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The diversity and distribution of introduced plant species reflects eight thousand years of settlement history

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Abstract

1. Human population has affected natural ecosystems since prehistoric times in many ways, causing disturbances in existing ecosystems and creating novel habitats, and altering the colonisation and extinction rates with potentially long-lasting effects on biodiversity. Here, we explored the pervasive effects of past human occupancy on present-day diversity and the distribution of plant species introduced by humans in the distant past – archaeophytes – at the regional spatial scale.

2. We analysed spatial relations between the present-day species richness of archaeophytes and native flora, the environmental setting, archaeological evidence, and the relationship between the residence time of archaeophytes and their regional range size. We used fine-scaled gridded information on plant diversity and archaeological records for the period 6000 BCE to 1000 CE summarised as average occupancy probability (AOP) in Czechia, Central Europe.

3. The proportion of archaeophytes in the local flora positively correlated with AOP. Variation partitioning revealed largely overlapping effects of AOP, environmental conditions, and present-day land use on the relative diversity of archaeophytes in local flora. The relationship between the minimum residence time of introduced species and their regional range size was non-significant.

4. *Synthesis.* Present-day regional diversity of archaeophytes mirrored the intensity of past human settlement. Our results suggest that the main underlying mechanism is the environmental filtering of non-native species pools, while dispersal limitation plays a minor role in the regional patterns of archaeophyte diversity.

Introduction

Since prehistoric times, wherever human populations have appeared they have significantly impacted multiple aspects of natural ecosystems (Ellis et al., 2021; Nikulina et al., 2022; Steffen et al., 2011; Thomas, 2020; Vareilles et al., 2021), and the distribution and diversity of plant species in the temperate zone during the Holocene is no exception (Kalis et al., 2003; Pokorná, 2018; Kuneš et al., 2015). Global or local extinctions causally linked to increasing anthropogenic pressure have been documented, particularly for animals (Andermann et al., 2020; Braje & Erlandson, 2013; Dirzo et al., 2014), but on the flip side are human-driven colonisation events, which, in contrast, may increase regional diversity (Storch et al. 2022).

In modern times, we are witnessing an unprecedented rate of plant invasions, but the introduction of plants by humans, either intentionally to introduce plant species with high nutritional, medicinal, ornamental or other value, or unintentionally, as in the case of weeds spreading with contaminated seed stock, has a long history (Colledge et al., 2004; Pyšek and Jarošík, 2005; Richardson & Pyšek, 2006; Pokorná et al., 2018; Rösch, 1998). The main geographic source area of species introduced to central Europe prior to the discovery of America (1492 CE), aka 'archaeophytes', is supposed to be the Mediterranean region (Pyšek et al., 2012). These introduced species are mostly well-adapted to open, human-modified habitats (fields, meadows, and ruderal stands) with a specific disturbance regime or nutrient conditions, although some of them also colonised natural habitats (Sádlo et al., 2007; Pyšek et al., 2012).

Besides anthropogenically increased colonisation rates, the suppression of dominant species utilising most resources available in an ecosystem and the creation of new habitats in the landscape may change local biodiversity equilibria and compensate for the negative effects of increased extinction rates at local scales (Storch et al., 2022). Forest trees represent dominant species in the context of

temperate-zone vegetation. In the past and today alike, agriculture and animal herding have required at least a partially deforested landscape. In central Europe, post-glacial expansion of forests led to gradual suppression of open habitats and their diversity, but from the Neolithic onward this trend has been reversed by intensifying human activities (Kuneš et al., 2015; Pokorný et al., 2015). Humans changed the land cover and its species composition both intentionally through active land use (i.e. conversion from forests or other natural habitats to pastures, fields, and settlements) or unintentionally, as a side-effect of ecosystem disturbance and altered environmental conditions, or game densities, linked to human activities in the landscape (Bernhardt-Römermann et al., 2015). The impact of prehistoric human communities may have had long-lasting effects to changes in plant diversity for several reasons, in particular due to following phenomena:

(i) Dispersal limitation. The ability for long-distance dispersal in plants is limited, and therefore current plant distribution reflects past colonisation events, dating back over millennia. Plants do not fill their whole potential range (Dullinger, et al., 2012; Giesecke et al., 2012; Svenning & Skov, 2004), which results in a positive relationship between range size or abundance, and time since introduction (Pyšek et al., 2012; Pyšek & Jarošík, 2005). Similarly, plant species that went locally extinct, e.g. due to large-scale deforestation, manifest lagged recolonization (Naaf & Kolk, 2015).

(ii) Long-term persistence. Plants use various strategies to survive in a changing environment. Once established in a region, species may locally persist despite episodic periods of unsuitable conditions for growth and reproduction. One strategy is to form a persistent seed bank, which is most common in the communities of weeds of arable land (Thompson et al., 1998). This strategy allows habitat specialists to survive periods of landscape abandonment in the medium-term. Alternatively, effective migration at shorter distances enables metapopulations to survive in a dynamic landscape mosaic.

(iii) Environmental alterations. Human activities have long-lasting or irreversible effects on environmental conditions (Dupouey et al., 2002). Soil development is generally a slow process, and human activities complexly alter soil conditions by means of differentiated soil development, with

increased soil erosion on arable land and the accumulation of eroded material in flood plains, soil fertilisation, or nutrient extraction (Closet-Kopp & Decocq 2015; Dotterweich, 2008; Juříčková et al., 2020). Similarly, an anthropogenically altered fire-regime has long-lasting effects on biota and soil properties (Bobek et al., 2018). These processes can be further intertwined with altered seed banks (Plue et al., 2008).

Studying human land-use legacies requires an interdisciplinary approach that combines ecology with those humanities examining the past – archaeology and history (Szabó, 2015). Historical ecology, working mostly with written records and maps of past land use, tells us about the impact of more recent centuries on current vegetation (Abadie et al., 2021; Bergès & Dupouey, 2021). Landscape changes and the pervasive effects of past land use can be quantified using a combination of precise historical maps and current and past vegetation plots. It has been documented that traditional woodland management involving litter raking, charcoal production, or coppicing, changed soil conditions and plant biodiversity on a local or even regional level, with effects persisting over centuries (e.g. Vild et al., 2018; Máliš et al. 2020). However, palaeoecological (archaeobotanical) research, integrating archaeology and vegetation ecology or palynology, shows us a much longer history of anthropogenic impacts on vegetation, dating back to the Mesolithic (Berglund et al., 2008; Dambrine et al., 2007; Kuneš et al., 2008; Kuneš et al., 2015, Nikulina et al., 2022).

Besides these legacy effects, present-day land-use and environmental conditions doubtlessly determine the current diversity of both native and alien flora (Palmer, 2006). Current biodiversity patterns thus necessarily reflect interactions between historical and present-day drivers. The relative importance of contemporary versus past drivers is scale-dependent; it is expected that historical processes matter at larger spatial scales, while current conditions are thought to be the primary driver at the local scale (Sádlo et al., 2007). However, studying vegetation diversity patterns at large spatial and temporal scales remains challenging, because standardised sampling is not feasible at such scales. The extent of most available studies is limited to a site, set of sites, or homogeneous region where similar landscape histories can be expected or have been proven by previous

archaeological excavations or surveys (e.g. Dambrine et al., 2007; Kozáková et al., 2015; Kuneš et al., 2008). Large-scale and long-term perspectives are still scarce, although the datasets and tools are increasingly available.

These 'lessons from the past' provide a much needed long-term perspective on the sustainability of human activities with regard to biodiversity under increasing anthropogenic pressure. It has been proposed that anthropogenic pressure does not automatically imply biodiversity loss – on the contrary 'intermediate' levels of human pressure may lead to greater biodiversity, at least at local to regional scales (Berglund et al., 2008; Storch et al., 2022; Thomas, 2020). Finding the optimal strategy to secure the growing demands of the human population at which the overall anthropogenic effects on biodiversity remain sustainable is a key task of the present, and historical ecology (also using knowledge from archaeology) and paleoecology can contribute significantly in resolving it (Vareilles et al., 2021).

In this study we aimed to explore large-scale patterns of plant diversity in the Czech Republic with respect to settlement history. Specifically, we hypothesised that the present-day distribution of plant species supposed to have been introduced by humans prior to 1500 CE (*archaeophytes*) will reflect past settlement intensity. Because the accumulation of archaeophytes is a long-term process, we assume that relative archaeophyte diversity will integrate settlement intensity after the onset of agro-pastoral subsistence strategies in the Neolithic (beginning around 5400 BCE in this region). Further, we propose that the extent of the present-day species distribution range will increase with the time that has elapsed since species were introduced to the region.

To test our ecological hypotheses, quantitative data on harmonised spatial and temporal scales on plant diversity, the environment, and human settlement history are needed. The advantage of our study region (Czechia, Central Europe) is that it belongs to one of most explored areas, both in terms of botanical and archaeological evidence. This enabled us to conduct our study at an unprecedented spatial resolution, with the study extent covering the whole country, and a record of settlement history dating back eight thousand years (1000 CE–6000 BCE).

Materials and Methods

Study region

The extent of this study covers the whole of Czechia, Central Europe (12°05'E–18°51'E; 49°33'N–51°04'N; 78,890 km²; Figure 1). This landlocked country belongs to the temperate forest biome, with natural vegetation represented by temperate broad-leaved deciduous forests covering the majority of the area, coniferous forests in the mountains, and limited areas of alpine tundra at the highest elevation. Currently, forests cover 34% of the area, 57% belongs to the agricultural land, and approx. 6% to urban areas. Human settlement has been recorded since the Palaeolithic, and continuous land use by farming communities in the warm lowlands has been recorded since the Neolithic (5400 BCE; Figure 2). Whereas the occupied area decreased during the subsequent Eneolithic (Copper Age), from the Bronze Age (starting ca. 2200 BCE) onwards farming population increased significantly and colonised previously sparsely inhabited areas with lower soil quality and relatively higher altitudes. From the Iron Age (especially ca. 500 BCE - 1 CE) we have evidence of beginnings of urbanisation (emergence of large fortified settlements - oppida and hillforts). During the following Roman and Migration Period many (peripheral) regions have been abandoned for centuries and the agropastoral settlement concentrated mostly again in the most fertile lowlands. Human settlement rapidly spread again after the start of the Mediaeval period (ca. 600 CE) (Kolář et al. 2022; Jiráň & Venclová, 2008; Podborský et al., 1993). The current human population is 10.3 million (density: 136/km²). The area was only marginally affected by glaciation during the Pleistocene, allowing the local survival of some boreal and even temperate woody species. Gradual post-glacial expansion of forests reached its maximum during the Holocene climatic optimum (Middle Holocene), suppressing species of open-habitats to environmentally extreme or anthropogenically disturbed refugia (Kuneš et al., 2015).

Plant diversity data

To explore the long-term impacts of human settlement history on vegetation, we focused on the geographic spatial patterns of plant occurrence. We used plant presence in a regular grid of quadrants (5x3 arc minutes; approx. 33.3 km²; Figure 1) from the most comprehensive source of floristic records for the Czech Republic – the PLADIAS database, which combines plant occurrence and trait data, including information about plant origin in the region (Chytrý et al., 2021; Wild et al., 2019). Plant occurrence recorded in the PLADIAS database covers the whole area of the Czech Republic, but sampling effort and primary sources of botanical data vary geographically (Wild et al., 2019). In consequence, absolute numbers of species richness are biased by sampling intensity and strategy, and cannot be easily corrected. Therefore, we focused mostly on the relative richness of species according to their origin, specifically the richness of archaeophytes relative to the species richness of indigenous plants, according to the species classification in Pyšek et al. (2012). Prior to analysis, crops and ornamental species occurring only in cultures and hybrids were excluded, while taxonomically complicated taxa such as apomicts (*Achillea* spp., *Rubus* spp., *Taraxacum* spp., and *Sorbus* spp.) were aggregated to sections. Subspecies were considered as independent entities only if their origin status differed. From the list of plant occurrences for each quadrant, we calculated the total species richness and species richness of native plants, archaeophytes, and neophytes classified according to Pyšek et al. (2012). Finally, we excluded from the analyses the 1% of quadrants with the lowest sampling effort (less than 109 records), as diversity estimates from these quadrants are unreliable. In this study, we worked with 13.39 million plant occurrences exported from the PLADIAS database on 21/06/2020. The application of our filtering criteria resulted in a dataset comprising 13.18 million records of 2,853 taxa, out of which 1,749 were classified as native, 259 as archaeophytes, and 826 as neophytes.

To analyse the effect of residence time on current range size within the studied region, we adapted minimum residence time (MRT) from Pokorná et al. (2018) based on the first occurrence of plant

macroremains in archaeological sites recorded in the Archaeobotanical Database of the Czech Republic. MRT was available for a subset of 113 of 259 (43.6%) archaeophytes (Supplementary table S3).

Archaeological evidence

The archaeological evidence for our study area was compiled from two comprehensive databases of archaeological sites and finds: the database maintained by the Institute of Botany of the Czech Academy of Sciences, which collates all available records from the eastern part of the country - Moravia and Czech Silesia (Kolář et al., 2016a), and from the database covering the western part of the country (Bohemia) maintained by the Institute of Archaeology of the Czech Academy of Sciences in Prague (Kuna et al., 2015; <https://digiarchiv.aiscr.cz/>), using the content available up to August 2019.

Temporal coverage of the records used in this study was set for the period between 6000 BCE and 1000 CE (7,950 to 950 cal. BP). 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 an archaeological component. An archaeological component is an aggregate of related archaeological artefacts defined by its function (e.g. settlement, burial, hillfort, hoard), chronological definition (period, phase, or archaeological culture; records without sufficient chronological accuracy were omitted from further analyses), and spatially limited to an archaeological site or its specific part documented during archaeological fieldwork (cf. Kuna et al., 2015). All components localised at least to the level of a civil parish (average parish area is 6 km²) or more precisely were used. In total, 65,511 archaeological components were used for further analyses.

To estimate the local human presence at different times, we partially followed previously elaborated procedures (Kolář et al., 2016b). We used components' spatial coordinates to assign them to the same quadrants as were used for plant occurrence data. Next, we randomly assigned a calendar year to each component within the temporal range of its dating, assuming a uniform probability of

component dating within period limits. A quadrant was considered as occupied in a particular 500-yr period if at least one component was assigned to the given period and grid cell. We repeated this procedure 1000 times and we quantified occupancy probability as the proportion of simulation runs where the grid cell was considered as occupied in a particular period. Finally, we calculated the average occupancy probability (AOP) of each grid cell over the sequence of periods, with increasing length from 500 to 7,000 years; all ending in 1,000 CE.

Environmental data

To characterise the environmental conditions of quadrants, we extracted quadrant-level average elevations from the digital elevation model (30 m Shuttle Radar Topography Mission DEM, <https://doi.org/10.5066/F7PR7TFT>; Figure 1C), modern mean annual temperature (MAT) and mean annual precipitation (MAP) from the CHESA database, version 2.1 (Karger et al., 2017) and historical mean annual temperature over last eight millennia from CHESA-TraCE21k v1.0. database (Karger et al., 2021), and the representation of soil types in quadrants was obtained by spatial intersection with the soil map (Tomášek, 2003).

Land use was represented by the proportion of forested area in the quadrant extracted from the satellite-based tree cover map for the year 2019, provided by the Forest Management Institute (www.uhul.cz; Figure 1D).

Spatial projection of the data layers was harmonised to WGS-84 / UTM zone 33N. Spatial data analyses were performed using *sp* and *raster* packages in R (Pebesma & Bivand, 2005; Hijmans, 2020).

To reduce the dimensionality of environmental data and to deal with the multicollinearity of predictors, we performed a principal component analysis (PCA) of the environmental variables using the *vegan* R package (Oksanen et al., 2020). Elevation, MAT, and MAP were standardised to unit range over the entire area, and the representation of soil types was standardised to unit sum in the quadrant for PCA. We used the first six principal component scores, accounting for 77.2 % of

variability in environmental variables, for further analysis. For principal component scores see Supplementary table S6.

Statistical analyses

First, we explored bivariate relations between native and archaeophyte diversity. Despite the exceptional quality and quantity of available primary data resources, the true geographic and temporal extent of past settlement and current plant distribution can be underestimated and geographically biased by the preferences of data collectors. Protected areas and protected species are typical examples of over-represented records in the PLADIAS database, while quadrants dominated by agricultural land are under-represented (Wild et al., 2019). To avoid confusion by sampling intensity, we divided the dataset into ten equally large subsets using the number of records per quadrant as the criterion and for each subset we calculated the Spearman's rank correlation coefficient (Spearman's rho) and visualised bivariate relationships using a generalised additive model with a cubic regression spline for the bivariate relationship between number of archaeophytes and native flora.

To analyse the drivers of variability in archaeophyte plant diversity, we fitted binomial generalised regression models with the share of archaeophytes over the sum of native and archaeophyte taxa in a quadrant as a dependent variable. The explanatory variables were put into three groups: archaeological evidence (AOP); environment (the median elevation, annual temperature, and precipitation of the quadrant) and land use. First, we evaluated the predictive power of AOP for different period lengths in a simple model with AOP as the only predictor; using AOP of single 500-yr periods and AOP for sequences of periods with increasing length.

In the next step, we used AOP over the whole study period (6000 BCE to 1000 CE) in multiple regression models together with environment and land use explanatory variables. To partition the variability explained either uniquely or jointly by each group of predictors, we fitted seven separate models for all combinations of predictor groups. Then we constructed a partition table from the

deviances explained by particular models and visualised it using a Venn diagram. Next, we evaluated the spatial autocorrelation of the dependent variable and the model residuals using Moran's I.

To test correlation between minimum residence time and spatial extent we used Spearman's correlation coefficient and computed p-values using asymptotic approximation.

Statistical analyses were performed using R (R Core Team, 2020) and packages ggplot2 (Wickham, 2016), modEVA (Barbosa, et al., 2013), ncf (Bjornstad, 2020), and vegan (Oksanen, 2020).

Results

AOP displayed a strong spatial pattern, with high and stable levels in the two main lowland regions, moderate levels in two regions (Pilsen region in the west of the country and the region of southern Bohemia in the south-west) and low levels in the highlands, i.e. the country's central and border regions (Figure 1B). The diversity of archaeophytes displayed more smooth spatial patterns:

The observed species richness of archaeophytes ranged between 0 and 178 per quadrant (median 52 species) and contributed by 0% to 37.03% (median 9.95%) to the summed species richness of both native and archaeophytes within quadrants (Figure 1A). The species richness of archaeophytes in quadrants was strongly positively correlated with native species richness at all levels of sampling-intensity (Figure 3; Spearman's rho varied between 0.59 and 0.89 among sampling intensities; all correlations were significant at the level $p < 0.001$).

The relative species richness of archaeophytes positively correlated with AOP (Figure 4 B). The strength of this correlation generally increased with the total time-span of the archaeological record used for calculating AOP, while the correlations between archaeophyte diversity and single 500-yr periods showed no clear trend with the age of the period (Figure 4 A). The full model, using AOP over the whole study period (6000 BCE to 1000 CE) together with environmental variables and current land use as predictors explained 60.1% of the variability in relative archaeophyte species richness and revealed significant positive relation between AOP and relative diversity of

archaeophytes (Table 1). The reduced model, with AOP as the only predictor, explained 32.3 % of variability. Variation partitioning showed that a major part of the explained variability in the full model (23.2 %) is shared between all predictor groups: archaeological evidence, environmental conditions, and land use (Figure 5). Independent contribution to explained variation was highest for environmental variables (9.2%), followed by land-use (6.7%) and only 1.1% of variability was uniquely attributed to archaeological evidence, but this contribution was significant at $p < 0.001$. Analysis of autocorrelation (Supplementary Figure S2) revealed that the full model considerably reduced residual autocorrelation, which remained high only in the first (0–20 km) distance class.

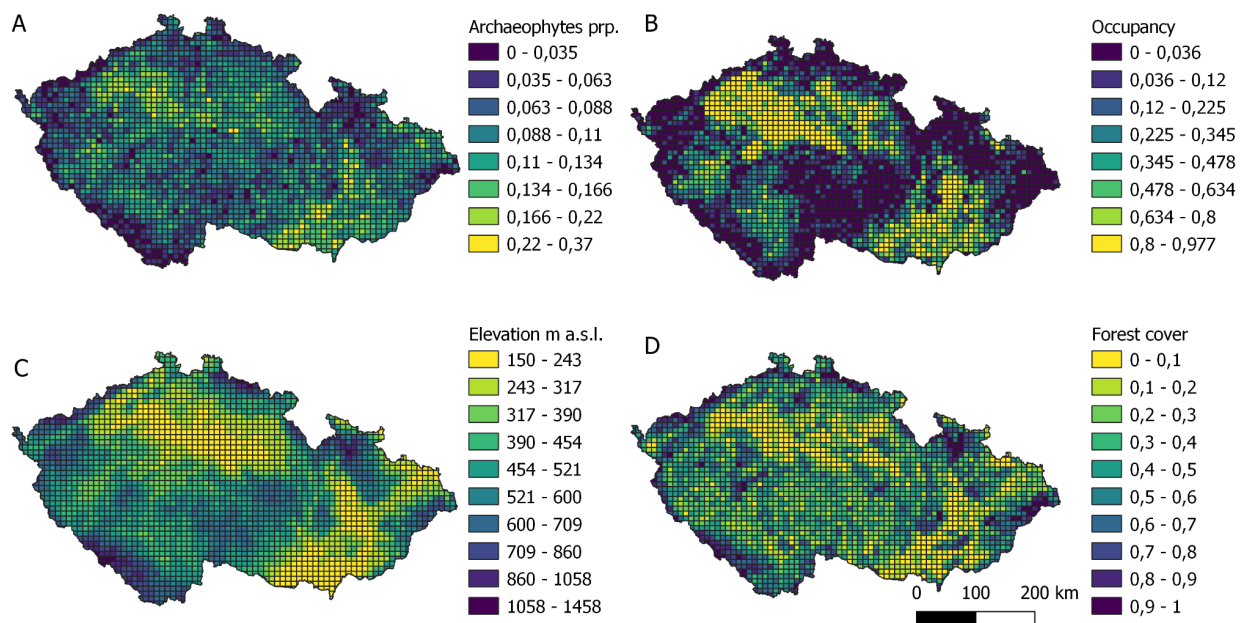


Figure 1 Maps showing the spatial patterns of the representative variables used in models summarised for 2,552 quadrants covering the study area (Czechia): (A) proportion of archaeophytes; (B) average archaeological occupancy modelled from the archaeological record covering the period 6000 BCE – 1000 CE; (C) median elevation; (D) Land use represented by current forest cover. Climate variables in the study area (not shown here) closely follow elevational gradients.

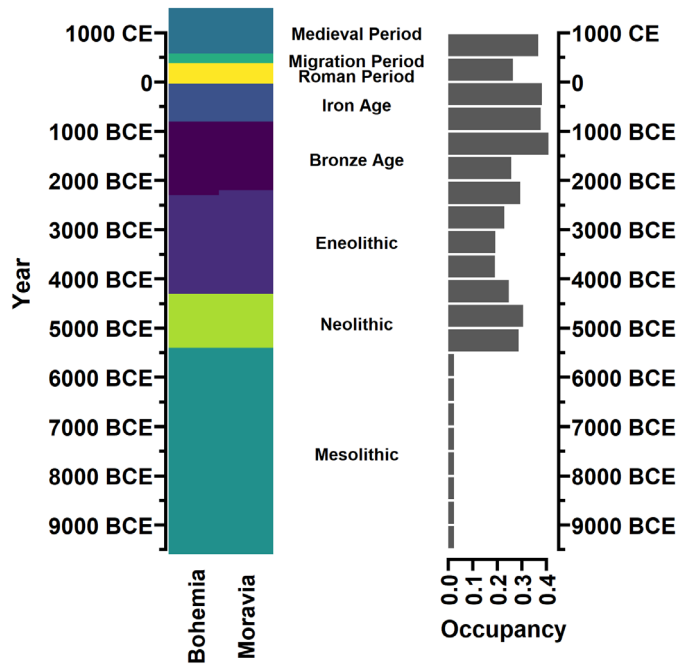


Figure 2 Timeline showing archaeological periodization of the area (left) and averaged occupancy probability aggregated over the whole study area (right).

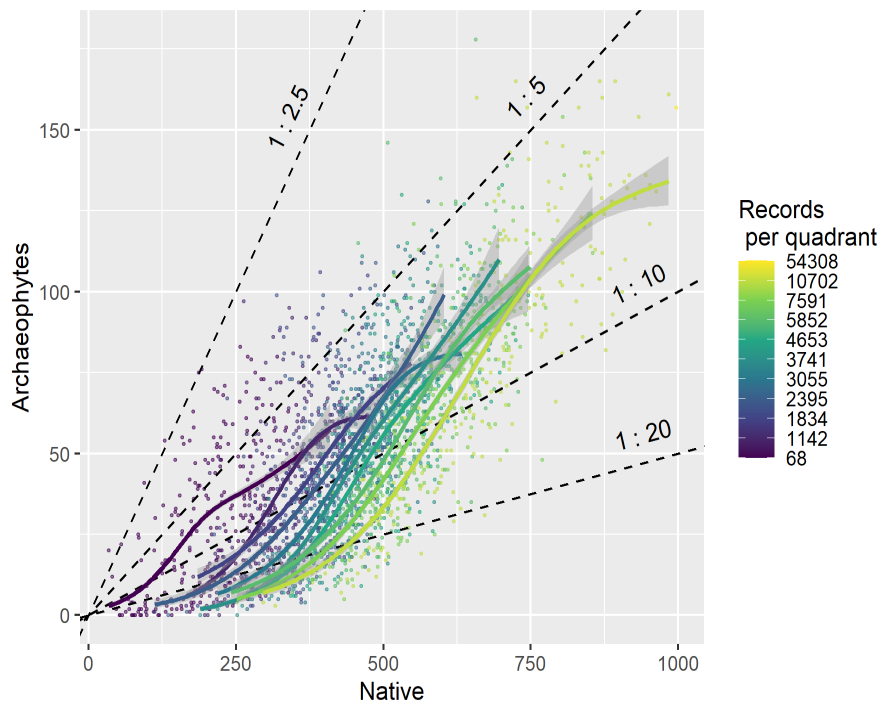


Figure 3 Absolute species richness of archaeophytes and native flora in quadrants (~33km²) according to the total number of records (colour scale) in quadrants from the PLADIAS database. Curves show the GAM cubic regression smoothers and a 95 % confidence interval for groups divided by deciles of the number of records from the PLADIAS database.

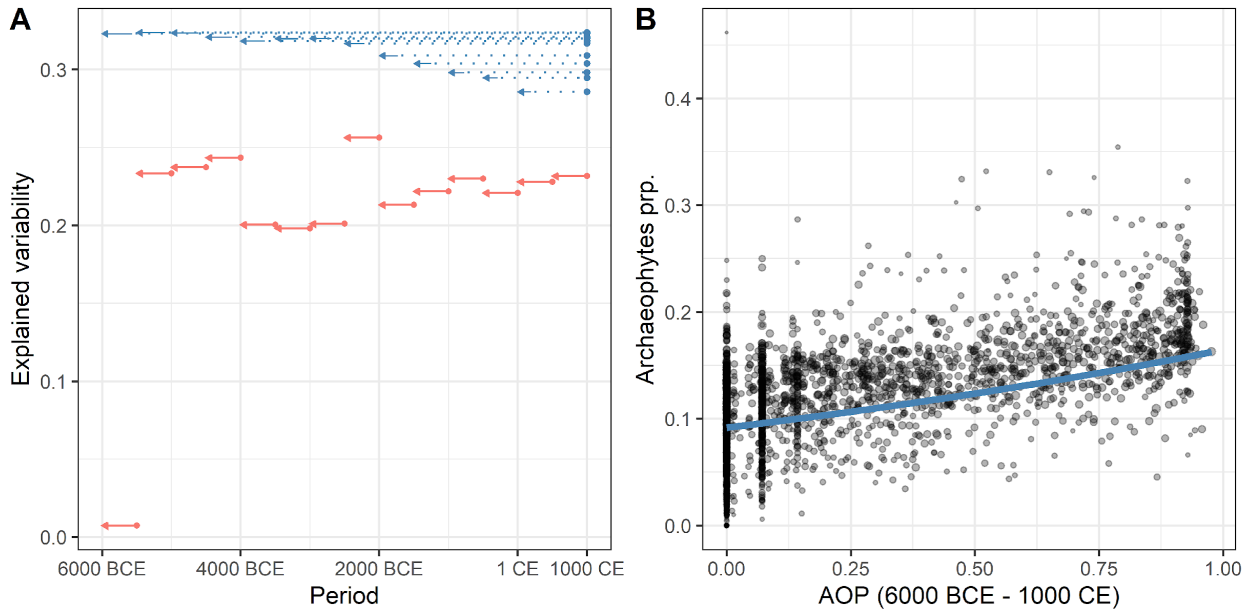


Figure 4 (A) Explained variability in relative archaeophyte diversity by AOP in 500-yr periods (red arrows) and by AOP integrated over longer periods (blue arrows). Arrow length indicates period length. (B) Relationship between averaged occupancy over the period 6000 BCE–1000 CE and relative species richness of archaeophytes in quadrants. Point size is proportional to total species richness in a quadrant. The blue line is the regression line.

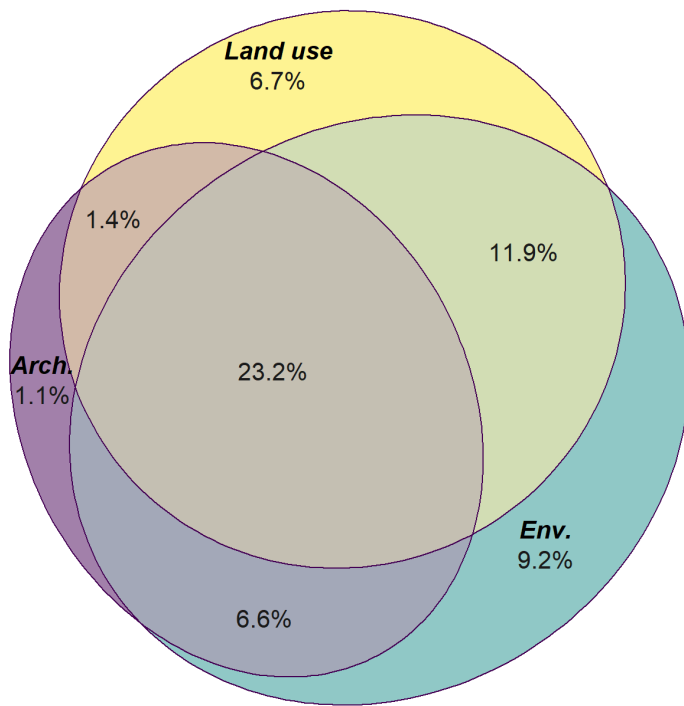


Figure 5 Variance partitioning diagram showing fractions of explained variability in the proportions of archaeophytes in the regional flora. Total explained variability is 60.1%. Most of the explained variability (23.2%) was shared between all three predictor groups. The independent effect of archaeological evidence (Arch.) accounted for 1.1% of variability.

Table 1 Model coefficients for a set of multiple regression models on proportion of archaeophytes. Predictors PC1-6 are principal components scores for environmental variables (climatic and edaphic). Slope estimate \pm standard error for predictor variables is presented here, significant terms ($p < 0.05$) are marked by *. PC1 is positively associated with temperature gradient (Supplementary Figure S1)

	Arch. + Land use + Env.	Arch. + Land Use	Arch. + Env.	Land Use + Env.	Land Use	Env.	Arch.
Intercept	-1.953 $\pm 0.008^*$	-1.87 $\pm 0.008^*$	-2.218 $\pm 0.005^*$	-1.882 $\pm 0.007^*$	-1.638 $\pm 0.005^*$	-2.142 $\pm 0.003^*$	-2.293 $\pm 0.004^*$
AOP	0.179 $\pm 0.012^*$	0.375 $\pm 0.009^*$	0.263 $\pm 0.012^*$	-	-	-	0.669 $\pm 0.008^*$
Land Use	-0.611 $\pm 0.017^*$	-0.895 $\pm 0.015^*$	-	-0.658 $\pm 0.016^*$	-1.185 $\pm 0.013^*$	-	-
PC1	1.479 $\pm 0.038^*$	-	2.032 $\pm 0.035^*$	1.75 $\pm 0.033^*$	-	2.509 $\pm 0.027^*$	-
PC2	0.612 $\pm 0.028^*$	-	0.81 $\pm 0.027^*$	0.526 $\pm 0.027^*$	-	0.704 $\pm 0.027^*$	-
PC3	0.015 ± 0.023	-	-0.164 $\pm 0.022^*$	0.015 ± 0.023	-	-0.186 $\pm 0.022^*$	-
PC4	0.036 ± 0.03	-	0 ± 0.03	0.027 ± 0.03	-	-0.018 ± 0.03	-
PC5	0.085 $\pm 0.025^*$	-	0.035 ± 0.025	0.133 $\pm 0.025^*$	-	0.101 $\pm 0.025^*$	-
PC6	-0.103 $\pm 0.021^*$	-	-0.082 $\pm 0.021^*$	-0.145 $\pm 0.02^*$	-	-0.144 $\pm 0.021^*$	-
<i>Null Deviance</i>	20377.29	20377.29	20377.29	20377.29	20377.29	20377.29	20377.29
<i>Resid. Deviance</i>	8133.53	10008.13	9502.85	8360.31	11587.58	10012.79	13792.28
<i>AIC</i>	22067.05	23929.64	23434.37	22291.82	25507.09	23942.3	27711.79

Range size and residence time

The range size of archaeophytes with assigned MRT varied between 10 and 2,388 occupied quadrants (0.4 % to 93.4 % of the total area) with a median of 787 quadrants (30.7 %).

Our hypothesis that the range size of archaeophytes increases with residence time was not supported at 5 % significance level (Figure 6; Spearman's $\rho = 0.173$, $p = 0.066$).

Fossil pollen evidence showed possible occurrence in the study region even several millennia prior to the first record from macro remains (Supplementary material S4; Supplementary Figure S5).

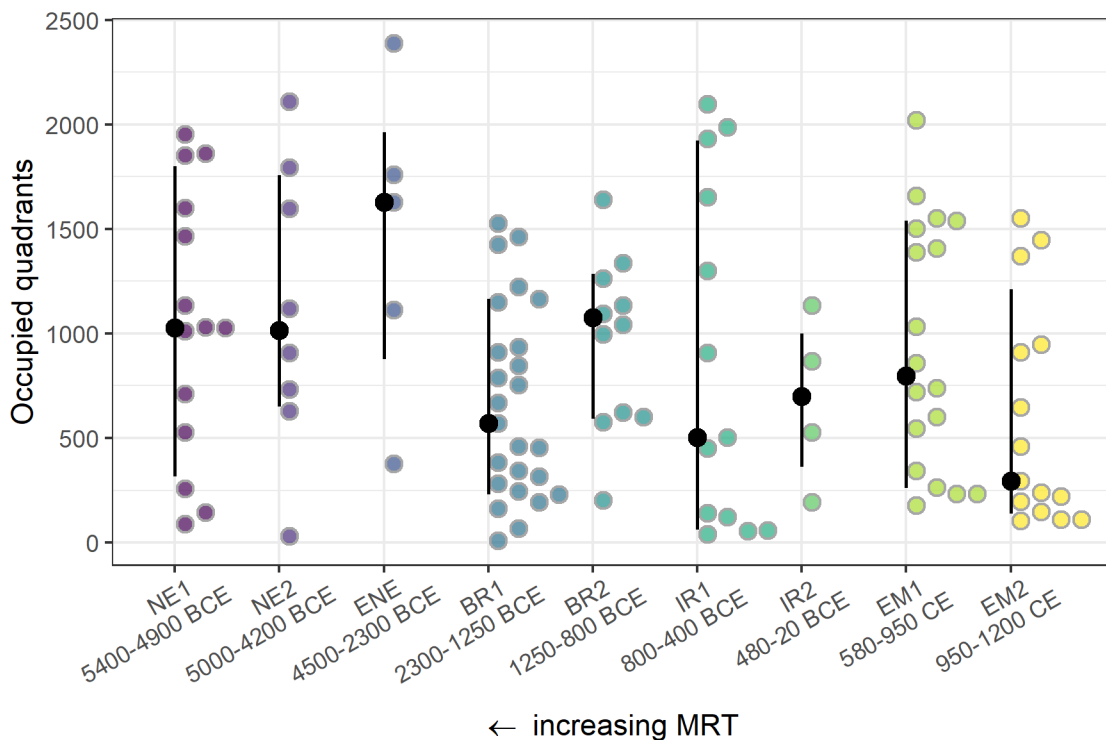


Figure 6 Occupied quadrants by archaeophyte species according to increasing minimum residence time (MRT), defined by the period of first appearance (NE1 = Early Neolithic, 5400-4900 BCE; NE2 = Late Neolithic, 5000-4200 BCE; EN = Eneolithic, 4500-2300 BCE; BR1 = Early to Middle Bronze Age, 2300-1250 BCE; BR2 = Late to Final Bronze Age, 1250-800 BCE; IR1 = Early Iron Age, 800-400 BCE; IR2 = Late Iron Age, 480-20 BCE; EM1 = Early Middle Ages 1–3, 580-950 CE; EM2 = Early Middle Ages 4, 950-1200 CE). Black dots indicate median values, line segments the 66% distribution interval. A non-

significant positive relationship between MRT and number of occupied quadrants was found for archaeophytes (Spearman's $\rho=0.173$, $p = 0.066$).

Discussion

In this study we documented that the species richness of plant species introduced in the past reflects settlement history. Remarkably, the longer the period over which human occupancy was integrated, the better the fit to archaeophyte diversity was achieved. This indicates that the accumulation of introduced species was a continuous process and the contribution of the distant past should not be neglected. However, the effects of settlement history largely overlapped with environmental conditions and current land-use, as the proportion of archaeophytes in the flora was higher in the warmer lowlands with less forest cover. These factors alone explained more variability in archaeophyte proportion than settlement history. Large overlap in explained variability corresponds to inter-correlation between these predictors. This inter-correlation is not surprising in Central Europe, where human settlement and subsequent land-conversion for agricultural use preferentially took place in warm lowlands on nutrient-rich soils. The prevailing spatial adherence of archaeophytes to the area characterised both by longer settlement history and by specific environmental conditions suggests a dominant role of environmental filtering and niche conservatism: the main migration or trade routes and environmental conditions and habitats, which were favoured/created by prehistoric human communities predefined the selection of the species pool of introduced species with specific ecological preferences. The majority of archaeophytes originate from the Mediterranean region (Pyšek et al., 2012), and this corresponds well with the spread of Europe's earliest farmers from Greece and north-western Anatolia (Hofmanová et al., 2016). This dominant introduction pathway predetermined the ecological requirements of archaeophytes and therefore even their contemporary geographic distribution within the study region. The extent of the area with ideal farming conditions seems generally consistent throughout

prehistory. Based on that fact, it is possible to use current environmental descriptors as strong predictors for past farming settlement. Deviations from this standard model do of course exist, but due to the nature of the human activities they reflect (travelling, gathering, hunting, rituals etc.), the environmental impacts are usually marginal (cf. Demján et al., 2022).

An alternative explanation for affinity of archaeophytes to the regions with longer settlement history would be their limited dispersal ability. Nevertheless, our second hypothesis supposing the geographic range size of archaeophytes would increase with residence time, was not confirmed neither in this study, nor by Pokorná et al. (2018), who have concluded that evidence for a relationship between current invasion status and MRT is not convincing. In contrast, Pyšek & Janošík (2005) reported a weak but significant positive relationship between MRT and archaeophyte frequency in Czech flora. Here, we employed a slightly different methodology from Pyšek & Janošík (2005), using a nonparametric test and geographic range expressed as the number of occupied quadrants instead of an index of species frequency, and we worked with an updated species occurrence dataset from the PLADIAS database. The weak relationship between range size and the MRT of archaeophytes together with the marginal independent effect of settlement history on relative archaeophyte diversity suggests that most archaeophytes have already reached their equilibrium range size, since range filling of ecologically suitable area following a successful introduction event can be relatively quick. Further, the enormous statistical spread of range sizes for species with the same MRT indicates that other factors like species ecological niche, govern their realised range size. According to Pyšek & Janošík (2005), recently introduced aliens (neophytes) with well-known time of introduction were able to colonise up to 10% of the study area in just 100 years. Given much longer residence time of archaeophytes, we can expect that most archaeophytes had enough time to fill their potential range within the region, and therefore the main driver of current archaeophyte diversity patterns is environmental filtering. The true residence time of many species is likely much larger than minimum residence time inferred from macroremains: fossil pollen evidence suggests that residence time for some species may be underestimated by thousands years

(Supplementary materials S4). This means that archaeophytes had even more time to colonise the suitable habitats within the region. In contrast, neophytes show higher affinity to urban areas compared to archaeophytes (Pyšek P., 1998, Chytrý et al. 2021). This marked affinity of neophytes to larger cities may be only temporal, as neophytes commonly start to spread from these cities serving as traffic hubs and have not yet filled their whole potential range.

With regard to our results, we consider long-distance dispersal (i.e. dispersal from source areas in Mediterranean) and environmental filtering to be a significant limiting factor at millennial time-scale, while the regional colonisation dynamic following a successful introduction event to be of secondary importance.

The relationship between archaeophyte diversity and archaeological settlement represents a synchronic viewpoint on a similar phenomenon described by many diachronic studies which suggest a correspondence between the rise of plant diversity in the past and the human impact (Roleček et al., 2021; Šizling et al., 2016; Woodbridge et al., 2021). New anthropogenic habitats to Central Europe, such as fields, were colonised by annual weeds brought with the first cereals from the Mediterranean area (e.g. *Adonis aestivalis*; Pokorná et al., 2018). However, the rise of diversity was more complex than the history of the iconic archaeophyte, and we also need to take into account the reaction of the native taxa to anthropogenic pressure and competition with newly introduced species.

Although the relative proportion of archaeophytes increases with settlement intensity over the study period, we found no indication of negative effects of the increasing number of introduced species on the indigenous plant diversity: a strong positive correlation between the absolute diversity of both native and introduced plant species was found at all levels of sampling intensity (Figure 3). This is consistent with previous empirical studies on the relationship between regional native and non-native plant diversity (Sádlo et al., 2007; Pyšek & Jarošík, 2005). The primary reason for this positive correlation is that the direct effects of species interactions (competition, mutualism) at larger spatial scales are less important than external drivers of species diversity (e.g. productivity

and environmental heterogeneity), which affect both introduced and native plant diversity in similar ways (Fridley et al., 2004; Gilbert & Lechowicz, 2005). It has been documented that historical human activity increased soil heterogeneity with positive effects on vegetation heterogeneity lasting centuries after abandonment (Closet-Kopp & Decoq, 2015). Storch et al. (2022) in their equilibrium theory of biodiversity dynamics suggested that human activity would increase regional equilibrium biodiversity level through two mechanisms: (i) increased immigration rates by human-mediated dispersal; and (ii) reduction of extinction risk for herbs under intermediate anthropogenic pressure thanks to partial suppression of dominant competitors represented by forest trees, utilising most resources.

Independent evidence for the spread of species and increase in plant diversity facilitated by anthropogenic disturbances had been provided by fossil pollen analysis (Kuneš et al., 2019). The persistence and continuity of anthropogenic disturbances in the settlement oecumene, and their fluctuation on the periphery in all spatial scales (Kolář et al., 2022), provided great variation of niches and ecological opportunities for taxa of different origins. Human impact led to an increase of the species pool size, which completely rewrote the ecological rules. Before 4500 BP (end of the Eneolithic), the greatest diversity was mainly found in regions with the intermediate disturbance regime, in accordance with the intermediate disturbance hypothesis, but in later periods plant diversity reached its maximum under the most frequent disturbance regime (Kuneš et al., 2019). The positive effect of anthropogenic disturbances on the species richness of native taxa in the distant past is supported by modern analogy from repeated surveys in disturbed landscapes, which document an increase in local and total species richness attributed to both native and exotic taxa (McCune & Vellend, 2013). These findings suggest, in accordance with the predictions of Storch et al. (2022), that anthropogenic disturbance regimes induced by ancient societies did not reach levels threatening plant diversity levels at the regional scale

Conclusions

The current diversity and distribution of archaeophytes – ancient plant invaders – mirror to a certain degree past distribution of human settlement. However, this similarity of patterns is more likely linked indirectly to the past extent of human settlements through environmental filtering of the ecological niches of introduced species than by any pervasive effect of dispersal limitation at the regional scale. Our results support the hypothesis that increased long-distance dispersal, in combination with human-induced landscape-opening and the creation of novel habitats, would lead to increased regional diversity equilibria.

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Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

Data and code used in this study are available on Dryad repository:

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Author Contributions

Martin Macek, Vojtěch Abraham, Peter Tkac and Jan Kolář conceived the ideas; Jan Kolář, Peter Tkac and David Novák prepared the archaeological data; Vojtěch Abraham prepared and analysed fossil pollen data; Jan Kolář acquired the project funding, Martin Macek analysed the data and led the writing of the manuscript; all authors contributed to writing and editing the draft, and have given their final approval for publication.

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