Journal of Biogeography (J. Biogeogr.) (2015) 42, 951–963

ORIGINAL ARTICLE

Origin of the forest steppe and exceptional grassland diversity in Transylvania (central-eastern Europe)

Angelica Feurdean[1,2]*, Elena Marinova[3], Anne B. Nielsen[4], Johan Liakka[1,2], Daniel Veres[5], Simon M. Hutchinson[6], Mihaly Braun[7], Alida Timar-Gabor[8,9], Ciprian Astalos[10], Volker Mosburgger[1] and Thomas Hickler[1,2,11]

[1]Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany, [2]Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main, Germany, [3]Centre for Archaeological Sciences, University of Leuven, Leuven, Belgium, [4]Department of Geology, Lund University, Lund, Sweden, [5]Institute of Speleology, Romanian Academy, [6]School of Environment and Life Sciences, University of Salford, Salford, UK, [7]Hertelendi Laboratory of Environmental Studies, Institute of Nuclear Research of the Hungarian Academy of Sciences, Debrecen, Hungary, [8]Faculty of Environmental Science, Babeş-Bolyai University, Cluj Napoca, Romania, [9]Interdisciplinary Research Institute on Bio-Nano-Science of Babeş-Bolyai University, Cluj-Napoca, Romania, [10]Satu Mare County Museum, Romania, [11]Department of Physical Geography, Goethe University, Frankfurt am Main, Germany

*Correspondence: Angelica Feurdean, Biodiversity and Climate Research Centre (BiK-F), Senckenberg Gesellschaft für Naturforschung, Senkenberganlage 25, D-60325, Frankfurt am Main, Germany.
E-mails: angelica.feurdean@senckenberg.de; angelica.feurdean@gmail.com

ABSTRACT

Aim The forest steppe of the Transylvanian Plain is a landscape of exceptionally diverse steppe-like and semi-natural grasslands. Is this vegetation a remnant of a once continuous temperate forest extensively cleared by humans, or has the area, since the last glacial, always been a forest steppe? Understanding the processes that drive temperate grassland formation is important because effective management of this biome is critical to the conservation of the European cultural landscape.

Location Lake Stiucii, north-western Romania, central-eastern Europe.

Methods We analysed multi-proxy variables (pollen, coprophilous fungi, plant macroremains, macrocharcoal) from a 55,000 year discontinuous sequence (*c.* 55,000–35,000; 13,000–0 cal. yr BP), integrating models of pollen-based vegetation cover, biome reconstruction, global atmospheric simulations and archaeological records.

Results Needleleaf woodland occurred during glacial Marine Isotope Stage (MIS) 3, but contracted at the end of this period. Forest coverage of *c.* 55% (early Holocene) and 65% (mid-Holocene) prevailed through the Holocene, but Bronze Age humans extensively cleared forests after 3700 cal. yr BP. Forest coverage was most widespread between 8600 and 3700 cal. yr BP, whereas grasses, steppe and xerothermic forbs were most extensive between 11,700 and 8600 cal. yr BP and during the last 3700 cal. yr BP. Cerealia pollen indicate the presence of arable agriculture by *c.* 7000 cal. yr BP.

Main conclusions We have provided the first unequivocal evidence for needleleaf woodland during glacial MIS 3 in this region. Extensive forests prevailed prior to 3700 cal. yr BP, challenging the hypothesis that the Transylvanian lowlands were never wooded following the last glaciation. However, these forests were never fully closed either, reflecting dry growing season conditions, recurrent fires and anthropogenic impacts, which have favoured grassland persistence throughout the Holocene. The longevity of natural and semi-natural grasslands in the region may explain their current exceptional biodiversity. This longer-term perspective implies that future climatic warming and associated fire will maintain these grasslands.

Keywords

Anthropogenic impact, Bronze Age, fire, grassland diversity, Holocene, MIS-3, palaeoecology, REVEALS, Romania, steppe.

INTRODUCTION

Eurasian forest steppe is an intermediate biome between the temperate forests and the temperate grasslands that extends intermittently from the Carpathian foothills to the Altay. Because forest steppe has been continuously transformed by human activities, the biogeography of this biome in Europe now has a cultural, rather than natural legacy, primarily in

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/jbi.12468

regions where local environmental factors favour forest (Ellenberg & Leuschner, 2010).

The forest steppe of Transylvania (north-western Romania) is a landscape whose origin has been much debated and which has an exceptional biodiversity of steppe-like and semi-natural grasslands (Ruprecht *et al.*, 2009; Dengler *et al.*, 2012). According to Bohn *et al.* (2003) the natural vegetation of the region is a mixed thermophilous deciduous forest, whereas Kun *et al.* (2004) classified this zone as a forest steppe unit. The origin of the open landscape of the Transylvanian Plain has been disputed for nearly two centuries since Kerner (1863) noted the unusual openness of this region (see Badarau, 2005). Two contrasting hypotheses have been put forward to account for how and when the region's extensive openness and grasslands were created. The first scenario proposes that the Transylvanian Plain was never extensively wooded following the last major glaciation, during which steppe and forest steppe extended over much of Europe. The region's forest steppe, according to this hypothesis, is a consequence of a relatively dry continental climate that predominated throughout the Holocene (Frenzel, 1968; Badarau, 2005; and references therein). According to the second scenario, the forest patches in the Transylvanian Plain are remnants of once continuous forests (Borza, 1936) that were extensively cleared by humans, probably in the last one to two millennia (Ruprecht *et al.*, 2009). To date, the sole palaeovegetation record close to the study region covers the period *c.* 13,000–5000 cal. yr BP and shows that the landscape was covered by forest until 5000 years ago (Feurdean *et al.*, 2007). Anthropogenic land cover change models (ALCCs) offer an alternative assessment of land-cover variability over time, but often show contrasting results to proxy reconstructions, depending on the region. There are also discrepancies between the models used. For example, modelling incorporating adaptive changes in land-use systems over time (e.g. KK10), indicates an earlier and stronger impact on land cover than that resulting from conservative models, which assume that land use per capita is constant over time, e.g. the HYDE model (Kaplan *et al.*, 2011). An accurate quantification of anthropogenic impact is necessary to adequately determine the magnitude and the timing of land-cover change brought about by human land use. It is therefore an important dimension in projecting future trajectories of environmental change.

Shedding light on the origin of this region's forested steppe landscape and its marked grassland diversity has an ecological relevance beyond the study area, especially in terms of understanding the processes that drive temperate grassland formation, variability and the reasons for their diversity. In addition to environmental factors, disturbance by fire helps to maintain tropical and North American temperate grasslands, and thus landscape openness (Hoffmann *et al.*, 2012). Simulations using dynamic global vegetation models that include fire disturbance indicate that in the absence of fire, many regions that currently support shrubs and herbaceous vegetation would turn into forests (Bond *et al.*, 2005). How fire–grass interactions have served to limit woody cover in European temperate grasslands and to facilitate grassland preservation over shrub and forest remain to be demonstrated.

Here, we present an integrated palaeoecological record from Lake Stiucii (pollen, coprophilous fungi, plant macroremains, macrocharcoal), along with pollen-based vegetation modelling (using REVEALS; Sugita, 2007) and biome reconstruction, as well as global climate simulations and archaeological records, to examine the dynamics of the forest and grassland in this region, as well as the timing and amplitude of alterations in vegetation cover by humans. The Lake Stiucii record is a 55,000 year discontinuous sequence (*c.* 55,000–35,000; 13,000–0 cal. yr BP), whose continuity has been affected by erosional hiatus. Nevertheless, this long-term sedimentary record does allow the examination of vegetation sensitivity to climate fluctuations during glacial conditions and is one of the first such records from the region.

We tested two main hypotheses: (1) the forest steppe of the Transylvanian Plain and its highly diverse grassland have persisted in this region throughout the Holocene; and (2) the forest patches in this region are remnants of early post-glacial continuous temperate forests that were extensively cleared by humans sometime during the Holocene and never fully recovered. Our emphasis lies on the processes that drive natural and semi-natural grassland formation, in particular climate–fire–vegetation interactions and human legacies. This is important as these habitats now play a key role in conserving biodiversity in European agricultural landscapes (Dengler *et al.*, 2012).

MATERIALS AND METHODS

Geography, climate and vegetation

The climate of the region surrounding Lake Stiucii (239 m a.s.l.; 46°58′ 044 N; 23°54′ 106 E; 38 ha; watershed *c.* 131 ha (Feurdean *et al.*, 2013a) is temperate continental with a mean annual temperature of *c.* 8–9 °C, January temperature *c.* −1 °C and July 18–20 °C. Annual precipitation is 550–650 mm with the highest values occurring in spring and summer (May–July) and the lowest in late autumn–winter (October–March). The geology comprises mainly Neogene marine marls and sands intercalated with volcanic tuffs and salt deposits. Soils are predominantly haplic and luvic chernozioms and phaenozems with gleic soils predominating along valley floors (IUSS Working Group WRB, 2007).

Anthropogenic activities have significantly changed the land cover near the study site so that it consists of approximately 16% forest, 17% pasture and meadows, and 60–70% arable land and orchards, today mostly in an abandoned state (Fig. 1). The remnant forest patches are confined to the hilltops and are primarily composed of *Quercus robur, Q. petraea, Q. pubescens, Carpinus betulus, Fagus sylvatica* and plantations of *Robinia pseudoacacia*, *Pinus sylvestris* and *P. nigra*. At present, the steppe-like grasslands are confined to south-facing, sunny slopes or marly soils where competition from tree species and agriculture yields are low (Badarau, 2005; Dengler

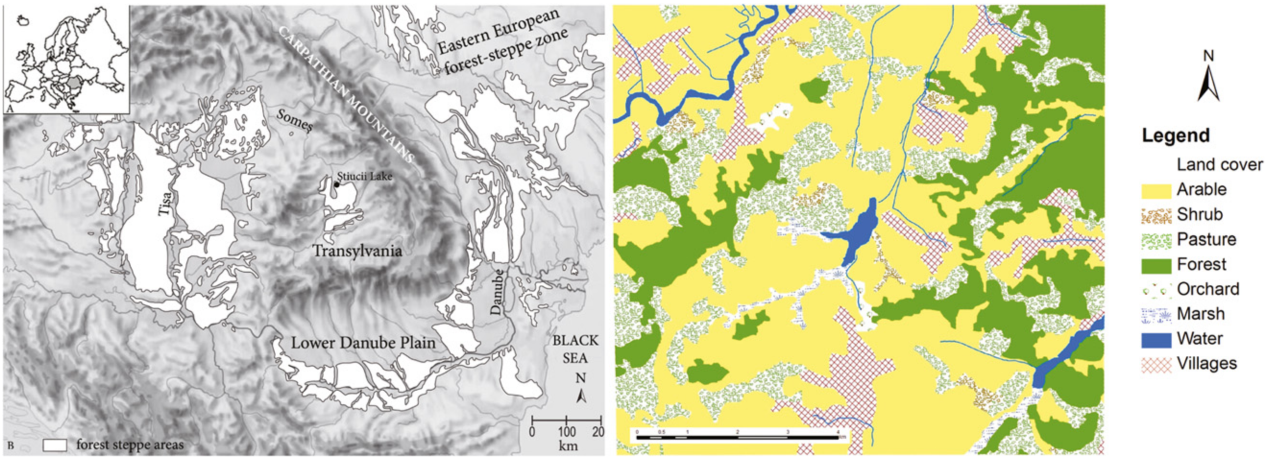

Figure 1 (a) Location of the study area in Europe, (b) distribution of forest steppe in Eurasia [redrawn after Varga *et al.* (2000) and Magyari *et al.* (2010)], and (c) CORINE Land Cover 2006 map.

et al., 2012). On the salt-rich soils, halophytesilous plants, including *Suaeda maritima, Petrosimonia triandra, Salicornia herbacea, Plantago cornuti* and *Artemisia salina*, occur. Plant nomenclature follows Tutin *et al.* (1964–1980).

Core collection, chronology and analyses

Sediment cores were extracted from the deepest (6 m) part of Lake Stiucii. The construction of a composite sedimentary record (total 726 cm) and a chronology of the upper 626 cm (last 12,000 years) were presented in Feurdean *et al.* (2013a). For the bottom part of the sediment profile (726–626 cm), the radiocarbon and optically stimulated luminescence (OSL) dates are described in Appendix S1 in Supporting Information. The chronological results indicate that the Lake Stiucii basin records environmental conditions from about 55,000 cal. yr BP (full glacial) with likely erosional events between 38,000 and 13,000 cal. yr BP. However, sediment accumulation during the last 12,000 cal. yr BP was continuous and the rate varied between 8 and 40 cm yr^{-1} (Feurdean *et al.*, 2013a).

Pollen was extracted from sediment samples (1.5 cm^3) at intervals ranging between 1 and 10 cm along the core following the standard procedures of Bennett & Willis (2001). The total pollen counts, excluding Cyperaceae, spores and aquatics at each level varied between 197 and 746 (343 mean). Pollen and spore counts were converted into percentages of the terrestrial pollen sum. Non-pollen palynomorphs were also tallied to identify grazing by domestic animals or wild herbivores (Baker *et al.*, 2013). The pollen record was divided into pollen zones using optimal splitting based on an information content technique as implemented in PSIMPOLL (Bennett, 2007).

The macroscopic charcoal content (160 μm) of contiguous sediment samples (1 cm^3) was analysed to document local fire history (Feurdean *et al.*, 2013a).

Analysis of plant macroremains, including charred remains, was performed on a sample volume of 10 to 30 cm^3 (measured by volumetric displacement). The plant macrofossils were sieved using a 0.2 mm mesh with no chemical treatment prior to the sieving. The macrocharcoals were selected and identified under a reflected light microscope, whereas the other plant macroremains were sorted and identified under a binocular microscope after wet sieving. The results are presented as the concentration of identifiable items in a 30 cm^3 sample volume.

Quantitative reconstruction of land cover using the REVEALS model

The pollen–vegetation relationship is not straightforward, but depends on the size and type (lake or bog) of the sedimentary basin, and differences in the pollen productivity and dispersal characteristics of taxa (Sugita, 1994, 2007; Broström *et al.*, 1998; Nielsen *et al.*, 2012). To correct for these biases, and thereby to produce a quantitative reconstruction of the vegetation cover in the region surrounding Lake Stiucii, we used the REVEALS model (Sugita, 2007). This model is designed to obtain estimates of regional vegetation, i.e. within 50–100 km (Hellman *et al.*, 2008) from pollen data from both lakes and bogs. Pollen productivity estimates (PPE) and the fall speed (FSP) for each of the 28 pollen types considered (15 woody and 13 herbaceous taxa) were obtained from the literature, including estimates from the Czech Republic (Abraham & Kozáková, 2012; Mazier *et al.*, 2012; Table 1, Appendix S2). Over time the site has undergone a change between lake and peatland (Feurdean *et al.*, 2013a). We took this into consideration when running the REVEALS model by applying the appropriate pollen dispersal and deposition models: the Prentice (1985) model for peatland period (11,450–4700 cal. yr BP), and the Sugita (1994) lake model for the open water phases (55,000–11,450 cal. yr BP and 4700–0 cal. yr BP). However, switching dispersal model does not fully account for vegetation that grows on the site itself during the peatland phase, hence we excluded Cyperaceae from the REVEALS analysis. In addition, Cyperaceae

Table 1 Pollen fall speed, relative pollen productivity estimates (PPE) and standard error estimates (SE) for 28 taxa. Data are from Mazier *et al.* (2012) except those marked with an asterisk, which are from Abraham & Kozáková (2012).

Pollen taxa	Fall speed (m s^{-1})	PPE	SE
Abies	0.120	6.88	1.44
Alnus	0.021	2.56*	0.32*
Betula	0.024	3.09	0.27
Carpinus	0.042	3.55	0.43
Corylus	0.025	1.99	0.20
Fagus	0.057	2.35	0.11
Fraxinus	0.022	1.03	0.11
Juniperus	0.016	2.07	0.04
Picea	0.056	2.62	0.12
Pinus	0.031	6.38	0.45
Salix	0.022	1.22	0.11
Tilia	0.032	1.36*	0.26*
Ulmus	0.032	1.27	0.05
Quercus	0.035	1.76*	0.20*
Sambucus	0.013*	1.30*	0.12*
Apiaceae	0.042	0.26	0.01
Artemisia	0.025	2.77*	0.39*
Asteraceae Tululiflorae	0.029	0.10	0.01
Asteraceae Liguliflorae	0.051	0.16	0.02
Cerealia	0.060	1.85	0.38
Chenopodiaceae	0.019*	4.28*	0.27*
Filipendula	0.006	2.81	0.43
Galium	0.019	2.61	0.23
Plantago lanceolata	0.029	3.7*	0.77*
Plantago major	0.024	1.27	0.18
Poaceae	0.035	1.00	0.00
Potentilla	0.018	1.19	0.13
Ranunculaceae	0.014	1.96	0.36
Rumex acetosa	0.018	2.14	0.28
Urtica	0.007*	10.52*	0.31*
Secale	0.060	3.02	0.05

may be over-represented as a result of the prevalence of wetland conditions. Over-representation of other peatland taxa, such as certain species of Poaceae, could also lead to inaccuracies in modelled forest openness (see Discussion), although the Poaceae pollen percentages are not generally higher during the peatland than lake phases. Kuneš *et al.* (2011) discuss the uncertainties associated with the REVEALS model, and conclude that it can be regarded as the best available method to estimate vegetation openness and the ratio between deciduous and conifer forest. We therefore chose to apply the REVEALS model to obtain a more realistic reflection of vegetation composition and openness than raw pollen percentages provide. A full description of the application of the REVEALS model is given in Appendix S2.

Biome reconstruction

Biomization was applied to the REVEALS output using a modified biome scheme of Prentice *et al.* (2000) developed by the EMBSeCBIO members to represent the major vegetation types in the study region. This scheme recognizes 14 biomes (Appendix S2). Affinity scores for any given pollen spectrum and biome were calculated as the sum of pollen values for the taxa that may occur in that biome. Prior to this calculation, the REVEALS estimates were square-root transformed in order to increase the signal-to-noise ratio. The minimum threshold for inclusion of a pollen type is 0.5%.

Climate simulations

To simulate the climate conditions during the last 12,000 years, we employed the NCAR CAM3.1 Global Atmospheric Model coupled to the CLM3.0 Land Surface Model and a slab-ocean model (Collins *et al.*, 2004; see details in Feurdean *et al.*, 2013a). In the present study, growing season temperature, precipitation and potential evapotranspiration values were extracted and interpolated to the site location. In the temperate zone, the temperature limit of the growing season is 5 °C, which coincides with the April–October period in most simulations. Monthly mean potential evapotranspiration was calculated according to Hargreaves *et al.* (1985), which requires top-of-the-atmosphere incoming solar radiation, monthly mean temperature and daily temperature range as input variables.

Archaeological literature survey

From the archaeological literature (Crişan *et al.*, 1992; Boroffka, 1994) and online databases (e.g. the Archaeological Repertorium of Romania, http://ran.cimec.ro/), we determined the number of archaeological sites (settlements and cemeteries) within a 10 km radius of Lake Stiucii.

RESULTS

Land-cover and biome reconstruction

Six major periods of change in land cover were detected over a 55,000 year period, as follows.

c. 55,000–35,000 cal. yr BP: evergreen needleleaf forest

The REVEALS estimate of tree cover varied between 50% and 60% and was dominated by *Pinus* pollen with small proportions of *Betula, Alnus, Picea abies, Salix* and *Juniperus*, and isolated finds of *Tilia* and *Ulmus* pollen (LS-10, Fig. 2). Poaceae (maximum 50% in the REVEALS model and 15% as a raw pollen percentage), Chenopodiaceae and *Artemisia* were the main components of the herbaceous cover and these were associated with high macrocharcoal concentrations (Fig. 2). Biome reconstruction indicates the predominance of evergreen needleleaf woodland or forest.

c. 35,000 cal. yr BP hiatus)–13,000 cal. yr BP: grasslands

The REVEALS estimate of tree cover declined around 650 cm to an average of 35% (LS-9a, Fig. 2). High proportions of Poaceae (*c.* 60% REVEALS model and *c.* 25% raw pollen percentages), Chenopodiaceae and *Artemisia* led to a

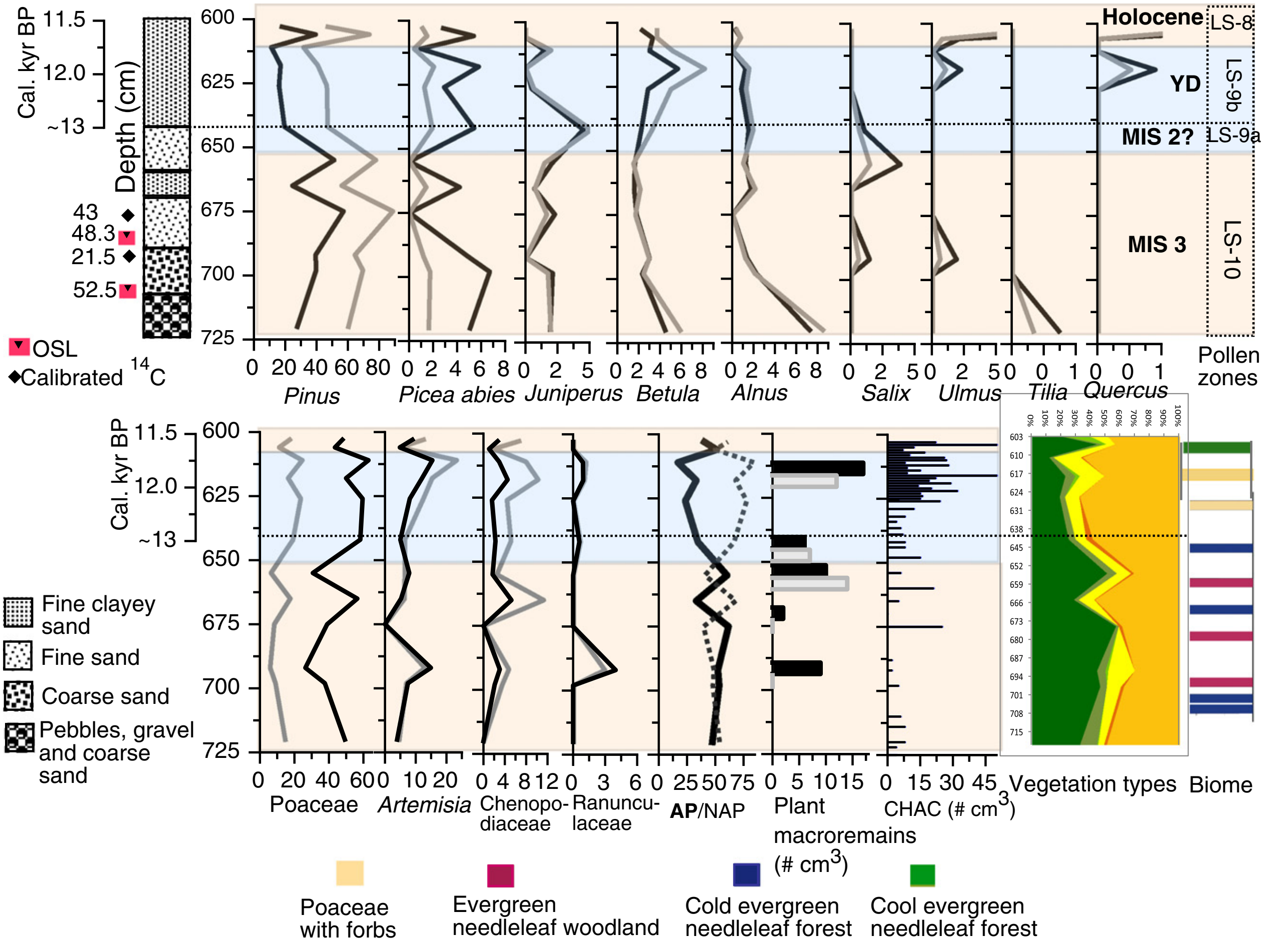

Figure 2 Estimated regional vegetation cover based on the REVEALS model (black lines) and pollen percentages (grey lines); tree (arboreal pollen, AP) versus herbaceous cover (non-arboreal pollen, NAP) at Lake Stiucii, north-western Romania (LS denotes local pollen assemblage zones at this site); total macroremains of herbaceous plants (black) and Poaceae (grey); macrocharcoal concentration (CHAC); main vegetation types (see Fig. 4 for colour coding), and biome reconstruction. Lithostratigraphy, calibrated radiocarbon accelerator mass spectrometry (AMS) ^{14}C and optically stimulated luminescence (OSL) ages are also given. The orange rectangle highlights warmer periods such as the early Marine Isotope Stage 3 (MIS 3) and the early Holocene, whereas the blue rectangle highlights cold periods possibly the end of MIS 3/beginning of MIS 2 and the Younger Dryas (YD). The dashed horizontal line shows the likely occurrence of a hiatus.

biome reconstruction dominated by grassland (Fig. 2). However, most of this interval is likely to be a hiatus.

c. 13,000–11,700 cal. yr BP*: grasslands*

The proportion and composition of the vegetation assemblages (LS-9b), as well as of biome reconstruction (grasslands), remained largely similar to the zone above. However, compared to the previous zone, there is an increased proportion of temperate trees (*Ulmus* and *Quercus*) and macrocharcoal concentrations (Fig. 2).

11,700–8600 cal. yr BP*: mixed evergreen needleleaf and deciduous broadleaf forest*

The REVEALS estimate of tree cover increased to an average *c.* 57% after 11,700 cal. yr BP (LS-8; Fig. 3a). Significant changes were the decline of *Betula* and *Alnus* and an increase in *Picea abies*, which showed a pronounced peak between 11,350 and 10,350 cal. yr BP. *Ulmus, Quercus* and *Fraxinus* also increased from 11,300 cal. yr BP (Fig. 3a). The relative abundance of all forbs, Asteraceae Liguliflorae, Chenopodiaceae, *Artemisia, Plantago major*, *Thalictrum,* Brassicaceae, Caryophilaceae and *Filipendula* diminished, whereas Poaceae remained dominant (Fig. 3b). *Pinus* levels dropped markedly from 10,500 cal. yr BP (LS-7), whereas *Corylus avellana* abundance increased at the expense of *Ulmus* from 9500 cal. yr BP (LS-6). Biome reconstruction indicates the occurrence of cool mixed evergreen needleleaf and deciduous broadleaf forest (Fig. 4). The arboreal pollen percentage was *c.* 10% higher than in the REVEALS model (Fig. 4). Dominant taxa in the plant macroremains record were Poaceae undiff. and *Phragmites* (Fig. 5). Macrocharcoal accumulation rates were the highest in the record during this period (Fig. 6).

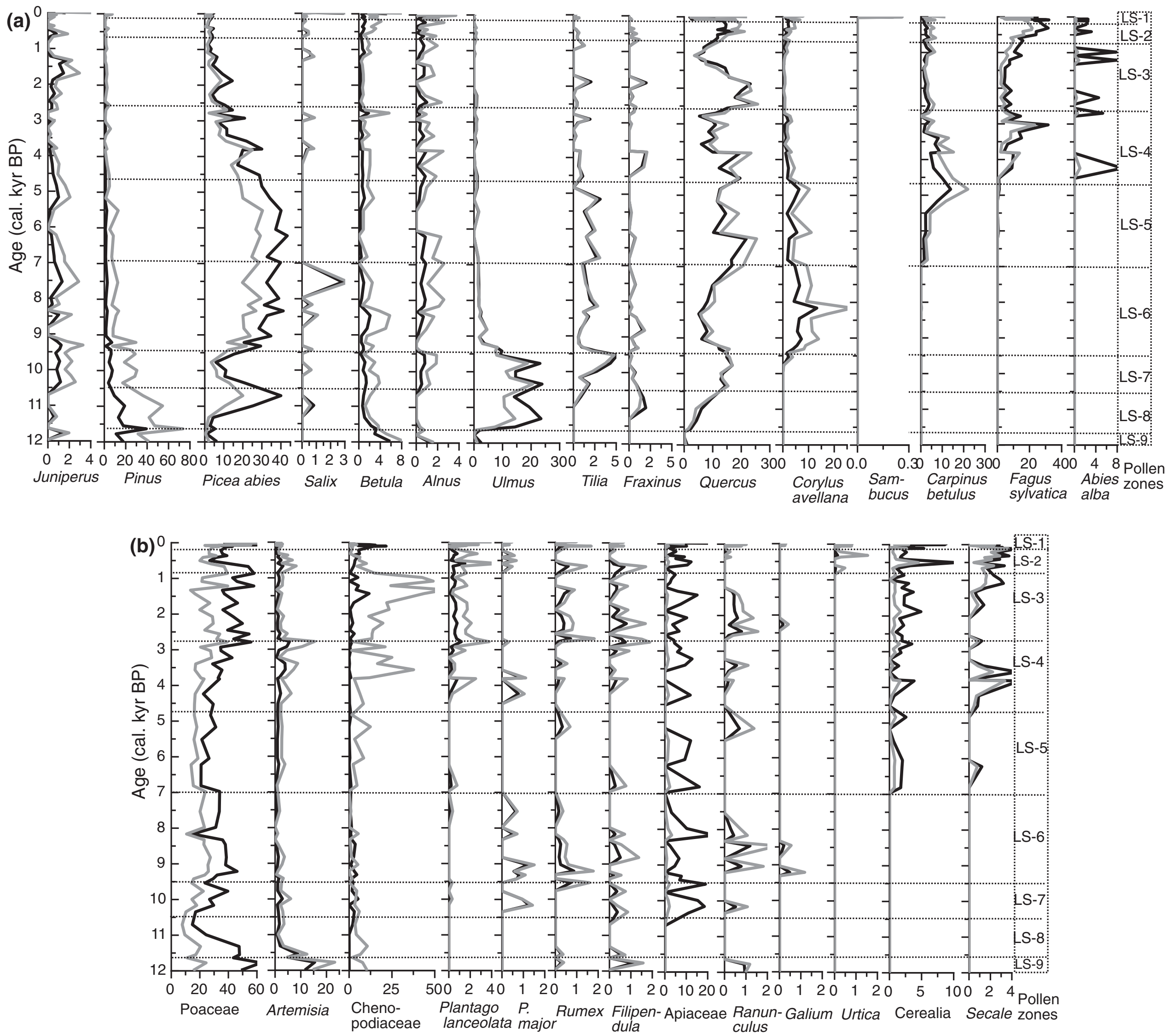

Figure 3 Estimated regional vegetation cover based on the REVEALS model (black lines) and pollen percentages (grey lines) for 28 taxa over the last 12,000 cal. yr BP at Lake Stiucii, north-western Romania: (a) trees and shrubs, and (b) herbaceous taxa.

8600–3700 cal. yr BP: temperate deciduous broadleaf forest

In the REVEALS reconstruction, the relative abundances of tree taxa rose gradually to about 60–70%, mainly represented by *Picea abies, Quercus, Corylus avellana, Carpinus betulus* (LS-5) and *Fagus sylvatica* (LS-4). Percentages of Poaceae and forbs pollen types declined (Figs 3b & 4). The main differences between REVEALS and raw pollen percentage estimates were that REVEALS predicted a greater cover of Poaceae and *Picea*, and slightly lower cover values for most other tree species and for Chenopodiaceae than found in the raw data. Biome reconstruction indicates the prevalence of temperate deciduous broadleaf forest until 7000 cal. yr BP and warm-temperate deciduous malacophyll broadleaf forest between 7000 and 3700 cal. yr BP (Fig. 4). Dicotyledonous herbs, *Phragmites* and Poaceae undiff. were the main elements in the macrofossil assemblages (Fig. 5). Macrocharcoal accumulation rates in this period were the lowest in the profile (Fig. 6).

3700–0 cal. yr BP: declining forest cover

Tree cover declined slightly from 4800 cal. yr BP, but a rapid reduction in the relative abundance of tree pollen taxa occurred after 3700 cal. yr BP (Figs 3a & 4). Intervals of tree cover increase (up to 55–60%) between 700 and 200 cal. yr BP (LS-2) and during the last 20 years (LS-1) are indicative of temperate and warm-temperate deciduous malacophyll broadleaf forest, whereas periods of decrease (on average 30%) from 2700 cal. yr BP (LS-3) and between 1700 and 700 cal. yr BP, and AD 1700 and 1850, are indicative of a biome dominated by grassland (Figs 3a,b & 4). Pollen abundances and the diversity of all herbaceous communities as well for cultivated plants also rose (Fig. 3b). Increased abundance of herbaceous plants is

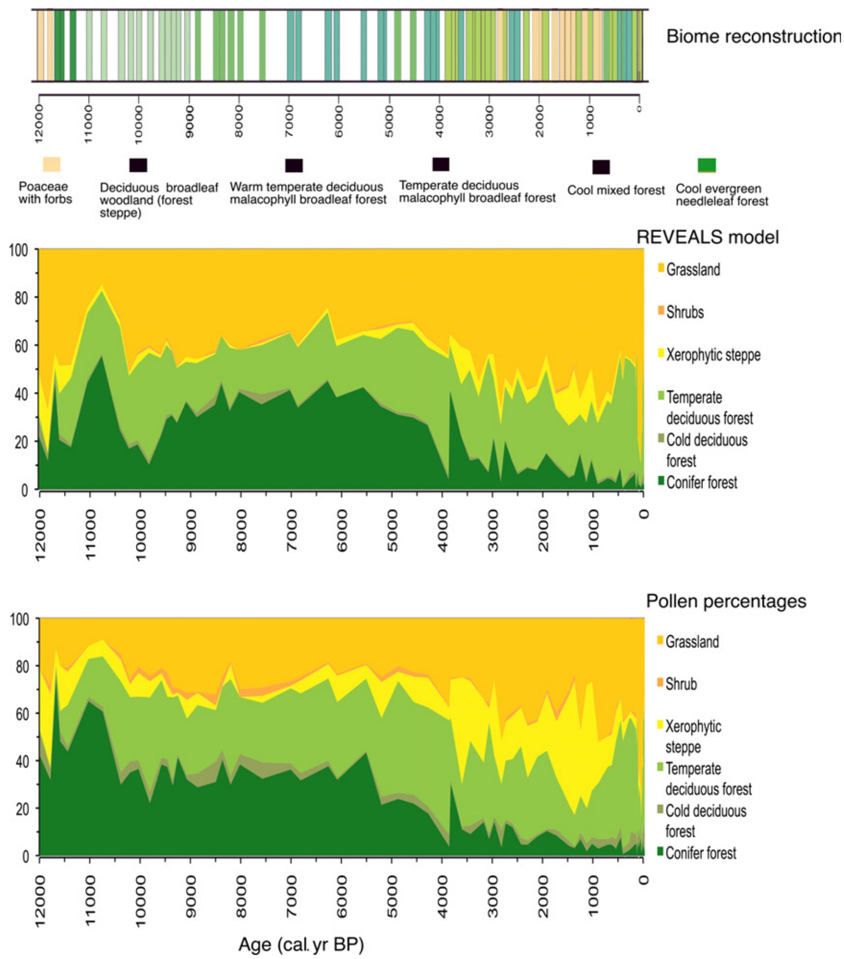

Figure 4 Summary of the vegetation type estimates based on the REVEALS model (percentages) and raw pollen percentages, as well as biome reconstruction at Lake Stiucii, north-western Romania.

also visible in the macrofossil assemblages (Fig. 5). Macro-charcoal accumulation rates increased between 3300 and 700 cal. yr BP to decline again over the last 700 years (Fig. 6).

Climate simulations

Between 11,500 and 8300 cal. yr BP, simulations of atmospheric climate conditions showed warm and dry growing season conditions (i.e. higher temperature and evapotranspiration and lower precipitation than today), followed by a gradual transition to cooler and wetter growing season conditions between 8300 cal. yr BP and the present (Fig. 6).

DISCUSSION

Full glacial and late glacial land-cover changes (55,000–35,000 cal. yr BP; 13,000–11,700 cal. yr BP)

The age–depth model indicates that the bottom part of the Lake Stiucii sequence registers a glacial environmental history from at least 55,000 cal. yr BP and is thus one of the few regional palaeoecological records reaching so deep into the last glacial cycle. REVEALS-based vegetation estimates that correct for the pollen productivity and transport differences of each taxon indicate a landscape with a tree cover of 20–60% (up to 80% in the uncorrected pollen percentages) that included *Pinus* (dominant), *Betula*, *Alnus*, *Picea abies*, *Juniperus*, Salix, *Ulmus* and *Tilia* from *c.* 55,000 to *c.* 35,000 cal. yr BP (Fig. 2). Biome reconstruction suggests the prevalence of cold evergreen needleleaf forest or woodland (similar to a forest steppe biome) during this interval. Chronologically, this interval could be a reflection of the warm and moist conditions of the early Marine Isotope Stage (MIS) 3 interstadial (Fletcher *et al.*, 2010; Panagiotopoulos *et al.*, 2013) that provided sufficient moisture for tree growth and local burning. Following this period of a more forested landscape, xerothermic herbs and grasses expanded to become the dominant biome from 650 cm in the core and this coincides with a slight decline in fire activity (Fig. 2). This biome is indicative of dry and cold growing season conditions that could represent the end of MIS 3 and the onset of cold MIS 2 (*c.* 29,000 cal. yr BP), that limited tree growth, biomass accumulation and fire activity. However, without a better-constrained chronology it is difficult to confidently ascribe any precise age to these sediments.

It has been debated whether tree pollen percentages from last glacial sequences in central-eastern Europe are indicative of gallery forest along river valleys or reflect more extensive open woodlands within the landscape (Willis & van Andel, 2004). As our reconstructed tree cover is corrected for pollen

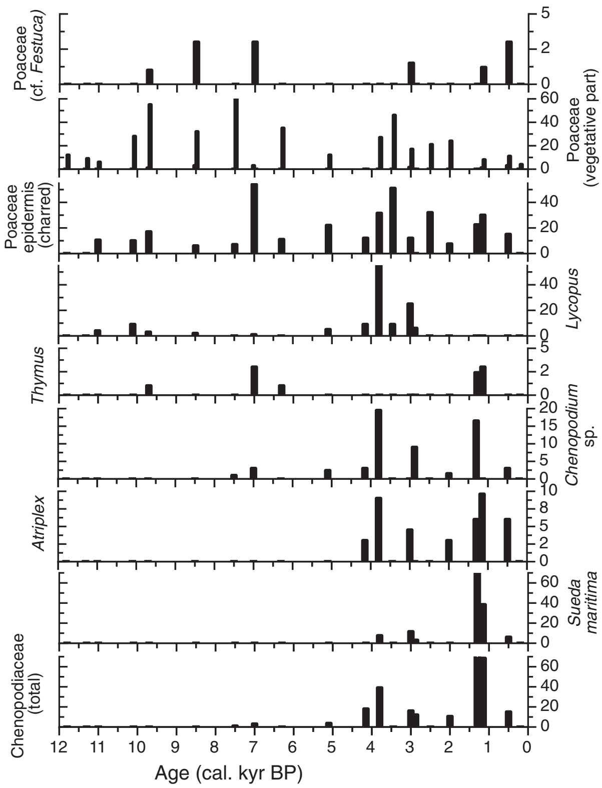

Figure 5 Selected plant macrofossil remains (concentrations of items in 30 cm^3 sample volume) indicative of open ground and saline meadows at Lake Stiucii, north-western Romania.

productivity and transport, the results are in favour of the view that although trees may have been more abundant along the river valley (in which Lake Stucii lies and which also accounts for the sandy nature of the sediment at this depth), widespread needleleaf woodlands prevailed on the surrounding landscape, at least during more favourable periods of the last glacial such as MIS 3. However, our REVEALS-based tree cover reconstruction is about 20% lower than that represented by pollen percentages and highlights that the proportion of the trees (mainly *Pinus*) during this glacial is overestimated using pollen percentages. Although fragmentary, other fossil records from central-eastern Europe sustain the idea that woodlands, composed primarily of needleleaf and cold deciduous trees, with a small population of temperate deciduous trees, persisted during MIS 3-2 (Willis & van Andel, 2004; Kuneš *et al.*, 2008; Magyari *et al.*, 2014). Our results also give support to model-based estimates of vegetation in MIS 3, which suggests that climate condition supported regional taiga forest in central-eastern Europe, results previously deemed unreliable because of their mismatch with a single palaeosequence from this region (Alfano *et al.*, 2003). However, recent vegetation simulations, including cold spells linked to Heinrich events, indicated treeless conditions during cold stadials and more forested conditions during interstadials (Huntley *et al.*, 2013).

The period *c.* 13,000–11,700 cal. yr BP was marked by the maximum extension of a grassland biome (grasses and xerothermic herbs), while the tree cover was dominated by *Pinus* (25–35%), with a small proportion of *Alnus, Betula, Fraxinus, Quercus* and *Ulmus* (Fig. 2). Local biomass appeared sufficient to sustain fire during the Younger Dryas (YD; Fig. 2). The vegetation composition during this time was a response to cold and dry GS-1 stadial conditions (YD), when a broad-scale drop in precipitation and winter temperatures led to a marked contraction in the forest cover in the lowlands of CE Europe (Willis *et al.*, 1997; Tantau *et al.*, 2006; Feurdean *et al.*, 2007; Connor *et al.*, 2013).

Holocene cover changes

Mixed needleleaf and deciduous broadleaf forest between 11,700 and 8600 cal. yr BP: warm and dry conditions

The land-cover reconstruction shows a *c.* 20% increase in tree cover around 11,700 cal. yr BP from an average of *c.* 33% to *c.* 57%, along with a decline in grasses and steppe communities. The reconstructed biome is a cool mixed evergreen needleleaf and deciduous broadleaf forest (Fig. 4). The *Picea abies* peak between 11,350 and 10,350 cal. yr BP probably represents local variability or possibly poor pollen preservation favouring more resistant pollen types, an interpretation supported by the absence of this feature in all low elevations pollen records in this region (Willis *et al.*, 1998; Feurdean *et al.*, 2007; Tantau *et al.*, 2006; Magyari *et al.*, 2010). Warm and dry site conditions in the early Holocene are suggested by the drying up of the lake and the onset of peat formation in the basin (Feurdean *et al.*, 2013a). Simulations of atmospheric conditions show an average growing season temperature (*c.* 14.5 °C) and evapotranspiration, which were regionally higher than today, and a lower growing season precipitation between 11,600 and 8500 cal. yr BP (Fig. 6). Fires were frequent in the early Holocene (Fig. 6). We suggest that the prevalence of warm and dry growing season conditions with prolonged summer droughts and frequent fire, prevented full forest extension and created conditions favourable for the persistence of grasses and forbs. These were probably not restricted to edaphically favourable locations and a considerable herbaceous cover developed outside forest patches and/or under an open forest canopy. This inference is based on the high proportion of pollen and macrofossils of grasses and open habitat forbs including steppic indicators (Figs 3–5). The occurrence of *Phragmites* on the site itself, which was a peatland during this period, may indicate that the REVEALS-reconstructed cover for Poaceae somewhat overestimates the regional abundance of grasses. However, our interpretation is further supported by a pedological study, which indicated the formation of darker soil (Phaeozems and Chernozems) associated with the extension of the forests and steppic grasslands and drier climate during the early Holocene in the Transylvanian Plain (Timar Gabor *et al.*, 2010). Pollen-based landscape openness has been documented to be greater in the early Holocene (11,700–9000 cal. yr BP) than in the mid-Holocene (9000–3000 cal.

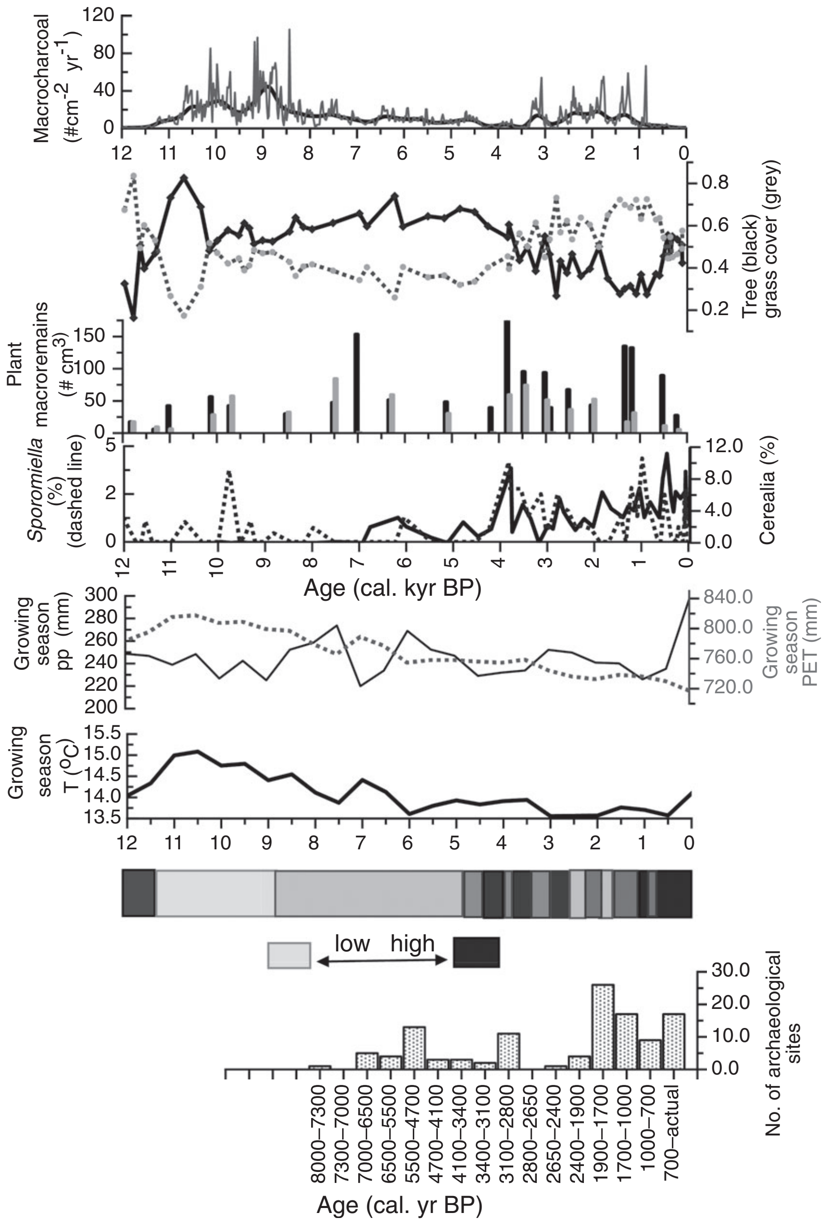

Figure 6 Synthesis figure including macrocharcoal accumulation rate; tree versus grass cover (REVEALS); Cerealia (% and REVEALS) and *Sporomiella* (%); total macroremains of herbaceous plants (black), total macroremains of vegetative parts of herbaceous plants (grey) at Lake Stiucii, north-western Romania; simulated growing season conditions (T = temperature, pp = precipitation; PET = potential evapotranspiration); archaeological finds (settlements and cemeteries within a 10-km radius); and lake level reconstruction (Feurdean *et al.*, 2013a).

yr BP), and in lowlands than at mid- to higher elevations in Romania (Tantau *et al.*, 2006; Feurdean *et al.*, 2013b). Grazing by wild herbivores may have additionally contributed to the maintenance of landscape openness (Vera, 2000). However, we have evidence for a moderate occurrence of coprophilous spores (*Sporomiellla*) between 11,700 and 9500 cal. yr BP (Fig. 6).

In Hungary, pollen-based reconstructions of landscape openness during the early Holocene varied between 25 and 60% (a temperate deciduous wooded steppe or temperate deciduous forest biome) (Willis *et al.*, 1997; Magyari *et al.*, 2010), whereas in the lowlands of Czech Republic (Moravia) and Slovakia it was *c.* 25% (Pokorný, 2011; Hájková *et al.*, 2013). There was also an increase in fire activity at most of these sites. These features also hold true for south-eastern Europe, including southern Romania (Tomescu, 2000; pollen) and eastern Bulgaria (Connor *et al.*, 2013; pollen and charcoal). Overall, these results suggest the prevalence of more open forests and extensive natural grasslands in the lowlands of central-eastern Europe during the early Holocene as a combined effect of enhanced dryness and fire activity.

Increased temperate deciduous broadleaf forest cover between 8600 and 4700 cal. yr BP: wetter and cooler conditions

Tree cover steadily increased from 8600 cal. yr BP to the highest levels in the record between 7000 and 4700 cal. yr BP. This paralleled a decline in herbaceous plants, notably of steppe and open habitat forbs (Figs 3–5). Biome reconstruction suggests the predominance of a temperate deciduous broadleaf forest (*Corylus, Quercus*) until 7000 cal. yr BP and of warm-temperate deciduous malacophyll broadleaf forest between 7000 and 4700 cal. yr BP (Fig. 4). This forest cover maximum coincides with low fire activity, a modest rise in the water table of the wetland and the reduction in simulated growing season temperature and a precipitation increase (Fig. 6). Grasses are known to be weak competitors against trees under sufficiently moist conditions (Hoffmann *et al.*, 2012; Hejcman *et al.*, 2013). Tropical and North American temperate grasslands depend on fire to persist (Hoffmann *et al.*, 2012), but temperate grassland–fire interactions have been less well explored in Europe. Our results suggest that the progressive increase in effective moisture and a climate-mediated decline in fire activity appear to have ensured a competitive advantage of trees over herbs. Based on the decline in the proportion of herbs, it is likely that a substantial proportion of the herbaceous layer under the forest canopy was also eliminated, while many of the steppe and forbs communities became constrained to areas edaphically unfavourable for forest growth.

There is evidence of Early Neolithic pastoral activity (8000 cal. yr BP) in the Lake Stiucii pollen and coprophilous records (Fig. 3a,b, Appendix S3). Signs of arable agriculture (Cerealia and *Secale*) are evident from 7000 cal. yr BP (Fig. 3b). On a regional scale, however, numerous archaeological sites of mid- to late Neolithic origin (7500–6000 cal. yr BP) are reported (Crişan *et al.*, 1992; Repertoriul Arheologic National, http://ran.cimec.ro/, accessed 2013). A wider expansion of the forest cover, sometime between 9000 and 3000 cal. yr BP, has been noted in the lowlands of central (Willis *et al.*, 1997; Magyari *et al.*, 2010; Nielsen *et al.*, 2012; Hájková *et al.*, 2013), eastern (Kremenetski, 1995) and southern Europe (Tonkov *et al.*, 2014). This regionally consistent pattern of vegetation change suggests that a wider scale increase in moisture availability dictated mid-Holocene afforestation across lower elevation areas in Europe.

Deforestation and transition to wooded steppe over the last 4700 cal. yr BP

The tree cover declined from *c.* 65% at 4700 cal. yr BP to *c.* 50% at 3700 cal. yr BP, while grasses, xerothermic and halophilous forbs and anthropogenic indicators expanded (Figs 3–5). Biome reconstruction suggests the persistence of warm-temperate deciduous broadleaf forest until 3700 cal. yr BP (*Fagus sylvatica* dominant) and a switch to deciduous broadleaved woodland (forest steppe; *Quercus* dominant) at 3700 cal. yr BP (Middle Bronze Age). Conversely, grasslands predominated between 2000 and 800 cal. yr BP (Dacian and Roman periods until the early Medieval Period), 200 and 100 cal. yr BP (Austro Hungarian Empire) and during the socialist period (1950–1989).

The lithology-based lake level reconstruction from Lake Stiucii shows a pronounced moist phase between 4700 and 3700 cal. yr BP and low fire activity (Fig. 6). There is also an increase in *F. sylvatica* at this time that paralleled a decline in *Picea abies, Corylus avellana* and *Carpinus betulus* (Fig. 3a). *Fagus sylvatica* requires moist summers and is a fire-sensitive taxon (Peterken & Mountford, 1996). This shift in the forest composition towards more mesic tree species is consistent with the hypothesis of enhanced moisture availability and diminished fire activity in the region. A climatic transition to wetter conditions in the study area is also indicated by a shift in soil properties from dark soil types towards Luvisols *c.* 4900–4000 years ago (Timar Gabor *et al.*, 2010) and an intensification of fluvial activity in several rivers in Romania (Persoiu, 2010). Our results therefore suggest that the onset of the opening of the forests at 4700 cal. yr BP resulted from the influence of something other than a climatically dry phase. Instead, a close association between the decline in forest cover and the corresponding increase in grasslands, enriched slightly by anthropogenic indicators, implies that humans were responsible for the initiation of the vegetation change after 4700 cal. yr BP (Figs 3 & 5, Appendix S3). Increased human impact in the study area is supported by a relatively high number of local archaeological sites of Late Copper Age (Cotofeni culture 5500-4500 cal. yr BP; Fig. 6). Subsequently, the timing of the biome shift from forest to forest steppe around 3700 cal. yr BP overlaps with a climatically dry phase, as suggested by the lithostratigraphically inferred lake level fall (Fig. 6). There is also a clear rise in anthropogenic indicators and coprophilous fungi. Therefore, the synergic effects of climate and human activities in opening the landscape at this time are apparent. The number of archaeological sites during this phase of marked deforestation (Middle Bronze Age) was low and they were represented mainly by the Wietenberg culture. However, this culture is characterized by short-lived settlements (Boroffka, 2013), which may explain the apparent mismatch between the level of anthropogenic disturbance and the evidence of human occupation (Fig. 5). Local biomass burning increased significantly between 3300 and 700 cal. yr BP concurrent with the development of a grassland biome, indicating the active role of natural and human-induced fires in this vegetation shift and grassy biome persistence. The extension of meadows after 2600 cal. yr BP (Iron Age) may also be a reflection of the technological improvements in agriculture brought about by the introduction of iron scythes in harvesting the grasslands (Hejcman *et al.*, 2013). The high proportion of saline species of Chenopodiaceae between 1800 and 1000 cal. yr BP indicate that herbaceous flora included saline floodplain meadows (Fig. 3b).

Our findings of a marked, anthropogenically induced ecosystem transformation in the lowlands of Transylvania from about 3700 cal. yr BP contrast with the situation for the mountainous areas of Eastern Europe, which retained most of their forests until 1000 years ago (Kaplan *et al.*, 2011; Feurdean *et al.*, 2013b). The timing of the initiation of landscape opening at the study site, however, resembles more that of other lowland areas in CE Europe such as Hungary, but is earlier than in Moravia and Slovakia (Willis *et al.*, 1997; Magyari *et al.*, 2010; Hájková *et al.*, 2011, 2013). A marked expansion of xerophitic steppe during the last 3000 cal. yr BP was noted in eastern (Kremenetski, 1995) and southern Europe (Tonkov *et al.*, 2014). This regional opening of the landscape appeared much earlier than the deforestation of this region indicated by ALCC models, i.e. from *c.* AD 1000 by the HYDE and after AD 1400 by the KK10 models (Kaplan *et al.*, 2011). Comparison between a pollen-based reconstruction and an ALCC modelled forest cover highlights that the relationship between population density and land-use productivity is dynamic and that simulations at a European scale sometimes appear unable to accurately capture regional details. This may reflect natural variations in environmental factors and shifting social, economic and cultural boundaries.

CONCLUSIONS

The pollen-based vegetation modelling applied here provides the first long-term quantitative reconstruction of vegetation cover changes from this part of Europe. Results from the REVEALS model suggest that landscape openness was *c.* 20% (*c.* 10–15%) greater during the glacial period (Holocene) than the estimates by the raw pollen data. Generally, REVEALS predicted a greater cover of Poaceae and *Picea*, and lower values for *Pinus*, *Artemisia* and Chenopodiaceae than the raw pollen data.

Open cool evergreen needleleaf forest occurred in the region during the last glacial (55,000 cal. yr BP; MIS 3), but became reduced thereafter probably marking the transition to the colder MIS 2. A forest coverage of *c.* 55% (early Holocene) and 65% (mid-Holocene) prevailed through the Holocene, but Bronze Age humans extensively cleared forests after 3700 cal. yr BP. This confirms our second hypothesis that the landscapes of Transylvanian Plain were more forested in the past, although there appears to have been a sufficient degree of landscape openness to sustain the hypothesized antiquity of grasslands. The assumption of a more recent ecosystem transformation is also challenged as we show that human activities have led to profound ecological impacts for almost four millennia.

Grasses, as well as steppe and xerothermic forbs, were most extensive during the glacial period, the Younger Dryas, the early Holocene (11,700–8600 cal. yr BP) and late Holocene (3700–0 cal. yr BP), reflecting a combination of dry growing conditions, intense fires, and human impact (from Bronze Age). Saline meadows and semi-natural grasslands were also part of the late Holocene grassy biome. Conversely, the xerothermic and steppe forbs became most reduced during the moister and less fire active period of the mid-Holocene. Our results demonstrate the long-term persistence of extensive natural and semi-natural grasslands in this region, thus giving support to the hypothesis that their exceptional diversity in CE Europe could be the result of their ancient nature and continuity in the landscape.

ACKNOWLEDGEMENTS

Financial support was received from the German Research Foundation (FE-1096/2-1) and 'LOEWE-Landesoffensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz'. We thank Carmen Bădăluţă, Viorica Nagavciuc and Diana Iegar for constructing Fig. 1. We also thank the two anonymous referees and the editors (Jack Williams, Robert Whittaker and Nicholas Gotelli) for constructive suggestions on earlier versions of the manuscript.

REFERENCES

Abraham, V. & Kozáková, R. (2012) Relative pollen productivity estimates in the modern agricultural landscape of Central Bohemia (Czech Republic). *Review of Palaeobotany and Palynology*, **179**, 1–12.

Alfano, M.J., Barron, E.J., Pollard, D., Huntley, B. & Allen, J.R.M. (2003) Comparison of climate model results with European vegetation and permafrost during Oxygen Isotope Stage 3. *Quaternary Research*, **59**, 97–107.

Badarau, A. (2005) *Transformation of the landscapes within the Transylvanian Plain (Romania) with special focus upon the biogeographical aspects*. PhD Thesis, Babes-Bolyai University, Cluj Napoca.

Baker, A.G., Bhagwat, S.A. & Willis, K.J. (2013) Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quaternary Science Reviews*, **62**, 21–31.

Bennett, K.D. (2007) *Psimpoll and pscomb programs for plotting and analysis*. Available at: http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html.

Bennett, K.D. & Willis, K.J. (2001) Pollen. *Tracking environmental change using lake sediments* (ed. by J.S. Smol, H.J.B. Birks and W.M. Last), pp. 5–32. Kluwer Academic Publishers, Dordrecht.

Bohn, U., Neuhäusle, R., Gollub, G., Hettwer, C., Neuhäuslová, Z., Raus, T., Schlüter, H. & Weber, H. (2003) *Map of the natural vegetation of Europe*. Explanatory text with CD-ROM. German Federal Agency for Nature Conservation, Bonn.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–37.

Boroffka, N. (1994) *Die Wietenberg-Kultur. Ein Beitrag zur Erforschung der Bronzezeit in Südosteuropa*. Universitätsforschungen zur prähistorischen Archäologie, Band 19. Bonn: Habelt.

Boroffka, N. (2013) Romania, Moldova, and Bulgaria. *The Oxford Handbook of the European Bronze Age* (ed. by H. Fokkens and A. Harding), pp. 877–897. Oxford University Press, Oxford.

Borza, Al. (1936) *Câmpia Ardealului. Studiu geobotanic*. Biblioteca Ateneului Român, No. 4, Bucuresti.

Broström, A., Gaillard, M.J., Ihse, M. & Odgaard, B. (1998) Pollen landscape relationship in modern analogues of ancient cultural landscapes in southern Sweden – a first step towards quantification of vegetation openness in the past. *Vegetation History and Archaeobotany*, **7**, 189–201.

Collins, W.D., Rasch, P.J., Boville, B.A., Hack, J.J., McCaa, J.R., Williamson, D.L., Kiehl, J.T. & Brieglebet, B. (2004)

Description of the NCAR Community Atmosphere Model (CAM 3.0). NCAR Technical Note NCAR/TN-464.STR. National Centre for Atmospheric Recourses, Boulder, CO.

Connor, S.E., Ross, S.A., Sobotkova, A., Herries, A.I.R., Mooney, S.D., Longford, C. & Iliev, I. (2013) Environmental conditions in the SE Balkans since the Last Glacial Maximum and their influence on the spread of agriculture into Europe. *Quaternary Science Reviews*, **68**, 200–215.

Crişan, I.H., Bărbulescu, M., Chirilă, E., Vasiliev, V. & Winkler, I. (1992) *Repertoriul arheologic al judetului Cluj Bibliotheca Musei Napocensis V*. Muzeul de Istorie al Transilvaniei, Cluj-Napoca.

Dengler, J., Becker, T., Ruprecht, E., Szabó, A., Becker, U., Beldean, M., Bita-Nicolae, C., Dolnik, C., Goia, I., Peyrat, J., Sutcliffe, L.M.E., Turtureanu, P.D. & Uğurlu, E. (2012) *Festuco-Brometea* communities of the Transylvanian Plateau (Romania) – a preliminary overview on syntaxonomy, ecology, and biodiversity. *Tuexenia*, **32**, 319–359.

Ellenberg, H. & Leuschner, C. (2010) *Vegetation Mitteleuropas mit den Alpen*. Eugen Ulmer KG, Stuttgart.

Feurdean, A., Mosbrugger, V., Onac, B., Polyak, V. & Veres, D. (2007) Younger Dryas to mid-Holocene environmental history of the lowlands of NW Transylvania, Romania. *Quaternary Research*, **68**, 364–378.

Feurdean, A., Liakka, J., Vanniere, B., Marinova, E., Hutchinson, S.M., Mossbruger, V. & Hickler, T. (2013a) Holocene fire regime drivers in the lowlands of Transylvania (Central-Eastern Europe): a data-model approach. *Quaternary Science Reviews*, **81**, 48–61.

Feurdean, A., Parr, C., Tanţău, I., Fărcaş, S., Marinova, E. & Persoiu, I. (2013b) Biodiversity variability across elevations in the Carpathians: parallel change with landscape openness and land use. *The Holocene*, **23**, 869–881.

Fletcher, W.J., Sánchez Goñi, M.F., Allen, J.R.M., Cheddadi, R., Coumbourieu-Nebout, N., Huntley, B., Lawson, I.T., Londeix, L., Magri, D., Margari, V., Müller, U.C., Naughton, F., Novenko, E., Roucoux, K.H. & Tzedakis, P.C. (2010) Millennial-scale variability during the last glacial in vegetation records from Europe. *Quaternary Science Reviews*, **29**, 2839–2864.

Frenzel, B. (1968) *Grundzuge der pleistozanen Vegetationgeschichte Nord-Eurasiens*. F. Steiner, Wiesbaden.

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

Hájková, P., Jamrichová, E., Horsák, M. & Hájek, M. (2013) Holocene history of a *Cladium mariscus*-dominated calcareous fen in Slovakia: vegetation stability and landscape development. *Preslia*, **85**, 289–315.

Hargreaves, G., Hargreaves, G. & Riley, J. (1985) Irrigation water requirements for Senegal River Basin. *Journal of Irrigation Drainage Engineering*, **111**, 265–275.

Hejcman, M., Hejcmanová, P., Pavlů, V. & Beneš, J. (2013) Origin and history of grasslands in Central Europe – a review. *Grass and Forage Science*, **68**, 345–363.

Hellman, S., Gaillard, M.J., Broström, A. & Sugita, S. (2008) The REVEALS model, a new tool to estimate past regional plant abundance from pollen data in large lakes: validation in southern Sweden. *Journal of Quaternary Science*, **23**, 21–42.

Hoffmann, W.A., Geiger, E.L., Gotsch, S., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M. & Franco, A.C. (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters*, **15**, 759–768.

Huntley, B., Allen, J.R.M., Collingham, Y.C., Hickler, T., Lister, A.M., Singarayer, J., Stuart, A.J., Sykes, M.T. & Valdes, P.J. (2013) Millennial climatic fluctuations are key to the structure of last glacial ecosystems. *PLoS ONE*, **8**, e61963.

IUSS Working Group WRB (2007) *World reference base for soil resources 2006, first update 2007*. World Soil Resources Reports No. 103. FAO, Rome.

Kaplan, J.O., Krumhardt, K.M., Ellis, E.C., Ruddiman, W.F., Lemmen, C. & Goldewijk, K.K. (2011) Holocene carbon emissions as a result of anthropogenic land cover change. *The Holocene*, **21**, 775–791.

Kerner, A.J. (1863) *Das Pflanzenleben der Donauländer*. Wagner, Innsbruck.

Kremenetski, C.V. (1995) Holocene vegetation and climate history of southwestern Ukraine. *Review of Palaeobotany and Palynology*, **85**, 289–301.

Kun, A., Ruprecht, E. & Szabo, A. (2004) Az Erdélyi-medence bioklimatológiai jellemzése [The bioclimatological characteristics of the Transylvanian Basin (Romania)]. *Muzeum Füzetek*, **13**, 63–81 (in Hungarian, with English abstract).

Kuneš, P., Pelánková, B., Chytrý, M., Jankovská, V., Pokorný, P. & Petr, L. (2008) Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia. *Journal of Biogeography*, **35**, 2223–2236.

Kuneš, P., Odgaard, B.V. & Gaillard, M.J. (2011) Soil phosphorous as a control of productivity and openness in temperate interglacial forest ecosystems. *Journal of Biogeography*, **38**, 2150–2164.

Magyari, E.K., Chapman, J.C., Passmore, D.G., Allen, J.R.M., Huntley, J.P. & Huntley, B. (2010) Holocene persistence of wooded steppe on the Great Hungarian Plain. *Journal of Biogeography*, **37**, 915–935.

Magyari, E.K., Kuneš, P., Jakab, G., Sümegi, P., Pelánková, B., Schäbitz, F., Braun, M. & Chytrý, M. (2014) Late Pleniglacial vegetation in eastern-central Europe: are there modern analogues in Siberia? *Quaternary Science Reviews*, **95**, 60–79.

Mazier, F., Gaillard, M.J., Kuneš, P., Sugita, S., Trondman, A.K. & Broström, A. (2012) Testing the effect of site selection and parameter setting on REVEALS-model estimates of plant abundance using the Czech Quaternary Palynological Database. *Review of Palaeobotany and Palynology*, **187**, 38–49.

Nielsen, A.B., Giesecke, T., Theuerkauf, M., Feeser, I., Behre, K.E., Beug, H.J., Chen, S., Christiansen, J., Dörfler, W., Endtmann, E., Jahns, S., de Klerk, P., Kühl, N., Latałowa, M., Odgaard, B.V., Rasmussen, P., Stockholm, J.R., Voigt, R., Wiethold, J. & Wolters, S. (2012) Quantitative reconstructions of changes in regional openness in north-central Europe reveal new insights into old questions. *Quaternary Science Reviews*, **47**, 131–149.

Panagiotopoulos, K., Böhm, A., Schäbitz, F. & Wagner, B. (2013) Climate variability since MIS 5 in SW Balkans inferred from multiproxy analysis of Lake Prespa sediments. *Climate of the Past Discussion*, **9**, 1321–1362.

Persoiu, I. (2010) *Reconstruction of Holocene geomorphological evolution of Somesu Mic Valley*. PhD Thesis, 'A. I. Cuza' University, Iasi, Romania (in Romanian).

Peterken, G.F. & Mountford, E.P. (1996) Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry*, **69**, 125–136.

Pokorný, P. (2011) *Neklidné casy. Kapitoly ze spolecných dejin prírody a lidí [Unstable times. Chapters from the common history of nature and people]*. Dokorán, Praha.

Prentice, I.C. (1985) Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. *Quaternary Research*, **23**, 76–86.

Prentice, I.C., Jolly, D. & BIOME 6000 participants (2000) Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa. *Journal of Biogeography*, **27**, 507–519.

Ruprecht, E., Szabó, A., Enyedi, M.Z. & Dengler, J. (2009) Steppe-like grasslands in Transylvania (Romania): characterisation and influence of management on species diversity and composition. *Tuexenia*, **29**, 353–368.

Sugita, S. (1994) Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology*, **82**, 881–897.

Sugita, S. (2007) Theory of quantitative reconstruction of vegetation: pollen from large sites REVEALS regional vegetation composition. *The Holocene*, **17**, 229–241.

Tantau, I., Reille, M., de Beaulieu, J.L. & Farcas, S. (2006) Late Glacial and Holocene vegetation history in the southern part of Transylvania (Romania): pollen analysis of two sequences from Avrig. *Journal of Quaternary Science*, **21**, 49–61.

Timar Gabor, A., Vasiliniuc, S., Badarau, A.S., Begy, R. & Cosma, C. (2010) Testing the potential of optically stimulated luminescence dating methods for dating soil covers from the forest steppe zone in Transylvanian basin. *Carpathian Journal of Earth and Environmental Sciences*, **5**, 137–144.

Tomescu, A. (2000) Evaluation of Holocene pollen records from the Romanian Plain. *Review of Palaeobotany and Palynology*, **109**, 219–233.

Tonkov, S., Marinova, E., Filipova-Marinova, M. & Bozilova, E. (2014) Holocene palaeoecology and human environmental interactions at the coastal Black Sea Lake Durankulak, northeastern Bulgaria. *Quaternary International*, **10**, 277–286.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds) (1964–1980) *Flora Europaea*, Vols 1–5. Cambridge University Press, Cambridge.

Varga, Z., Borhidi, A., Fekete, G., Debreczy, Zs., Bartha, D., Bölöni, J., Molnár, A., Kun, A., Molnár, Zs., Lendvai, G., Szodfridt, I., Rédei, T., Facsar, G., Sümegi, P., Kósa, G. & Király, G. (2000) *Alföldi erdossztyepp-maradványok Magyarországon* (ed. by Zs. Molnár and A. Kun), pp. 7–19. WWF Magyarország, Budapest.

Vera, F.M.V. (2000) *Grazing ecology and forest history*. CABI Publishing, Wallingford, Oxon.

Willis, K.J. & van Andel, T.H. (2004) Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quaternary Science Reviews*, **23**, 2369–2387.

Willis, K.J., Braun, M., Sumegy, P. & Toth, A. (1997) Does soil change cause vegetation change or vice verse? A temporal sequence from Hungary. *Ecology*, **78**, 740–750.

Willis, K.J., Sümegi, P., Braun, M., Bennett, K.D. & Toth, A. (1998) Prehistoric land degradation in Hungary: who, how and why? *Antiquity*, **72**, 101–113.

SUPPORTING INFORMATION

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

Appendix S1 Chronology and age–depth construction at Lake Stiucii.

Appendix S2 Description of the REVEALS model and biomization at Lake Stiucii.

Appendix S3 Pollen percentage (raw) diagram at Lake Stiucii.

BIOSKETCH

Angelica Feurdean is a palaeoecologist with research interests in the long-term interactions between vegetation, climate and the disturbances in temperate forests and grasslands of central-eastern Europe, as well as in exploring ecological hypotheses using palaeoecological records.

Author contributions: A.F. conceived the paper; A.F. C.A., M.B., S.M.H. and D.V. collected the sediments; A.F. conducted the pollen, spore and charcoal analyses; E.M. conducted plant macrofossil analysis and biome reconstruction; A.B.N. applied the REVEALS model; J.L. undertook the climate simulations and analysed the results; C.A. conducted the archaeological survey, A.T.G. conducted the OSL analysis; A.F. led the writing with contributions from T.H. All authors contributed to the final writing.

Editor: Jack Williams