Grass and Forage Science
The Journal of the British Grassland Society | The Official Journal of the European Grassland Federation

Review Article

Origin and history of grasslands in Central Europe – a review

M. Hejcman*,†,‡, P. Hejcmanová§, V. Pavlů*,‡ and J. Beneš¶
*Faculty of Environmental Sciences, Department of Ecology, Czech University of Life Sciences Prague, †Faculty of Arts, Institute of Prehistory and Early History, Charles University Prague, ‡Crop Research Institute Prague – Ruzyně, §Faculty of Tropical AgriSciences, Czech University of Life Sciences Prague, ¶Faculty of Science, Laboratory of Archaeobotany and Palaeoecology, University of South Bohemia, České Budějovice, Czech Republic

Abstract

In terms of origin, grasslands in Central Europe can be classified into (i) natural grasslands, predetermined by environmental conditions and wild herbivores; (ii) seminatural grasslands, associated with long-term human activity from the beginning of agriculture during the Mesolithic–Neolithic transition; and (iii) improved (intensive) grasslands, a product of modern agriculture based on sown and highly productive forage grasses and legumes. This review discusses the origin, history and development of grasslands in Central Europe from the Holocene (9500 BC) to recent times, using archaeobotanical (pollen and macroremains), archaeozoological (molluscs, dung beetles, animal bones) and archaeological evidence, together with written and iconographic resources and recent analogies. An indicator of grasslands is the ratio of non-arboreal/arboreal pollen and the presence of pollen of species such as *Plantago lanceolata* and *Urtica dioica* in sediments. Pastures can be indicated by *Juniperus communis* pollen and charcoal present in sediments and the soil profile. Insect-pollinated species can be studied using cesspit sediments and pollen (from honey) in vessels in graves. In Central Europe, natural steppe, alluvial grasslands and alpine grasslands occurred before the start of agriculture in the early Neolithic (5500 BC); their area was small, and grassland patches were fragmentary in the forested landscape. Substantial enlargement of grasslands cannot be expected to have occurred before the late Bronze Age. The first scythes come from the 7th–6th century BC; therefore, hay meadows probably did not develop before this time. There is evidence of hay meadows in Central Europe during the Middle Ages, documented by macroremains of *Arrhenatherum elatius* in sediments, written records and long scythes in archaeological assemblages. Based on macroremains analyses, we conclude that there was generally high diversity of seminatural grasslands in the cultural landscape in the Middle Ages, and individual grassland communities were generally species rich. From the beginning of the agriculture until the 18th century, pastures and pasture forests were dominant sources of forage. Large-scale enlargement of hay meadows and decline of pastures in many regions occurred from the 18th century. Hay making is associated with enlargement of arable fields and the use of cattle as draught animals for ploughing and soil preparation. The spread of *A. elatius* in Central Europe was enabled by the decline of grazing management and an increased proportion of hay meadows in the 18th and 19th centuries. In some mountain areas, there are no records of large-scale deforestation and enlargement of grasslands until the 14th century, and the peak of the agriculturally used area was recorded for the period from the 18th to the first half of the 20th century. Grasslands were converted into arable land during periods of war; conversely, grasslands replaced arable land after the collapse of agriculture in many regions of former communist countries following political regime change in the 1990s. The dynamics of the grassland area reflect the development of human society and the political situation, because grasslands are an integral part of the cultural landscape in Central Europe.

Keywords: Holocene, pastures, meadows, pollen analysis, prehistory, Middle Ages

Nomenclature of vascular plants
Kubát *et al.* (2002)

Nomenclature of plant communities
Chytrý (2007)

Correspondence to: M. Hejcman, Faculty of Environmental Sciences, Department of Ecology, Czech University of Life Sciences, Kamýcká 129, CZ 165 21 Prague 6 – Suchdol, Czech Republic.
E-mail: hejcman@fzp.czu.cz

Received 6 August 2012; revised 20 March 2013

doi: 10.1111/gfs.12066

Introduction

In terms of their origin, grasslands in Central Europe can be divided into three broad categories: (i) natural grasslands, predetermined by natural conditions such as shortage of moisture in steppe regions on the eastern border of Central Europe or by low temperature and a short growing season above the upper tree limit in high mountains (Jeník, 1961; Ellenberg, 1988; Hejcman *et al.*, 2006); (ii) seminatural grasslands with a wide range of species richness of vascular plants, ranging from 1 to 67 species per 1 m^2 (Klimeš *et al.*, 2001; Hejcman *et al.*, 2010a) and herbage production from 1 to 10 t dry matter (DM) ha^{-1} per year (Pavlů *et al.*, 2006; Smit *et al.*, 2008; Hrevušová *et al.*, 2009; Merunková *et al.*, 2012); the existence of seminatural grasslands is closely associated with long-term human activity from the beginning of agriculture during the Mesolithic–Neolithic transition; and (iii) improved (syn. intensive) grasslands, a product of modern intensive agriculture, which comprise swards of several sown and highly productive forage grasses, of which *Dactylis glomerata*, *Lolium perenne*, *Phleum pratense*, *Festuca arundinacea* and *F. pratensis* are the most important (Pavlů *et al.*, 2011a; Hejcman *et al.*, 2012), together with legumes such as *Trifolium repens* and *T. pratense* (Rochon *et al.*, 2004; Komárek *et al.*, 2010). Although some authors have argued that grassland intensification started in the 18th or 19th century (Semelová *et al.*, 2008), the first detailed written records about intensification of grasslands come from Roman authors, Marcus Porcius Cato (234–149 BC, *De Agricultura*; Hooper and Ash, 1935), Marcus Terentius Varro (116–27 BC, *Rerum rusticarum libri III*; Hooper and Ash, 1935) and finally from Lucius Junius Moderatus Columella (4 AD (?) – 70 AD, *De Re Rustica*; Ash, 1941). According to these authors, pastures and hay meadows can be intensified by resowing, removal of mosses and fertilization by dung and ashes. Roman authors also highly appreciated the high value of legumes such as *Medicago sativa*, *Trifolium* spp. and *Vicia* spp. for improving soil fertility, herbage production and forage quality.

Until now, relatively little attention has been paid to the origin and history of grasslands in Central Europe and to the sources of information which can be used for such a study. The aim of this review was therefore to discuss the origin, history and development of natural and seminatural grasslands in Central Europe since start of the Holocene (9500 BC) up to recent times, using archaeobotanical, archaeozoological and archaeological evidence, together with written and iconographic resources and recent analogies. The paper makes particular reference to information sources that relate to the land area of the present-day Czech Republic, but has relevance to a wider area of Central Europe. A unique feature of this review is that it draws on information from many data sources that are of great importance for the history of grasslands, some of which are relatively inaccessible to international readers. First, we delimit the area of Central Europe and then discuss the origin and history of natural grasslands, particularly steppe, alluvial and alpine grasslands. We then discuss the origin of seminatural grasslands, demonstrating the importance of honey for the study of grassland history, and discuss the history of pastures and meadows. In the last part of the review, we discuss the transport of diaspores of grassland species through Central Europe and provide an example of the development of a grassland area at the scale of a typical mountain village.

The Central European phytogeographic province

Europe can be divided into several phytogeographical provinces with different species pools and extent of natural grasslands (Figure S1). According to the phytogeographical map of Rivas-Martinez *et al.* (2004), the Central European province includes the present-day lands of Germany, Poland, Czech Republic, Lithuania, Latvia and Estonia and also extends partly into north-east France, Belgium, Netherlands, Denmark, southern Norway and Sweden. The Central European province experiences moderately hot summers and cold winters, conditions that favour the development of forests with trees adapted to overwintering and competition for light during the vegetation season. Natural grasslands in this province are therefore relatively rare. There is a gradual transition from the eastern continental climatic conditions, which support plant communities of dry, low-productive calcareous grasslands, with the occurrence of species from the eastern continental steppes such as *Festuca vallesiaca*, *Adonis vernalis*, *Linum flavum*, *Verbascum phoeniceum*, *Astragalus exscapus*, *Campanula sibirica*, *Crambe tataria* or *Iris pumila* (described in detail by Kaplan, 2012). On the other side of the province, in the grasslands in the western part of Central Europe, steppe species gradually disappear and sub-Mediterranean and suboceanic species occur, for instance *Bromus erectus*. Fragmentary natural heathlands occur only under the specific edaphic conditions of extremely acid- and nutrient-poor soils (Svenning, 2002). Together with *Nardus stricta* grasslands, heathlands with the dominant species of *Calluna vulgaris*, *Luzula campestris*, *Danthonia decumbens*, *Carex pilulifera* and *Potentilla erecta* occur towards the Atlantic and sub-Atlantic parts of Europe. Atlantic elements common in Central Europe include, for example, *Cirsium acaule*, *Lathyrus linifolius* and *Galium saxatile* (Ellenberg, 1988; Hejný and Slavík, 1997).

Alpine grasslands are confined to the Central European high mountains above the timberline, where the short and cold season of vegetation growth is the essential driver of vegetation development. Most of the alpine species evolved from Tertiary lowland species, and others represent relicts from glacial times. The Alpine flora of the Carpathians and the Central European Hercynian mountains is due to former glaciation and is of recent evolution, rather species poor, and few endemic species are found there (Jeník, 1961; Ellenberg, 1988).

Dry grasslands on calcareous soils are generally the most species-rich grasslands in Europe (Karlík and Poschlod, 2009). Pärtel *et al.* (1996) recorded 43 vascular plant species per m^2 in the Estonian Alvar limestone grasslands, and Merunková *et al.* (2012) found 38 and 40 species per m^2 in the SE part of the Czech Republic and Slovakia respectively. Klimeš *et al.* (2001) recorded 67 species per m^2 in grasslands in the White Carpathians Mountains at the borderland of the Czech Republic and Slovakia, and these grasslands are considered to be among the most species-rich grasslands in the world. They compare with the highest recorded species richness of vascular plants in grasslands, which were 89 vascular plant species per m^2 in the mountains of Argentina, 87 per m^2 in the Russian steppe and 79 per m^2 in a semidry basiphilous grassland in Romania (Wilson *et al.*, 2012). Species richness of common grasslands in Central Europe is mainly in the range of 10–25 species per m^2 (Pavlů *et al.*, 2003, 2011b; Hejcman *et al.*, 2010a), but natural and seminatural grasslands with fewer than 10 species per m^2 can also be recorded, especially on highly acidic soils above the upper tree limit (Semelová *et al.*, 2008; Hejcman *et al.*, 2009, 2010b). The extraordinary high species richness of calcareous grasslands can be explained by larger pools of calcicole than of calcifuge species, despite the contemporary predominance of acid soils in Central Europe (Chytrý *et al.*, 2003; Ewald, 2003). This disparity in the species pool has resulted from historical and evolutionary processes that took place on high pH soils (Pärtel, 2002). In the Pleistocene (glacial times, 2·588 million to 9500 BC), calcareous soils dominated in the dry continental landscapes of Central Europe and in the glacial refugia of temperate flora situated mostly in southern European mountains with abundant limestone and dolomite.

Pollen and mollusc analysis and natural steppe grasslands in Central Europe

The occurrence and range of natural grasslands in Central Europe is a topic for discussion that began at the start of the 20th century by 'the steppe theory' of Gradmann (1933). According to this theory, the first farmers in Central Europe colonized the steppe grasslands that had survived in the forested landscape from the last glaciation. This theory was soon criticized by palynologists. In sediments from the Neolithic (5500–2000 BC), the pollen is predominately of forest species (85–90% of arboreal pollen; see Kreuz, 2008) with minimal indices for open steppe or grassland vegetation (Margielewski *et al.*, 2010). A problem with pollen analysis is its low sensitivity for indication of grasslands in highly forested landscapes or in heavily grazed forests. Forests serve as pollen filters, and therefore, small areas of natural grasslands in highly forested landscapes can be detected only if the pollen from sediments that accumulated in close vicinity to such grasslands is analysed. Further, there is a substantially higher pollen production by wind-pollinated woody species, especially pine (*Pinus* spp.) or birch trees (*Betula* spp.), than by understorey species, from vegetation in clearings and from other grassland species particularly under grazing management. In heavily grazed forests, pollen production of understorey species is generally low, because of removal of plant reproductive organs by grazers and the presence of insect-pollinated species.

A further problem with pollen analysis is the frequent absence of suitable sediments for the preservation of pollen grains in close vicinity of steppe grasslands and frequently also in close vicinity of densely inhabited Neolithic areas. For example, in the Czech Republic, the most suitable sediments for pollen analysis are in peat bogs located in mountains without any traces of Neolithic agricultural activities. Fragmentary steppe grasslands were probably present only in the driest lowland regions of Central Europe and on alkaline soils, which do not enable good preservation of pollen grains. Low proportions of non-arboreal pollen in analysed sediments cannot therefore be regarded as evidence that open steppe and other grassland sites were completely missing in the forested landscape. Palaeobotanical studies must, in these cases, be complemented by investigations of mollusc communities, which reflect both the vegetation and pedological conditions. Molluscs are well preserved, particularly in alkaline soils, and due to their reliable identification to species level, they provide very precise information about the presence of grasslands at the small scale (Svenning, 2002). Specific mollusc communities are therefore able to bring a record about forest-free patches in the forested landscape. On this basis, fragmented areas of continuous glacial steppes were identified through the whole Holocene in the driest and warmest areas with predominantly chernozem soils and in lowlands on south-exposed slopes in Central Europe. Continuous existence of steppe grasslands was indicated by the presence of steppe mollusc species in sediments, *Chondrula tridens* and *Helicopsis striata* particularly, which are unable to survive in closed forests (Ložek, 2007). In these areas, with annual precipitation below 500 mm, the post-glacial development of vegetation did not tend towards forest dominance, but expansion of plant species restricted to forests was blocked, and steppe elements survived there from the Pleistocene. These isolated steppe grasslands (in the lands that are now in Germany and the Czech Republic) were the most western-located fragments of steppe in Central Europe (Buček *et al.*, 2006). Larger-scale natural wooded steppes with continuous existence from the Pleistocene with many southern continental, Pontic–Pannonian and sub-Mediterranean floristic elements probably existed in the Carpathian basin in Hungary (Magyari *et al.*, 2010). On grasslands on south-exposed slopes, the border between steppe and forest vegetation can be very sharp, as is clear from some recent examples from the Czech Middle Mountains (České středohoří) in the north-west of the Czech Republic (Figure S2a). There have been discussions about whether the sharp border between steppe and forest is of natural or human-induced origin (Hilbig, 2000; Dulamsuren *et al.*, 2005). However, clearly natural analogies of a sharp border between steppe and forest from the South Ural Mountains (Figure S2b) or from southern Siberia (Figure S2c) indicate that very sharp borders can be of natural origin (see also Horsák *et al.*, 2010). High similarity of 'exposition forest steppes' in the Czech Republic and in Russia indicates that the existence of such grasslands was probably predetermined by natural conditions rather than by human activity, although human activity certainly enabled their enlargement in Central Europe.

Sediments suitable for pollen analysis were recently discovered close to the current 'steppe area' in the north-west of the Czech Republic [sediments of Ohře (Eger) River close to village Tvršice] and analysed by R. Kozáková (Pokorný, 2011). In this unique profile, the proportion of non-arboreal pollen was higher than 25% even during the Boreal (7000–5500 BC) before the start of the Neolithic 5500 years BC. Pollen of *Artemisia* sp., an indicator of open steppe grasslands, was permanently high without any interruption over the last 9000 years. Results clearly indicate natural origin of steppe grasslands in this part of Central Europe and that typical steppe species survived the development of forests in the Pre-boreal and Boreal period before the start of Neolithic agricultural activities in the Atlantic period (6000–4000 BC).

Analysis of macroremains and steppe grasslands

In addition to pollen analysis, long-term existence of steppe grasslands in Central Europe can be indicated by botanical macroremains of steppe species recorded during archaeological excavations of prehistoric sites. Such records are still rare, but they exist in Central Europe. Important evidence has recently been made by analysis of the early Neolithic archaeobotanical assemblages that belonged to the Linear Pottery culture (*Linienbandkeramik* - LBK, 5500–4800 BC) in South Germany (Kreuz and Shäfer, 2011). The structure of recorded species reflects a gradual increase in field weeds and grassland species during this period. A new way of land use in core areas of the LBK in lowland regions with primary grassland areas probably led to its gradual transformation into a secondary seminatural grassland, which began to spread considerably, as documented by the archaeological evidence of a dense network of originating farming settlements (Beneš, 2004). Grassland species whose macroremains were recorded in South Germany in the Earliest LBK settlements were *Alchemilla vulgaris*, *Phleum pratense*, *Rumex acetosella*, *Stipa* sp. and *Trifolium* spp. particularly (Kreuz and Shäfer, 2011).

In north-east Austria, for example, remnants of *Stipa pennata*, *Teucrium chamaedrys*, *Asperula cynanchica* and *Plantago media* have been recorded in burnt houses of late Neolithic Baden and Jenišovice Cultures (3600–2800 BC, Kohler-Schneider and Caneppele, 2009). In the central part of the Czech Republic, well-preserved remnants of *Stipa* sp. (feather grass) were recorded in the storage pit of a Unětická Culture from the early Bronze Age (2300–1600 BC; Bieniek and Pokorný, 2005). Well-preserved awns of *Stipa* sp. were recorded in the storage pit in very high quantities, indicating their intentional gathering probably for decorative or fire-making purposes. In addition, caryopses of *Stipa* spp. are considered to be edible, and they were probably collected intentionally as food. Remnants of *Stipa* clearly indicate there was a large area of steppe grasslands in this part of the Czech Republic during the Bronze Age. Recently, remnants of *Stipa pennata* s. l. awns were also recorded in the same locality in destroyed remains of houses of the Řivnáčská Culture from the late Neolithic (ca 3000 BC, Dobeš *et al.*, 2011). In central Poland, macroremains of *S. pennata* s. l. were recorded in large quantities in Neolithic settlements of the Linear Pottery (LBK, 5400–5000 BC) and Lengyel (4400–4000 BC) cultures in the Kujawy region (Bieniek, 2002). The presence of this grass in archaeological situations can be explained by gathering of this plant and by the presence of steppe grasslands in this part of the Poland during the Neolithic.

Based on pollen and mollusc analysis, together with analysis of macroremains, we concluded that at least small-scale steppe grasslands of natural origin were present in the forest zone of Central Europe even before the start of agricultural activities in the Neolithic, and they represent relicts of Pleistocene steppes.

Herbivores and alluvial grasslands

In addition to steppe grasslands, some natural alluvial or wetland grasslands probably existed in Central Europe before the Neolithic, in the Pre-boreal and Boreal period. They were predetermined by floods and by the activities of the European beaver (*Castor fiber*). The presence of beaver in Central Europe during prehistory was evidenced by the discovery of its skeletal remains (Polet *et al.*, 1996; Kyselý, 2005; Komosa *et al.*, 2007) and by characteristically cut trees (Pokorný, 2011). Beavers build dams on shallow rivers, which increase the water table substantially, and therefore, the surrounding alluvial forests become waterlogged (Figure S3a). Trees die in waterlogged conditions, and the result is treeless alluvial grassland after destruction of the dam. In addition to the effects of increasing the water table, beavers also prevent forestation by direct cutting of trees and by eating bark of standing trees, thereby increasing their mortality. Because of beaver activity, strips of alluvial grasslands can be assumed to have developed around rivers even without any human activity. Alluvial grasslands are well supplied with water and nutrients, and therefore, they produce large amounts of herbage of relatively high quality during the whole vegetation season (Hrevušová *et al.*, 2009). We can therefore suppose that there was selective and intensive grazing by large herbivores on these grasslands, which would have prevented their forestation. Density of large herbivores can be studied using macroremains of dung beetles in sediments (Svenning, 2002), although this has not yet been investigated in Central Europe. In addition to beavers, large herbivores such as wild horses (*Equus* sp.), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), aurochs (*Bos primigenius*) and European bison (*Bison bonasus*) were present in prehistoric forests, and they could have maintained areas of open forests or treeless plots with dominant grasses by grazing and in wintertime by browsing on trees and shrubs (Vera, 2000). Hunting of large herbivores was common during the Mesolithic (9000–5500 BC) and Neolithic periods, indicating their permanent occurrence in the landscape. Kyselý (2005) investigated the occurrence of bones of wildlife on thirty-nine Neolithic localities in the Czech Republic. The most frequently hunted animal was red deer, recorded on 69% of studied archaeological localities, followed by roe deer (41%), aurochs (38%), hare (*Lepus europaeus*, 36%), wild boar (*Sus scrofa*, 36%) and beaver (23%). Although the importance of the effect of large herbivores on the presence of open prehistoric forests has been much criticized (Mitchell, 2005; Kreuz, 2008), it is highly probable that large herbivores were able to open the forests in places where they concentrated.

We have personally studied behaviour and grazing ecology of European bison in the Cherga enclosure (Russia, the Altai Mountains) in summer 2011. Almost every tree of *Larix sibirica* (Figure S3b) or *Betula pendula* (Figure S3c) was damaged by scratching, resulting in increased tree mortality. Although the total density of animals was relatively low in the enclosure (12 adults per 45 ha), all animals concentrated into a small part of the reserve where they had opened the forest substantially. We learned that for the development of open forest vegetation with the presence of grassland species, it is more important that animals are able to build up herds and to concentrate into particular places where they affect the forest vegetation heavily, rather than achieving a particular mean density of animals per total area of the reserve. In winter, bison stripped shrubs and trees and browsed twigs if left for several days without any supplementary feeding. The most preferred woody plants were *Salix* sp. and *Betula pendula*. A similar experience with winter feeding of bison was recorded in the Białowieza old-growth forest in Poland by Kowalczyk *et al.* (2011). The amount of woody materials (trees and shrubs) consumed by bison increased with decreasing access to supplementary fodder, ranging from 16% in intensively fed bison to 65% in non-fed bison utilizing forest habitats. Conversely, the amount of forbs, grasses and sedges decreased from 82% in intensively fed bison to 32% in non-fed bison utilizing forest habitats. The woody species that were browsed by bison were mainly *Carpinus betulus*, *Corylus avellana*, *Betula* sp. and *Salix* sp. We personally recorded similar feeding behaviour and stripping of trees in winter enclosures with red and roe deer and also with Highland cattle, in the Giant Mountains. During the Middle Ages, there was a progressive increase in grazing by cattle and horses and pannage of pigs, especially in open deciduous forests. This competition for food, together with hunting, resulted in extinction of the aurochs, and the last specimen died in Poland in 1627 (Szafer, 1968). Since that time, the key driver for maintaining the grassland area in Central Europe has predominantly been provided by domesticated animals. Finally, we concluded that large herbivores were able to open *Quercus* forests in Central Europe, but not equally at all sites. The herbivores were able to maintain fragments of grasslands in places where they concentrated. Such small-scale grasslands, which can hardly be detected by pollen analysis, probably enabled the survival of grassland species in a predominantly forested landscape.

Alpine grasslands

Alpine grasslands are common in areas above the upper tree limit in large mountain regions such as the Carpathians (Kliment *et al.*, 2010) and the Alps (Mayer and Erschbamer, 2011). A small area of (sub) alpine grasslands also occurs in the Hercynial middle mountains of Central Europe, in the Hrubý Jeseník Mts. (Altvatergebirge in German) with the highest peak Mt. Praděd (1493 m a.s.l.) in the north-eastern part of the Czech Republic, in the Kralický Sněžník Mts. (Masyw Śnieżnika and Glatzer Schneegebirge in Polish and German, respectively) with the highest peak Mt. Kralický Sněžník (1424 m a.s.l.) in the Polish–Czech borderland, in the Giant Mts. (Krkonoše, Karkonosze and Riesengebirge in Czech, Polish and German) with the highest peak Mt. Sněžka (1602 m a.s.l., Figure S4) also on the Polish–Czech border, and in the Harz Mts. with the highest peak Mt. Brocken (1142 m a.s.l.) in central Germany. The upper tree limit (sensu Körner, 1999) decreases from east to west and is at 1310, 1310, 1230 and 1100 m a.s.l. in the Hrubý Jeseník Mts., in the Kralický Sněžník Mts., in the Giant Mts. and in the Harz Mts. respectively (Treml and Banaš, 2000; Novák *et al.*, 2010; Hertel and Schöling, 2011). Despite doubts about the areas of natural alpine grasslands in these mountains and historical fluctuations of the upper tree limit, continuous existence of alpine grassland vegetation in the Hrubý Jeseník Mts. over the last 5000 years is supported by results of pollen analyses (Rybníček and Rybníčková, 2004; Treml *et al.*, 2008; Novák *et al.*, 2010), by the presence of charcoal of the heliophyte *Juniperus communis* subsp. *alpina* in the soil profile (Novák *et al.*, 2010) and, over the last 10 000 years, by the presence of patterned tundra soils (soil material sorted according to size by melting and freezing of soil water), which cannot survive under dense forest vegetation, and also by the survival of several arctic–alpine and other plant species typical of open stands from glacial times until the present, particularly *Bartsia alpina*, *Campanula barbata*, endemic *C. gelida*, *Carex bigelowii*, *Gentiana punctata*, *Hieracium alpinum* agg., *Hypochoeris uniflora*, *Juncus trifidus*, *Juniperus communis* subsp. *alpina*, *Phleum rhaeticum*, *Potentilla aurea*, *Rhinanthus pulcher*, *Salix herbacea* and *Viola lutea* subsp. *sudetica* (Jeník, 1961; Kubát *et al.*, 2002). In the Hrubý Jeseník Mts., the first fires indicating human activities on the top of mountains are dated according to ^{14}C analysis of charcoal discovered in the soil profile of alpine grasslands into the second or the first century BC (Novák *et al.*, 2010). Alpine grasslands were largely used for hay making and cattle grazing from the late Middle Ages, and the most intensive agricultural exploitation occurred in the 18th and 19th centuries; lately, they have been abandoned as agricultural activities became uneconomic (Rybníček and Rybníčková, 2004).

In the Kralický Sněžník Mts., alpine grasslands are developed only on the top of the Kralický Sněžník Mountain itself. Arctic–alpine and other plant species that have survived there since the last glaciation until today include *Campanula barbata*, *Hieracium alpinum* agg., *Hypochoeris uniflora*, *Potentilla aurea*, *Rhinanthus pulcher* and *Viola lutea* subsp. *sudetica* (Jeník, 1961; Kubát *et al.*, 2002).

In the Giant Mts., alpine grasslands are present on both of the highly elevated plateaus and have existed over the last 10 000 years. This is documented by the proportion of non-arboreal pollen, which comprises more than 10% in pollen diagrams of peat bogs on the top of mountains (Speranza *et al.*, 2000; Jankovská, 2004; Svobodova, 2004; Treml *et al.*, 2008). Although 10% of non-arboreal pollen seems a low proportion, the presence of *Pinus mugo* shrubs on the top of mountains, which produces very high amounts of pollen, would have reduced the proportion of non-arboreal pollen. In addition, there is a presence of patterned soils together with high number of arctic–alpine and other species typical of open stands, which have survived from the glaciation: *Bartsia alpina*, endemic *Campanula bohemica*, *Carex bigelowii*, *Gnaphalium supinum*, *Hieracium alpinum* agg., *Hypochoeris uniflora*, *Juncus trifidus*, *Phleum rhaeticum*, *Potentilla aurea*, *Primula minima*, *Pulsatilla alpina*, *Rhinanthus pulcher*, *Salix herbacea*, *Saxifraga oppositifolia*, *Rubus chamaemorus*, and *Viola lutea* subsp. *sudetica* particularly (Jeník, 1961; Kubát *et al.*, 2002; Kaplan, 2012). Although alpine grasslands are considered to be natural in the Giant Mountains, they were substantially enlarged by cutting of *Pinus mugo* shrubby stands to enlarge the area for cattle grazing and hay making, which was carried out intensively from the 16th to the 19th centuries (Lokvenc, 1978; Hejcman *et al.*, 2006; Figure S4). All agricultural activities on the top of mountains were terminated after the resettlement of German inhabitants after World War II (Semelová *et al.*, 2008).

In the Harz Mountains, the area of alpine grasslands is restricted to the top of the Brocken Mountain itself. Arctic–alpine and other plant species typical of open stands that have survived there from the glaciation until today include *Hieracium alpinum*, *H. nigrescens* agg. and *Pulsatilla alpina* (Damm, 1994).

Alpine grasslands in the Hercynian mountains can be divided into low-production swards, especially with *Nardus stricta* and *Avenella flexuosa* as dominant grasses, medium-production swards with dominance of *Calamagrostis villosa*, *C. arundinacea* or *Molinia caerulea* on places with higher nutrient availability and, finally, highly productive grasslands with a dominance of tall forbs and ferns such as *Adenostyles alliariae* (not in the Harz), *Athyrium distentifolium* and *Cicerbita alpina* typical of alluvial plains and the lower parts of avalanche tracks well supplied by water and nutrients (Damm, 1994; Hejcman *et al.*, 2005, 2009, 2010b; Chytrý, 2007).

We have concluded therefore that, historically, there have been three main categories of natural grasslands in Central Europe: fragmentary steppe grasslands in lowland regions especially on south-facing exposed slopes; alluvial grasslands maintained by flooding, beaver-induced deforestation and the subsequent grazing by large herbivores; and (sub)alpine grasslands situated above the upper tree limit. In addition, some additional temporary grasslands probably existed in forests because of disturbances created by wind, fires and landslides.

Origin of seminatural grasslands in Central Europe

It is likely that Central Europe was densely forested in the Holocene climatic optimum (also called the Atlantic period). There are also indications of differences between fully forested regions and areas of semi-open landscape. The 'virgin forest' cannot be perceived as a closed canopy cover, but more or less as an open mixture of woodland with scattered islands of small steppe-like areas in the lowlands. This concept was developed by Ložek (1973, 1981, 2007) on the basis of malacostratigraphic data, postulating a continuity of xerothermic herbaceous vegetation in some Czech regions. Important changes in the natural forest composition occurred during the Holocene climatic optimum (Beneš, 2004). At all altitudinal zones, previous pine- and/or birch-dominated woodlands were replaced by a new set of forest trees. In the lowlands, mixed oak woodlands developed, characterized by the occurrence of broadleaf trees (*Quercus*, *Tilia*, *Ulmus*, *Corylus*, *Fraxinus*) (Pokorný, 2004). How open the woodland actually was, and how much energy was spent by humans in its initial clearing, is still being researched. The origin of seminatural grasslands should be connected with the presence of Neolithic settlers (LBK culture, 5500–4800 BC) and with their preference for loess-based soils (Bellwood, 2005; Pavlů and Zápotocká, 2007). Although Czech LBK sites generally correspond with loess-based soils, this correlation is not quite strict. It is little realized that the distribution of LBK sites in the Czech Republic more accurately reflects a relationship with easily tilled soils, rather than the fertile but heavy chernozem soils. In younger Neolithic periods [Stroked Pottery (4800–4000 BC) and Lengyel (4300–4000 BC) cultures)], there is a greater tendency to occupy heavier soils (Rulf, 1983). It is uncertain whether these soil preferences reflect the actual settlement choices of the earliest farmers, or whether this process indirectly records the expansion of secondary anthropogenic grassland and therefore an increase in the development of chernozem soils. The second possibility seems more probable (Beneš, 2004). The start of agricultural activities can be detected by a decrease in the proportion of pollen of woody species in sediments and by an increase in pollen of non-arboreal species in forested Central Europe. The presence of arable agriculture is indicated by pollen of cereals, wind-pollinated *Secale cereale* being the most frequent, and of arable-field weeds from the families *Chenopodiaceae*, *Brassicaceae* and *Poaceae* and determinable weedy species such as *Centaurea cyanus* or *Polygonum aviculare* in sediments (Kreuz, 2008; Margielewski *et al.*, 2010). A problem of pollen analysis is the inability to determine many taxa at the level of individual species according to their pollen; therefore, in many cases, the pollen analysis must be supplemented by other methods such as macroremains or phytolite analyses to determine the presence of individual plant species in the landscape. A species with easily determinable pollen is *Plantago lanceolata*, and this species is considered to be a good indicator of seminatural grasslands in the landscape (Poschlod and Baumann, 2010; Brun, 2011). An advantage of *P. lanceolata* is its occurrence in all types of grasslands irrespective of biomass production and soil pH. In the Rengen Grassland Experiment (SW Germany) for example, *P. lanceolata* was the only forb species recorded in all fertilizer treatments, from the low-productive *Nardus stricta* grassland with annual herbage production of 3 t ha^{-11} in the control up to the tall grass community under NPK application with dominant *Arrhenatherum elatius* and herbage production of over 10 t ha^{-1} (Hejcman *et al.*, 2010a; Figure S5). Pollen of *Plantago lanceolata* together with pollen of *Calluna vulgaris* and *Artemisia* sp. was present in sediments from Zahájí (Czech Republic) continuously over the last 5000 years, indicating continuous existence of seminatural grasslands in this lowland site since the late Neolithic, and this is in accordance with remnants of settlement activities revealed by archaeological research (Pokorný, 2005). In the Tišice locality close to Elbe River, a lowland site 30 km east of Zahájí, seminatural grasslands existed, according to the presence of pollen of *P. lanceolata* in sediments, since the late Bronze Age (1000 BC). This indicates high regional variability in the area of seminatural grasslands in prehistory even in the most productive lowland regions of Czech Republic.

Using charcoal of woody species in the soil profile together with pollen analysis of alluvial sediments, Poschlod and Baumann (2010) suppose a continuous existence of dry calcareous grasslands in Franconia (Bavaria, southern Germany), certainly from Roman times (approximately 30 BC) and most probably since at least the early Bronze Age (1800 BC). This assumption is based on the presence of charcoal and pollen grains of the light-demanding shrub *Juniperus communis* subsp. *communis.* This shrub is typical for open pastures in Central Europe and cannot survive for a long time in closed forests that are not grazed by livestock. In addition, the amount of *J. communis* pollen in alluvial sediments was well correlated with pollen of typical grassland taxa such as *Plantago lanceolata*, *Galium* type, *Apiaceae*, *Ranunculaceae* and *Ballota/Galeopsis* types. Another example comes from the central part of the Czech Republic. Charcoal of *J. communis* has been recorded in the infill of sunken houses from the 6th and 7th century AD in Roztoky close to Prague (Novák *et al.*, 2012). The presence of charcoal in houses indicates the use of *J. communis* as firewood and also the existence of large pastures in the valley of the Vltava (Moldau) River around the village.

Another indicator of grasslands and ruderal sites in the landscape with identifiable pollen is *Urtica dioica* (Kozáková and Kaplan, 2006). A disadvantage of this species is its occurrence also in alluvial forests and its affinity to soils that are well supplied with N, P and K. Therefore, an increase in pollen of *U. dioica* in sediments can indicate human settlement activity in the landscape and also intensive livestock grazing. *Urtica dioica* can become a dominant species within 2 or 3 years of increased nutrient availability, as documented by Hejcman *et al.* (2012). According to our personal observations and other reports (e.g. Taylor, 2009), *U. dioica* is generally avoided by grazing animals but is consumed in the form of hay and silage, or as fertile parts of fresh plants in the autumn, and as whole plants after the first winter frosts, which interrupt the antiherbivore function of its stinging trichomes. *Urtica dioica* was a common species in the first agricultural settlements since the LBK Culture in Central Europe, as evidenced by its presence in pollen diagrams and by frequently recorded remnants of seeds in sediments and cultural layers (Bakels, 1992; Margielewski *et al.*, 2010; Out, 2010). The next indicator of grasslands and ruderal sites since prehistory is *Trifolium repens*-type pollen (a strict determination of *T. repens* according to its pollen is not possible). As *T. repens* is an insect-pollinated species, only a relatively small amount of its pollen is frequently recorded in sediments, as compared with many wind-pollinated species (Brun, 2011). During the period from the start of the Neolithic until the Iron Ages, the area of grasslands and arable fields was relatively small in Central Europe, and forests still predominated, even in the most densely populated lowland regions with loess soils (Pokorný, 2005, 2011). Large-scale deforestation is supposed to have started around 1000 BC in Central Europe (Kaplan *et al.*, 2009), causing extensive soil erosion (Beneš, 1995). Despite the forest dominance, it is important to note that many prehistoric settlements were located on the border of present-day extraordinarily species-rich calcareous grasslands, indicating their long-term continuity in the landscape since at least the Iron Age (Pärtel *et al.*, 2007; Hájková *et al.*, 2011). Seminatural grasslands in close vicinity of Neolithic settlements in Central Europe can be identified according to macroremains of grasses typical for managed grasslands. Grazing-tolerant *Phleum pratense* was the most common grass species recorded in prehistoric settlements in South Germany since the Neolithic (Kreuz and Shäfer, 2011). In the Czech Republic, the oldest record of *Anthoxanthum odoratum*, a species typical for low-production grasslands across a wide altitudinal range, is of two caryopses discovered during archaeological excavations of the hillfort Denemark close to Kutná Hora (Řivnáčská Culture, 3000–2800 BC) (Čulíková, 2008).

In the Czech lowlands, the highest wave of deforestation was recorded after the 13th century AD, when the structure of contemporary high medieval settlements was established. The vicinities of many towns were free of forests in the 15th century, as was evidenced by the low proportion of pollen of arboreal species in anthropogenic sediments collected from the main Czech towns (Beneš *et al.*, 2002; Kozáková *et al.*, 2009; Jankovská, 2011). Low proportions of forests in the vicinity of towns were also documented in written records, and the shortage of high-quality timber was responsible for the first known restrictions of livestock grazing in forests (Novotný, 2000). In addition, high numbers of macroremains of different grassland species were recorded in anthropogenic and natural alluvial sediments collected during archaeological research of medieval settlements in the Czech Republic (Čulíková, 1994, 1999, 2003, 2011; Opravil, 2000). In Prague, for example, macroremains of more than 300 plant species were recorded in the Vltava River and anthropogenic sediments from the 8th to 14th centuries, as described in detail by Čulíková (2010). Mesophilic, probably cut, grasslands (order *Arrhenatherion elatioris*) were represented by macroremains of forbs including *Achillea millefolium*, *Campanula patula*, *Cerastium vulgare*, *Chrysanthemum leucanthemum*, *Crepis biennis*, *Galium mollugo*, *Heracleum sphondylium*, *Hypericum perforatum* and *Knautia arvensis*. Indicators of mesophilic pastures (order *Cynosurion cristati*) were rosette and prostrate species such as *Leontodon autumnalis*, *L. hispidus*, *Medicago lupulina*, *Plantago lanceolata*, *P. media*, *Prunella vulgaris*, *Taraxacum officinale* agg. and *Trifolium repens*. Indicators of alluvial grasslands (order

Deschampsion cespitosae) were *Glechoma hederacea*, *Lychnis flos-cuculi*, *Potentilla repens*, *Ranunculus acer*, *R. repens*, *Rumex acetosa*, *R. crispus*, *R. obtusifolius*, *Stellaria graminea* and *Sysimbrium officinale*. Wetland grasslands (order *Calthion palustris*) were represented by macroremains of *Caltha palustris*, *Carex flava*, *C. nigra*, *Juncus* spp., *Epilobium hirsutum*, *Filipendula ulmaria*, *Lysimachia vulgaris*, *Linum catharticum*, *Lythrum salicaria*, *Scirpus sylvaticus*, *Theucrium flavum* and *Viola palustris*. Grasslands of temporary wet soils (order *Molinion caeruleae*) were represented by *Angelica sylvestris*, *Betonica officinalis*, *Potentilla erecta*, *Dianthus superbus*, *Hypericum tetrapterum* and *Stachys palustris*. Discovered indicators of dry grasslands (order *Bromion erecti*) were *Agrimonia eupatoria*, *Anthemis tinctoria*, *Calamintha clinopodium*, *Dianthus armeria*, *D. carthusianorum*, *Hieracium pilosella*, *Medicago minima*, *Origanum vulgare*, *Potentilla argentea*, *Stachys erecta*, *Silene vulgaris* and *Thalictrum minus*. Also of interest was the discovery in the surroundings of Prague of macroremnants of *Orlaya grandiflora* and *Turgenia latifolia*, which are species of dry grasslands that are now extinct in that area. *Orlaya grandiflora* is today restricted to the Pálava hills in SE part of Czech Republic (Kozáková and Pokorný, 2007). High numbers of recorded species indicate very high species diversity of seminatural grasslands in the surrounding of Prague in the Middle Ages. Based on all these macroremains analyses, we concluded that (i) there was generally high diversity of seminatural grasslands in the cultural landscape in the Middle Ages, and (ii) individual grassland communities were generally species rich, in many cases probably more species rich than today. A high decline in species richness of grasslands has been recorded; especially in the last sixty years, as many grasslands were abandoned or intensified (Bochenková *et al.*, 2012; Pavlů *et al.*, 2012).

Honey and its use for the study of grassland history

The presence of many insect-pollinated grassland species in the landscape in different historical periods can be studied using anthropogenic sediments in cesspits or in vessels placed in graves, which were originally filled with honey or products made from honey. From prehistoric times until the 19th century, honey was the main sweetener in Europe. The pollen spectrum in honey reflects the spectrum of insect-pollinated species in the landscape and therefore the geographical origin of the honey (Anklam, 1998). After the use of the honey as a foodstuff, the pollen it contains accumulates in faecal sediments, because pollen grains are not destroyed by cooking or by the human digestive tract (Jankovská, 1987). By pollen analysis, the import of honey from floristically different regions can be well identified. For example, Deforce (2010) determined that honey used by the aristocracy in Bruges (Belgium) in the 15th century was imported from the western Mediterranean, as the cesspit sediments were rich in pollen of insect-pollinated species typical for Spain. *Calluna vulgaris* has frequently been recorded in cesspit sediments, and this species was substantially more common during the late Middle Ages than it is today in the Czech Republic, and it indicates the presence of oligotrophic acid pastures in the neighbourhood of large medieval towns (Kozáková *et al.*, 2009; Jankovská, 2011). Food prepared from *Avena sativa* and sweetened with honey was identified in a ceramic vessel from a grave from the 10th century close to Libice above the Cidlina River in the central part of the Czech Republic by Pokorný and Mařík (2006). Honey of local origin was identified according to dominance of insect-pollinated species in the sediment and according to the presence of immature pollen grains that can be transported only by insects from flowers. Species richness of pollen grains was very high in comparison with recent honey, indicating high diversity of biotopes in the landscape of the 10th century. Taxa indicating the presence of alluvial grasslands were *Filipendula*, *Cirsium*, *Carduus*, *Centaurea jacea* type, *Plantago lanceolata*, *Campanula*, *Daucus* type, *Mentha* type, *Rhinanthus*, *Asteraceae*, *Lamiaceae*, *Serratula* type and *Peucedanum* type. Taxa indicating the presence of dry grasslands were *Helianthemum*, *Hypericum perforatum* type, *Calluna vulgaris*, *Brassicaceae*, *Artemisia*, *Poaceae*, *Centaurea scabiosa*, *Aster* type, *Rubiaceae*, *Anthemis* type, *Plantago media*, *Gentianella germanica* type, *Pulsatilla* and *Sedum*. A wide spectrum of identified species indicates that honey was collected in autumn, as both early- and late-flowering species were recorded together. Local origin of the honey can be supposed because of the presence of pollen of *Nymphoides peltata*, a water plant that occurs in the lowland region of the Czech Republic where the vessel with honey remnants was discovered. Pollen of arable weeds was almost absent, indicating the presence of grasslands and alluvial forests (pollen of *Tilia cordata*, *Alnus glutinosa* and *Humulus lupulus*) in the neighbourhood of the hive. High diversity and species richness of grasslands in the study area in the 10th century, and with few or no arable fields in the area's close vicinity, were also in accordance with the results of palynological analysis of alluvial and anthropogenic sediments performed by Kozáková and Kaplan (2006) and by macroremains analyses of anthropogenic sediments performed by Čulíková (1999, 2006). As shown by this unique finding, remnants of honey discovered during archaeological excavations are extremely valuable for the study of vegetation history with respect to insect-pollinated plant species and for grasslands particularly.

History of pastures and meadows

According to their management, seminatural grasslands can be divided into pastures, meadows and grazed meadows. Pastures are managed by livestock grazing, meadows are managed by regular cutting, and grazed meadows are cut in spring and then grazed in summer and/or in autumn (Pavlů *et al.*, 2007; Hejcman *et al.*, 2010c). We use this clear and simple categorization of seminatural grasslands according to their management as this terminology is well followed in the agronomic literature (Allen *et al.*, 2011), although not in archaeology or ecology. In archaeological or ecological literature, the term ‘pasture’ is frequently used for low-productive grasslands and ‘meadow’ for highly productive grasslands, irrespective of their actual management. In the classification study of grassland vegetation by Rozbrojova *et al.* (2010), for example, the terms ‘meadow’ or ‘pasture’ are derived from the knowledge of plant species composition without information about real grassland management. In the period from the Neolithic up to the Iron Age, only pastures (from the management point of view) and forest pastures existed because there were no tools available for extensive grass cutting. From Neolithic times up to the Middle Ages, and in some regions up to modern times, leaf fodder from woody species was frequently used instead of grass hay or silage for the winter feeding of livestock. The most valuable woody species were *Acer* spp., *Corylus avellana*, *Fraxinus* spp., *Quercus* spp., *Tilia* spp., *Salix* spp. and *Ulmus* spp. (Sádlo *et al.*, 2005; Delhon *et al.*, 2008), although collection of other species, even coniferous species, has also been recorded. In addition to woody species, species with wintergreen leaves such as *Hedera helix* and *Viscum album* were also collected during the wintertime and used as green fodder for livestock (Deforce *et al.*, 2012). Collection of leaf fodder was replaced by hay making in many regions because hay making was, according to the amount of herbage dry matter collected per unit of time, at least ten times more efficient than the collection of leaf fodder. In addition, the intake rate of cattle is much higher on hay than on dried leaves of shrubs and trees (Prins, 1998).

The first iron short scythes suitable for cutting grasslands come from the Iron Age and are dated to the 7th–6th century BC (Beranová and Kubačák, 2010). Therefore, in Central Europe, hay meadows could not be established before the late Hallstatt Period (ca 600 BC). In the Czech Republic, the oldest scythes discovered so far come from the depot of iron agricultural instruments hidden under the floor of a sunken house from the 5th century BC, in Chýnov near Prague. The next oldest scythes were from two depots from the 1st century BC, discovered in Kolín and in Strádonice close to Beroun (Waldhauser, 2001). In South Germany, existence of hay meadows from the La Tène period (500–0 BC) is documented by macroremains of *Arrhenatherum elatius* (Kreuz and Shäfer, 2011), a grass species that is typical for cut grasslands and which suffers under intensive grazing (Mahmoud *et al.*, 1975). Hay making is indisputably connected with the enlargement of arable fields and with the use of cattle as draught animals for ploughing and soil preparation. Ploughing and soil preparation before seeding is a very costly operation in terms of energy, and therefore, good winter feeding of draught animals with high-quality hay was necessary to have them in good physical condition for spring work (Prins, 1998). In addition, the breeding of horses for military and transport purposes was common from the Iron Age, and these horses also required high-quality forage over winter to maintain them in good condition all times.

Long scythes of today’s shape have been used since the Middle Ages. The oldest discovered long scythe from archaeological sources comes from Belgium from the 8th century AD, and the oldest illustration of the long scythe is from Handwritings of Charles the Great from the 9th century (Klápště, 2006). In the Czech Republic, the oldest long scythe comes from the turn of the 13th and 14th centuries from archaeological excavations of the small castle of Bradlo (Beranová and Kubačák, 2010). Although it seems certain that some hay meadows existed in the landscape in the Middle Ages, large-scale enlargement of hay meadows was not recorded until the 18th century, when the livestock were moved into barns for the whole year to produce farm yard manure, which was used to increase crop production on arable land in many regions of Central Europe (Petrášek, 1972). Existence of hay meadows from the Middle Ages is documented by the macroremains of the tall grass *Arrhenatherum elatius* discovered in several Czech medieval towns (Čulíková, 1994, 1999). In the town of Most, for example, written records from the 14th century document the existence of meadows (Klápště, 2006). Hay meadows belonging to the town were under juridical protection, and the sale of fresh herbage or hay from them out of the town was strictly prohibited. In this unique case, the written records are in excellent agreement with results of archaeobotanical research–with the presence of *A. elatius* caryopses in sediments from the 14th century.

The existence of hay meadows is also documented by several medieval illuminations with a motif of hay making, from the discovery of scythes during archaeological excavations of several deserted medieval villages from the 15th century (Klápště, 2006), and finally by written testimony of the first Czech chronicler Kosmas (1045 (?)–1125) of Sadská, a settlement 30 km east of Prague, which was surrounded by meadows during his lifetime. Evidence of hay making is also indicated indirectly by pottery shards collected on former arable fields. The oldest pottery shards that were applied with manuring on former fields come from the 13th century; it is likely that they were thrown away with household waste into the farmyard manure and then redistributed on the field (Klápště, 2006). To produce manure, livestock were kept for at least part of the year in barns and fed with hay. Pottery shards as manuring scatters that were collected in deserted villages on former arable fields thus indicate (i) the presence of hay meadows in the landscape and hay production,(ii) housing of livestock, (iii) intensity of manure application on arable fields and (iv) transport of nutrients from grasslands to arable fields. There is evidence of the stalling of cattle in the Netherlands and western Germany at least since the Iron Age (Prins, 1998), but not before the 13th century in the Czech Republic.

Since the 18th century, large areas of pasture have been converted into either arable land or hay meadows, and grazing in forests was prohibited because of a general shortage of wood in the territory of the Czech Republic (Novotný, 2000). Remnants of former pasturelands in Central Europe that represent grasslands with a presence of scattered shrubs of *Juniperus communis* subsp. *communis*, which were common in the past, are present today only in several nature reserves in the Czech Republic (Chytrý *et al.*, 2010) or in Germany (Figure S6). Remnants of pasturelands are more common in the mountain regions of Slovakia, Ukraine or Romania, where grazing management is still practised (Buček, 2000).

Forests grazed by livestock were generally open, short and with a dense and species-rich understorey of grassland species up until the 19th century in the Czech Republic. In addition, there were diffuse borders between grasslands and forests. Strict borders between forests and grasslands developed in the 19th century when a stable cadastre (land register) was established. Each plot had a strictly defined purpose for the calculation of land taxes and the intensification of landscape management. As the landscape changed rapidly during that time, aristocrats started to establish 'English parks' with scattered trees and short swards, which retained the style of the open pasture landscape that had been present in Central Europe from prehistory until the 18th century (Buček, 2000; Novotný, 2000). Tall and dense forests as we know them today, with low numbers of grassland and other species and low biomass of the understorey, are thus a result of modern forest management in the last two centuries in Central Europe.

Grasslands were not only established, but they also disappeared frequently from the landscape in different historical periods. An example is the La Tène Iron Age hillfort at Vladař, in the western Czech Republic, where grasslands existed approximately from the establishment of the fortification (400 BC to ca 0 BC) according to the evidence showing that the proportion of non-arboreal pollen in water-cistern sediments was higher than 50% (Pokorný *et al.*, 2006). There was then a sudden event, most probably of military origin, resulting in a major fire (evidenced by melted stones of the fortification and charcoal layers), which terminated life in the hillfort and its neighbourhood. The area was naturally reforested as the proportion of non-arboreal pollen decreased suddenly to <10% and the proportion of pioneer woody species *Betula* (*pendula*) increased sharply. The next grasslands appeared in the 9th century AD, and they continue to the present. In addition, there are many deserted medieval villages together with their former grasslands in contemporary forests in Central Europe. Many of them disappeared during the Hussite wars in the 15th century or during the Thirty Years' War in the 17th century (Klápště, 2006; Klír, 2010; Hejcman *et al.*, 2013). In contrast, many medieval arable fields at higher elevations were converted into grasslands during the Little Ice Age in the 17th century because arable farming became ineffective; this is indicated by analysis from the Bohemian Forest Mts. (Bayer and Beneš, 2004). In the Czech Republic, the last villages, together with their grasslands, disappeared and were artificially or naturally reforested after resettlement of German inhabitants after World War II (Vojta, 2007). Many such villages were not settled again because of reasons connected with the post-1945 'Cold War'– they were in mountain and upland areas close to the border with Austria and Germany where non-populated military zones were designated.

Transport of seeds of grassland species through Europe

A frequently discussed question has been the transport of diaspores of grassland species during the colonization of new areas and establishment of seminatural grasslands. The natural transport of diaspores by windstorms was the main driver for the dispersal of species over long distances independent of human activities (Sádlo *et al.*, 2005). In addition, since prehistory, there have been intensive movements of people and livestock among the different regions of Europe because of trade and wars. These movements are also associated with epizoochoric and endozoochoric transport of germinable diaspores of many grassland species. We recorded, for example, massive germination of

Trifolium repens in cattle faeces (Hejcman, 2005), indicating the ability of legumes to be transported via endozoochory. There are several methods for estimating historical livestock movement and therefore the potential for transport of diaspores. Viner *et al.* (2010), using strontium isotopic analysis of late Neolithic cattle teeth from Durrington Walls (Wiltshire, UK), determined that only two of thirteen animals were native in the area; the others came from regions that were at least 100 km distant. Although such analysis has not yet been performed in Central Europe, we can suppose that similar movements of cattle would have taken place. Different examples of livestock movements over long distances obtained from written historical records include the war expeditions of the Czech Duke Břetislav I (Czech ruler in the period 1034–1055). Several settlements were relocated, together with their inhabitants and their livestock, from Poland into Czech territory in year 1039 as a result of its successful military attack of Poland. As the people came from the neighbourhood of the Hedče castle (Giecz in Polish; close to Poznaň), they established two villages with names of Hedčany in the eastern and central part of the Czech Republic (Žemlička, 1997). Resettlement of people, seizure of livestock and their transport over long distances were common practice during war expeditions in the Middle Ages, thus enabling massive transport of diaspores of grassland species between different regions. The next source of information is provided by archaeology. Many different objects originating from the Mediterranean area have been discovered during archaeological excavations in the Czech Republic and other countries north of the Alps, indicating intensive movement of people, animals and transport of goods through the Alps since at least the Bronze Age (Venclová *et al.*, 2008). There is also evidence that jewellery made from the black sedimentary rock sapropelite in the third century BC close to Prague was transported into Austria, Hungary, Slovakia, Germany and other regions (Blažková *et al.*, 2011). Long-distance transport of goods involved animals, especially horses, and therefore caused transport of diaspores of grassland species.

The next example of livestock and transport of diaspores is transhumance. In southern Germany, shepherding was common in the 19th century, and the distance between summer pastures in the Swabian Alb and winter pastures in the Lake Constance basin, or the Rhine Valley, was several hundred kilometres (Poschlod and WallisDeVries, 2002). As was demonstrated by Fischer *et al.* (1996), more than 8500 diaspores of eighty five plant species can be found in the fleece of an individual sheep. Although generally underestimated, livestock movement and transhumance have enabled massive transport of diaspores of grassland species within the landscape and therefore genetic communication between populations of grassland species.

There are also direct written examples how people intentionally transported grassland species. Together with their cattle, the timber-working families who resettled from the Alps to the Giant Mountains in the 16th century intentionally took *Rumex alpinus* from their fatherland as a vegetable, forage and medicinal plant (Šťastná *et al.*, 2010). Today, *R. alpinus* is a troublesome grassland weedy species on soils that are well supplied with water and nutrients in the Giant Mountains. *Onobrychis viciifolia*, a legume native in the Mediterranean, was used as a fodder plant in Central Europe from the 16th century (Poschlod and WallisDeVries, 2002). Today, *O. viciifolia* is considered as a characteristic plant of species-rich calcareous grasslands in many countries north of the Alps. *Arrhenatherum elatius* is the dominant grass species of two-cut lowland meadows in Central Europe (Chytrý, 2012), but the species was probably rare in Central Europe before modern times. Some authors have suggested that *A. elatius* was a neophytic species (i.e. it appeared after 1492) in Central Europe (Pyšek *et al.*, 2002; Poschlod *et al.*, 2009), but results of macroremain analyses from several archaeological localities in South Germany indicate that the species was present in Central Europe since La Téne period (Kreuz and Shäfer, 2011). Discovery of *A. elatius* in medieval sediments in the Czech Republic (Čulíková, 1994) was the reason for the reclassification of this species from neophytic to archeophytic (appeared before 1492) in the list of alien species in Czech Republic (Pyšek *et al.*, 2012). One of the oldest records of *A. elatius* in the Czech Republic comes from Libice nad Cidlinou from the 10th century (Čulíková, 1999, 2006). In this locality, remnants of *A. elatius* seeds were recorded together with seeds of many other typical grassland grasses such as *Agrostis stolonifera*, *Brachypodium pinnatum*, *Dactylis glomerata*, *Elytrigia repens*, *Festuca pratensis*, *F. ovina*, *Lolium perenne*, *Phleum pratense*, *Poa pratensis* and *Trisetum flavescens*, the forbs *Centaurea jacea*, *Geranium pratense*, *Hypericum perforatum* and *Knautia arvensis*, and legumes *Lathyrus pratensis*, *Lotus uliginosus*, *Medicago falcata*, *Secugirea varia*, *Trifolium hybridum*, *Vicia hirsuta*, *V. sativa* subsp. *angustifolia*, *V. sepium* and *V. tetrasperma*. The large-scale spread of *A. elatius* has been recorded since the 18th century and still continues. This spread was enabled by the decline of grazing management and by an increase in the proportion of hay meadows from the grassland area in Central Europe in the 18th and 19th centuries (Buček, 2000). In addition, recent spread of *A. elatius* into species-rich dry grasslands has been supported by their absence of management, or infrequent defoliation management, together with high deposition of nitrogen compounds (Fiala *et al.*, 2011; Dostálek and Frantík, 2012).

Development of the grassland area from the 17th century to 2009: an example of a typical central European mountain village

To demonstrate the dynamics of land use in relation to grassland management, the mountain village of Oldřichov v Hájich (Ullersdorf in German) in the Jizera Mountains (Jizerské hory, Góry Izerskie and Isergebirge in Czech, Polish and German) located in the borderland between the Czech Republic, Poland and Germany was selected. This village was chosen because its development in terms of total agricultural area, and proportions of grasslands and arable land, is directly comparable to that of many mountain villages in Central Europe (Štrobach, 2010). The background for this case study was the chronicle of the village (Ulrych, 2006), the historical map of stable cadastre from the year 1843 and military aerial photographs collected in years 1938 and 2003. The first written records about this village come from an Urbarium (a special book for economic survey) from the year 1381. The 13th and 14th centuries were the time of 'colonization' in Central Europe, when mountain areas were gradually settled, deforested and used for agricultural activities (Klápště, 2006). The inhabitants of Oldřichov worked as woodcutters; however, they also kept some cattle and paid a tax from their grasslands. The first written record about the area of agricultural land is from the year 1651, and the number of livestock was counted in 1654 for the first time to provide an economic survey for the payment of taxes. The total agricultural area was approximately 150 ha in year 1651, but more than 400 ha was recorded in the period from the second half of the 18th century to the first half of the 20th century (Figure S7). Then, there was a decrease recorded in the area of agricultural land, and it was approximately 300 ha in 2009. This decrease was as a result of reforestation of marginal grasslands and partly due to an increase in built-up areas.

The peak of arable land area was recorded during the period of World War I, due to the general shortage of food. During that war, more than 100 ha of grasslands in the study area was converted to arable land. In the second half of the 20th century, arable fields were gradually grassed down until the 1980s. A sudden change in the land use occurred after the change of the political regime in the 1990s, when a partial (and in many regions, total) collapse of agriculture occurred in former communist countries. At this time, the arable land reverted completely and naturally to grassland, without sowing any grass-seed mixtures, similar to many other abandoned arable fields in the Czech Republic (Lencová and Prach, 2011), and the number of livestock also decreased dramatically (Figure S8). In 2009, there was the same livestock loading in the study area as there was in year 1651, but the grassland area was six times larger. The majority of grasslands are thus delivering little agricultural production, and they have been managed by mulching, infrequent cutting or highly extensive grazing because of state subsidies since the 1990s making their management, even under low livestock loading, profitable (Gaisler *et al.*, 2004).

This case study clearly demonstrates that the grassland area in the landscape has been largely affected by the political situation. We have learned that small changes in land use have occurred gradually, but dramatic changes have generally occurred very quickly, over a time scale of one or several years. Grasslands in the landscape were not only established, but they were also converted into arable land and naturally or artificially reforested in different historical periods.

Conclusions

In Central Europe, natural steppe, alluvial grasslands and alpine grasslands existed in the post-glacial period on only a small area (probably up to 5% of the total land area of Central Europe) in the Mesolithic period and at the beginning of agriculture in the Neolithic. The majority of grasslands were developed by human activity, and they are therefore considered to be secondary vegetation replacing original forest and open woodland vegetation. The history of grasslands can be studied using archaeobotanical (pollen and macroremains) and archaeozoological (molluscs, beetles and animal bones) analyses performed on natural as well as on anthropogenic sediments. A phytogeographical approach by comparison of different floristic regions, together with knowledge of the area of individual species, enables the study of differences and similarities in plant species composition of grasslands on large spatial scales. Management of grasslands can be studied using archaeological methods and, finally, by the use of different written and iconographic resources. Study of past processes in the landscape can help to understand current species composition of many grassland areas.

Acknowledgments

The review is a revised version of the invited paper that was presented at the 24th General Meeting of the European Grassland Federation in Lublin, Poland, in June 2012. The useful comments of Milan Chytrý and anonymous reviewers are gratefully acknowledged.

The completion of the article was funded by projects GAČR 521/08/1131 and GA JU 138/2010/P.

References

Allen V.G., Batello C., Berretta E.J., Hodgson J., Kothmann M., Li X., McIvor J., Milne J., Morris C., Peeters A. and Sanderson M. (2011) An international terminology for grazing lands and grazing animals. *Grass and Forage Science*, **66**, 2–28.

Anklam E. (1998) A review of the analytical methods to determine the geographical and botanical origin of honey. *Food Chemistry*, **63**, 549–562.

Ash H.B. (1941) *Columella On agriculture, Books I – IV*. Loeb Classical Library No. 361. Harvard: Harvard University Press.

Bakels C.C. (1992) The botanical shadow of two early Neolithic settlements in Belgium: carbonized seeds and disturbances in a pollen record. *Review of Paleobotany and Palynology*, **73**, 1–19.

Bayer T. and Beneš J. (2004) Středověká terasová pole na Šumavě jako hydropedologický fenomén a archeologický problém (Medieval terraced fields in the Bohemian Forest as a hydropedological phenomenon and problem of landscape archaeology). *Archeologické Rozhledy*, **56**, 139–159.

Bellwood P. (2005) *First farmers – The origin of agricultural societies*. Oxford, UK: Blackwell.

Beneš J. (1995) Erosion and accumulation processes in the late holocene of Bohemia, in relation to prehistoric and mediaeval landscape occupation. In: Kuna M. and Venclová N. (eds) *Wither archaeology?*, pp. 133–144. Prague: Papers in honour of Evžen Neustupný.

Beneš J. (2004) Palaeoecology of the LBK: earliest agriculturalist and landscape of Bohemia, Czech Republic. In: Lukes A. and Zvelebil M. (eds) LBK Dialogues. *Studies in the formation of the Linear Pottery Culture*, pp. 143–150. BAR International Series 1304. Oxford: Archaeopress.

Beneš J., Kaštovský J., Kočárová R., Kočár P., Kubečková K., Pokorný P. and Starec P. (2002) Archaeobotany of the Old Prague Town defence system, Czech Republic: archaeology, macro-remains, pollen, and diatoms. *Vegetation History and Archaeobotany*, **11**, 107–119.

Beranová M. and Kubačák A. (2010) *Dějiny zemědělství v Čechách a na Moravě (The history of agriculture in Bohemia and Moravia)*. Prague: Libri.

Bieniek A. (2002) Archaebotanical analysis of some early Neolithic settlements in the Kujawy region, central Poland, with potential plant gathering activities emphasised. *Vegetation History and Archaeobotany*, **11**, 33–40.

Bieniek A. and Pokorný P. (2005) A new find of macrofossils of feather grass (*Stipa*) in an Early Bronze Age storage pit at Vliněves, Czech Republic: local implications and possible interpretation in a Central European context. *Vegetation History and Archaeobotany*, **14**, 295–302.

Blažková K., Sedláček F., Stolz D., Stolzová D. and Venclová N. (2011) *Příběh nejkrásnější keltské hlavy – pohled do života Keltů nejen na Novostrašecku (Story of the most beautiful Celtic head – view into life of Celts not only in area of Nové Strašecí)*. Prague: Ústav archeologické památkové péče středních Čech a Muzeum T. G. M Rakovník.

Bochenková M., Hejcman M. and Karlík P. (2012) Effect of plant community on recruitment of *Pulsatilla pratensis* in dry grassland. *Scientia Agriculturae Bohemica*, **43**, 127–133.

Brun C. (2011) Anthropogenic indicators in pollen diagrams in eastern France: a critical review. *Vegetation History and Archaeobotany*, **20**, 135–142.

Buček A. (2000) Krajina české republiky a pastva (The landscape of Czech Republic and livestock grazing). *Veronika*, **14**, 1–7.

Buček A., Lacina J. and Laštůvka Z. (eds) (2006) Pannonian steppe grasslands in Moravia. *Veronica*, **20**, 1–40.

Chytrý M. (ed.) (2007) *Vegetation of the Czech Republic 1. Grassland and heathland vegetation*. Prague: Academia.

Chytrý M. (2012) Vegetation of the Czech Republic: diversity, ecology, history. *Preslia*, **84**, 1–78.

Chytrý M., Tichý L. and Roleček J. (2003) Local and regional patterns of species richness in Central European vegetation types along the pH/calcium gradient. *Folia Geobotanica*, **38**, 429–442.

Chytrý M., Kučera T., Kočí M., Grulich V. and Lustyk P. (eds) (2010) *Katalog biotopů České republiky (Habitat Catalogue of the Czech Republic)*. edn 2. Prague: Agentura ochrany přírody a krajiny ČR.

Čulíková V. (1994) Rekonstrukce synantropní vegatace středověkého města Mostu (Reconstruction of synanthropic vegetation in the medieval town of Most). Medievalia Archaeologica Bohemica 1993. *Památky Archeologické*, Supplementum **2**, 181–204.

Čulíková V. (1999) Rostlinné makrozbytky z objektu č. 126 na předhradí slovanského hradiska v Libici nad Cidlinou (Plant macroremnants from the feature no. 126 in settlement around Slavic castle Libice nad Cidlinou). *Památky Archeologické*, **90**, 166–185.

Čulíková V. (2003) Rostlinné makrozbytky z raně středověkého hradu Stará Boleslav (Plant macro-remains from the early medieval stronghold Stará Boleslav). *Mediaevalia Archaeologica*, **5**, 367–379.

Čulíková V. (2006) Rostlinné makrozbytky z prostor raně středověkého opevnění v sondě 236 na jz. okraji předhradí v Libici nad Cidlinou (Plant macro-remains from the area of the Early Medieval fortification at the south-western edge of the bailey at Libice nad Cidlinou). *Archeologické Rozhledy*, **58**, 527–539.

Čulíková V. (2008) *Rostlinné makrozbytky* (Plant macro-remains). In: Zápotocký M., Zápotocká M.: Kutná hora – Denemark – Hradiště řivnáčské kultury (ca 3000–2800 př. Kr.). Památky Archeologické – Supplementum **18**, pp. 255–264.

Čulíková V. (2010) Středověká údolní niva Vltavy v Praze na Malé Straně (Valdštejnská čp. 154/III, Kolovratský palác) (Medieval floodplain of the river

Vltava in the neighbourhood of the Lesser Town in Prague (Valštejnská St. No. 154/III, Kolovratský Palace). *Archeologické Rozhledy*, **63**, 72–116.

Čulíková V. (2011) Rostlinné zbytky jedním z pramenů pro interpretaci čáslavského středověkého objektu (Plant remains as one of the sources for interpretation of the Čáslav Medieval sunken building). *Forum Urbes Medii Aevi*, **6**, 276–303.

Damm C. (1994) Vegetation und Florenbestand des Brockengebietes (Vegetation and phytogeography of the Mt. Brocken, Harz, Germany). Hercynia N. F. Halle. *Hercynia*, **29**, 5–56.

Deforce K. (2010) Pollen analysis of 15th century cesspits from the palace of the dukes of Burgundy in Bruges (Belgium): evidence for the use of honey from the western Mediterranean. *Journal of Archaeological Science*, **37**, 337–342.

Deforce K., Bastiaens J., Van Neer W., Ervynck A., Lentacker A., Sergant J. and Crombé P. (2012) Wood charcoal and seeds as indicators for animal husbandry in a wetland site during the late mesolithic-early neolithic transition period (Swifterbant culture, ca. 4600–4000 B.C.). *Vegetation History and Archaeobotany*, **22**, 51–60.

Delhon C., Martin L., Argant J. and Thiébault S. (2008) Shepherds and plants in the Alps: multi-proxy archaeobotanical analysis of neolithic dung from "La Grande Rivoire" (Isere, France). *Journal of Archaeological Science*, **35**, 2937–2952.

Dobeš M., Limburský P., Kyselý R., Novák J. and Šálková T. (2011) Příspěvek k prostorovému uspořádání obytných areálů z konce středního eneolitu, Řivnáčské osídlení ve Vlíněvsi (The contribution to the spatial structure of the residential area at the end of the Middle Eneolithic period, Řivnáč settlement in the Vlíněves, Central Bohemia). *Archeologické Rozhledy*, **63**, 375–424.

Dostálek J. and Frantík T. (2012) The impact of different grazing periods in dry grasslands on the expansive grass *Arrhenatherum elatius* L. and on woody species. *Environmental Management*, **49**, 855–861.

Dulamsuren C., Hauck M. and Mühlenberg M. (2005) Ground vegetation in the Mongolian taiga forest-steppe ecotone does not offer evidence for the human origin of grasslands. *Applied Vegetation Science*, **8**, 149–154.

Ellenberg H. (1988) *Vegetation ecology of Central Europe*. Cambridge UK: Cambridge University Press.

Ewald J. (2003) The calcareous riddle: why are there so many calciphilous species in the Central European flora? *Folia Geobotanica*, **38**, 357–366.

Fiala K., Tůma I. and Holub P. (2011) Effect of nitrogen addition and drought on above-ground biomass of expanding tall grasses *Calamagrostis epigejos* and *Arrhenatherum elatius*. *Biologia*, **66**, 275–281.

Fischer S., Poschlod P. and Beinlich B. (1996) Experimental studies on the dispersal of plants and animals by sheep in calcareous grasslands. *Journal of Applied Ecology*, **33**, 1206–1222.

Gaisler J., Hejcman M. and Pavlů V. (2004): Effect of different mulching and cutting regimes on the vegetation of upland meadow. *Plant, Soil and Environment*, **50**, 324–331.

Gradmann R. (1933) Die Steppenheidetheorie (Steppe grassland theory). *Geographishe Zeitschrift*, **39**, 265–278.

Hájková P., Roleček J., Hájek M., Horsák M., Fajmon K., Polák M. and Jamrichová E. (2011) Prehistoric origin of the extremely species-rich semi-dry grasslands in the Bílé Karpaty Mts. (Czech Republic and Slovakia). *Preslia*, **83**, 185–204.

Hejcman M. (2005) *Grassland management in mountain and upland areas of the Czech Republic*. Ph.D. thesis, Prague: Faculty of Environmental Sciences, Czech University of Life Sciences.

Hejcman M., Nežerková P., Pavlů V., Gaisler J., Lokvenc T. and Pavlů L. (2005) Regeneration of Nardus stricta subalpine grasslands in the Giant Mountains (Krkonoše). *Acta Societatis Botanicorum Poloniae*, **74**, 253–258.

Hejcman M., Pavlů V., Hejcmanová P., Gaisler J., Hakl J. and Rauch O. (2006) Farmer decision making and its effect on the subalpine grassland succession in the Giant Mountains, Czech Republic. *Acta Societatis Botanicorum Poloniae*, **75**, 165–174.

Hejcman M., Klaudisová M., Hejcmanová P., Pavlů V. and Jones M. (2009) Expansion of *Calamagrostis villosa* in sub-alpine *Nardus stricta* grassland: cessation of cutting management or high nitrogen deposition? *Agriculture, Ecosystems and Environment*, **129**, 91–96.

Hejcman M., Češková M., Schellberg J. and Pätzold S. (2010a) The Rengen Grassland Experiment: effect of soil chemical properties on biomass production, plant species composition and species richness. *Folia Geobotanica*, **45**, 125–142.

Hejcman M., Češková M. and Pavlů V. (2010b) Control of *Molinia caerulea* by cutting management on sub-alpine grassland. *Flora*, **205**, 577–582.

Hejcman M., Schellberg J. and Pavlů V. (2010c) Long-term effects of cutting frequency and liming on soil chemical properties, biomass production and plant species composition of Lolio-Cynosuretum grassland after the cessation of fertilizer application. *Applied Vegetation Science*, **13**, 257–269.

Hejcman M., Strnad L., Hejcmanová P. and Pavlů V. (2012) Response of plant species composition, biomass production and biomass chemical properties to high N, P and K application rates in *Dactylis glomerata*- and *Festuca arundinacea*-dominated grassland. *Grass and Forage Science*, **67**, 488–506.

Hejcman M., Karlík P., Ondráček J. and Klír T. (2013) Short-term medieval settlement activities irreversibly changed forest soils and vegetation in Central Europe. *Ecosystems*, **16**, 652–663.

Hejný S. and Slavík B. (eds) (1997) *Květena České republiky 1*. (Flora of Czech Republic 1). Prague: Academia.

Hertel D. and Schöling D. (2011) Below-ground response of Norway spruce to climate conditions at Mount Brocken (Germany) – a re-assessment of Central Europe's northernmost treeline. *Flora*, **206**, 127–135.

HILBIG W. (2000) Forest distribution and retreat in the forest steppe ecotone of Mongolia. *Marburger Geographische Schriften*, **135**, 171–187.

HOOPER W.D. and ASH H.B. (1935) *Cato and Varro on Agriculture*. Loeb Classical Library No. 283. Harvard: Harvard University Press.

HORSÁK M., CHYTRÝ M., POKRYSZKO B.M., DANIHELKA J., ERMAKOV N., HÁJEK M., HÁJKOVÁ P., KINTROVÁ K., KOČÍ M., KUBEŠOVÁ S., LUSTYK P., OTÝPKOVÁ Z., PELÁNKOVÁ B. and VALACHOVIČ M. (2010) Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. *Journal of Biogeography*, **37**, 1450–1462.

HREVUŠOVÁ Z., HEJCMAN M., PAVLŮ V., HAKL J., KLAUDISOVÁ M. and MRKVIČKA J. (2009) Long-term dynamics of biomass production, soil chemical properties and plant species composition of alluvial grassland after the cessation of fertilizer application in the Czech Republic. *Agriculture, Ecosystems and Environment*, **130**, 123–130.

JANKOVSKÁ V. (1987) Netradiční interpretace pylových spekter ze středověké Prahy (Untraditional interpretation of pollen analyses from medieval Prague). *Archeologické Rozhledy*, **39**, 435–444.

JANKOVSKÁ V. (2004) Krkonoše v době poledové (The Giant Mts. in Holocene). *Opera Corcontica*, **41**, 111–123.

JANKOVSKÁ V. (2011) The middle ages in pollen-analytical research on the territory of the Czech Republic. *Bulletin of Geography – Physical Geography Sciences*, **4**, 47–70.

JENÍK J. (1961) *Alpinská vegetace Krkonoš, Kralického Sněžníku a Hrubého Jeseníku: teorie anemo-orografických systémů (Alpine vegetation of the Giant Mts., the Kralický Sněžník Mts. and the Hrubý Jeseník Mts.)*. Prague: Nakladatelství AVČR.

KAPLAN Z. (2012) Flora and phytogeography of the Czech Republic. *Preslia*, **84**, 505–573.

KAPLAN J.O., KRUMHARDT K.M. and ZIMMERMANN N. (2009) The prehistoric and preindustrial deforestation in Eu rope. *Quaternary Science Reviews*, **28**, 3016–3034.

KARLÍK P. and POSCHLOD P. (2009) History or abiotic filter: which is more important in determining the species composition of calcareous grasslands? *Preslia*, **81**, 321–340.

KLÁPŠTĚ J. (2006) *Proměna českých zemí ve středověku (Transformation of Czech Lands in the Medieval)*. Prague: Nakladatelství Lidové noviny.

KLIMENT J., ŠIBÍK J., ŠIBÍKOVÁ I., JAROLÍMEK I., DÚBRAVCOVÁ Z. and UHLÍŘOVÁ J. (2010) High-altitude vegetation of the Western Carpathians – a syntaxonomical review. *Biologia*, **65**, 965–989.

KLIMEŠ L., DANČÁK M., HÁJEK M., JONGEPIEROVÁ I. and KUČERA T. (2001) Scale-dependent biases in 29 species counts in a grassland. *Journal of Vegetation Science*, **12**, 699–704.

KLÍR T. (2010) Rural settlements in Bohemia in the Age of Transition (14th – 16th century): research concept and preliminary report. *Medieval Settlement Research*, **25**, 52–61.

KOHLER-SCHNEIDER M. and CANEPPELE A. (2009) Late Neolithic agriculture in eastern Austria: archaeobotanical results from sites of the Baden and Jenišovice cultures (3600–2800 BC). *Vegetation History and Archaeobotany*, **18**, 61–74.

KOMÁREK P., PAVLŮ V. and HEJCMAN M. (2010) Effect of depth and width of cultivation and sowing date on establishment of red clover (*Trifolium pratense* L.) by rotary slot seeding into grassland. *Grass and Forage Science*, **65**, 154–158.

KOMOSA M., FRACKOWIAK H. and GODYNICKI S. (2007) Skulls of Neolithic Eurasian beavers (*Castor fiber* L.) in comparison with skulls of contemporary beavers from natural biotopes of Wielkopolska region (Poland). *Polish Journal of Environmental Studies*, **16**, 697–705.

KÖRNER C. (1999) *The Alpine plant life*. Berlin: Springer.

KOWALCZYK R., TABERLET P., COISSAC E., VALENTINI A. and MIQUEL C. (2011) Influence of management practices on large herbivore diet – Case study of European bison in Białowieża Primeval Forest (Poland). *Forest Ecology and Management*, **261**, 821–828.

KOZÁKOVÁ R. and KAPLAN M. (2006) Příspěvek pylové analýzy k rekonstrukci přírodních poměrů v okolí Libice nad Cidlinou (The contribution of pollen analysis to the reconstruction of natural conditions around the enclosure at Libice nad Cidlinou). *Archeologické Rozhledy*, **58**, 540–549.

KOZÁKOVÁ R. and POKORNÝ P. (2007) Dynamics of the biotopes at the edge of a medieval town: pollen analysis of Vltava river sediments in Prague, Czech Republic. *Preslia*, **79**, 259–281.

KOZÁKOVÁ R., POKORNÝ P., HAVRDA J. and JANKOVSKÁ V. (2009) The potential of pollen analyses from urban deposits: multivariate statistical analysis of a data set from the medieval city of Prague, Czech Republic. *Vegetation History and Archaeobotany*, **18**, 477–488.

KREUZ A. (2008) Closed forest or open woodland as natural vegetation in the surroundings of Linearbandkeramik settlements? *Vegetation History and Archaeobotany*, **17**, 51–64.

KREUZ A. and SHÄFER E. (2011) Weed finds as indicators for the cultivation regime of the early Neolithic Bandkeramik culture? *Vegetation History and Archaeobotany*, **20**, 333–348.

KUBÁT K., HROUDA L., CHRTEK J., KAPLAN Z. and ŠTĚPÁNEK J. (2002) *Klíč ke květeně České republiky (Key to the flora of Czech Republic)*. Prague: Academia.

KYSELÝ R. (2005) Archeologické doklady divokých savců na území ČR v období od neolitu po novověk (Archaeological evidence of wild mammals in the Czech Republic from the Neolithic to the Modern times). *Lynx*, **36**, 55–101.

LENCOVÁ K. and PRACH K. (2011) Restoration of hay meadows on ex-arable land: commercial seed mixtures vs. spontaneous succession. *Grass and Forage Science*, **66**, 265–271.

LOKVENC T. (1978) *Toulky krkonošskou minulostí (Wandering through history of the Giant Mts.)*. Kruh: Hradec Králové.

Ložek V. (1973) *Příroda ve čtvrtohorách (Nature in Quaternary)*. Prague: Academia.
Ložek V. (1981) Změny krajiny v souvislosti s osídlením ve světle malakologických poznatků (Changes in the landscape in context of settlement in the light of molusc analysis). *Archeologické Rozhledy*, **33**, 176–188.
Ložek V. (2007) *Zrcadlo minulosti: Česká a slovenská krajina v kvartéru (Mirror of the past: Czech and Slovak landscape in the Quaternary)*. Prague: Dokořán.
Magyari E.K., Chapman J.C., Passmore D.G., Allen J.R.M., Huntley J.P. and Huntley B. (2010) Holocene persistence of wooded steppe in the Great Hungarian Plain. *Journal of Biogeography*, **37**, 915–935.
Mahmoud A., Grime J.P. and Furness S.B. (1975) Polymorphism in *Arrhenatherum elatius* (L.) Beauv. EX J. & C. Presl. *New Phytologist*, **75**, 269–276.
Margielewski W., Krapiec M., Valde-Nowak P. and Zernitskaya V. (2010) A Neolithic yew bow in the Polish Carpathians – Evidence of the impact of human activity on mountainous paleoenvironment from the Kamiennik landslide peat bog. *Catena*, **80**, 141–153.
Mayer R. and Erschbamer B. (2011) Seedling recruitment and seed-/microsite limitation in traditionally grazed plant communities of the alpine zone. *Basic and Applied Ecology*, **12**, 10–20.
Merunková K., Otýpková Z. and Chytrý M. (2012) White Carpathian grasslands: can local ecological factors explain their extraordinary species richness? *Preslia*, **84**, 311–325.
Mitchell F.J.G. (2005) How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology*, **93**, 168–177.
Novák J., Petr L. and Treml V. (2010) Late-Holocene human-induced changes to the extent of alpine areas in the East Sudetes, Central Europe. *Holocene*, **20**, 895–905.
Novák J., Lisá L., Pokorný P. and Kuna M. (2012) Charcoal analysis as an environmental tool for the study of Early Medieval sunken houses infills in Roztoky, Czech Republic. *Journal of Archaeological Science*, **39**, 808–817.
Novotný G. (2000) Pastva hospodářských zvířat v lesích českých zemí v minulosti (Livestock grazing in forests of Czech lands in the past). *Veronika*, **14**, 1–7.
Opravil E. (2000) Zur Umwelt des Burgwalls von Mikulčice und zur pflanzlichen Ernährung seiner Bewohner mit einem Exkurs zum Burgwall Pohansko bei Břeclav (Environment of the Mikulčice settlement and plant food of its inhabitants with excursion also into the Pohansko settlement by Břeclav). In: Poláček L. (ed.). *Studien zur Burgwall von Mikulčice 4*, pp. 9–169. Brno: Institute of Archaeology. Masaryk University.
Out W.A. (2010) Integrated archaeobotanical analysis: human impact at the Dutch Neolithic wetland site the Hazendonk. *Journal of Archaeological Science*, **37**, 1521–1531.
Pärtel M. (2002) Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, **83**, 2361–2366.
Pärtel M., Zobel M., Zobel K. and van der Maarel E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, **75**, 111–117.
Pärtel M., Helm A., Reitalu T., Liira J. and Zobel M. (2007) Grassland diversity related to the Late Iron Age human population density. *Journal of Ecology*, **95**, 574–582.
Pavlů I. and Zápotocká M. (2007) *Archeologie pravěkých Čech 3 – Neolit (Archaeology of prehistoric Czechia 3 – Neolithic)*. Prague: Archeologický ústav AVČR.
Pavlů V., Hejcman M., Pavlů L. and Gaisler J. (2003) Effect of rotational and continuous grazing on vegetation of the upland grassland in the Jizerské hory Mts, Czech Republic. *Folia Geobotanica*, **38**, 21–34.
Pavlů V., Hejcman M., Pavlů L., Gaisler J. and Nežerková P. (2006) Effect of continuous grazing on forage quality, quantity and animal performance. *Agriculture, Ecosystems and Environment*, **113**, 349–355.
Pavlů V., Hejcman M., Pavlů L. and Gaisler J. (2007) Restoration of grazing management and its effect on vegetation in an upland grassland. *Applied Vegetation Science*, **10**, 375–382.
Pavlů V., Schellberg J. and Hejcman M. (2011a) Cutting frequency vs. N application: effect of a 20-year management in *Lolio-Cynosuretum* grassland. *Grass and Forage Science*, **66**, 501–515.
Pavlů L., Pavlů V., Gaisler J., Hejcman M. and Mikulka J. (2011b) Effect of long-term cutting versus abandonment on the vegetation of a mountain hay meadow (Polygono-Trisetion) in Central Europe. *Flora*, **206**, 1020–1029.
Pavlů V., Gaisler J., Pavlů L., Hejcman M. and Ludvíková V. (2012) Effect of fertiliser application on plant species composition of *Festuca rubra* grassland under cutting management and its after effect under abandonment. *Acta Oecologica*, **45**, 42–49.
Petrášek F. (1972) *Geneze chovu skotu v českých zemích (Genesis of cattle breeding in Czech lands)*. Prague: Academia.
Pokorný P. (2004) Postglacial vegetation distribution in the Czech Republic and its relationship to settlement zones: review from off-site pollen data. In: Gojda M. (ed.) *Prehistoric settlement patterns in Bohemia – the potential of non-destructive archaeology*, pp. 395–407. Prague: Academia.
Pokorný P. (2005) Role of man in the development of Holocene vegetation in Central Bohemia. *Preslia*, **77**, 113–128.
Pokorný P. (2011) *Neklidné časy – kapitoly ze společných dějin přírody a lidí (Restless times – chapters from collective history of nature and people)*. Prague: Dokořán.
Pokorný P. and Mařík J. (2006) Nález zbytku medem slazené potraviny ve výbavě raně středověkého hrobu v Libici nad Cidlinou – Kaníně: zhodnocení nálezu z hlediska rekonstrukce krajiny a vegetace (The find of honey-sweetened cereal food residues from Early Medieval burial site near Libice nad Cidlinou - Evaluation of the find from the point of landscape and vegetation reconstruction). *Archeologické Rozhledy*, **68**, 559–569.
Pokorný P., Boenke N., Chytráček M., Nováková K., Sádlo J., Veselý J., Kuneš P. and Jankovská V.

(2006) Insight into the environment of a pre-Roman Iron Age hillfort at Vladař, Czech Republic, using a multi-proxy approach. *Vegetation History and Archaeobotany*, **15**, 419–433.

Polet C., Dutour O., Orban R., Jadin I. and Louryan S. (1996) A healed wound caused by a flint arrowhead in a Neolithic human innominate from the Trou Rosette (Furfooz Belgium). *International Journal of Osteoarchaeology*, **6**, 414–420.

Poschlod P. and Baumann A. (2010) The historical dynamics of calcareous grasslands in the central and southern Franconian Jurassic mountains: a comparative pedoantracological and pollen analytical study. *The Holocene*, **20**, 13–23.

Poschlod P. and WallisDeVries M.F. (2002) The historical and socioeconomic perspective of calcareous grasslands – lessons from the distant and recent past. *Biological Conservation*, **104**, 361–376.

Poschlod P., Baumann A. and Karlík P. (2009) Origin and development of grasslands in Central Europe. In: Veen P., Jefferson R., de Smidt J. and van der Straaten J. (eds) *Grasslands in Europe of high nature value*. Utrecht, NL: KNNV Publishing.

Prins H.H.T. (1998) Origins and development of grassland communities in northwestern Europe. In: WallisDeVries M.F., Bakker J.P. and Van Wieren S.E. (eds) *Grazing and conservation management*. Dordrecht: Kluwer Academic Publishers.

Pyšek P., Sádlo J. and Mandák B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.

Pyšek P., Danihelka J., Sádlo J., Chrtek J.J., Chytrý M., Jarošík V., Kaplan Z., Krahulec F., Moravcová L., Pergl J., Štajerová K. and Tichý L. (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. *Preslia*, **84**, 155–255.

Rivas-Martinez S., Penas A. and Diaz T. (2004) *Biogeographic map of Europe*. Spain: Cartographic Service, University of León.

Rochon J.J., Doyle C.J., Greef J.M., Hopkins A., Molle G., Sitzia M., Scholefield D. and Smith C.J. (2004) Grazing legumes in Europe: a review of their status, management, benefits, research needs and future prospects. *Grass and Forage Science*, **59**, 197–214.

Rozbrojova Z., Hájek A. and Hájek O. (2010) Vegetation diversity of mesic meadows and pastures in the West Carpathians. *Preslia*, **82**, 289–306.

Rulf J. (1983) Přírodní prostředí a kultury českého neolitu a eneolitu (Environment and cultures of Czech Neolithic and Eneolithic). *Památky Archeologické*, **74**, 35–95.

Rybníček K. and Rybníčková E. (2004) Pollen analysis of sediments from the summit of the Praděd range in the Hrubý Jeseník Mts (Eastern Sudetes). *Preslia*, **76**, 331–347.

Sádlo J., Pokorný P., Hájek P., Dreslerová D. and Cílek V. (2005) *Krajina a revoluce – významné přelomy ve vývoji kulturní krajiny českých zemí (The landscape and revolution – important brakes in development of the cultural landscape in Czech lands)*. Prague: Malá Skála.

Semelová V., Hejcman M., Pavlů V., Vacek S. and Podrázský V. (2008) The Grass Garden in the Giant Mts. (Czech Republic): residual effect of long-term fertilization after 62 years. *Agriculture, Ecosystems and Environment*, **123**, 337–342.

Smit H.J., Metzger M.J. and Ewert F. (2008) Spatial distribution of grassland productivity and land use in Europe. *Agricultural Systems*, **98**, 208–219.

Speranza A., van der Plicht J. and van Geel B. (2000) Improving the time control of the Subboreal/Subatlantic transition in a Czech peat sequence by 14C wiggle-matching. *Quaternary Science Reviews*, **19**, 1589–1604.

Šťastná P., Klimeš L. and Klimešová J. (2010) Biological flora of Central Europe: *Rumex alpinus* L. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 67–79.

Štrobach J. (2010) *Studium biodiverzity agrofytocenóz ve vztahu ke způsobům hospodaření na trvalých travních porostech (Study of agrophytocoenoses biodiversity in relation to the management of permanent grassland)*. Ph.D. thesis, Czech University of Life Sciences in Prague.

Svenning J.C. (2002) A review of natural vegetation openness in north-western Europe. *Biological Conservation*, **104**, 133–148.

Svobodova H. (2004) Vyvoj vegetace na Upskem rašeliništi v holocenu (Development of the vegetation on Úpské rašeliniště Mire in the Holocene). *Opera Corcontica*, **41**, 124–131.

Szafer W. (1968) The ure-ox extinct in Europe since the seventeenth century: an early attempt at conservation that failed. *Biological Conservation*, **1**, 45–47.

Taylor K. (2009) Biological flora of the British Isles: *Urtica dioica* L. *Journal of Ecology*, **97**, 1436–1458.

Treml V. and Banaš M. (2000) Alpine timberline in the high sudetes. *Acta Universitatis Carolinae, Geographica*, **15**, 83–99.

Treml V., Jankovská V. and Petr L. (2008) Holocene dynamics of the alpine timberline in the High Sudetes. *Biologia*, **63**, 73–80.

Ulrych L. (2006) *První česká kronika obce Oldřichov v Hájích (The first Czech chronicle of the village Oldřichov v Hájích)*. Oldřichov v Hájích: Obecní úřad.

Venclová N., Drda P., Michálek J., Militký J., Salač V., Sankot P. and Vokolek V. (2008) *Archeologie pravěkých Čech – doba Laténská (Archaeology of prehistoric Czechia – Laténe period)*. Praha: Archeologický ústav AV ČR.

Vera F.W.M. (2000) *Grazing ecology and forest history*. Wallingford, UK: CABI.

Viner S., Evans J., Albarella U. and Pearson M.P. (2010) Cattle mobility in prehistoric Britain: strontium isotope analysis of cattle teeth from Durrington Walls (Wiltshire, Britain). *Journal of Archaeological Science*, **37**, 2812–2820.

Vojta J. (2007) Relative importance of historical and natural factors influencing vegetation of secondary forests in abandoned villages. *Preslia*, **79**, 223–244.

Waldhauser J. (2001) *Encyklopedie Keltů v Čechách (Encyclopaedia of Celts in Bohemia)*. Prague: Nakladatelství Libri.

Wilson J.B., Peet R.K., Dengler J. and Pärtel M. (2012) Plant species richness: the world records. *Journal of Vegetation Science*, **23**, 796–802.

Žemlička J. (1997) *Čechy v době knížecí (Czechia in the Princes period)*. Prague: Nakladatelství lidové noviny.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Schematic phytogeographical division of Europe into main floral provinces.

Figure S2. (a) Expositional steppe grasslands of natural origin can be recorded in the NW part of the Czech Republic on south-facing slopes on basic-rich volcanic soils. The border between steppe grassland and forest with *Quercus robur*, *Q. petrea* and *Carpinus betulus* is very sharp and fully corresponds to similar borders between expositional steppe grasslands and (b) *Acer platanoides* forests in the South Ural Mts. (Russia) or (c) to *Betula pendula* forests in the Altai Mts. (South Siberia, Russia, photograph Michal Hejcman, Milan Chytrý and Pavla Hejcmanová).

Figure S3. (a) Beaver dam on a small river in the western part of the Czech Republic. In the background are visible dead waterlogged trees of *Alnus glutinosa*. (b) Male of European bison damaging *Larix sibirica* tree in Cherga enclosure the Altai Mts., South Siberia, Russia. (c) Tree of *Betula pendula* heavily damaged by European bison in Cherga Reserve (photograph Aleš Vorel, Michal Hejcman and Pavla Hejcmanová).

Figure S4. Although subalpine *Nardus stricta* grasslands are considered to be natural in the Giant Mts., they were substantially enlarged by agricultural activities in 16th–19th centuries by cutting of *Pinus mugo* shrubs (see Hejcman *et al.*, 2006).

Figure S5. Cover of *Plantago lanceolata* in control (C) and other fertilizer treatments in the Rengen Grassland Experiment in late June 2011.

Figure S6. Remnants of low-productive pastures with shrubs of *Juniperus communis* subsp. *communis* surrounded by improved grasslands in the Eifel Mountains in SW Germany (photograph Michal Hejcman).

Figure S7. Total agricultural area, area of grasslands and area of arable land in the village of Oldřichov v Hájích in the period from 1651 to 2009.

Figure S8. Livestock units (one LU is 500 kg of live weight) in the village of Oldřichov v Hájích over the period from 1654 to 2009.