The influence of refugial population on Lateglacial and early Holocene vegetational changes in Romania

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Received 2 March 2006; received in revised form 30 November 2006; accepted 14 December 2006
Available online 5 January 2007

Abstract

Romania has for a long time been lacking good palaeoenvironmental records, particularly for the Late Quaternary. A chronological framework had been nearly absent and the vegetation development had been reconstructed entirely from pollen data. Data sets from this part of Europe are important for assessing the spatial variability of past vegetation and climatic changes and to reconstruct tree migration routes at the end of the last glacial period. New palaeobotanical evidence has enabled us to address this gap and to provide a more comprehensive picture of the Lateglacial and early Holocene continental environment. This paper reviews results from radiocarbon dated sequences in Romania with the aim to place them in a larger perspective with regard to glacial refugia and tree immigration, and to assess the vegetation response to climatic oscillation from the end of the Last Glacial Maximum (LGM) to the early Holocene. This study documents that some coniferous and broad-leaved trees were present prior to 14,700 cal. yr BP in Romania, and thus it appears that this region may have been a refugial area for some tree species. During the Lateglacial, the vegetation shows a distinct response to climatic oscillations at all elevations, although the response is stronger at mid altitude (800–1100 m. a.s.l.) than at high altitudes. Moreover, smaller climatic oscillations are only recorded at sites situated at mid altitudes, probably because these areas were located close to the tree line ecotone.

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Keywords: glacial refugia; vegetation fluctuation; climate; pollen; plant macrofossils; Lateglacial; Romania

1. Introduction

The importance of palaeoecological studies as a way of placing contemporary environmental and climatic changes in a long-term perspective is increasingly recognized. Of particular interest are the millennial to
centennial climate fluctuations, which were characteristic of the Late Quaternary, and their impact on terrestrial ecosystems. By studying the biological response to these abrupt changes, it is possible to assess the sensitivity of vegetation to future climatic changes. Specifically, palaeoecological studies allow reconstructing shifts in the composition and abundance of plant communities, location of tree refugia and immigration routes. Palaeoecological research also becomes increasingly recognized as a tool for biodiversity evaluation and conservation management (Gillison and Willis, 2005; Willis et al., 2005). Because Romanian territory was not extensively glaciated during the full glacial, this region may have been glacial refugia for temperate trees and therefore may represent areas of special values for long-term persistence on biodiversity.

Numerous studies show a clear response of the vegetation to the distinct climatic fluctuations during the Lateglacial in Europe, but the amplitude of the response varied greatly across regions (Lotter et al., 1992; Ammann et al., 1983; Farcas, 1995, 1996; Buz, 1999). Only very long tradition (Pop, 1929, 1932, 1942, 1957, 1960; Diaconeasa, 1969, 1977; Lupsa, 1977, 1980; Boscaiu et al., 1983; Farcas, 1995, 1996; Buz, 1999). Only very recent studies, however, provide radiocarbon chronologies. The present discussion is therefore based on pollen stratigraphies established at these sites.

Palaeovegetational investigations in Romania have a long tradition (Pop, 1929, 1932, 1942, 1957, 1960; Diaconeasa, 1969, 1977; Lupsa, 1977, 1980; Boscaiu et al., 1983; Farcas, 1995, 1996; Buz, 1999). Only very recent studies, however, provide radiocarbon chronologies for Lateglacial fluctuation in vegetation dynamics (Farcas, 2001; Farcas et al., 1999; Feurdean et al., 2001; Wohlfarth et al., 2001; Björkman et al., 2002, 2003; Tantau et al., 2003; Tantau et al., 2003; Feurdean, 2004; Feurdean and Bennike, 2004; Tantau et al., 2006). These studies show that steppe environments with Pinus and Betula developed before 14,700 cal. yr BP. During the Lateglacial, herbs and open woodlands with Pinus, Betula and some Larix, Salix and Alnus, alternated with expansion of woodlands that also included Picea, Ulmus and Populus. At the Lateglacial–Holocene transition at 11,500 cal. yr BP, Pinus, Betula, Larix woodlands spread, followed rapidly by the expansion of Ulmus and Picea, and the arrival of Quercus, Tilia, Fraxinus, Acer and Corylus.

The sites Avrig, Preluca Tiganului, Steregoiu, Mohos, Luci, Iezerul Calimani and Taul Zanogutii are the only available Lateglacial radiocarbon dated sequences in Romania (Figs. 1, 3–9). The aim of this paper is to summarize results from these sites and (i) to place them in a regional context with regard to glacial refugia and tree immigration, (ii) to discuss the vegetation response to the climatic oscillations during the Lateglacial and early Holocene, (iii) to examine the sensitivity of vegetation to climate change and (iv) to examine the refugial role of Romania for temperate vegetation and highlight the potential of this region in terms of its genetic diversity and conservation implication.

2. Geographic setting and methodology

Romania is characterized by a high degree of topographical variation, which leads to steep climatic gradients that are sensitive indicators for climatic changes. The modern vegetation shows clear latitudinal zonation: the steppe zone, the forest-steppe zone and the nemoral zone, the latter being the most extensive vegetation type (Donita, 1962; Csurös and Vegetatia, 1976; Cristea, 1993). The vegetation is also arranged in altitudinal belts according to climatic, topographic and edaphic conditions (Fig. 2). The limits of the altitudinal belts vary in the Carpathians with latitude, distribution of air masses and orientation of the mountains. Four altitudinal belts can be distinguished: (1) the foothill woodland belt (300–600 m a.s.l.), which includes several oak species (the most common is Quercus petraea), Tilia cordata, Corylus avellana, Carpinus betulus, Fagus sylvatica; (2) the montane belt can be subdivided into three sub-belts: F. sylvatica woodlands between 600 and 1000 m a.s.l., F. sylvatica–Pinus abies or F. sylvatica–Abies alba woodlands between 1000 and 1200 m a.s.l. and P. abies woodlands between 1200 and 1800 m a.s.l. Small stands of Larix decidua, Pinus sp. (most common P. sylvestris and P. cembra) also occur; (3) the sub-alpine belt (1800–2000 m a.s.l.) is dominated by mixtures of Pinus mugo ssp. mugo, Juniperus communis and Rhododendron kotschyi; (4) the alpine belt occurs above 2000 m a.s.l. and is characterized by communities dominated by Salix spp. and herbaceous plants such as Silene acaulis, Saxifraga bryoides, Festuca glacialis, Sesleria coerulea, Carex curvula, etc.

Only seven Lateglacial sites from Romania, situated in or close to the Carpathian Mountains, at altitudes ranging from 400 to 1840 m a.s.l. (Fig. 1, Table 1), provide absolute chronologies. The present discussion is therefore based on pollen stratigraphies established at these localities. Avrig is situated in the southern part of the Transylvanian Depression, close to the southern Carpathians and is influenced by a montane climate (Tantau et al., 2006). Preluca Tiganului and Steregoiu are located on the western flank of the Gutaiului Mountains (Wohlfarth et al., 2001; Björkman et al., 2002, 2003; Feurdean, 2004;
Feurdean and Bennike, 2004), and Mohos and Luci (Tantau, 2003) in the Harghita Mountains of the eastern Carpathians. The modern climate is continental temperate, but the western part (Gutauiului Mountains) is influenced by western oceanic air masses. Iezerul Calimani is located in the Calimani Mountains of the eastern Carpathians, and Taul Zanogutii in the Retezat Mountains in the western part of the southern Carpathians (Fig. 1, Table 1). Both sites are situated in high montane subalpine areas (Farcas et al., 1999). Among these sites, Preluca Tiganului and Steregoiu (Gutauiului Mountains) are the only one where pollen analysis was complemented by macrofossil data.

Three sites (Avrig, Preluca Tiganului and Steregoiu) out of seven were originally published on a calibrated age scale. Therefore, the chronology for Avrig (Fig. 3) follows the model outlined by Tantau et al. (2006), and for Preluca Tiganului (Fig. 4) and Steregoiu (Fig. 5) we use the age-depth relationship established by Björkman et al. (2002, 2003). The pollen sequences at Mohos (Fig. 6), Luci (Fig. 7), Iezerul Calimani (Fig. 8) and Taul Zanogutii (Fig. 9) were formerly published on a depth scale (Farcas et al., 1999; Tantau et al., 2003), and these radiocarbon dates had to be converted into calibrated years. The calibration was performed with the CALIB REV 4.4 calibration program (Stuiver and Reimer, 1993). The dates used to construct age models for the pollen diagrams (Figs. 6–9) were the midpoint of the calibrated interval (at 2σ). The plot of all diagrams on a comparable temporal scale is essential for a better visualization of the time when changes in the pollen assemblages at different sites occurred. The pollen diagrams are presented as percentages diagram with terrestrial pollen included in the total sum. Aquatic pollen and spores were excluded from the total sum at all sites and Cyperaceae from Avrig, Mohos and Luci due to their high representation.

3. Examining the refugial role of Romania for temperate vegetation

Long-standing discussions regarding the location of tree refugia in Europe (Faegri, 1963; Lang, 1970; West, 1977; Huntley and Birks, 1983; Bennett et al., 1991; Willis, 1994, 1996) have been challenged by palaeoenvironmental records from central and eastern Europe during the last decade, which indicate the existence of at least coniferous trees (Pinus, Picea, Larix) and cold tolerant deciduous taxa (Betula and Salix) during and before the LGM (Willis et al., 1995; Damblon, 1997; Follieri et al., 1998; Haesaerts et al., 1998; Willis et al., 2000; Rudner and Sümege, 2001; Ravazzi, 2002).
According to the most recent palaeoenvironmental review for central and eastern Europe, coniferous (Pinus, Picea, Larix, Juniperus) and broad-leaved trees and shrubs (Salix, Betula, Corylus, Ulmus, Fagus, Quercus, Carpinus, Sorbus, Populus, and Rhamnus), persisted here between ca. 42,000 and 19,000 cal. yr BP (Willis and van Andel, 2004).

Four sites with sediments potentially dating to >14,700 cal. yr BP are available so far in Romania: Avrig (A-1, 2, 3, Fig. 3, ca. 17,000 cal. yr BP), located in

Table 1
Information on studied sites. The abbreviations are as follows: $[T_{ann}]=$mean annual temperatures; $[T_{win}]=$mean winter temperatures; $[T_{summ}]=$mean summer temperatures and $[P_{ann}]=$mean annual precipitation. For location see Fig. 1. All sites are peat, except of Taul Zanogutii, which is a lake

<table>
<thead>
<tr>
<th>Site name</th>
<th>Coordinates</th>
<th>Mountain chain</th>
<th>Altitude m a.s.l.</th>
<th>Size ha</th>
<th>Climate ($T/P$)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preluca</td>
<td>N 47°48,83′</td>
<td>Gutaiului Mountains; Eastern Carpathians</td>
<td>730</td>
<td>1</td>
<td>$[T_{ann}]=8, ^\circ C$  $[T_{win}]=−3, ^\circ C$  $[T_{summ}]=700, \text{mm to ca. 1200–1400 mm}$ above 1200 m a.s.l.</td>
<td>Wohlfarth et al. (2001)  Björkman et al. (2002)  Feurdean (2004)</td>
</tr>
<tr>
<td>Tiganului</td>
<td>E 23°31,91′</td>
<td></td>
<td>790</td>
<td>0,5a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Steregoiu</td>
<td>N 47°48,48′</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>E 23°32,41′</td>
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<tr>
<td>Mohos</td>
<td>N 46°05′</td>
<td>Harghita Mountains, Eastern Carpathians</td>
<td>1050</td>
<td>80</td>
<td>$[T_{ann}]=8, ^\circ C$  $[T_{summ}]=15, ^\circ C$  $[P_{ann}]=1000, \text{mm}$</td>
<td>Tantau (2003)  Tantau et al. (2003)</td>
</tr>
<tr>
<td>Luci</td>
<td>N 46°16′</td>
<td></td>
<td>1079</td>
<td>120</td>
<td></td>
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<tr>
<td></td>
<td>E 25°45′</td>
<td></td>
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<tr>
<td>Avrig</td>
<td>N 45°43′</td>
<td>Transylvanian depression</td>
<td>400</td>
<td>10</td>
<td>$[T_{ann}]=9, ^\circ C$  $[T_{summ}]=20, ^\circ C$  $[P_{ann}]&gt;600, \text{mm}$</td>
<td>Tantau et al. (2006)</td>
</tr>
<tr>
<td></td>
<td>E 24°23′</td>
<td></td>
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<tr>
<td>Iezerul</td>
<td>N 47°19′40″</td>
<td>Calimani Mountains, Eastern Carpathians</td>
<td>1650</td>
<td>1</td>
<td>$[T_{ann}]=4–6, ^\circ C$  $[P_{ann}]=1022$</td>
<td>Farcaş et al. (1999)</td>
</tr>
<tr>
<td>Calimani</td>
<td>E 25°16′25″</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Taul Zanogutii</td>
<td>N 45°19′40″</td>
<td>Retezat Mountains, Southern Carpathians</td>
<td>1840</td>
<td>1</td>
<td>$[T_{ann}]=−4–0, ^\circ C$  $[T_{h}]=10, ^\circ C$  $[T_{coldest, month}]=−7, ^\circ C$  $[P_{ann}]=1400, \text{mm}$</td>
<td>Farcaş et al. (1999)</td>
</tr>
<tr>
<td></td>
<td>E 22°48′10″</td>
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southern Transylvania (Tantau et al., 2006); Preluca Tiganului (PT-1a, Wohlfarth et al., 2001) and Stereogoiu (S-1, Fig. 5, ca. 17,000 cal. yr BP) in NW Romania (Björkman et al., 2002, 2003); and Iezerul Calimani (IC-1a, Fig. 8, ca. 18,000 cal. yr BP) in the eastern Carpathians (Farcas et al., 1999). The bottom sediments in the latter site had earlier been attributed to the Lateglacial. The pollen records suggest the presence of Pinus stands or open woodland vegetation dominated by Pinus at all sites. Alongside, Betula, Juniperus, Hippophaë, Salix and scarce Picea grains were present at Avrig (Fig. 3); Betula, Juniperus and Salix were frequent at Preluca Tiganului (Wohlfarth et al., 2001) and Stereogoiu (Fig. 5); and some Betula and Picea pollen were reported at Iezerul Calimani (Fig. 8). No macro-remains of these trees were recorded in the bottom sediments of Preluca Tiganului (Wohlfarth et al., 2001) and Stereogoiu (Fig. 5), but two pine logs were found at Magherus, in the lowland of northern Transylvania (14,500 $^{14}$C yr BP ca. 17,000 cal. yr BP, Wohlfarth et al., unpublished; Lascu, 2003). Although the age assignment of the oldest sediments at Avrig, Preluca Tiganului, Stereogoiu and Iezerul Calimani still remains somewhat ambiguous, the pine log found at Magherus clearly indicates that trees were present in the lowlands as early as 17,000 yr BP.

Low pollen values in sediments older than 14,700 cal. yr BP may be connected with the quantity of pollen available for deposition. Studies on pollen productivity show that pollen production is strongly related to temperature (Hicks, 1994, 2006). Trees may cease producing pollen under cold conditions, and variations in pollen production do therefore not necessarily coincide with variations in tree density (Hicks, 2006). Another factor that may affect pollen productivity are changes in atmospheric CO₂ concentration (Jackson and Williams, 2004). Experimental research has shown that plants (e.g. Ambrosia artemisiifolia) produce more pollen at the elevated concentration of 700 ppm than at the current concentration of 350 ppm (Ziska and Caulfield, 2000). Although the influence of low CO₂ concentration on pollen productivity is not known, low CO₂ values throughout glacial time may have reduced productivity thus making it even more difficult to detect pollen in sediments.

Fig. 3. Simplified pollen diagram from Avrig, after Tantau et al. (2006). PB—Preboreal; YD—Younger Dryas; AV—Avrig oscillation equivalent to the Older Dryas; LGI—Lateglacial interstadial; OSD—Oldest Dryas.
Fig. 4. Simplified pollen and macrofossil diagram and from Preluca Tiganului, after Feurdean and Bennike (2004). PB—Preboreal; YD—Younger Dryas; Al—Allerød; BO—Bølling. Macrofossils are presented as concentration.

Fig. 5. Simplified pollen and macrofossil diagram from Steregoiu, after Feurdean and Bennike (2004). PB—Preboreal; YD—Younger Dryas; Al—Allerød; BO—Bølling; OSD—Oldest Dryas. Macrofossils are presented as concentration.
Another body of evidence, which can offer insights into the phylogeography of different species is genetic material (chloroplasts, nuclear and mitochondrial DNA), and the value of such studies in combination with fossil evidence has been increasingly recognized (Taberlet and Bouvet, 1994; Taberlet and Cheddadi, 2002; Petit et al., 2003; Hewitt, 2004; Lascoux et al., 2004; Willis and van Andel, 2004; Deffontaine et al., 2005; Gugerli et al., 2005; McLachlan et al., 2005; Magri et al., 2006; Duriez et al., in press). The genetic evidence considers two main ideas: (1) the population in the glacial refugia show taxonomic and genetic diversity, which decreases away from these areas, and such information can be used to reconstruct postglacial migration routes; (2) the populations between refuges are highly divergent as a result of prolonged isolation. Studies of 22 woody plant species from 25 European woodlands show that, along with the Balkan Peninsula, Italy and Croatia, Romania is among the areas with the most genetically unique populations, which could be the results of a long-standing isolation in

Fig. 6. Simplified pollen diagram from Mohos, after Tantau et al. (2003). PB—Preboreal; YD—Younger Dryas; LGI—Lateglacial interstadial.

Fig. 7. Simplified pollen diagram, from Luci, after Tantau et al. (in preparation). PB—Preboreal; YD—Younger Dryas; LGI—Lateglacial interstadial.
a glacial refuge (Petit et al., 2003; Lascoux et al., 2004). A more recent study using combined fossil and genetic data for the reconstruction of the history of *F. sylvatica* indicate that the Romanian Carpathians do not appear to be a major refugia for beech. Some population, however, may have survived in the Apuseni Mountains as suggested by both an early appearance in the pollen record during the Holocene and high allelic richness of *F. sylvatica* (Magri et al., 2006). Indirect evidence for glacial refugia of European temperate woodlands can also be obtained from phylogeographic and palaeontological studies of those species strongly connected to woodland habitats. For instance, the analyses of mitochondrial DNA of the bank vole (*Clethrionomys glareolus*), a temperate woodland mammal species, show high genetic diversity for central Europe (Austria, Hungary, Slovakia and Romania) and these areas appear as very important glacial refugia for the western bank vole group (Deffontaine et al., 2005). The very recent study on the bank vole suggests the persistence of this species in the Carpathians between 25000 and 10,000 uncal. years BP, and a strong contribution of the Carpathian population to the postglacial colonization of Europe (Kotlik et al., 2006). According to Kotlik et al. (2006), these findings provide the clearest phylogeographic evidence to date of a northern glacial refugium for temperate species in Europe. Further genetic evidence comes from the Western capercaillie (*Tetrao*...
urogallus), a keystone species of coniferous boreal and altitude forests suggesting that this distinct lineage of birds (aqutinus) were only found in the Pyrenees and Cantabrians mountains and the Romanian Carpathians (Duriez et al., in press) as a result of possible glacial refugia in these areas. Studies on mDNA of the brown bear (Ursus arctos) also indicate the glacial isolation of a special lineage in Romania (Taberlet and Bouvet, 1994).

4. Lateglacial and earliest Holocene vegetational changes (14,700–11,300 cal. yr BP)

The Lateglacial and early Holocene period was characterized by several climate oscillations at global and regional scales. In order to see how the vegetation dynamic across the Romanian Carpathians was affected by these climatic changes seven radiocarbon dated pollen diagrams from sequences located at different altitudes were compared (Figs. 3–9; Table 2). We also present independent evidence on climate variability derived from the δ18O and δ13C record of stalagmites (Table 2) from the Apuseni Mountains, NW Romania (Tamas, 2003; Tamas et al., 2005).

4.1. Lateglacial interstadial (~14,700–12,500 cal. yr BP)

Increasing pollen percentages of Pinus from about 14,700 cal. yr BP in lowland (A-4, Fig. 3), and at mid-altitude sites in the Carpathian Mountains, i.e. Preluca Tiganului (P-1, 2, 3, Fig. 4; PT-1b) and Steregoiu (S-2, 3, Fig. 5), indicate that pine woodlands started expanding their area. These woodlands also contained Betula, Salix, Picea and Juniperus (Figs. 3–5), and at Steregoiu also Alnus, which was most probably derived from very local individuals (Fig. 5). The macrofossil records at Preluca Tiganului (P-1, 2, 3, Fig. 4) and Steregoiu (S-2, 3, Fig. 5) support the local presence of these taxa and of Larix, Populus tremula and Prunus padus, and strongly indicate that they reached at least elevations of about 800 m a.s.l. Pollen of Larix have also been noted by single pollen grains at Luci (Fig. 7) across the Lateglacial. Low pollen production and preservation, poor dispersal capacity and difficulties in identification results in a strong under-representation of Larix and Populus in fossil pollen records (Lang, 1994). At Iezerul Calimani (1650 m a.s.l), the poorly constrained chronology and no clear fluctuations in the pollen assemblages throughout the Lateglacial make identifications of any changes in the vegetation composition difficult (IC-1a, 1b, Fig. 8). At Taul Zanogutii (1840 m a.s.l), the sharp rise in pollen of Pinus and of some Betula along with the decrease of NAP (strongest for Artemisia) represents the transition to the Lateglacial interstadial (TZ-1, Fig. 9). These high elevation areas have remained mostly tree-less, or perhaps scattered trees have occurred, thus most of the tree pollen is likely to represent a signal from lower elevations.

Trees surviving before >14,700 cal. yr BP in the Carpathians (Pinus, Betula, Picea, Alnus, Larix, Salix and Juniperus) were the first to expand as a response to climate warming at the beginning of the Lateglacial interstadial. The more rapid and widespread reaction of Betula and Pinus could be due to broad spatial scale refugia in the Carpathians and could also represent an increase in pollen and fruit production of locally existing populations in response to higher temperature. Furthermore, Pinus and Betula are important pioneer types that can survive on nutrient poor soils. Picea and Alnus also survived in the Romanian Carpathians, but their weak and slow response as compared to Pinus and Betula may have been due to more restricted refugial areas (e.g. low-density populations and less numerous spots).

A brief re-expansion of Juniperus, Salix, Artemisia, Poaceae and Chenopodiaceae combined with a decline of Pinus is recorded at three sites: in the lowland at Avrig (A-5, Fig. 3) and at mid-elevation, i.e. Preluca Tiganului (P-3, Fig. 4) and Luci (second half of L-1, Fig. 6), suggesting a temporary opening of woodland. The calibrated ages at Luci (14,800–14,200 cal. yr BP) are older than those of Avrig (14,200–13,800 cal. yr BP, Tantau et al., 2006) and Preluca Tiganului (14,100–13,800 cal. yr BP, Björkman et al., 2002). The common characteristics of the pollen diagrams at these three sites may, however, indicate synchronicity in the vegetation development (Figs. 3, 5, 7), although a better-constrained chronology is clearly needed for such assumptions. If true, then this vegetation change could be a response to the Older Dryas cold episode. Pollen-based temperature reconstructions for Preluca Tiganului point to a 5–10 °C drop in winter temperatures and to ca. 200 mm in annual precipitation (Furdean et al., submitted for publication).

A distinct change in the vegetation composition is evidenced along the altitudinal transect in the Carpathians between ca. 13,800 and 12,500 cal. yr BP by the increase in pollen percentages for Picea and Betula, the appearance of thermophilous trees (see discussion below), alongside with a decrease of helophilous herbaceous plants and of Pinus, Salix and Juniperus. In the pollen diagrams at Avrig (A-6, Fig. 3) and Luci (L-3, Fig. 7), Picea pollen account for ca. 5% of the pollen sum, at Taul Zanogutii (TZ-2, Fig. 9) of ca. 10 %, whereas at Preluca Tiganului (P-5, Fig. 4) and Steregoiu (S-4, Fig. 5) these values are comparatively higher (15–20%). The high representation of Picea from the total...
A tentative correlation between climatic events inferred from the $\delta^{18}$O and $\delta^{13}$C of the stalagmites from the Apuseni Mountains (Tamas, 2003; Tamas et al., 2005) and the time and changes in vegetation development derived from the pollen and macrofossil records is valuable for understanding the regional vegetation changes. The amount of pollen at Preluca Tiganului and Steregoiu basins and the presence of *Picea* woodlands in the immediate vicinity of these basins. The corresponding abundant macrofossil record for *P. abies* (needles) confirms the local importance of *Picea* in the catchment vegetation (P-5, Fig. 4; S-4, Fig. 5). As large basins receive regional pollen loading, the amount of particular tree taxa is diluted (Sugita, 1994; Hicks, 2006). This fact may have caused a lower representation of *Picea* pollen in the sediments from Luci and Mohos. Furthermore, studies on *Picea* pollen production, dispersion, transport and representation have shown that it usually has low pollen values even in *Picea*-dominated stands and that long-distance transported *Picea* pollen rarely exceed 5% (Huntley and Birks, 1983; Hicks, 1994; Lang, 1994; Giesece and Bennett, 2004; Latalowa and van der Knaap, 2006). In pollen maps of *Picea* generally threshold values of around 0.5–2% are considered as indicative of building up populations and percentages around 5–10% mark their spatial expansion phase (Ravazzi, 2002; Giesece and Bennett, 2004; van der Knaap et al., 2005). These lines of evidence suggest that *P. abies*-dominated woodlands covered the surroundings at Preluca Tiganului and Stereogoiu (Gutauiul Mountains) between 13,800 and 12,500 cal. yr BP, whereas a mixture of *Picea, Pinus* and *Betula* occurred in the lowland and at other sites in the Carpathians. This picture is very different from the woodland composition in central Europe and the Balkan Mountains (e.g. Bulgaria) where *Picea* was nearly absent, illustrating that the Carpathians acted as an important refugial area for *Picea*.

Apart from coniferous and cold deciduous trees, the pollen diagrams also indicate the presence of thermophilous deciduous trees between 13,800 and 12,500 cal. yr BP. *Ulmus* is recorded with highest pollen values (between 1% and 5%) at Preluca Tiganului (P-5, Fig. 4) and Stereogoiu (S-4, Fig. 5), which is a clear indication for its local establishment. The other five pollen diagrams show discontinuous occurrences of pollen of *Ulmus* or continuous curves with less then 1%. This observation may be related to the size of the former basins of Avrig Luci, and Mohos (Figs. 3, 6, 7), which may have lead to a dilution of pollen of *Ulmus* and of other deciduous trees in the sediment. Scattered *Ulmus* stands may thus have occurred nearby at mid elevation sites during the Allerod (M-1, Fig. 6; L-3, Fig. 7), although higher altitude must have been too cold and *Ulmus* pollen grains were most probably blown in from lower sites (IC-1b, Fig. 8; TZ-2, Fig. 9). In addition, scattered pollen grains of *Quercus, Tilia* and *Corylus* were found at most sites (Figs. 3–9). These pollen percentages could represent small local populations of deciduous trees occurring at low and mid-

### Table 2: Timeframe for change in vegetation

<table>
<thead>
<tr>
<th>$\delta^{18}$O</th>
<th>$\delta^{13}$C</th>
<th>Timeframe</th>
<th>Vegetation development</th>
</tr>
</thead>
<tbody>
<tr>
<td>11,600 $\delta^{18}$O</td>
<td>11,500 $\delta^{13}$C</td>
<td>11,600</td>
<td>Low and mid altitude: reforestation with <em>Pinus</em> and <em>Betula</em>, rapidly followed by <em>Picea</em> and <em>Ulmus</em> and then by <em>Quercus, Tilia</em> and <em>Fraxinus</em></td>
</tr>
<tr>
<td>12,600–11,600 $\delta^{18}$O</td>
<td>11,500–12,900 $\delta^{13}$C</td>
<td>12,600–11,500</td>
<td>Low and mid altitude: reduction of woodland to stands of <em>Pinus</em>, <em>Betula</em>, <em>Salix</em> and <em>Alnus</em>; high altitude: open herbaceous vegetation and probably stands of shrubs</td>
</tr>
<tr>
<td>12,900–12,600 $\delta^{18}$O</td>
<td>11,600–12,900 $\delta^{13}$C</td>
<td>12,900–12,600</td>
<td>Low and mid altitude: <em>Picea</em> dominated woodlands with <em>Betula</em>, and probably <em>Quercus</em> and <em>Tilia</em>; high altitude: open herbaceous vegetation and probably stand of shrubs and <em>Pinus</em></td>
</tr>
<tr>
<td>13,200–12,800 $\delta^{18}$O</td>
<td>11,600–13,200 $\delta^{13}$C</td>
<td>13,200–12,800</td>
<td>Opening of <em>Picea</em> woodland (only at Preluca Tiganului and Luci)</td>
</tr>
<tr>
<td>13,600–13,200 $\delta^{18}$O</td>
<td>11,600–13,600 $\delta^{13}$C</td>
<td>13,600–13,200</td>
<td>Low and mid altitude: expansion of <em>Picea</em> dominated woodland with <em>Betula</em>, <em>Pinus</em>, <em>Salix</em>, <em>Alnus</em>, <em>Larix</em>, <em>Ulmus</em> and probably <em>Quercus</em> and <em>Tilia</em>; high altitude: open herbaceous vegetation and probably stands of shrubs and <em>Pinus</em></td>
</tr>
<tr>
<td>14,500–14,000 $\delta^{18}$O</td>
<td>11,600–14,500 $\delta^{13}$C</td>
<td>14,500–14,000</td>
<td>Opening of <em>Pinus–Betula</em> woodland (only recorded at Avrig, Preluca Tiganului and Luci)</td>
</tr>
<tr>
<td>14,800–14,300 $\delta^{18}$O</td>
<td>11,500–14,800 $\delta^{13}$C</td>
<td>14,800–14,300</td>
<td>Low and mid altitude: expansion of open <em>Pinus–Betula</em> woodland with <em>Betula</em>, <em>Salix</em>, <em>Alnus</em>, <em>Picea</em>, <em>Larix</em>, <em>Populus</em> and <em>Prunus</em>; high altitude: open herbaceous vegetation, shrubs and probably stands of trees</td>
</tr>
<tr>
<td>&gt;14,800 &gt;14,700 $\delta^{18}$O</td>
<td>11,500 &gt;14,800 $\delta^{13}$C</td>
<td>&gt;14,800</td>
<td>Low and mid altitude: open vegetation with <em>Pinus</em>. Stands of <em>Betula</em>, <em>Picea</em>, <em>Alnus</em>, <em>Juniperus</em> and <em>Salix</em> also existed; high altitude: open herbaceous vegetation and shrubs</td>
</tr>
</tbody>
</table>
altitude within the coniferous-dominated woodlands with higher pollen productivity, which may have masked their small pollen signal. At the same time, coniferous trees could have generated favorable micro-environmental conditions for the development of temperate trees (see Willis et al., 2000, 2001). Several studies show that in the case of a very small population only a small amount of pollen is deposited and it may even happen that these pollen types are not at all detectable in sediments (Willis et al., 2001; Seppä and Bennett, 2003; Hicks, 2006). Other researchers consider the presence of scattered or low percentages of deciduous tree pollen in the USA and northwestern Europe as a result of long distance transport (Birks, 2003). This assumption may also be valid for Romania, specifically for trees with good dispersal capability such as Quercus and Corylus, but not for trees with low pollen productivity and low dispersal capacity as Tilia and Ulmus. In Bulgaria there is pollen evidence for the presence of Quercus and Corylus in a Pinus–Betula-dominated woodland during the Allerød (Bozilova and Tonkov, 2000; Stefanova et al., 2006; Tonkov et al., 2006). A substantially higher pollen percentage of meso-thermophilous deciduous trees (Ulmus, Quercus, Tilia and Carpinus) recorded in Hungary suggests the local presence of these trees (Willis et al., 1995).

Overall, the expansion of P. abies woodlands in sites from lowlands (Fig. 3) to high altitudes in the Romanian Carpathians (Figs. 4–9), and the presence of mesophilous trees such as Ulmus, Prunus and probably of Quercus, Corylus and Tilia around 13,800 cal. yr BP at low and mid altitudes, are good indicators of warmer and moisture conditions. Pollen-based climate reconstructions show a temperature increase from \( \sim -13 \) to \( \sim -7 \) °C during the coldest month, temperatures close to modern values (ca. 16 °C) during the warmest month, and precipitation of ca. 600 mm in the Gutauiul Mountains (Feurdean et al., submitted for publication). The distinct response of the vegetation in Romania, which is seen at sites situated at low, mid and high altitudes, is remarkable. The time interval between ca. 13,800 and 12,600 cal. yr BP may be regarded as the major and longest warm period during the Lateglacial in Romania. The tree limit must have been located above 800 m a.s.l., as is showed by macrofossil finds in the Gutauiul Mountains (Figs. 4 and 5).

A short-term opening in the Allerød woodland is indicated by the marked reduction of Picea pollen, the disappearance of Ulmus and the increase of Betula, Artemisia and Chenopodiaceae at Preluca Tiganului between 13,400 and 13,200 cal. yr BP (middle of P-5, Fig. 4) and at Luci between 13,100 and 12,900 cal. yr BP (towards the upper part of L-3, Fig. 7). None of the other Romanian pollen diagrams, neither at low nor at high elevation, revealed this change in vegetation. The opening in woodland could be attributed to the intra-Allerød cooling or to the Gerzensee oscillation in Switzerland (Lotter et al., 1992; Ammann et al., 2000).

4.2. Younger Dryas

Around ca. 12,900–12,600 cal. yr BP, pollen diagrams indicate again major changes in pollen percentages, i.e. Picea pollen starts to decline, deciduous mesophilous trees almost disappeared and Pinus, Juniperus, Salix, Artemisia, Poaceae, Chenopodiaceae and Cyparaceae increased at all investigated sites (Figs. 3–9). This change in pollen composition witnesses a general reduction in woodland cover, although not uniformly at all sites. For instance, pollen of Betula increase markedly along with a reduction of Pinus in the lowlands (A-7, 8, Fig. 3), while Pinus rises along with a slight reduction of Betula at middle altitudes i.e. Preluca Tiganului (P-6, 7, Fig. 4), Steregoiu (S-5, 6, Fig. 5) and Luci (L-4, 5, Fig. 7), or Pinus and Betula both decrease at Mohos (M-2, Fig. 6) and at higher elevations, i.e. Taul Zanoguitii (TZ-3, Fig. 9). The local topography and microclimate may explain these dissimilarities: more humid condition at Avrig may have favored the local development of Betula, and considerably higher pollen values for Betula and Pinus at higher altitudes are most probably due to wind-blown pollen from trees stands situated at lower elevations. Similarly, differences in pollen composition between sites situated along an altitudinal transect from the Swiss Plateau to the Southern Alps have been demonstrated based on numerical analyses (Lotter et al., 1992; Ammann et al., 1993). The corresponding abrupt decline in macrofossil remains for Pinus sp., Betula sect. Albae (includes Betula pubescens and Betula pendula) and P. abies at Preluca Tiganului (P-6, 7, Fig. 4) and Steregoiu (S-5, 6, Fig. 5) at 12,900 cal. yr BP supports the marked deforestation, but stands of L. decidua, Salix sp., Pinus sp., Betula sect. Albae and P. abies still persisted at 800 m a.s.l. (Ampel, 2004; Feurdean and Bennike, 2004). Although these trees reduced their area, they persisted in stands or patches from low to mid altitudes (Figs. 3–7). At higher elevation they were most probably no longer present and a tree-less montane-steppe vegetation dominated (Fig. 9).

Picea was the most affected taxon and its dramatic reduction indicates a substantial moisture decline. Dry and also cold conditions are also implied by the disappearance of deciduous trees and by a marked re-expansion of continental steppe vegetation type. The pollen-based temperature reconstruction for the time interval between
12,700 and 11,700 cal. yr BP in the Gutaiului Mountains indicates that winter temperatures were ca. 14 °C colder, summer temperatures ca. 2–6 °C lower and that precipitation declined by 50% (ca. 500 mm) as compared to the modern values (Feurdean et al., submitted for publication). The distinct vegetation responses from lowlands to high altitudes in Romania suggest that this interval was the most pronounced cold interval of the Lateglacial. Apparently, the response of the vegetation was strongest between 800 and 1100 m a.s.l. (Figs. 3–7).

Pollen and macrofossil records from the Swiss Alps indicate that tree line was lowered by ca. 300–500 m during the Younger Dryas (Ammann et al., 1993; Lotter et al., 2000; Tobolsky and Ammann, 2000; Wick, 2000). On the Hungarian plain, the composition of the vegetation seems to have remained fairly stable during the whole Lateglacial interval (Willis et al., 1995). Pinus dominated woodlands, however, remained well-represented most probably due to drier climatic conditions at lower elevations. On the contrary, at higher elevations in the Bulgarian mountains, arboreal pollen was strongly reduced during the Younger Dryas (Stefanova et al., 2006; Tonkov et al., 2006).

### 4.3. Early Holocene vegetational development

At around 11,500 cal. yr BP, pollen diagrams show a general reduction of open grass communities (Artemisia, Chenopodiaceae, Poaceae), accompanied by slightly increasing values for Betula in the lowlands (A-9, 10, Fig. 3) and for Picea and Pinus at mid-elevation (P-8, 9, 10, Fig. 4; S-7, 8, Fig. 5; M-3, 4, Fig. 6; L-6, Fig. 7), an indication of the onset of the Holocene. A hiatus is, however, present at Preluca Tiganului (end of P-8, Fig. 4) and Mohos (end of M-3, Fig. 6) at this transition. Picea, Populus, Alnus and Salix were part of these earliest Holocene woodlands. Pollen profiles at higher elevation show an expansion of the montane and subalpine vegetation types with Pinus sp., Pinus mugo, Betula and Alnus viridis (IC-2a, 2b, Fig. 8; TZ-4, Fig. 9). These tree taxa spread almost synchronously at all sites in the east, south and north-western Carpathians, suggesting that they had widespread refugia across the Romanian Carpathians. The low values of Picea pollen at the onset of the Holocene may be connected to a strong reduction of Picea woodlands during the cold Younger Dryas. The very similar shape of the pollen curves for Picea in Romanian pollen diagrams indicates that Picea started to spread from local residual populations, situated in different areas in the Romanian Carpathians, which acted as an important repopulation centre for Picea. This is consistent with a Picea im-

migration route in Europe that shows a clear east to west direction at the beginning of the Holocene (Huntley and Birks, 1983; Huntley and Prentice, 1993; Giesecke and Bennett, 2004; van der Knaap et al., 2005). Judging from the pollen percentages of Picea, it seems that Picea was more dominant at mid-higher elevation than at lower sites, which fits well with the present day ecological preferences for Picea. Currently, Picea is the dominant taxon at mid and higher mountain belts in Romania, and the second taxon represented in woodlands (after Fagus) making 23% of the total stem area (Toader and Dumitru, 2004).

The rapid increase of Ulmus pollen percentages from ca. 11,300 cal. yr BP is similarly shown at all recently investigated localities and points to an early Holocene establishment of Ulmus in the Romanian Carpathians (Figs. 3–7). At high elevation these pollen may have come from tree stands at lower elevation (Figs. 8, 9). The slight difference in timing for the establishment of Ulmus could probably be attributed to altitudinal upward migration (from suitable habitats at lower elevation where Ulmus populations survived during the Lateglacial) to higher elevation of each mountain massif. If Ulmus would have migrated only from areas situated to the south in Romania, then a distinct time-transgressive pattern could be expected during the early Holocene.

### 4.4. Sensitivity of the vegetation to climatic change

Generally, the palaeoecological results from Romania show a distinct response of the vegetation to climatic changes, although only stronger oscillations are recorded at all elevations. The response is most pronounced at middle to higher elevations between 800 and 1100 m a.s.l. where also minor climatic oscillations are detectable (e.g. Preluca Tiganului, Stereogiu, Luci). Short oscillations are not recorded at elevations above 1600 m a.s.l. This observation is in good agreement with comparable studies performed in the Swiss Alps, which show altitudinal differences in the vegetation response to climatic fluctuations (Ammann et al., 1993, 2000; Birks and Ammann, 2000; Wick, 2000). Although it is often said that vegetation at higher elevations is more sensitive to climatic changes (Willis, 1994; Ammann et al., 2000; Birks and Ammann, 2000; Wick, 2000; Peteet, 2000), a stronger response is seen at medium elevation sites in the Carpathians. Low pollen-sampling resolution and accumulation ratio at higher elevation most probably have hampered the identification of such short changes. Furthermore, palaeoecological investigations at sites located between 1100 and 1600 m a.s.l. are
unfortunately still lacking. Thus, our conclusions are preliminary and new data are necessary to understand the vegetation dynamics between 1100 and 1600 m a.s.l. (e.g. the tree line ecotone zone may have been located higher than 1100 m). Only one site is situated at low elevation (400 m a.s.l.) and it shows a vegetation pattern that is rather similar to that at mid-altitude sites.

4.5. Was Romania an important glacial refugium?

Summarising, the available palaeoecological evidence (pollen and mega-fossils) suggests the occurrence of Pinus, Juniperus, Betula, Salix and Picea in lowland areas and the Romanian Carpathians prior to 14,700 cal. yr BP (potentially between 18,000 and 14,700 cal. yr BP). This agrees with areas indicated as glacial refuges by genetic data. However, no fossil evidence for other deciduous trees have been found so far, despite of the genetic data that suggest otherwise. Furthermore, the presence of Larix, P. tremuloides, Ulmus, P. padus and probably of Quercus and Tilia throughout the Lateglacial, and the very rapid expansion at the very beginning of the Holocene (particularly for Ulmus), could also suggest the glacial refugia of these species in the Romania.

Apart from genetic studies on plants there are several genetic studies on phylogeographic patterns of animal species connected to the woodlands, which point to a glacial isolation of these species in Romania (Taberlet and Bouvet, 1994; Deffontaine et al., 2005; Kotlik et al., 2006; Duriez et al., in press). The presence of these species and the fact that they are associated with temperate and coniferous woodlands strongly suggest that such woodland types covered Romania or the Romanian Carpathians during glacial times. They also suggest that Romania is particular important as a genetically diverse region.

Modern palaeoecological and palaeoenvironmental investigations in Romania have only recently been initiated and mainly cover the Lateglacial and Holocene, whereas full-glacial environments are poorly documented. The current results show, however, the potential of Romania as a refugia during the last glacial. Identification of the region containing refugial population is important as they represent areas of special value for a long-term persistence on biodiversity and therefore have a high priority for conservation biodiversity.

5. Conclusions

(1) This paper reviews results from radiocarbon dated pollen sequences in Romania with the aim to place them in a larger perspective with regard to glacial refugia and tree immigration and to study the vegetation response to climatic oscillations from the end of the LGM (GS-2) to the early Holocene. Although the available pollen diagrams are few they cover a large part of Romania, except for the southern part. The pollen stratigraphy is similar at most of the sites suggesting a regional signal.

(2) The pollen data indicate that coniferous (Pinus, Picea and Larix) and cold-tolerant deciduous trees (Betula, Alnus and Salix) survived prior to 14,700 cal. yr BP in Romania. During the Lateglacial Pinus (P. sylvestris, P. cembra, P. mugo), Betula (B. pubescens, B. pendula), Picea abies, Larix decidua, Populus tremula, Prunus padus and Alnus were present at mid-altitude areas in the Carpathians. Ulmus occurred in low to mid elevation areas during the Lateglacial in particular between 13,200 and 12,900 cal. yr BP. Quercus, Tilia, Fraxinus and Corylus were also probably present in few isolated places during the Lateglacial, although their pollen percentages are significantly lower than Ulmus. Genetic evidence on plants and on animals associated with woodlands, points to a full glacial isolation of these trees in Romania, showing the potential of Romania as a glacial refugia. This study documents that important refugia for Picea existed in the Romanian Carpathians.

(3) The Lateglacial vegetation development shows distinct responses to climatic changes. Apart from regional climate, local factors determined by the elevation and topography of the study sites were also important. The amplitude of the response is largest at sites located at 800 to 1100 m a.s.l., and rather significant around 400 m a.s.l., but was much less at higher elevations (above 1600 m a.s.l.). Probably the tree line ecotone was situated around 1100 m a.s.l. and thus these sites were more sensitive to short climatic shifts as compared to sites at higher elevations. However, at higher elevation sites sampling resolution was low, thus the capture of clear oscillations was hampered. In the future, a network of sites covering altitudes between 1100 and 1500 m a.s.l. is needed in order to increase the spatial resolution of earlier palaeoecological studies.

(4) It appears that there is a good correlation between phases with open vegetation in Romania and cold events recorded regionally and between phases of tree expansion and regional warm climate intervals.

Acknowledgments

Wim Hoek and Björn Berglund are thanked for fruitful remarks and suggestions and Tudor Tamas is thanked for comments on an earlier version of the manuscript and for drawing Fig. 2. Comments from two anonymous reviewers are greatly acknowledged. Financial support...
came from Stockholm University, the Alexander von Humboldt Foundation and a Marie Curie Grant (MEIF-CT-2006-024296).

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