Ancient and Early Medieval man-made habitats in the Czech Republic: colonization history and vegetation changes

Synantropní biotopy v pravěku a raném středověku České republiky: kolonizační historie a změny vegetace

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The invasion history of archaeophytes (i.e. alien taxa that were introduced into Europe prior to AD 1500), their effect on past vegetation and their present status based on their residence time were studied. The residence times of archaeophytes range from 7500 to 500 years. It is likely that species with other functional traits came at different times. We summarized assemblages of macroremains obtained from the Archaeobotanical Database of the Czech Republic. The data based on 202 archaeological sites cover the period from the Neolithic to the Early Middle Ages. We found 123 alien species and 94 synanthropic species native in the Czech Republic. Three waves of immigration of increasing magnitude were distinguished: (i) the Neolithic, (ii) the Bronze Age, and (iii) the Early Middle Ages. The first phase of synanthropic plant immigration was characterized by the prevalence of native and alien generalist species, which are still very abundant, sharing both ruderal and segetal habitats. Specialist weeds of cereal fields occurred only since the Eneolithic. In the ruderal flora, the successive development started from a stage dominated by species associated with disturbance of less fertile soils and species that need nutrient-rich soils prevailed later. The composition of the oldest grassland flora corresponded with that of short lawns at disturbed and/or trampled sites, whereas a sudden increase in meadow species occurred in the Late Bronze Age. Since the Middle Ages, pastural species, avoided by grazing animals, indicate the intense use of pastures and their expansion into wet conditions. The species that arrived early in this era, i.e. in the Neolithic, are currently more successful than the later arrivals. Such a trend cannot be explained by the length of time they have had to naturalize and spread because all archaeophytes have been here long enough, whether they arrived early or late, to be

fully naturalized. The success of the abundant and invasive species is not due to their long resi-
dence times; on the contrary, they arrived early due to their invasiveness, which is a result of their
biological traits. A contrasting strategy is that of the specialized weeds of cereal fields. Unlike
ruderal species, they rarely spread from cultivated land. Therefore, many of these ecological spe-
cialists remained common until the early 20th century, but then modern agriculture practices
resulted in a great reduction in their abundance.

Introduction

In Europe, vascular plants of alien origin are divided into two groups according to their res-
idence time, archeophytes (introduced between the Neolithic and High Middle Ages), and
neophytes (introduced since the beginning of the Modern Period; Schroeder 1969, Pyšek et
al. 2004, 2017, La Sorte & Pyšek 2009). Unlike archaeophytes, neophytes are a well-
defined and intensely studied group, and the more familiar they are the more they are stud-
ied. On the contrary, archaeophytes are, in this respect, rather neglected due to their longer
residence time and even their archaeophyte status is uncertain in many cases (Pyšek et al.
2017). However, it is noteworthy that archaeophytes are commonly used as a reference
group in relation to neophytes or native flora (e.g. Chytrý et al. 2008, Hulme 2011).

   The archaeophyte flora is numerous (~300 species in central Europe; see e.g.
Lambdon et al. 2008, Medvecká et al. 2012, Pyšek et al. 2012) and results from succes-
sive immigrations over more than half of the Holocene period. In addition to the time of
their arrival, archaeophytes differ in their distribution, invasion success and conservation
status. Considering the environmental conditions, which changed dramatically during
this period, the formation of such a polymorphic species group was a complex process,
which needs further research. The period when the archaeophytes arrived coincided with
a huge change in the European cultural landscape. Its start (~5500 BC, in the middle of
the Holocene climatic optimum; Kalis et al. 2003) is associated with the beginning of
agricultural activities, which included the introduction of alien crops as well as weeds,
the beginning of sedentary life and the gradual formation of the cultural landscape (Birks
1988, Pokorný et al. 2015). This period ended about AD 1500, at about the time America
was discovered, which is, however, a too concise interpretation. The onset of modern
times coincides with the beginning of the cool oscillation in the so called Little Ice Age,
and is defined by substantial cultural and economic changes. It was notably highlighted
by the consolidations and further expansions of several large political units, such as the
Spanish, Roman and Ottoman Empires, as well as the Grand Duchy of Moscow, and by
the early transoceanic expeditions around the world.

   Two different approaches are valid in understanding the long-term developmental
changes of plant cover in the past. The first approach, called 'secular succession' (van der
Maarel 1988, or 'synchronology' sensu Braun-Blanquet 1964), deals mainly with vege-
tation and describes the development of plant cover as a long-term process driven by both
climate and cultural influences, such as lifestyle and management practices. The second
approach, called 'colonization history', deals with flora and describes this process in terms
of the ecology of invasions. This approach is applicable to the then newly established
alien plants, e.g. archaeophytes, and native plants that originated from the surrounding

landscape and locally colonized anthropogenic habitats. The concept of this study is closer to the latter approach in handling the data without aspiring to achieve a generalized holistic description.

Residence time is distinguished as a crucial attribute of the colonization history of aliens, influencing their range size, abundance and invasion status (Pyšek & Jarošík 2005, Richardson & Pyšek 2006, Wilson et al. 2007, Pyšek et al. 2015). In this context, colonization history is frequently studied, especially that of modern invaders (e.g. Pyšek et al. 2003, Castro et al. 2005, Pergl et al. 2016), because reliable information about their residence time is usually available and the whole process from introduction to invasion can be easily traced. However, archaeophytes are mostly studied as a group, and attempts to historically categorize them on a regional scale are rare. To help fill this gap in the knowledge of alien plant history, we used the macroremains found at archaeological settlement sites in the Czech Republic dated from the Early Neolithic to the end of the Early Middle Ages. The comparison of our results with those of other studies is, nevertheless, limited owing mainly to regional differences (e.g. Preston et al. 2004, Brun 2009) or different approaches (Trzcińska-Tacik & Wasylikowa 1982, Willerding 1986, Lityńska-Zając 2005, Poschlod 2015). Since it is not usually known exactly when a taxon was introduced, we adopted the term 'minimum residence time' (MRT) to express the time span since the first record of a species in this country (Rejmánek 2000, Pyšek et al. 2015).

In this study, we offer a first look at the invasion history of archaeophytes from a regional perspective, with the aim of providing a general outline to guide further detailed investigations; a special evaluation of the archaeological or taphonomical aspects of our data will be presented in separate papers. Our aims are to (i) define the periods of the archaeophyte stage in this region in terms of the established MRTs of particular species, (ii) infer the historical process by which the overall floristic diversity in man-made habitats developed, and (iii) judge how the current abundance and invasiveness of the archaeophytes is affected by their residence time.

Materials and methods

Data set

Our data consists of assemblages of macroremains obtained from the Archaeobotanical Database of the Czech Republic (Pokorná et al. 2011, Dreslerová & Pokorná 2015, Institute of Archaeology CAS 2017), supplemented by unpublished data of the authors of this study. All of the data were initially processed using the archaeobotanical database programme ArboDatMulti (Kreuz & Schäfer 2002, Pokorná et al. 2011).

The original data set contained ~5000 records of more than two hundred plant taxa from 223 sites (202 after our selection as described below). Each site represents one cultural phase at 197 localities dated to between the Early Neolithic (5600 BC) and end of the Early Medieval Period (AD 1200). The data from the High Middle Ages (AD ~1200 to 1500) could not be integrated into this study, because the process of transferring the data to the database is still ongoing. Moreover, these data are hardly comparable to that for ancient cultures as they are much more abundant and fossilized in a different way. Most of the prehistoric material was preserved by charring, with only a few exceptions at waterlogged sites, unlike the medieval material, which was mostly waterlogged.

The majority of the sites were studied between 2000 and 2014 (the oldest analysis was ~1960) and about one half of the reports have not been published in scientific journals. The number of independent determiners was 12.

Plant species and morphotaxa

The visually-based taxonomic identification of the macroremains resulted in a list of morphotaxa. Since most of them were identified to species level, we generally use the term 'species' instead of 'morphotaxon'. The collective taxa were established for the purpose of reducing potential identification bias, caused by the different determination criteria of various authors or by differences in the quality of the preservation of the seeds (e.g. *Amaranthus blitum/graecizans*, *Arctium* cf. *lappa/tomentosum*, *Chenopodium glaucum/ rubrum*, *Galeopsis angustifolia/ladanum*, *Lamium amplexicaule/purpureum*, *Melilotus albus/officinalis*, *Papaver dubium/rhoeas*, *Potentilla* sp., *Rumex crispus/obtusifolius*, *Setaria verticillata/viridis*, *Stachys annua/arvensis*, *Taraxacum* sp., *Veronica opaca/polita, Vicia hirsuta/tetrasperma*).

We targeted herbaceous plants, which presumably grew spontaneously in settlements and entered the archaeological sites without any human intention. Therefore, we excluded the following groups from our primary data: (i) trees and shrubs, (ii) species of natural habitats such as rocks (e.g. *Stachys recta*) or water pools, and (iii) crops harvested intentionally (e.g. *Triticum* sp., *Pisum sativum*), as well as wild herbaceous plants presumably collected for food (e.g. *Fragaria* sp.) or medical purposes (e.g. *Atropa belladonna*). We did, however, include several species of open land although they produce edible seeds (e.g. the genera *Bromus*, *Chenopodium*, *Fallopia*, *Sambucus*, *Stipa* and *Vicia*), which may have been semi-spontaneous, i.e. both wild and, perhaps, also potentially supported by man (see e.g. Bieniek 2002). For methodical reasons, we furthermore excluded (iv) rare native species occurring at less than five sites during all periods (e.g. *Cerastium arvense*), and (v) species with an extremely discontinuous occurrence in our data, in which, therefore, the MRT specification remained uncertain. For the list of taxa excluded for methodical reasons, see Electronic Appendix 1.

Sites and chronology

First, we excluded sites for which less than five species corresponding to the above criteria are recorded, as well as sites suspected of either being contaminated, containing plants wrongly identified or for which the archaeological dating is doubtful. To reflect the differences in the cultural/socioeconomic development in the individual periods, we classified the information into the 10 chronological phases summarized in Table 1. For general information about the localities and their references, see Electronic Appendix 2.

The Neolithic Period (Pavlů & Zápotocká 2013) was divided into two phases: the initial Early Neolithic or Linear Pottery Culture (NE1) and the following Late Neolithic (NE2), in order to distinguish the earliest stages in the invasion of alien plants. The Eneolithic Period (ENE), a commonly used term in the Czech Republic (Neustupný 2013), is the equivalent of the Late Neolithic in western, central and north-western Europe, and of the Chalcolithic (or Copper Age) in south-eastern and eastern Europe. In contrast to the commonly used archaeological periods of the Bronze Age (Jiráň 2013), we divided it into two phases: the Early to Middle Bronze Age (BR1) and the Late to Final

Table 1. – Chronology of the data examined. Absolute dating of prehistoric periods for the Czech Republic follows Jiráň & Venclová (2013). The sum of seeds means the total number of seeds of species meeting our criteria.

Abbr.	Periods of the Prehistory	Time span	Length (years)	Number of sites	Sum of seeds
NE1	Early Neolithic (Linear Pottery)	5600–4900 BC	600	10	5,894
NE2	Late Neolithic	5000–4200 BC	700	10	2,211
ENE	Eneolithic	4500/4400–2300 BC	2000	17	1,116
BR1	Early to Middle Bronze Age	2300/2200–1250 BC	1000	20	5,127
BR2	Late to Final Bronze Age	1250–800/750 BC	500	44	20,793
IR1	Early Iron Age (Hallstatt)	800–400/370 BC	350	25	17,467
IR2	Late Iron Age (La Tène)	480/460–50/20 BC	450	21	9,653
RMP	Roman to Migration Period	35/25 BC–AD 560/580	580	14	9,941
EM1	Early Middle Ages 1–3	AD 580–950	370	13	71,727
EM2	Early Middle Ages 4	AD 950–1200	250	28	73,870

Bronze Age (BR2), which differed markedly in both the technological progress in agriculture and the range of crops cultivated (Dreslerová & Kočár 2013, Dreslerová et al. 2017). The subsequent Early Iron (IR1) and Late Iron (IR2) Ages are used in the same sense as the Hallstatt and La Tène cultures, respectively (see Venclová 2013a, b). On the contrary, a short Migration Period was attached to the previous Roman Period (RMP), because these periods are alike both in terms of culture and technology in the Czech territory (Jiráň & Venclová 2013). The Early Medieval was divided into two periods (EM1 and EM2) reflecting the population increase and landscape changes and with respect to the homogeneity of the archaeobotanical data.

Residence time, invasiveness and development of flora

All species were categorized according to their estimated MRT based on their first occurrence in the archaeological records. In the following text, we use MRT of alien species for possible time of their immigration. At the same time, when talking about native species, we use the term first occurrence. Archaeophytes (sensu Pyšek et al. 2012) were classified into five groups according their current invasiveness and abundance (based on Danihelka et al. 2012 and Pyšek et al. 2012), ranging from common invasive to rare species.

We plotted the cumulative numbers of newly occurring aliens, and the proportions of alien and native species in each of the individual periods against the subsequent periods on a time axis. Principal component analysis (PCA) was performed using Canoco v. 5 (Lepš & Šmilauer 2003) based on the floristic composition in the individual periods.

Furthermore, we classified the species into groups according to their first occurrence, and their links to habitats. The ecological demands of a particular species were derived from Chytrý (2007–2013), regional species pools (Sádlo et al. 2007) and Ellenberg-type indicator values for the Czech flora (Chytrý et al. 2018). Each phase was characterized by the co-occurrence of several species groups. The names of the phytosociological units used in the description of some groups follow Chytrý et al. (2007–2013) and Mucina et al. (2016).

Results

Dynamics of invasion, species composition and vegetation development

The application of our selection criteria reduced the data studied from 223 to 202 sites (Fig.1) and from the original 278 to 217 taxa. Based on this data, we recorded 123 alien and 94 native taxa in the Czech Republic. The MRTs of these species are in Table 2. This flora was assessed using the following three approaches: invasion dynamics, species composition and vegetation development.

The invasion dynamics of the newly occurring aliens (Fig. 2) were expressed in terms of their cumulative numbers against the time of their first record. This approach distinguished three temporal phases, which were represented by waves of immigration of increasing magnitude followed by distinct declines. The wave/decline phases cover the periods (i) NE1–ENE, (ii) BR1–RMP, and (iii) EM1–EM2 (see Table 1 for the chronology and abbreviations). The gradual emergence of native species was similar to that of the alien species, but this coincidence results from the different dynamics of several species groups. Species of natural habitats such as grasslands rapidly increased only from the Late Bronze Age (BR2), whereas the proportion of ruderal/segetal native species was similar to the representation of aliens in the respective periods (Fig. 3).

The gradual changes in total species composition were expressed in terms of the floristic resemblance of the individual periods (Fig. 4). The ordination shows a similar pattern over the phases as the above-mentioned invasion dynamics, however the initial period (NE1) formed a separate unit distinct from the subsequent periods. The approach based on vegetation development (Table 2) offers a more detailed view of the formation of the synanthropic flora. This showed the successive emergence of particular species groups defined by their first occurrence and habitat affinities. Four developmental phases were distinguished based on the definitions of 11 species groups.
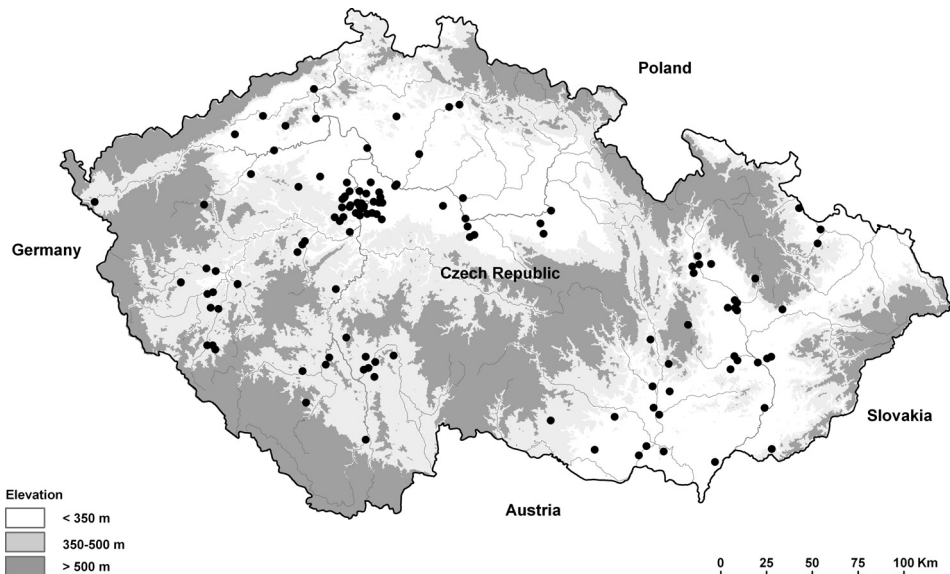

Fig. 1. – Map showing the locations of the archaeological sites included in the analyses. Note that the majority of sites in the Czech Republic are located in the fertile lowlands. The average altitude of the sites is 295 m a.s.l. Author of the map: Č. Číšecký.

Table 2. – List of plant species. For each taxon, its occurrence in the prehistoric period is shown semiquantitatively. Species are divided into ecological groups (for more details see the section 'Characterization of vegetation development'). Empty circle, occurred at less than 10% of the sites; solid circle, 10–50% of the sites; solid rectangle, more than 50% of the sites in the given period. The species status (alien or native) is based on Danihelka et al. (2012).

Plant species	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2	status
NE1 – NE2 (Early Neolithic - Late Neolithic)											
Weeds of contemporary fallow land or hoed crop fields											
Atriplex patula	○	---	○	○	●	●	●	●	■	●	alien
Bromus arvensis	○	●	●	●	●	●	●	○	---	●	alien
Bromus secalinus	●	●	●	■	●	■	■	●	---	●	alien
Bromus sterilis	○	●	○	●	●	●	●	●	---	●	alien
Chenopodium album	■	■	■	■	■	■	■	■	■	■	
Chenopodium polyspermum	●	---	○	---	●	○	○	○	●	●	
Digitaria ischaemum		○	---	○	○	○	○	○	---	○	alien
Digitaria sanguinalis		○	---	○	○	○	○	---	---	○	alien
Echinochloa crus-galli	○	●	---	●	●	●	●	●	●	■	alien
Euphorbia helioscopia		●	○	---	●	●	●	---	■	●	alien
Fallopia convolvulus	■	■	■	■	■	■	■	■	■	■	alien
Galium aparine	●	●	●	■	■	■	■	■	■	■	
Galium spurium	●	●	●	■	■	■	■	■	■	■	alien
Lapsana communis	○	---	---	---	○	○	○	○	●	●	alien
Lolium temulentum		○	○	○	●	●	○	○	---	○	alien
Persicaria lapathifolia agg.	●	●	○	●	●	■	●	●	●	■	
Persicaria maculosa	●	●	●	●	●	●	●	●	■	●	
Setaria pumila	○	●	○	○	●	●	●	●	●	■	alien
Setaria viridis		●	●	●	●	●	0	---	---	---	alien
Sinapis arvensis	○	---	○	---	---	○	●	○	●	●	alien
Solanum nigrum	●	●	●	●	●	●	●	●	■	■	alien
Stellaria media agg.		○	○	○	●	●	●	---	●	●	
Thlaspi arvense	○	---	---	○	●	●	●	---	■	■	alien
Annual species of trampled and/or dunged bare soils											
Arenaria serpyllifolia agg.		○	---	○	○	---	○	---	●	●	
Capsella bursa-pastoris		○	---	---	---	○	---	---	●	●	alien
Chenopodium hybridum	●	●	●	●	■	■	■	■	■	■	
Chenopodium murale	●	○	●	○	●	●	●	●	○	●	alien
Chenopodium urbicum	○	---	○	---	---	○	---	---	○	●	alien
Poa annua	○	---	---	○	---	○	○	---	○	○	
Polygonum aviculare agg.	●	●	●	●	■	■	■	■	■	■	
Perennial species of mezic ruderal grasslands											
Convolvulus arvensis		○	---	●	○	○	●	---	●	●	alien
Elymus repens	○	---	○	●	○	●	●	---	---	●	
Medicago lupulina	○	---	---	○	●	●	●	●	---	●	
Ranunculus repens	○	---	○	○	---	○	●	○	■	■	
Rumex acetosa	○	---	---	---	○	○	---	---	●	●	
Sambucus ebulus		●	●	●	●	●	●	●	■	●	alien
Securigera varia		○	---	---	●	---	●	---	○	○	
Silene vulgaris	○	---	---	---	○	○	○	○	●	●	
Trifolium pratense	○	---	○	○	●	●	●	●	●	●	
Urtica dioica	●	●	---	○	○	○	○	○	●	■	
Vicia hirsuta/tetrasperma		●	●	●	●	■	●	●	●	●	

Plant species	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2	status
Other species											
Acinos arvensis		○	---	---	○	○	○	---	●	●	
Atriplex sagittata	○	---	---	○	○	---	---	---	●	●	alien
Papaver dubium/rhoeas	○	---	---	---	○	●	○	---	●	●	alien
Rumex acetosella	○	●	●	○	●	●	●	●	■	■	
Stipa pennata agg.		●	●	○	●	○	○	---	---	---	
ENE – BR1 (Eneolithic, Early and Middle Bronze Age)											
Annual cereal weeds											
Adonis aestivalis				○	---	○	○	○	●	●	alien
Aethusa cynapium				○	---	---	---	---	■	●	
Agrostemma githago			●	●	●	●	●	●	■	■	alien
Anagallis arvensis agg.			○	---	---	○	---	---	●	●	alien
Anthemis arvensis				○	---	○	○	○	●	●	alien
Apera spica-venti				○	---	---	---	---	---	---	alien
Buglossoides arvensis			●	●	●	●	●	●	●	●	alien
Bupleurum rotundifolium				○	○	○	○	○	■	■	alien
Consolida regalis				○	---	○	○	---	---	○	alien
Fumaria officinalis				○	●	●	●	○	■	■	alien
Fumaria vaillantii				○	---	---	---	---	---	○	alien
Galeopsis tetrahit agg.			○	○	○	○	●		■	■	
Kickxia elatine				○	---	○	---	---	---	○	alien
Lolium remotum				○	---	---	---	---	---	---	alien
Nigella arvensis				○	---	---	---	---	○	○	alien
Polycnemum arvense				○	○	○	---	●	●	●	alien
Raphanus raphanistrum			○	○	---	○	○	---	●	●	alien
Scleranthus annuus			○	●	●	○	●	○	●	●	
Silene noctiflora				○	---	○	---	○	○	○	alien
Stachys annua/arvensis			○	---	●	○	●	●	■	●	alien
Thymelaea passerina				○	---	---	○	---	●	○	
Veronica hederifolia agg.			○	●	●	●	○	---	○	○	
Veronica opaca/polita				○	○	---	---	---	---	○	alien
Viola cf. *arvensis*			○	---	○	○	○	---	●	●	
Tall biennial and perennial herbaceous plants of dry and nitrogen-poor substrata											
Artemisia vulgaris				○	---	○	○	---	---	○	
Camelina microcarpa				○	●	●	●	---	●	●	alien
Cirsium arvense			○	○	●	○	---	---	●	●	alien
Daucus carota				○	○	○	○	○	●	●	
Echium vulgare			○	---	○	○	---	---	---	○	
Galeopsis angustifolia/ladanum				○	○	○	●	○	●	●	
Geranium columbinum				○	○	---	---	---	---	○	alien
Lathyrus tuberosus				○	○	---	---	---	---	---	alien
Medicago falcata				○	○	○	●	○	---	○	
Melilotus albus/officinalis				○	○	○	○	---	●	●	alien
Reseda lutea				○	---	---	---	○	●	●	alien
Silene latifolia			○	---	○	○	○	○	■	■	alien
Trifolium arvense				○	○	○	○	●	---	○	
Vicia cf. *pannonica/sativa*				○	○	○	○	○	○	○	alien
Species of nutrient-rich trampled and grazed lawns											
Carex muricata agg.			○	---	○	○	---	○	●	○	
Galium mollugo				○	○	○	●	○	●	○	
Glechoma hederacea				○	○	○	○	---	●	●	
Mentha arvensis				○	○	○	○	○	●	●	

Plant species	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2	status
Plantago lanceolata			○	○	●	●	●	●	○	●	
Potentilla anserina				○	---	○	---	---	○	●	
Prunella vulgaris				○	○	○	○	---	●	●	
Rumex crispus/obtusifolius			○	●	●	●	●	●	●	●	
Sonchus arvensis				○	---	---	---	---	●	○	alien
Trifolium campestre			○	---	●	---	○	○	○	---	
Trifolium repens			○	○	●	●	●	●	○	●	
Verbena officinalis				○	---	○	---	○	●	●	alien

Other species

Plant species	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2	status
Arctium cf. *lappa/tomentosum*			●	---	---	○	---	---	●	○	alien
Atriplex oblongifolia				○	○	---	---	---	●	○	alien
Centaurea jacea			○	○	●	○	○	---	●	○	
Galium verum agg.				○	●	○	●	---	---	○	
Glaucium corniculatum				○	---	---	○	---	●	●	alien
Heracleum sphondylium			○	---	---	---	○	---	●	○	
Hyoscyamus niger				○	○	○	●	---	●	●	alien
Lamium amplexicaule/purpureum				○	●	●	●	---	■	●	alien
Leucanthemum vulgare agg.				○	○	---	●	---	●	●	
Lithospermum officinale				○	○	---	○	○	●	---	
Malva neglecta				○	---	○	○	○	●	●	alien
Mercurialis annua				○	---	---	○	---	---	○	alien
Scirpus sylvaticus			○	---	○	---	○	---	●	●	
Senecio vulgaris				○	---	---	---	---	○	○	alien
Trisetum flavescens				○	○	○	○	---	○	○	

BR2, IR1, IR2, RMP – Late and Final Bronze Age, Early and Late Iron Age, Roman and Migration Period

Ruderal species of sunny, unevenly disturbed substrata rich in bases and organic nutrients

Plant species	BR2	IR1	IR2	RMP	EM1	EM2	status
Anthemis cotula		○	---	---	●	○	alien
Bromus tectorum	○	○	---	---	---	---	alien
Bryonia alba	○	---	---	---	---	---	alien
Carduus acanthoides		○	---	---	●	●	alien
Chenopodium bonus-henricus	○	---	---	---	---	---	alien
Erodium cicutarium	○	---	---	---	---	---	alien
Geranium pusillum		○	---	---	---	○	alien
Lepidium campestre			○	---	●	●	alien
Lepidium ruderale	○	○	---	○	---	○	alien
Malva pusilla		○	---	○	---	○	alien
Malva sylvestris	○	○	---	---	●	●	alien
Onopordum acanthium		○	---	---	○	○	alien
Stachys germanica			○	---	●	○	
Urtica urens		○	---	---	■	●	alien

Species of meadows, pastures and dry grasslands

Plant species	BR2	IR1	IR2	RMP	EM1	EM2	status
Ajuga genevensis/reptans	○	---	●	○	●	●	
Barbarea vulgaris	○	---	---	---	●	●	
Carex hirta	○	●	○	●	○	●	
Carex leporina	○	○	●	---	●	●	
Carex pallescens		○	---	---	●	●	
Centaurea scabiosa	○	○	---	○	●	●	
Clinopodium vulgare	○	○	---	---	●	●	
Hypericum perforatum	○	---	●	○	■	●	
Knautia arvensis				○	●	●	
Linum catharticum			○	---	●	○	
Lychnis flos-cuculi	○	○	○	---	●	●	

Plant species	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2	status
Melampyrum arvense							○	○	○	●	alien
Phleum pratense					○	○	○	○		○	
Pimpinella saxifraga						○	---	---	○	○	
Plantago media					○	○	○	---		○	
Ranunculus acris						○	●	○	●	●	
Silene nutans						○	---	---	●	●	
Stellaria graminea					○	---	○	---	●	●	
Taraxacum sp.							○	---	●	●	
Thalictrum minus					○	---	---	○	○	○	
Vicia cracca/sepium					○	○	●	●	○	○	

Other species

Plant species	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2	status
Aegopodium podagraria							○	---	---	●	
Ajuga chamaepitys						○	---	---	---	○	alien
Aphanes arvensis							○	---	●	●	
Asperula arvensis						○	○	---	---	●	alien
Avena fatua					○	○	---	●	●	○	alien
Chelidonium majus						○	---	---	●	●	alien
Chenopodium ficifolium					●	○	●	●	●	●	
Chenopodium foliosum						○	---	---	---	---	alien
Chenopodium glaucum/rubrum					○	○	○	○	●	●	
Descurainia sophia					○	---	○	---	---	○	alien
Galium tricornutum					○	---	○	---	---	○	alien
Hibiscus trionum							○	---	---	---	alien
Myosotis arvensis						○	○	---	●	○	alien
Neslia paniculata							○	●	■	■	alien
Odontites vernus					○	---	---	---	●	○	
Papaver argemone					○	---	---	---	●	○	alien
Potentilla sp.					○	○	●	---	■	●	
Stachys palustris						○	---	---	○	●	
Tripleurospermum maritimum						○	---	---	---	---	alien
Valerianella dentata					○	○	●	---	■	●	alien
Valerianella rimosa							○	---	---	---	alien

EM1, EM2 – Early Middle Ages

Nitrophilous ruderal species of human-made substrata

Plant species	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2	status
Amaranthus blitum/graecizans									●	●	alien
Anthriscus caucalis										○	alien
Atriplex prostrata									○	●	
Ballota nigra									●	●	alien
Chenopodium vulvaria										○	alien
Conium maculatum									●	●	alien
Euphorbia peplus									○	○	alien
Hordeum murinum									○	---	alien
Lactuca serriola										○	alien
Lamium album									●	●	alien
Leonurus cardiaca									●	○	alien
Nepeta cataria									○	●	alien
Portulaca oleracea										●	alien
Rumex conglomeratus										●	
Setaria verticillata/viridis									○	○	alien
Sisymbrium officinale										○	alien
Sonchus asper									●	●	alien
Sonchus oleraceus									●	○	alien
Xanthium strumarium									●	●	alien

Plant species	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2	status
Pastural species avoided by grazing animals											
Agrimonia eupatoria									●	●	
Anchusa officinalis									○	○	alien
Berteroa incana									●	●	alien
Cerinthe minor									●	●	
Cichorium intybus									●	●	alien
Cirsium vulgare									○	○	
Euphorbia cyparissias									○	●	
Linaria vulgaris									●	●	alien
Marrubium vulgare										○	alien
Species of wet forests and alluvial meadows											
Fallopia dumetorum									●	●	
Filipendula ulmaria										●	
Pastinaca sativa									●	○	
Ranunculus flammula									●	●	
Rumex sanguineus									●	○	
Silene dioica									●	○	
Stellaria palustris									●	●	
Thalictrum flavum									●	●	
Valeriana officinalis									●	●	
Other species											
Anthemis austriaca										○	alien
Caucalis platycarpos									○	●	alien
Centaurea cyanus									●	●	alien
Crepis capillaris										○	alien
Geranium dissectum									●	●	alien
Geranium molle										○	alien
Microrrhinum minus										○	alien
Ranunculus arvensis										○	alien
Reseda luteola									●	●	alien
Silene dichotoma										○	alien
Silene gallica										○	alien
Spergula arvensis										●	alien
Vaccaria hispanica										○	alien

The historical periodization of the archaeophyte phase studied is summarized and the main expansion/invasion processes responsible for the floristic changes are listed in Table 3. The recorded differences in periodization based on the individual methods reflect distinct aspects of temporal floristic changes. Still, the periodization using the invasion dynamics was based on a simple and quantitative criterion unlike the other two methods, which reflected only partial and qualitative features of vegetation changes.
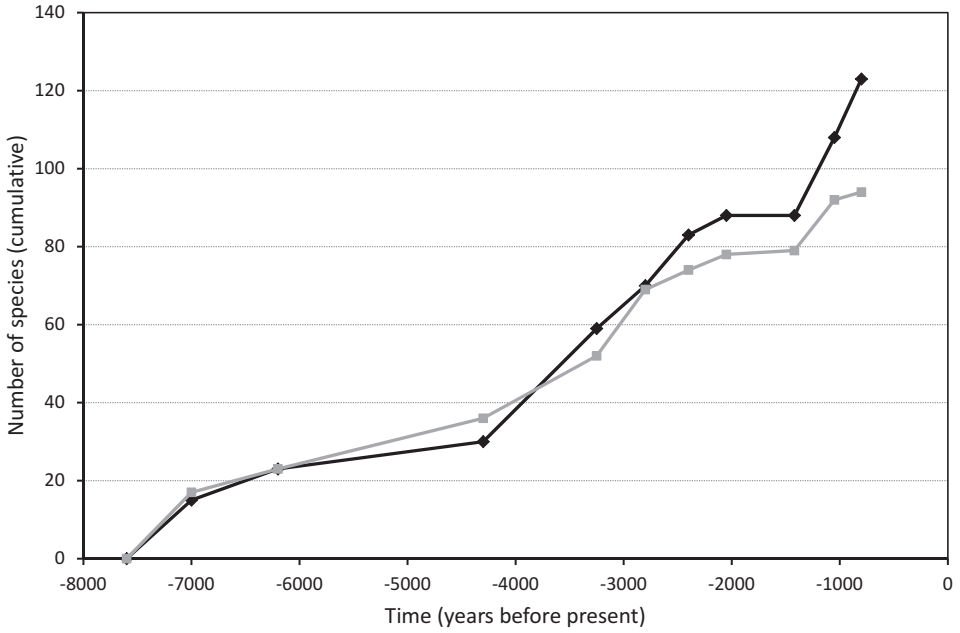
Fig. 2. – The cumulative number of alien species (black line) and native species (grey line) plotted against the time of their first record.
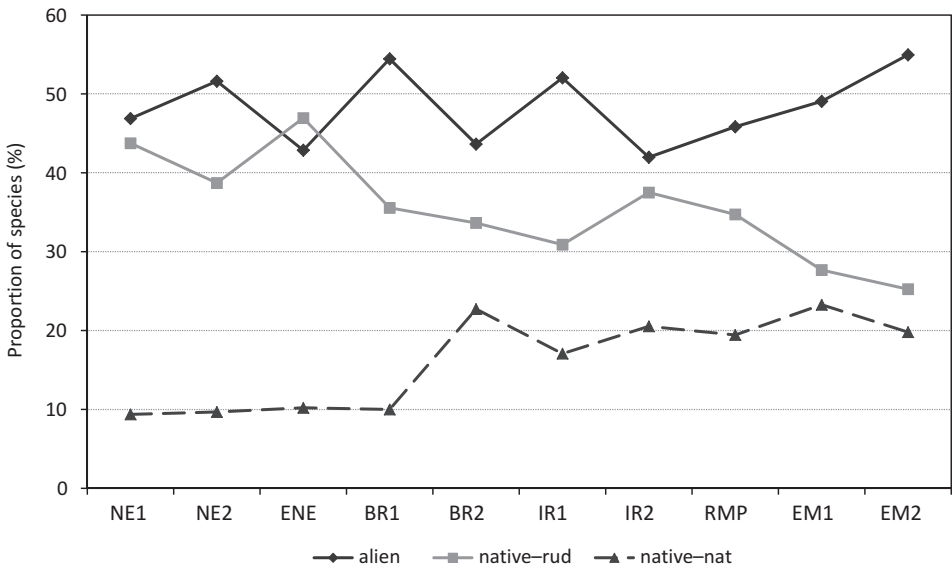
Fig. 3. – The relative percentages of the species in the individual periods (see Table 1 for an explanation of the abbreviations). Within the native flora, species of ruderalized habitats (native–rud) were distinguished from species of semi-natural habitats (native–nat).
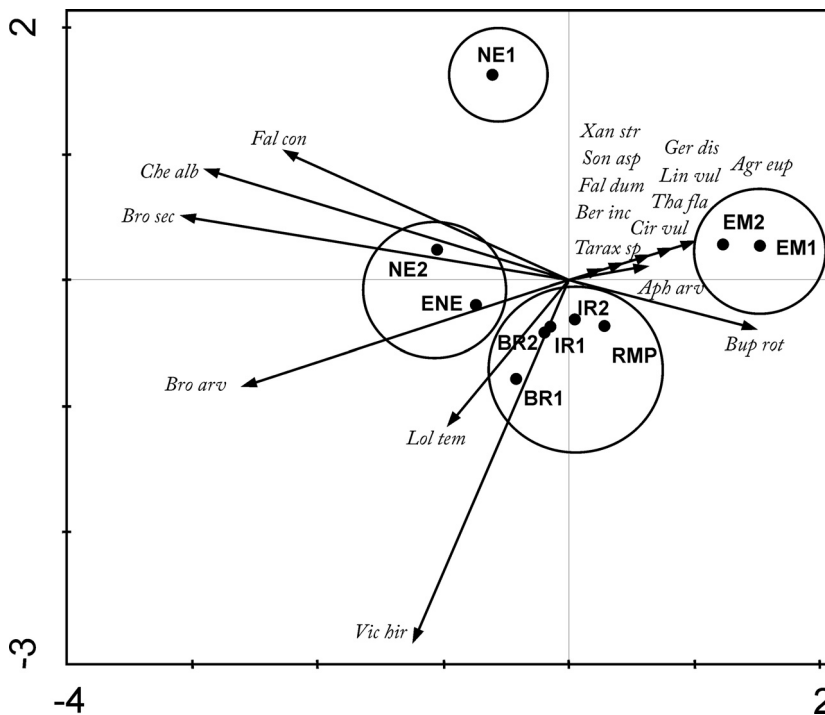
Fig. 4. – Ordination diagram showing results of a PCA analysis of the individual periods and the species relationship. The first axis explained 37.7% of the variability, and the first two axes together explained 53.8% of the variability. Only species fitting well on the first two PCA axes are shown. Species abbreviations: Agr eup, *Agrimonia eupatoria*; Aph arv, *Aphanes arvensis*; Ber inc, *Berteroa incana*; Bro arv, *Bromus arvensis*; Bro sec, *Bromus secalinus*; Bup rot, *Bupleurum rotundifolium*; Cir vul, *Cirsium vulgare*; Che alb, *Chenopodium album*; Fal con, *Fallopia convolvulus*; Fal dum, *Fallopia dumetorum*; Ger dis, *Geranium dissectum*; Lin vul, *Linaria vulgaris*; Lol tem, *Lolium temulentum*; Son asp, *Sonchus asper*; Tarax sp, *Taraxacum* sp.; Tha fla, *Thalictum flavum*; Vic hir, *Vicia hirsuta/tetrasperma*; Xan str, *Xanthium strumarium*.

Table 3. – Periodization of the archaeophyte phase based on different classification approaches: invasion dynamics (see Fig. 2); species composition (Fig. 4); vegetation development (Table 2). See Table 1 and text for abbreviations of the periods.

Period	NE1	NE2	ENE	BR1	BR2	IR1	IR2	RMP	EM1	EM2
Invasion dynamics										
Species composition										
Vegetation development										

Main species groups:

                    Ruderal / segetal generalists

                             Specialized segetal weeds

                                      Species of meadows and pastures

                                            Nitrophilous ruderal weeds

Characterization of vegetation development

The following classification (see also Table 2) is based on first occurrences of the species (both aliens and natives) and their present-day links to anthropogenic habitats.

Phase 1 (NE1–NE2; 5600–4200 BC)

Weeds of contemporary fallow land or hoed crop fields. Species of nutrient-rich, frequently disturbed soils are common. This group is composed of annual dicotyledons (e.g. *Chenopodium album*, *Fallopia convolvulus*, *Persicaria lapathifolia*), winter annual grasses (*Bromus arvensis*, *B. secalinus*, *B. sterilis*) and late-germinating C4 annual grasses with an autumnal optimum (*Digitaria ischaemum*, *D. sanguinalis*, *Echinochloa crus-galli*, *Setaria pumila*, *S. viridis*). At present, most of these species occur in sandy-loamy soils in ruderal habitats, fields and gardens. Aliens such as *Atriplex patula*, *Euphorbia helioscopia*, *Sinapis arvensis*, *Solanum nigrum* and *Thlaspi arvense* and natives such as *Chenopodium polyspermum* and *Stellaria media* indicate repeatedly disturbed, nutrient-rich soils occurring, at present, in hoed root crops, maize fields or vegetable gardens. This species composition clearly indicates weedy vegetation of the phytosociological units *Spergulo arvensis-Erodion cicutariae* and *Veronico-Euphorbion*. These units often occur together as autumnal and vernal phenological variants, respectively.

   Annual species of trampled and/or dunged bare soils. This group includes ruderal species of bare soils. Trampling is indicated by the presence of e.g. *Capsella bursa-pastoris*, *Poa annua*, *Polygonum aviculare* and the presence of ammonia nitrogen by *Chenopodium hybridum*, *C. murale* and *C. urbicum*. In modern times, this species combination typically occurs on open grounds alongside buildings, walls, and various human defecation/urination sites, sites for livestock breeding and near dung holes.

   Perennial species of mesic ruderal grasslands. This group is formed by generalist species that are widespread in the current landscape and easily colonize periurban, industrial or mining areas, road embankments or field boundaries. These successional stages mostly last for several tens of years and are not regularly managed excluding the occasional trampling, cutting or the deposition of waste. They are often dominated by rhizomatous geophytes, e.g. *Convolvulus arvensis*, *Elymus repens*, *Sambucus ebulus* and *Urtica dioica*.

Phase 2 (ENE–BR1; 4500–1250 BC)

Annual cereal weeds. Thermophilous annual aliens of cereal fields (e.g. *Adonis aestivalis*, *Agrostemma githago*, *Bupleurum rotundifolium*) and stubble fields (e.g. *Polycnemum arvense*, *Silene noctiflora*, *Stachys annua/arvensis*) clearly correspond to the unit *Caucalidion*, which represents weedy field vegetation on fertile soils rich in mineral nutrients such as chernozem. Similarly, a group of less nutrient-demanding species on base-poor soils (aliens such as *Anthemis arvensis* and *Raphanus raphanistrum;* natives such as S*cleranthus annus* and *Galeopsis tetrahit*) may indicate *Scleranthion*, i.e. weedy vegetation of less fertile cereal fields.

   Tall biennial and perennial herbaceous plants of dry and nitrogen-poor substrata. This species-rich group includes alien geophytes spreading clonally by roots (e.g. *Cirsium arvense*, *Lathyrus tuberosus*) and short-lived herbaceous plants, which are both

of alien origin (e.g. *Melilotus albus/officinalis*, *Reseda lutea*, *Silene latifolia*) and natives (e.g. *Artemisia vulgaris*, *Daucus carota*, *Echium vulgare*). These species indicate dry and sunny sites with bare loamy or stony soils that are rich in mineral nutrients but poor in phosphorus and nitrogen. In a modern landscape, this species composition corresponds to the *Dauco-Melilotion* unit, the type of vegetation resulting from a major disturbance followed by several years of succession, e.g. in newly abandoned fields, road margins, eroded slopes or stone pits.

Species of nutrient-rich trampled and grazed lawns. Species such as *Potentilla anserina*, *Prunella vulgaris* and *Verbena officinalis* characteristically occur in short ruderalized grasslands. Most of the species are native. In modern times, such vegetation occurs in villages (*Potentillion anserinae*, pastures with compacted and nitrified soils, mostly maintained by poultry or goats) or in their vicinity (*Alchemillo-Ranunculion repentis*, eutrophic short lawns).

Phase 3 (BR2, IR1, IR2, RMP; 1250 BC–AD 580)

Ruderal species of sunny, unevenly disturbed substrata rich in bases and organic nutrients. The present cooccurrence of these species results from early succession on bare or repeatedly disturbed soils around sites where animals are bred. Tall xerophilous and thermophilous biennial herbaceous plants (e.g. *Carduus acanthoides*, *Onopordon acanthium*, *Stachys germanica*) and small annuals (e.g. *Bromus tectorum*, *Erodium cicutarium*) may indicate the *Onopordion acanthii* unit. Similar, but moderately wet and highly nitrified habitats may be indicated by the species in *Malvion neglectae* (small annuals *Anthemis cotula*, *Malva pusilla*, *Urtica urens*), and *Arction* (tall perennials *Bryonia alba*, *Chenopodium bonus-henricus*, *Malva sylvestris*). In rural settlements, these three phytosociological units often form a tessellate pattern, which is spatially differentiated according to the quality and intensity of the effects of man or animals.

Species of meadows, pastures and dry grasslands. Most of these species are native in central Europe. The species, which are associated with mesic or wet habitats, may indicate a recurring cycle of disturbance events (e.g. grazing by cattle) separated by periods of abandonment (e.g. *Carex hirta*, *C. leporina*, *C. pallescens*, *Lychnis flos-cuculi*, *Stellaria graminea*, *Stachys palustris*). Species such as *Clinopodium vulgare*, *Plantago media*, *Silene nutans* and *Thalictrum minus* indicate dry grasslands, shrubby fringes or, possibly, grazed forests.

Phase 4 (EM1, EM2; 580–AD 1200)

Nitrophilous ruderal species on human-made substrata. This group includes mesophilous and nitrophilous plants demanding or tolerating high contents of nitrogen and other nutrients. Tall and robust perennials (e.g. *Ballota nigra*, *Conium maculatum*, *Leonurus cardiaca*) indicate nutrient-rich substrata, disturbed infrequently. Short annuals such as *Anthriscus caucalis*, *Chenopodium vulvaria* and *Xanthium strumarium* prefer intensely disturbed sites rich in ammonia nitrogen. Tall annuals (e.g. *Lactuca serriola*, *Sisymbrium officinale*, *Sonchus asper*) are, in modern times, common on rubbish dumps or refuse heaps. These three groups of species correspond to the units *Arction*, *Malvion neglectae* and *Atriplicion*, respectively.

Pastural species avoided by grazing animals. Indigestible, aromatic or poisonous pastural weeds were present in this period. Aliens such as *Anchusa officinalis*, *Cichorium intybus* and *Linaria vulgaris*, and natives such as *Agrimonia eupatoria*, *Cerinthe minor*, *Cirsium vulgare* and *Euphorbia cyparissias* indicate pastural degradation of mesic or dry grasslands, or possibly also pasture on fallow land.

Species of wet forests and alluvial meadows. This species group indicates wet and nutrient-rich habitats in fluvial plains or spring beds. Tall herbaceous plants such as *Filipendula ulmaria*, *Thalictrum flavum* and *Valeriana officinalis* indicate moist meadows whereas *Fallopia dumetorum*, *Silene dioica* and *Rumex sanguineus* may indicate forest edges or clearings.

Residence time and invasion success

We asked whether differences among the species in their MRTs were still reflected in their current invasion status, many centuries or millennia after their arrival. According to our data, the earlier periods, in general, brought a higher number of currently common species than the later periods in which, on the contrary, species with low invasion success were more abundant. Three archaeophytes of Neolithic origin are invasive today (*Atriplex sagittata*, *Digitaria ischaemum* and *Echinochloa crus-galli*). On the contrary, three species of the same origin are rare today (*Bromus arvensis*, *B. secalinus* and *Lolium temulentum*). Common species (including those locally abundant) represent 65% of all the aliens of Neolithic origin.

Several archeophytes, which arrived during the later phases of prehistoric times, are rare or uncommon today although they are rather common in our data (*Agrostemma githago*, *Bupleurum rotundifolium*, *Glaucium corniculatum*, *Polycnemum arvense* and *Asperula arvensis*). Others are rarely recorded in the archaeobotanical data and are currently also rare (*Kickxia elatine*, *Lolium remotum*, *Nigella arvensis*, *Ajuga chamaepitys*, *Galium tricornutum*, *Hibiscus trionum*, *Chenopodium foliosum* and *Valerianella rimosa*). Only one species in this group is invasive today (*Cirsium arvense*).

Two currently invasive species (*Conium maculatum* and *Portulaca oleracea*) and seven rare species (*Anthriscus caucalis*, *Xanthium strumarium*, *Marrubium vulgare*, *Caucalis platycarpos*, *Geranium molle*, *Silene gallica* and *Vaccaria hispanica*) arrived in the Early Middle Ages. Common species (including those locally abundant) make up only 42% of all the aliens introduced in the Early Medieval Period.

Discussion

Sources of the progressive increase in species diversity

Two factors greatly affected the increasing, but fluctuating number of species since the Neolithic to the Early Medieval Period. These are the long term (centuries, millenia) processes that occurred in the past in the vegetation and the taphonomic distortion of the palaeorecords (for more details about taphonomy in archaeobotany, see e.g. Greig 1981, Behre & Jacomet 1991, Jacomet & Kreuz 1999, Heimdahl 2005, Bosi et al. 2011, Święta-Musznicka et al. 2013). The recorded increase in diversity is no doubt affected by the total amount of data available in the different periods. The number of sites investigated

varied between 10 in NE1 and 46 in BR2 or 36 in EM2, but the differences in the numbers of seeds recorded are much more significant. The seed sum did not reach 6000 until BR2, but it exceeded 70,000 in EM1 and EM2 (Table 1).

Necessarily, our data includes only a portion of the original local vegetation and cannot be entirely free of imperfections. Above all, the different preservation processes of macroremains result in a considerably different composition of the archaeological records. Waterlogging, which was common in the Medieval Period, generally results in more numerous and species-rich assemblages than the carbonization of seeds, which predominate at ancient sites. Fossilization by charring is mainly connected to crop processing after harvest, and thus crop weeds are much more likely to be found than other plants. Therefore, the composition of most archaeobotanical samples is usually distorted by the harvesting technology or crop processing such as threshing or winnowing (see e.g. Hillman 1981, Reynolds 1985, Jones 1990, Colledge & Conolly 2014, Kočár et al. 2015) and may result in a biased interpretation.

In addition, the floristic composition indicates that different sections of the landscape were recorded in the different periods. The collecting area for macroremains increased during the archaeophyte period. For example, the Neolithic flora was dominated by species that indicate fields and the vicinity of buildings. Later, the share of seminatural grasslands increased. Finally, this area extended as far as on the dry slopes or swamps in the Early Medieval Period. The sudden increase in meadow species occurred in BR2, which requires further study, since the oldest findings of a scythe only date back to the Hallstatt Period (Venclová 2013a).

Special attention needs to be paid to the number of native species and their proportion relative to number of alien species. The vegetation in archaic settlements, including their close vicinity, was dominated by native species, as at present (see e.g. Pyšek 1998, Chocholoušková & Pyšek 2003, Pyšek et al. 2003, 2004, Celesti-Grapow et al. 2006, Lososová & Simonová 2008, Lososová et al. 2012, 2016). However, the number of native species was rather low in the assemblage of macroremains studied with their percentage in relation to alien species ranging only from 42 to 55% of the total species number in the respective periods. The stable percentage of native species may be partly due to the extensive standardization of the data in which many species were excluded for taphonomic reasons (see Electronic Appendix 1). Furthermore, the above-mentioned share of species in natural habitats such as grasslands (Fig. 3) implies that the ostensible concurrence of natives with aliens resulted from the representation of two independent species groups. Several other factors contributed to the suppression of natives. In many native species, either seed production is low (e.g. clonal grasses subject to human pressure) or they are not used by man. In addition, cereal weeds are better adapted to persist in harvested grain (de Wet & Harlan 1975) than the more easily separated natives.

The increase in species diversity recorded in the fossil flora was, in the first place, caused by the immigration of aliens. However, the changing number of the types of habitats and complexity of the cultural landscape also played a considerable role, though this effect may be partially hidden by the above-mentioned increase in the collecting area. Although landscape development did not follow a straight and smooth progress, the general trend of an increase in cultural diversity is obvious in settlements from the Neolithic to Medieval Periods, which is reflected in the floristic development. Rather the cumulative increase in the number of species and types of vegetation implies an increase in the

number of habitats. For example, the sequence of *Dauco-Melilotion – Onopordion – Arction* communities may indicate the successive emergence of nutrient-rich anthrosols formed by long-term human habitation. However, especially the succession of ruderal vegetation is not sufficiently interpretable without further comparison with archaeological knowledge.

Invasion history of the segetal and ruderal flora

The positive dependence of the present invasion success of alien plants on their MRT has been established many times at various time scales and using different indicators of success (e.g. Pyšek et al. 2003, 2015, Pyšek & Jarošík 2005, La Sorte & Pyšek 2009). In neophytes, this relationship can be easily explained by the length of time they have had to naturalise and spread (Wilson et al. 2007) and the distribution of the more recent arrivals was delayed and retarded by their yet incomplete naturalization.

We wanted to check whether this dependence applies even to archaeophytes, which have been fully naturalized for a long time whether they arrived early or late. Considering the fact that our data are still rather sketchy, the results are, unfortunately, not reliable for this purpose. Still, those archaeophytes, which are currently widespread, are mainly associated with earlier phases of Prehistory and especially with the Neolithic, whereas in later phases, their share gradually decreased. In the case of the current rare species, the time changes in the number of species showed no obvious trend.

As Pyšek et al. (2015) proved, MRT is not an independent cause of invasion success, but results from the sequence of biological traits that were present both in the native area and during the invasion. This finding implies that the early-established archaeophytes are probably not currently successful because of their long residence time, but quite the opposite, they arrived early due to their permanent invasiveness. The generalist species colonized both ruderal and segetal habitats and their broad environmental tolerance facilitated their spread. During the 2000 years of the Neolithic cultural expansion from the Near East and the Mediterranean, they rapidly overcame the consecutive changes in macroclimate, habitats and cultural patterns, and appeared in the Neolithic paleorecord in a very similar composition throughout central Europe (Coward et al. 2008). It is no wonder that most of them are currently still common invaders (Kalusová et al. 2017). Some species with a neolithic MRT produce large edible seeds, which served as a substitute for cereals both in the distant past and even in recent times (Harlan 1989, Barakat & Fahmy 1999, Behre 2008), e.g. *Bromus secalinus*, *Chenopodium album*, *Echinochloa crus-galli*, *Fallopia convolvulus*, *Persicaria lapathifolia* and *Setaria pumila*. This indicates that (i) their invasion could have been strengthened by them being collected or even cultivated, which are important invasion drivers (Pyšek et al. 2015), and (ii) the boundary between alien and native species, and between crops and weeds, is fuzzy and intricately definable (see e.g. Chapman 1992, Hancock 2012, Zohary et al. 2012). Especially *Fallopia convolvulus*, which is regarded as an alien in the Czech Republic, is suspected of being a native species since it is recorded from Mesolithic settlements in Sweden (Regnell 2012), Scotland (Bishop et al. 2014), Russia (Dolukhanov 2016) and Belgium (Crombé et al. 2015).

Specialized cereal weeds and the generalist species of Neolithic origin have very different strategies. The native ranges of the former includes the East-Mediterranean steppes, where these species grow today in tall annual grasslands formed by e.g. the genera *Aegilops*, *Avena*, *Secale* and *Bromus* (Zohary 1973, Danin 1988), unlike the ruderal

species that are associated with disturbed places. In central Europe, the segetal weeds only spread out of cereal crops to a limited extent. The archaeobotanical record detected two waves of invasion by those weeds, the first in the Eneolithic/Early Bronze Age and the second in the Early Middle Ages, probably in connection with the changing management of crops and the processing of grain.

The invasion of cereal weeds was less successful, i.e. weaker, slower and delayed in comparison to the less specialized synanthropic plants (see Table 2). The main cause probably lies in their lower propagule pressure, which is stabilized by their exclusive spreading strategy consisting of grain circulation between fields. Therefore, many of these ecological specialists remained common until the early 20th century, but modern agriculture greatly restricted them, unlike the generalists. Some newer invaders of Mediterranean origin are rather common today, but are not invasive (e.g. archaeophytes *Centaurea cyanus* and *Neslia paniculata*, or neophytes *Consolida orientalis* and *Senecio vernalis*). Moreover, most of them (e.g. the genera *Aegilops* and *Malcolmia*) occur only as rare transient casuals in ruderal habitats. This may suggest that the number of potential invasive weeds from the Mediterranean was limited and their supply was already exhausted during the archaeophyte period. For the future, new invasions of segetal weeds coming from this region to central Europe are unlikely. Nevertheless, they cannot be excluded due to their possible support by man-related transport or climate changes.

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Souhrn

Otázka, zda invazní chování rostlin závisí na době, která uplynula od data jejich imigrace, je předmětem řady současných studií. Pozornost se však soustředí hlavně neofyty, kdežto archeofyty bývají posuzovány jen souborně jako jejich referenční skupina. Přitom délka pobytu (doba od zavlečení, MRT) na našem území má u jednotlivých archeofytů rozpětí od 7500 do 500 let. Proto lze předpokládat, že v různých dobách mohly přicházet druhy s odlišnými vlastnostmi. Pro zhodnocení imigrační dynamiky archeofytů jsme použili výsledky analýz rostlinných makrozbytků, čerpaných především z Archeobotanické databáze České republiky. Výsledkem je přehled nálezů 123 archeofytů a 94 původních druhů, obývajících synantropní stanoviště na 202 archeologických lokalitách v období zemědělského pravěku a raného středověku. Identifikovali jsme tři období se zvýšenou intenzitou imigrace druhů: (i) neolit, (ii) doba bronzová, (iii) raný středověk. V neolitu převládaly nálezy méně specializovaných, zejména jednoletých druhů. Tyto ruderální i segetální, archeofytní i původní druhy jsou běžné i v dalších obdobích a dodnes tvoří nejhojnější složku synantropní vegetace. Teprve od eneolitu se v datech objevují makrozbytky archeofytních plevelů striktně vázaných na obilná pole. Víceleté ruderální rostliny ze starších období prorazují spíše jen jednorázové disturbance méně úrodných půd (okruh vegetace *Dauco-Melilotion*), teprve v pozdějších obdobích se připojují i druhy živinově bohatých skládek a navážek (*Onopordion*, *Arction*). Nejstarší nalezené druhy polopřirozených stanovišť indikují poloruderální mezofilní trávníky s převahou druhů snášejících sešlap. Později, od střední doby bronzové, se v archeobotanickém záznamu objevují i druhy luk a pastvin. V raném středověku se pak připojují druhy prorazující zvýšenou intenzitu využívání pastvin a zvětšování jejich plochy, a to především do vlhkých stanovišť. Druhy, které se na naše území rozšířily dříve, jsou dnes obecně úspěšnější než ty, které se zde objevily až později. Domníváme se, že tento trend nelze

vysvětlit samotnými rozdíly v délce pobytu archeofytů. Většina dnešních hojných a invazních archeofytů se k nám sice dostala brzy, ale dnes jsou již plně naturalizovány všechny archeofyty, a tak by teoreticky měly být také všechny stejně úspěšné. Spíš než ptát se, proč jsou tak úspěšné právě archeofyty, které přišly dříve, je potřeba se zeptat, proč se úspěšné druhy rozšířily do našeho synantropního prostředí tak brzy. Vysvětlujeme to tím, že tyto nepůvodní druhy měly potenciálně invazní vlastnosti již v okamžiku imigrace, a mimo jiné měly i schopnost rychle osídlovat různé typy stanovišť. Naproti tomu specializované plevele obilných kultur většinou nedokázaly trvale kolonizovat jiné habitaty než pole, takže dnes neinvadují, a navíc mohou být zásadně ohroženy inovacemi obilnářských technologií.

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