



European glacial relict snails and plants: environmental context of their modern refugial occurrence in southern Siberia

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Knowledge of present-day communities and ecosystems resembling those reconstructed from the fossil record can help improve our understanding of historical distribution patterns and species composition of past communities. Here, we use a unique data set of 570 plots explored for vascular plant and 315 for land-snail assemblages located along a 650-km-long transect running across a steep climatic gradient in the Russian Altai Mountains and their foothills in southern Siberia. We analysed climatic and habitat requirements of modern populations for eight land-snail and 16 vascular plant species that are considered characteristic of the full-glacial environment of central Europe based on (i) fossil evidence from loess deposits (snails) or (ii) refugial patterns of their modern distributions (plants). The analysis yielded consistent predictions of the full-glacial central European climate derived from both snail and plant populations. We found that the distribution of these 24 species was limited to the areas with mean annual temperature varying from -6.7 to 3.4 °C (median -2.5 °C) and with total annual precipitation varying from 137 to 593 mm (median 283 mm). In both groups there were species limited to areas with colder and drier macroclimates (e.g. snails *Columella columella* and *Pupilla loessica*, and plants *Kobresia myosuroides* and *Krascheninnikovia ceratoides*), whereas other species preferred areas with relatively warmer and/or moister macroclimates (e.g. snails *Pupilla turemenica* and *P. alpicola*, and plants *Artemisia laciniata* and *Carex capillaris*). Analysis of climatic conditions also indicated that distributional shifts of the studied species during the Pleistocene/Holocene transition were closely related to their climatic tolerances. Our results suggest that the habitat requirements of southern Siberian populations can provide realistic insights into the reconstruction of Eurasian, especially central European, glacial environments. Data obtained from modern populations also highlight the importance of wet habitats as refugia in the generally dry full-glacial landscape.

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Historical distribution patterns and species compositions of past communities are usually assessed based on direct fossil evidence from the target area and a particular time period, but these assessments can be improved by knowledge of modern analogues, i.e. present-day communities and ecosystems resembling those known from the fossil record (e.g. Jackson & Williams 2004). Modern analogues never provide a perfect match with past environments, but enable an examination of real ecological processes across multiple habitats, which may be hidden in the fossil record. They also help us deal with various biases existing in the fossil record caused by the varying capacity of the environment to preserve the fossils, mixing of multiple sediment beds and differential preservation amongst taxa (Kidwell & Holland 2002; Jackson & Williams 2004).

Recent research has provided plausible evidence that plant and animal communities, and whole ecosystems of the Altai-Sayan region in southern Siberia represent

possibly the closest modern analogue to those of full-glacial central Europe. Several land-snail species typical of central European full-glacial loess sediments, some currently extinct in Europe, have been found to possess extant populations in this part of central Eurasia and to exhibit community assemblages that are typical of the European full-glacial fossil record (Meng 2008; Meng & Hoffmann 2009; Horsák *et al.* 2010; Hoffmann *et al.* 2011). Likewise, present mammalian communities of the Altai-Sayan region display a marked similarity to the Last Glacial mammalian fauna of the same area (Agadjanian & Serdyuk 2005), harbouring more surviving Pleistocene full-glacial mammals than any other region of the Palaearctic (Pavelková Řičánková *et al.* 2014). Comparisons of the full- and late-glacial fossil pollen spectra from central Europe with modern pollen assemblages of various vegetation types from southern Siberia have also confirmed their considerable similarity in dominant plant species and vegetation types (Kuneš *et al.* 2008;

Magyari *et al.* 2014a; see also Jankovská & Pokorný 2008; Pelánková & Chytrý 2009). The Altai-Sayan region can thus be regarded as an important refugium for full-glacial fauna and flora, harbouring a unique mosaic of cold steppe (e.g. snails *Pupilla loessica* and *Vallonia tenuilabris*, mammals *Lagurus lagurus* and *Marmota bobak*, plants *Artemisia* spp. and Chenopodiaceae) and tundra/taiga species (e.g. snails *Columella columella* and *Vertigo parcedentata*, mammals *Lepus timidus* and *Microtus gregalis*, and plants *Betula rotundifolia* (*B. nana* s. lat.) and *Kobresia myosuroides*), occurring at the same or closeby sites (Kuneš *et al.* 2008; Horsák *et al.* 2010; Pavelková Řičánková *et al.* 2014). Therefore, data from this region can considerably enhance our knowledge of the structure and habitat heterogeneity of the European and northern Asian Last Glacial landscapes, and the autecology of glacial relict species. As several mollusc-based transfer functions have been developed to reconstruct past temperature and precipitation during the last glaciation (Rousseau 1991; Moine *et al.* 2002), the integration of these modern data can also help to improve the reliability of the reconstructions.

In this paper we examine climatic and habitat affinities of selected species of land snails and vascular plants in their continental refugium in the Altai Mts of southern Siberia with the aim of contributing to the biogeographical interpretation of the current isolated occurrences of these species in Europe, where they may be of relict origin, and to palaeoenvironmental reconstructions. We assume that species persisting in the southern Siberian refugium have retained their habitat requirements since the Last Glacial period (Horsák *et al.* 2010). For land snails, relict status is directly ascertained from their known presence in the glacial loess sediments of central Europe (e.g. Ložek 1954, 1964, 2001; Sümegei 2005; Mania 2006). For most species of vascular plants, however, relict status can only be indirectly inferred based on their modern distribution ranges, as identifications of most herbaceous plants to the species level are difficult or impossible based on fossil pollen (Bennett & Willis 2001) and macrofossils are generally rare. Therefore, only plant species with rare isolated occurrences in Europe and a major continuous distribution range in the continental central part of Asia, or those for which a more continuous distribution range in Europe during the Last Glacial is indicated by fossil records, were considered in this study as probable glacial relicts. We included not only species of zonal habitats, but also wetland plant species.

We assessed and compared climatic and habitat requirements of relict snails and (presumably) relict plants in parallel, using original data collected along a 650-km-long transect across the Russian Altai Mts, which follows the strongest climatic gradient in this area. Both macroclimatic and habitat requirements of

the target relict populations are summarized and discussed in the broader context of central European glacial-environment reconstructions. We aimed to review the modern distribution and fossil records of these species and put them into the context of the climatic and habitat affinities of their extant relict populations in southern Siberia. We believe that original field data on the ecology of these species that are often used as proxies for past environmental conditions can be very useful for interpretation of European full-glacial environments. Of prime importance are those species that are today extinct or extremely rare in central Europe, as data on their climatic and habitat affinities are very limited or completely missing. Such data may also help to understand the causes of their rarity in Europe with consequences not only for historical biogeography, but also for biodiversity conservation.

Material and methods

Study area

In order to define the climatic ranges and habitat requirements for modern populations of the target European full-glacial species, we sampled along an ~650-km-long NNW–SSE transect across a steep climatic gradient running across the northern Altai foothills and the Russian part of the Altai Mts in southern Siberia, from the Salairskii Kryazh range in the north to the Ukok plateau in the south (Fig. 1). The transect covered an elevational range from 192 to 2924 m a.s.l. and included three main climatic and vegetation zones (Kuminova 1960; Walter 1974), which differ greatly in average elevation, temperature and precipitation. Owing to increasing elevation, temperature sharply decreases from NNW to SSE. Whereas mean annual precipitation locally exceeds 800 mm in the northern Altai foothills, it decreases sharply to the south and south-east (e.g. Polikarpov *et al.* 1986), resulting in very dry conditions for the southeastern part of the Russian Altai, where intermontane basins receive <180 mm of annual precipitation (Beresneva 2006). At the scale of the whole Russian Altai, precipitation therefore decreases with the decrease in temperature. As a result, the climatic settings as well as the vegetation of the NNW part of the transect resemble those of modern central Europe except for longer winters with much lower temperatures and several months of continuous frost, in contrast to the SSE areas, which closely match the climate and biota reconstructed for the central European full-glacial (Horsák *et al.* 2010).

The low mountains in the northern part of the area are mainly forested, with *Abies sibirica*, *Betula pendula*, *Picea obovata*, *Pinus sibirica*, *P. sylvestris* and *Populus tremula* being the dominant trees. The central part is a forest-steppe and forest-tundra with woodland patches

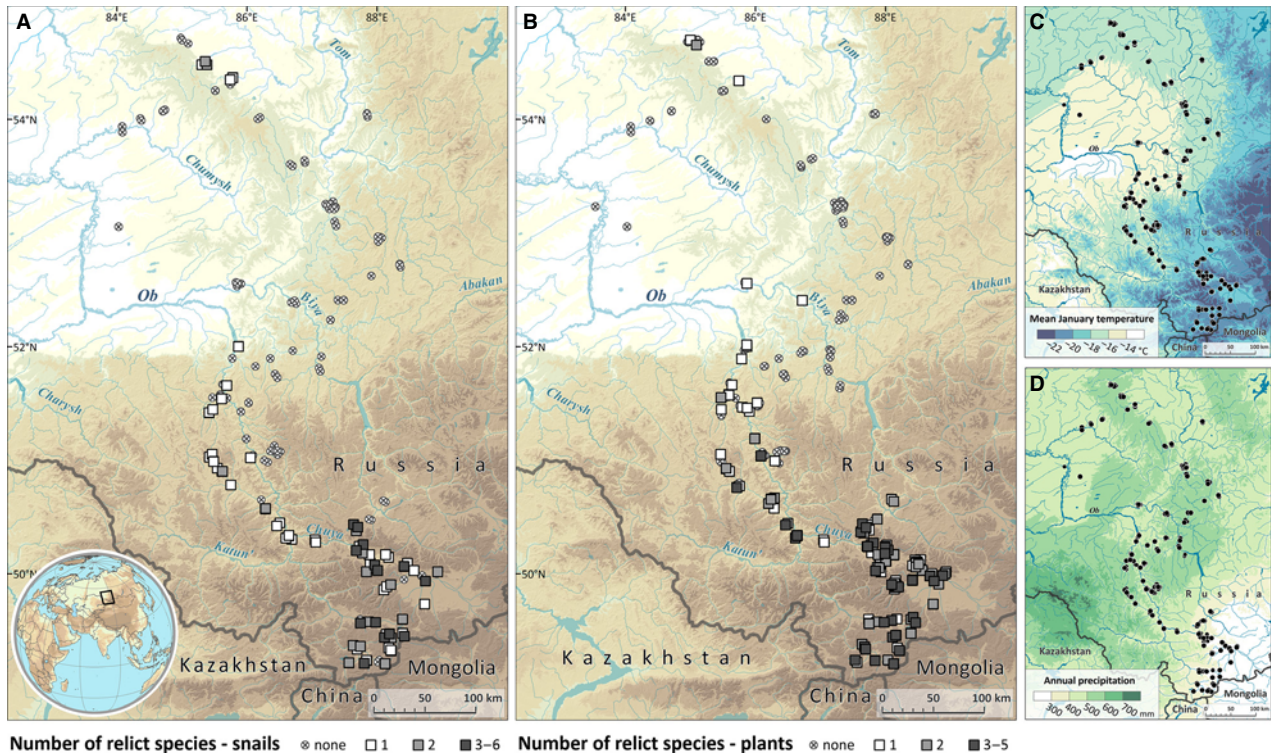


Fig. 1. Map of the study area with the position of sampling sites. Variation in numbers of recorded relict species of land snails (A) and vascular plants (B) discussed in this study is expressed by different symbols. Distributions of mean January temperature (C) and total annual precipitation (D) are shown across the study area.

dominated by *Larix sibirica*, *Picea obovata* and *Pinus sibirica*. The southern part is predominantly an open landscape with steppe and tundra grasslands, locally with small patches of *Larix sibirica* woodland. For further details on the environment of the Russian part of the Altai Mts see Horskák *et al.* (2010).

Species sampling

Vascular plants were recorded from 570 quadrats of 100 m² in area that represented locally predominant habitat types along the transect (Fig. 1). All vascular plant species were recorded in each plot. Species that could not be identified in the field were collected and identified subsequently using the Flora of Siberia (Krasnoborov 1987 *et seq.*) and a comparative herbarium collection. Plant specimens are stored at the Herbarium of Masaryk University (BRNU). In general, the taxonomy and nomenclature of vascular plants follow the Flora of Siberia as summarized by Baikov (2005). Wherever necessary, information is given on the taxonomic concept accepted for the purpose of this study.

Land snails were sampled from 315 of the 570 vascular plant quadrats using habitat-specific sampling techniques that allowed for optimal encounter rates and maximal inventory of the snail assemblage from each plot. In non-wetland habitats snails were carefully searched for by eye from all microhabitats. Sampling

continued until no new species were found over a 15-min period and until all species were represented by at least three individuals. Using this rule, species-poor sites (e.g. dry loess steppes) were never sampled for <30 min, whereas at richer sites (herb-rich forest plots or calcareous rock outcrops) sampling generally took no more than an hour to complete. In damper habitat types (i.e. mires, fens, wet tundra and alluvial vegetation), a 12-litre sample of the soil organic horizon including topsoil, litter, bryophytes and herbaceous vegetation was collected and processed in the field using the wet-sieving method (Horskák 2003). All recorded shells and live shelled snails were collected and kept dry; samples were identified under a dissecting microscope in the laboratory using the available literature (Meng 2009; Sysoev & Schileyko 2009; Horskák *et al.* 2010, 2013a) and the first author's comparative collection of Siberian snail specimens. All samples are stored in the collection of Michal Horskák (Brno). Nomenclature and taxonomy generally follow Sysoev & Schileyko (2009), with Nekola *et al.* (2015) used for the genus *Pupilla*.

Environmental variables and data analysis

For each site with a record of any of the target relict species, total annual precipitation and mean January and July temperatures were obtained from the WorldClim database (Hijmans *et al.* 2005,

www.worldclim.org) using the ArcGIS 8.3 program (www.esri.com). We chose then mean temperature of the coldest month as it has repeatedly emerged as the most important thermal parameter that may constrain the geographical distribution of land snails (e.g. Moine *et al.* 2002; more details also below). By contrast, total annual precipitation is amongst the most important predictors for vascular plants in continental areas (Adler & Levine 2007; Chytrý *et al.* 2007; Yang *et al.* 2010), although their direct effect on snails is not so obvious. Because of strong correlations amongst the sums of annual, summer and winter precipitation ($\rho > 0.87$), we used only the total annual precipitation, which appeared to be the most informative measure of precipitation in our previous study of the distribution of glacial snails in the study area (Horsák *et al.* 2010). As both taxa can also be influenced by summer temperatures, we completed the data by mean temperature of the warmest month. All above mentioned climatic characteristics were used, along with the annual temperature, to show the climate affinities of the target species and to provide data for comparisons with the estimates commonly derived from palaeoclimatic reconstructions and transfer functions.

Plots with target species present (95 plots for snails; 234 for plants) were classified into 11 habitat types according to vegetation structure, plant species composition and abiotic environmental factors (Table 2, Fig. 2). The number of sampled sites approximately reflected the frequency of a particular habitat type in the landscape.

The variation of individual climatic values for sites containing each target species was graphically presented using beanplots (Kampstra 2008). Apart from showing each measurement, the beanplots provide an easy visual comparison of the studied groups by showing the density of distribution. The overall median values were calculated separately from all records of glacial relict snail or plant species (Table 1). We used individual species records instead of plots to give a proportionally higher importance to plots with more species; e.g. climatic values of a plot with five species were used as five independent values. Beanplots were created in R (version 2.15.1, R Core Team 2012) with the use of the 'beanplot' package (Kampstra 2008).

Results and discussion

In the following text and graphs (Figs 3, 4), species are ordered by their temperature requirements, ranging from the most cold-adapted to the most warm-demanding.

Land snails

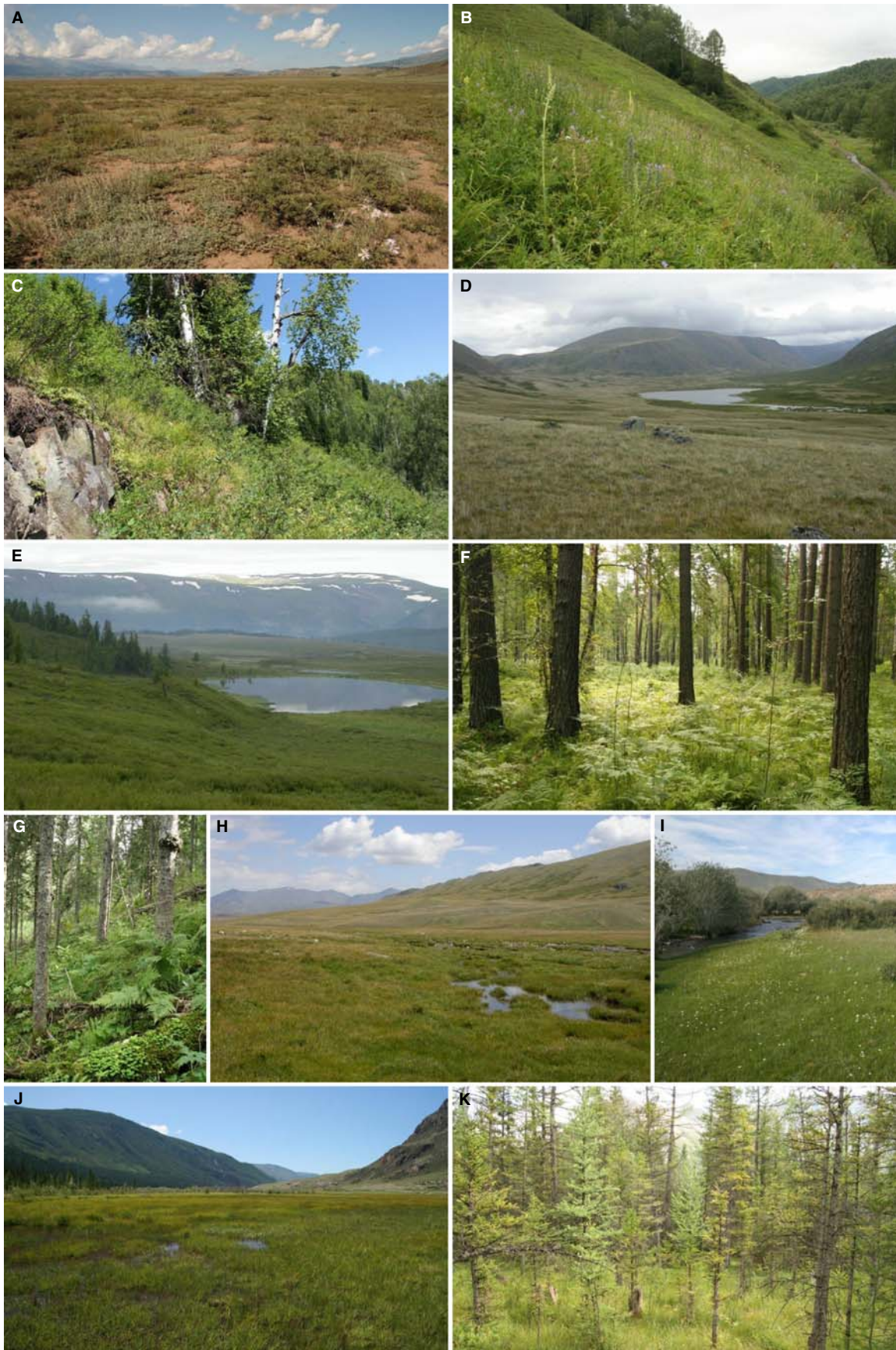
From 315 plots sampled for snails in the Russian Altai Mts (Fig. 1), we obtained 109 records of six target

land-snail species (i.e. *Columella columella*, *Pupilla alpicola*, *P. loessica*, *Vallonia tenuilabris*, *Vertigo parcedentata* and *V. pseudosubstriata*; Table 1) that, based on loess fossil evidence from central Europe (Ložek 1964, 2000), characterize full-glacial environments. Thirty-six records of *Pupilla turcmenica* and twenty-five records of *Vertigo* aff. *genesii* were also included. Both of these taxa are morphologically and ecologically similar central Asian or Beringian siblings of the European *Pupilla sterrii* (Nekola *et al.* 2015) and *Vertigo genesii* (Nekola unpubl. data), respectively, which are common and abundant in central European loess assemblages (e.g. Ložek 2000). *Pupilla sterrii* is common in contemporaneous limestone steppes of central and eastern Europe (Kerney *et al.* 1983), whereas *Vertigo genesii* is an arcto-alpine European endemic known from the UK and Scandinavia and extending to western Russia and south into the Alps (Cameron *et al.* 2003).

Pupilla loessica. – *Pupilla loessica* is a steppe-tundra species that is currently restricted to cold areas of the central Asian mountain systems (Meng & Hoffmann 2009; Horsák *et al.* 2010), with related sibling species occurring in southwestern (Hokkaido) and eastern (Alaska) Beringia (Nekola *et al.* 2015). However, it is also a characteristic full-glacial fossil in loess deposits across almost the whole of temperate Europe, except in areas west of the Rhine valley (e.g. Ložek 1964, 2001; Rousseau 2001). It was first described based on fossil material from Moravia (Czech Republic) and until recently was considered to be extinct (cf. Meng & Hoffmann 2009). Lately it has been found to occur commonly in the Tien Shan and Altai Mountains, northern Mongolia and near Lake Baikal (Meng & Hoffmann 2009; Horsák *et al.* 2010).

Its modern distribution in the Altai is limited to areas with a dry and cold climate (Figs 3, 4). In some places it represents the only snail species capable of surviving in extremely harsh environments, e.g. in the Chuya basin, Ukok plateau, and adjacent mountain passes in the southeastern part of the Russian Altai (Fig. 1). In these areas it is confined to *Betula rotundifolia* tundra or to sparse *Larix sibirica* woodlands with a well-developed moss layer. Although it commonly inhabits both grassland and shrub tundra, it can also be found in a variety of other habitats, including wetlands (Table 2) where shells may be almost twice as large (Nekola *et al.* 2015).

Given its modern ecological preferences, it is likely that it may have lived in various glacial habitats across the European steppe-tundra zone (Ložek 2001; Meng & Hoffmann 2009; Hoffmann *et al.* 2011). In some European loess deposits it represents the only snail species, yet occurs in high numbers. This is exactly the pattern observed in its driest habitats in the Altai. It is important to remember, however, that in contempora-



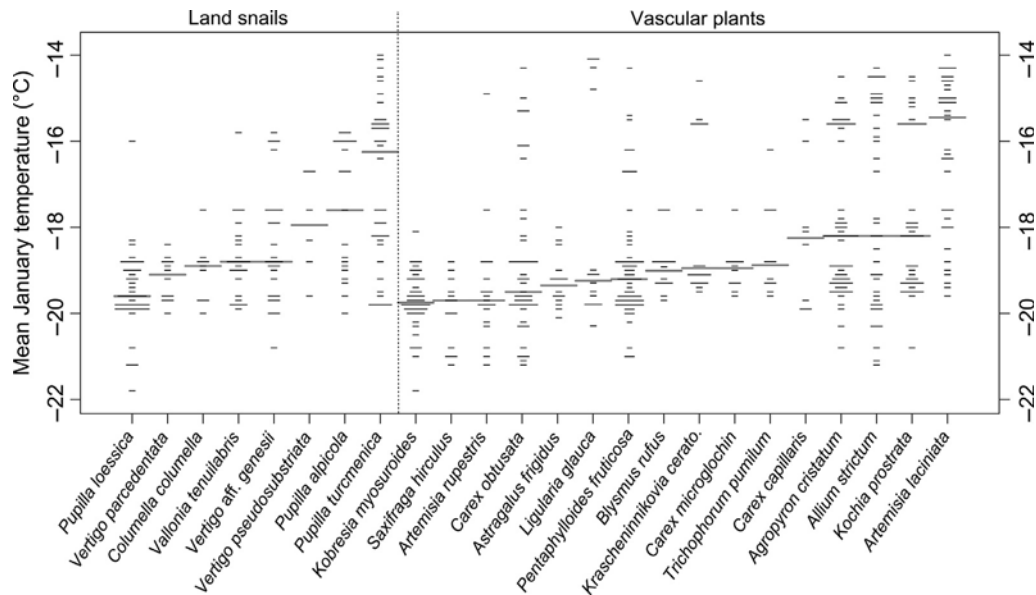


Fig. 3. Mean January temperatures of sites with records of relict snail and plant species. The longest grey line refers to the median value; lengths of the shorter black lines correspond to the number of sites with the same climatic value (ranges from one to six).

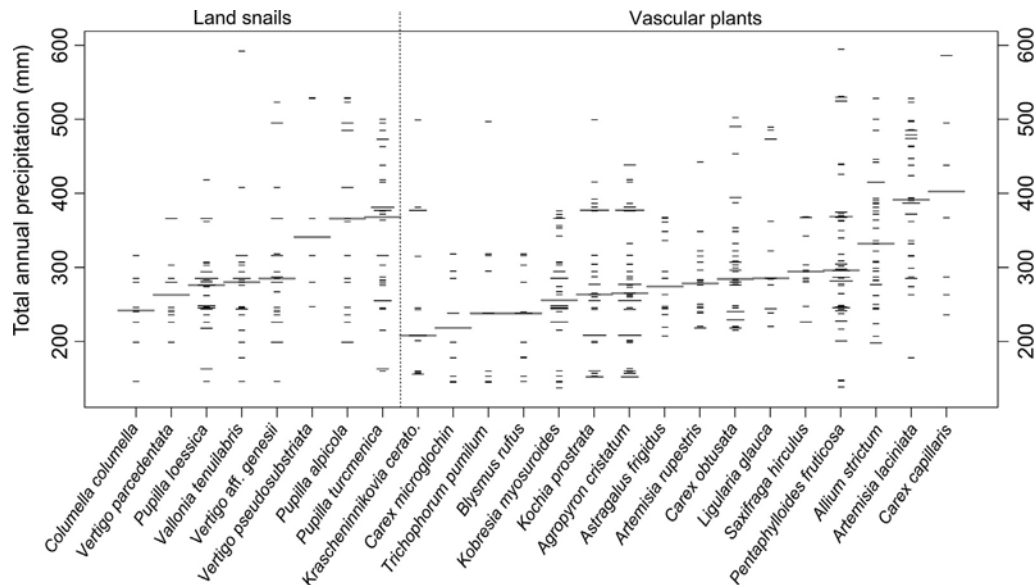


Fig. 4. Total annual precipitation of sites with records of relict snail and plant species. See Fig. 3 for details.

neous environments it also occurs in damper habitats where it may co-occur with species like *Pupilla alpicola* and *Vertigo parcedentata* (Table 2); however, such wet to mesic assemblages were much less likely to be preserved through loess deposition and are thus under-represented in the fossil record.

Vertigo parcedentata. – *Vertigo parcedentata* is a sub-alpine wetland species originally described on the basis of fossils from loess near Wiesbaden, Germany. It was later discovered living at four sites near Kongsvoll in the Dovrefjell National Park in central Norway (Pokryszko 1993). Very recently it was also recorded in the

Fig. 2. Habitats in which the studied land snail and vascular plant species occur in the Russian Altai Mountains (from left to right and top to bottom): A. Dry steppe. B. Meadow steppe. C. Steppe scrub. D. Tundra grassland. E. Tundra scrub. F. Herb-rich forest. G. Taiga forest. H. Wet grassland. I. Saline grassland. J. Open fen. K. Wet woodland. The habitat classification and the order of habitat types are as in Table 1. Photographs by P. Hájková (A–C, F, G, I, J), M. Horsák (D, E, H) and M. Chytrý (K).

Table 1. Climatic descriptors of the sites with records of at least one target species of snails and plants. Values are also provided for all snail species first and then for all snail species except *Pupilla turcmenica* (see text for explanation).

	Median	Mean	SD	Min.	Max.
All snails					
Mean January temperature (°C)	-18.8	-18.4	1.56	-21.8	-14.0
Mean July temperature (°C)	13.5	14.2	2.58	8.3	20.5
Mean annual temperature (°C)	-2.4	-1.9	2.00	-6.7	3.4
Total annual precipitation (mm)	283	304	93.5	146	592
Snails except <i>Pupilla turcmenica</i>					
Mean January temperature (°C)	-19.0	-18.8	1.25	-21.8	-15.8
Mean July temperature (°C)	13.1	13.5	2.19	8.3	19.5
Mean annual temperature (°C)	-2.9	-2.4	1.70	-6.7	1.6
Total annual precipitation (mm)	280	295	90.7	146	592
Plants					
Mean January temperature (°C)	-19.1	-18.4	1.83	-21.8	-14.0
Mean July temperature (°C)	13.4	14.2	2.77	8.3	20.5
Mean annual temperature (°C)	-2.5	-1.8	2.26	-6.7	3.4
Total annual precipitation (mm)	285	301	94	137	593

Altai (Meng 2008; Horsák *et al.* 2010) and Tien Shan (Meng 2008) mountains of central Asia. Based on both mitochondrial and nuclear markers, European and central Asian populations have been confirmed to be part of the same species-level clade (J.C. Nekola, unpublished data).

In the Russian Altai it is predominantly associated with willow scrub in riparian corridors and fens. Its association with such wet and patchily distributed habitats may explain its relatively common occurrence, but low numbers, in loess deposits (e.g. Ložek 2001): it is possible that in Pleistocene Europe this species occurred in wet habitats adjacent to the loess zone (wet depressions, toe-slope seepages etc.), and only accidentally strayed into the dry loess steppe matrix. This hypothesis is supported by its record from Lateglacial calcareous fen sediments in the intermountain basins of the Western Carpathians in Slovakia (Hájková *et al.* 2015a).

Columella columella. – *Columella columella* is a circumboreal arcto-alpine species typical of willow scrub, wet tundra and taiga seeps. It is common in cold regions of Norway (Pokryszko 1993), inhabits alpine tundra grasslands in the calcareous ranges of the Alps and Carpathians (Kerney *et al.* 1983; Horsák *et al.* 2013a), is known from several mountain systems of central Asia (e.g. Sysoev & Schilevko 2009) and occurs in similar habitats throughout boreal and arctic North America (Nekola & Coles 2010).

In the Altai refugium, most populations are associated with alluvial fen woodlands and treeless fens (Table 2). Despite this clear affinity for wetland sites (see also Hoffmann *et al.* 2011), climate data indicate that *C. columella* occurs in the driest regions, where annual precipitation is <300 mm. Perhaps this restriction is related to the fact that groundwater in such

regions will typically contain higher levels of dissolved cations.

These observations may help explain the presumed diversity of habitat preferences for this species at the Pleistocene/Holocene transition, when *C. columella* appeared not only as a xerophilous species able to persist in loess-mantled uplands (Ložek 1964), but was also capable of establishing large populations in calcareous wetlands (Ložek 2007; Hájková *et al.* 2015a). With Lateglacial climate amelioration and the increase in precipitation, calcareous wetlands may have become more frequent and provide the principal habitat for this species. It is also possible that shells found in loess deposits represent temporary populations that flourished only during wetter periods, as also suggested by the data from the Nussloch loess series (Moine *et al.* 2008). This is also the only characteristic glacial species commonly found in the Weichselian upper pleniglacial loess deposits west of the Rhine valley, especially close to the Channel coast (Moine 2014; O. Moine, pers. comm. 2014), i.e. in areas of high humidity. In Britain it persisted into the early Holocene (e.g. Preece & Bridgland 1999).

Vallonia tenuilabris. – *Vallonia tenuilabris* is typical of steppe-tundra, but also inhabits various habitats ranging from dry steppes to wet forests across central and southern Siberia (Gerber 1996). Its occurrence is concentrated in the mountain systems of central Asia (Meng 2009; Horsák *et al.* 2010), but it has also been found on the northern Siberian plains, such as in central Yakutia (Horsák *et al.* 2013b). It is a common and characteristic species of central European loess assemblages (Ložek 1964; Meng 2009), which became extinct in Europe at the onset of the Holocene (e.g. Horáček & Ložek 1988; Ložek & Cílek 1995).

Table 2. Habitat preferences of the studied full-glacial land-snail (shaded) and vascular plant species (nonshaded). The relative percentage of the species records amongst 11 habitat types is shown for each species with the highest percentage value given in bold. The species are classified as preferring steppe (i.e. mostly recorded in dry or meadow steppes), tundra (mostly recorded in tundra grassland or scrub) or wet habitats (mostly recorded in saline grassland, open or woodland fens). The last snail species was not classified as it was rare and exhibited no distinct habitat preferences. Dash (-) indicates species absence in the habitat.

Habitat types	Steppe										Tundra					Wet habitats								
	<i>Koehia prostrata</i>	<i>Agropyron cristatum</i>	<i>Krascheninnikovia ceratoides</i>	<i>Papilla turcmenica</i>	<i>Allium strictum</i>	<i>Carex obtusata</i>	<i>Artemisia lachnata</i>	<i>Kobresia myosuroides</i>	<i>Saxifraga hirculus</i>	<i>Artemisia rupestris</i>	<i>Ligularia glauca</i>	<i>Papilla loessica</i>	<i>Pentaphragmoides fruticosa</i>	<i>Astragalus frigidus</i>	<i>Trichophorum punctatum</i>	<i>Blysmus rufus</i>	<i>Carex microglochin</i>	<i>Papilla alpicola</i>	<i>Vallonia tenuilabris</i>	<i>Verigo aff. genesii</i>	<i>Verigo parcedentata</i>	<i>Carex capillaris</i>	<i>Columella columella</i>	<i>Verigo pseudosubstrata</i>
Dry/typical steppe	97	93	88	56	35	24	8	5	11	14	8	6	-	-	-	-	-	-	-	-	-	-	-	-
Meadow steppe	3	-	-	11	22	22	44	-	28	21	8	5	-	-	-	-	5	-	-	-	-	-	-	-
Steppe scrub	-	6	12	17	19	-	8	-	6	7	5	3	-	-	-	-	-	4	-	-	-	-	-	-
Tundra grassland	-	-	-	3	19	22	6	37	33	29	25	22	-	-	10	-	11	-	13	25	-	-	-	-
Tundra scrub	-	-	-	-	7	7	3	26	6	7	20	22	29	-	-	-	5	13	16	-	-	-	-	33
Herb-rich forest	-	2	-	11	5	22	17	3	11	14	13	5	21	-	-	-	5	4	4	-	-	-	-	-
Taiga forest	-	-	-	-	-	2	-	-	-	-	5	2	29	-	-	-	5	4	4	-	-	-	-	-
Wet grassland	-	-	-	-	-	-	3	8	6	7	3	9	14	-	-	16	16	9	8	8	13	11	33	-
Saline grassland	-	-	-	-	-	-	6	5	-	-	-	-	-	60	54	40	-	4	4	-	-	-	-	-
Open fen	-	-	-	3	-	-	6	16	23	-	10	11	-	30	31	50	32	13	32	25	-	33	-	-
Wet woodland	-	-	-	-	-	-	6	-	-	-	5	16	7	7	8	-	26	22	36	42	50	56	33	-
No. of records	38	54	17	36	37	41	36	38	13	14	40	64	14	10	13	10	19	23	25	12	8	9	6	6

Although it was found in almost all habitat types at high elevations in the Altai (Table 2) the largest populations were recorded from wet habitats such as open and wooded fens. However, it was also observed in two dry steppes and at one steppe scrub site. The ability of this species to occupy environmentally diverse conditions may explain its common occurrence in European loess (Meng 2009).

Vertigo aff. genesii. – *Vertigo aff. genesii* is the Berinian sibling to the European arctic/alpine *Vertigo genesii* that ranges from the Altai through Yakutia, Mongolia, Hokkaido and Alaska to central Manitoba and the Gulf of St Lawrence in Quebec (Nekola & Coles 2010; J.C. Nekola, unpublished data). Altaian populations of this species have previously been identified based on conchological characters as *V. genesii* (Meng 2008; Horsák et al. 2010; Hoffmann et al. 2011), which is otherwise known from calcareous parts of the Scandinavian mountains with isolated populations extending to the British Isles and the Alps (Schenkova & Horsák 2013). Prior contact between these two species is suggested by the introgression of typical *V. genesii* mtDNA into some Altaian populations of *V. aff. genesii* which possess typical nDNA sequence for that entity (J.C. Nekola, unpublished data).

Throughout its extensive range *Vertigo aff. genesii* is largely limited to graminoid-dominated fens or other wetlands (Nekola & Coles 2010). Its habitat thus basically mimics *V. genesii*, although the latter species appears more constrained to base-rich habitats. In the Altai, *V. aff. genesii* is the second most common full-glacial relict snail, being recorded from 25 sites, often in large populations, especially in graminoid-dominated fens and seepages. Several populations were also found in wet tundra habitats.

In the central European Quaternary, *V. genesii* was common during the warm phases of the Lateglacial and early Holocene (Ložek 1964; Hájková et al. 2015a). Although Ložek (2001) did not consider *V. genesii* characteristic of central European loess environments (fossil records from loess deposits are very rare; see Moine et al. 2008), the observed climatic preferences of *V. aff. genesii* in the Altai refugium are very similar to those of the characteristic loess species *Vallonia tenuilabris* and *Pupilla loessica* (Figs 3, 4). The general absence of *V. genesii* from loess assemblages is probably due to its restriction to wetland habitats. It is therefore likely that it only strayed accidentally into upland sites where loess was being deposited.

Vertigo pseudosubstriata. – *Vertigo pseudosubstriata* has a similar modern and Pleistocene/Holocene distribution to *Pupilla loessica*. Originally described from Czech Republic Pleistocene loess deposits (Dolní

Věstonice) in 1954 and it was discovered to be extant about 30 years later in the Tien Shan Mts and subsequently from several other central Asian mountain ranges (e.g. Meng 2009; Sysoev & Schileyko 2009; Horsák et al. 2010).

It is the least frequent glacial relict snail species found in the Altai, having a scattered distribution in isolated habitats such as fens, seepage slopes and humid shrublands. It was absent from a number of seemingly suitable sites across the region. Its climatic range in the Altai matches that of relict species that survived in temperate Europe such as *Pupilla alpicola*.

This species is also rare in loess deposits of central Europe (Ložek 2001). Perhaps its patchy contemporaneous distribution centred on wet-mesic sites helps to explain its rarity in loess deposits.

Pupilla alpicola. – *Pupilla alpicola* inhabits treeless alkaline fens and fen meadows, and until recently was only known from the Alps and Carpathians (Kerney et al. 1983; Horsák et al. 2011). Recent molecular studies (Nekola et al. 2015) have demonstrated that this species also includes the more highly calcified shells previously termed *Pupilla pratensis*. As a result, the modern distribution of this species has been considerably expanded both to the west (British Isles, Scandinavia) and east (Altai) (Horsák et al. 2010). It is likely that at least some (e.g. appendix S1 in Horsák et al. 2010) or all records of *P. muscorum* reported from interior Asia actually represent *P. alpicola*. Careful examination of shell microsculpture and architecture (rather than apertural characters) is required for accurate species assignment in this genus (Nekola et al. 2015).

In the Altai this species was found in various high-humidity habitats such as open fen and fen woodland, with some populations also occurring in wet shrub tundra (Table 2).

Pupilla alpicola, namely its form *densegyrata*, is characteristic of the younger loess sediments in central Europe (Ložek 2001), and should be considered a local Lateglacial relict (Ložek 1964; Horsák et al. 2011). Ložek (1964, 2001) reported various ecomorphological forms of *P. alpicola* from central European full-glacial deposits that may correspond to the ecophenotypic variation observed in modern populations.

Pupilla turcmenica. – *Pupilla turcmenica* is a central Asian species that inhabits steppe and other dry, treeless habitats (Sysoev & Schileyko 2009). Based on shell shape, whorl expansion and periostracal microsculpture, it resembles the characteristic central European loess species *Pupilla sterrii*, which was widespread and one of the most abundant species of loess assemblages (Ložek 2001). This species remains common across central and southeastern Europe (Kerney et al. 1983) where it is mainly confined to rocky or very stony

steppe or other open-land habitats (Horsák *et al.* 2013a). DNA sequence analysis has shown *P. sterrii* and *P. turcmenica* to be sibling taxa (Nekola *et al.* 2015), with the latter perhaps being a subspecies of the former.

Pupilla turcmenica, as an ecomorphological parallel to European *P. sterrii*, is the only characteristic glacial species found almost exclusively in the dry steppe habitats in the Altai, which were occupied by the species in climatically diverse areas including those with the highest temperature and precipitation (Figs 3, 4). Most populations were found in rocky or very stony dry habitats and the species expressed remarkable ecophenotypic variation in the development of apertural calcification, including the populations corresponding to putative *Pupilla altaica*, which was found to be conspecific with *P. turcmenica* on the basis of genetic analyses (Nekola *et al.* 2015). This variability appears to be linked to soil calcium content and aridity. Hoffmann *et al.* (2011) also reported *P. turcmenica* only from very dry habitats, but as they restricted it to only that part of the species' morphological variation corresponding to the putative species *P. altaica*, they biased the climatic affinities of the species to warm conditions. Based on our findings we suggest that loess populations of *P. sterrii* also expressed a strong affinity to very dry habitats in different macroclimatic contexts.

It is important to note that the characteristic and widespread snails of loess assemblages (*sensu* Ložek 2001), which managed to survive across the lowlands of temperate Europe, are species of either dry steppe habitats, e.g. *Pupilla sterrii* and *Helicopsis striata* or are generalists, e.g. *Succinella oblonga* and *Trochulus hispidus*.

Vascular plants

From 570 quadrats sampled for vascular plants in the Russian Altai (Fig. 1), we identified 16 species (i.e. *Agropyron cristatum*, *Allium strictum*, *Artemisia laciniata*, *A. rupestris*, *Astragalus frigidus*, *Blysmus rufus*, *Carex capillaris*, *C. microglochis*, *C. obtusata*, *Kobresia myosuroides*, *Kochia prostrata*, *Krascheninnikovia ceratoides*, *Ligularia glauca*, *Pentaphylloides fruticosa*, *Saxifraga hirculus* and *Trichophorum pumilum*) that occurred in at least seven quadrats while also being characteristic of full-glacial environments in central Europe. In total, these species were represented by 425 occurrences.

Kobresia myosuroides. – *Kobresia myosuroides* is a circumpolar species distributed in the arctic zone of Asia and North America, and in the mountains of the boreal and temperate zones of Eurasia and North America (Meusel *et al.* 1965). In Europe, it is found in

western Scandinavia, and the Pyrenees, Alps, Carpathians, Apennines and Dinarids.

In these mountain ranges it is generally confined to wind-exposed summits where it grows with short hemi-cryptophytes and chamaephytes (including cushion plants) and numerous species of bryophytes and lichens (Petřík *et al.* 2005, 2006). Many common features shared by *Kobresia* grassland across the whole of northern Eurasia (Ohba 1974) support the assumed relict status of *Kobresia myosuroides* in the mountain ranges of the European temperate zone.

In the Altai *K. myosuroides* is a typical species of high-mountain tundra in the dry continental parts of this mountain range (Figs 3, 4). In places it is a dominant or co-dominant species of mesic tundra grasslands (Table 2), but it also grows in patches of wind-swept tundra with *Dryas oxyodonta* or in tundra scrub dominated by *Betula rotundifolia*. It occasionally also occurs in valley bottoms or intermountain basins where it is usually confined to wetter sites such as fens, and wet and saline grasslands.

Saxifraga hirculus. – *Saxifraga hirculus* is a circumpolar arctic-boreal species with disjunct occurrences in the mountain systems of Europe and interior Asia including the Caucasus (Meusel *et al.* 1965). In Europe, scattered populations exist, or once existed, in Romania, Switzerland, France, the British Isles, northern Poland, the Baltic Countries and Scandinavia, but the species has been declining and is becoming endangered across Europe (Vitozz *et al.* 2006). A more continuous distribution starts in northern Poland and continues eastwards. Magyari *et al.* (2014a,b) found a continual pollen record of *S. hirculus* in a lake sediment dated back to the Last Glacial Maximum in the Harghita Mts in Romania, a region where the species has survived in fen refugia up to the present (Kerekes 2008). Refugial European populations are limited to brown-moss fens with a stable water table (either acidic or alkaline) situated close to the soil surface (Vitozz *et al.* 2006), where the species apparently experiences low competition pressure as it probably did in the cold glacial tundra. These sites tend to occur in lowlands or mountain basins rather than in once-glaciated sub-alpine or alpine zones.

In the Altai it grows in areas with a strongly continental climate where it prefers wet habitats such as tundra grasslands with *Dryas oxyodonta* and tundra scrub dominated by *Betula rotundifolia*, *Pentaphylloides fruticosa* and various *Salix* species. When the moss layer is well developed, *S. hirculus* reaches only low abundances. It also lives in open fens and wet grasslands (e.g. in the Dzhazator valley and on the Ukok plateau), where it can locally reach high abundance.

The genetic structure of European and North American populations reveals higher haplotype diversity outside the limits of the last glaciations, suggesting that it survived the cold stages in the periglacial zone (Oliver *et al.* 2006). Molecular sequencing of organic sediments preserved in permafrost documents its full-glacial presence in nonglaciated northeastern Russia (Sønstebo *et al.* 2010).

Artemisia rupestris. – *Artemisia rupestris* has a distribution range similar to that of *A. laciniata* (see below), including the southern half of Siberia and adjacent parts of central Asia (Jäger 1987; Meusel & Jäger 1992; Yourun *et al.* 2011) and was also reported from a single site in the southwestern Yukon Territory (Shultz 2006). However, this population was recently re-evaluated as a distinct species not closely related to *A. rupestris* (Riggins & Seigler 2012). In Europe, isolated populations are situated in northern Russia and on the Baltic islands of Saaremaa, Öland and Gotland. Occurrences in central Germany disappeared by the early 20th century (Jäger 1987). All of these regions are characterized by a rather continental climate.

At its German sites, *A. rupestris* was confined to saline pastures and meadows. The sites in the Baltic region are found on shallow limestone soils of alvars and seashores. In both habitats, the species is protected from competition either by salinity or by other soil properties (Jäger 1987).

In the Altai *A. rupestris* occurs in dry high-mountain landscapes, most typically at altitudes above 2000 m. It is also occasionally found on valley bottoms at lower altitudes. It occurs in various types of grasslands, most often in mesic high-mountain grasslands (steppe-tundra), but also in meadow steppes and dry steppes on south-facing slopes at high altitudes (Table 2). It can be rarely found in low scrub (*Betula rotundifolia* and *Caragana arborescens*) or in open larch forests.

Pentaphylloides fruticosa. – *Pentaphylloides fruticosa* (syn. *Potentilla fruticosa*) is a species with a continuous North American and central and east Asian distribution, and several disjunct occurrences in central and western Europe (Meusel *et al.* 1965), and being more frequent east of the Urals and Caucasus. One population is found in Bulgaria (Rhodopes Mts) and several in the Pyrenees, British Isles, Baltic Countries and southern Sweden. Although this species prefers cold, but usually neither high-mountain nor arctic regions in Eurasia, it occurs in North America in a wide variety of mostly calcareous habitats (including fens and xeric rock outcrops; Nekola 1990) ranging from near sea level to alpine meadows. A phylogeographical study based on chloroplast DNA, carried out on the Qinghai-Tibetan plateau, suggested that *P. fruticosa* expanded its range on the plateau during the periods

of climatic cooling and contracted to the interior high-mountain region during warmer periods (Shimono *et al.* 2010).

In the Altai this is a common species that occupies various habitats but favours tundra shrub and wet woodlands. Considering the climatic affinities of the modern Altai populations, it may be assumed that European and central Asian populations were interconnected during the last glacial period when the landscape was open and temperatures at low altitudes in central Europe were similar to those that currently occur in the south Siberian mountains (e.g. Isarin & Renssen 1999). Germination experiments (Meshinev 1975) showed that this species needs a sufficient amount of light to germinate and establish. This indicates that the bottleneck for *P. fruticosa* survival was probably the Holocene climatic optimum, when open, unproductive or disturbed habitats suitable for regeneration of this species were rather rare.

Carex obtusata. – *Carex obtusata* is a circumpolar species (Meusel & Jäger 1992) with a more or less continuous distribution range in southern Siberia (Malyshev 1990), occurring further in adjacent parts of central Asia in Kazakhstan, Mongolia and northern China (Tang *et al.* 2010). It is further present in the Caucasus and in North America (Ball & Reznicek 2002). Yurtsev (1982) considered *C. obtusata* to be a typical species of the Beringian steppe-tundra (see also Kucherov & Daniëls 2005). In Europe, it is scattered throughout European Russia and Ukraine, and is found on the Swedish island of Gotland, at four sites in central Germany (Schultze-Motel 1967–1980), and at two localities in the eastern part of the Czech Republic (Řepka 2007).

The German populations, of which only one is still extant, occur in dry grasslands or open pine forests on sandy soils (www.floraweb.de). Both Czech populations are found in dry steppe grasslands on shallow acidic soil.

In the Altai *C. obtusata* is a widespread species of various steppe and tundra grasslands and open larch forests especially in dry continental areas (Table 2). It often co-occurs with *Artemisia rupestris*, but it is more common than this species and shows a stronger preference for drier steppe and dry larch forests. These affinities suggest that it may have been common in the European glacial landscape and that the current isolated localities may be remnants of its past, larger range.

Astragalus frigidus. – *Astragalus frigidus* is a remarkably variable Eurasian taxon with a distribution extending from northernmost Europe and the lowlands of northern Siberia to the Far East, Japan, southern Siberian mountain systems and the adjacent parts of central Asia (Meusel & Jäger 1992; Xu &

Podlech 2010). It is now divided into three subspecies (e.g. Vydrina 1994; Elven 2014), of which the type subspecies is present both in Europe and in the Altai. The European distribution of *A. frigidus*, now rather fragmentary, was probably more continuous in the Pleistocene, as indicated by Lateglacial fossil records from the Baltic Sea area (Hultén & Fries 1986).

In the Alps it occurs most frequently in alpine grasslands on steep slopes or convex ridges on slightly calcareous soils, usually at elevations of 1700–2500 m a.s.l., whereas its northernmost localities in Norway are situated almost at sea level (Gams 1923–1924).

In the Altai *A. frigidus* is a species of continental high-mountain landscapes, in which it is confined to various types of forests and open woodlands dominated by *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, scrub with *Betula fruticosa* (*B. humilis* s. lat.) and *Pentaphylloides fruticosa*, and sub-alpine tall-forb vegetation. It avoids dry or mesic short grasslands (Table 2).

Ligularia glauca s. lat. – *Ligularia glauca* is a European-Siberian species with a strongly disjunct range in Europe and a continuous distribution in the southern parts of western and central Siberia (Ermakov *et al.* 1999). The European populations are morphologically slightly different from those in Siberia, sometimes being considered as different subspecies or as the species *L. carpathica* (e.g. Pojarkova 1961). In all European countries where the species occurs (Slovakia, Romania, Bulgaria and Ukraine) it is critically endangered and considered as a glacial relict (Tomescu & Chifu 2009; Kricsfalussy & Budnikov 2007). In Europe, *L. glauca* grows on limestone outcrops with semi-open vegetation (Slovakia; Hajdúk 1957), semi-dry grasslands (Romania, Ukraine), calcareous fens (Romania; Tomescu & Chifu 2009) and sub-alpine tall-herb vegetation (Bulgaria; Roussakova 2002). Although these habitats differ in many attributes, they all share an open or semi-open structure with certain continuity during the Holocene (Fajmonová *et al.* 2013). Presumably this species may have been widely distributed in central and eastern Europe under the strongly continental climate of the glacial period.

In the Altai *L. glauca* has two ecological optima. In the more humid climate of the northern Altai, it prefers meadow steppes with *Brachypodium pinnatum*, *Calamagrostis arundinacea*, *Crepis sibirica* and *Phlomis tuberosa*, but it also occurs in drier steppes (with *Aster alpinus* and *Iris ruthenica*) and in herb-rich birch forests (Table 2). By contrast, it occupies tundra grasslands and tundra scrub in the continental southern part of the Altai (e.g. Ukok plateau, Kurai and Chuya ranges).

The fact that most European localities are concentrated at low or middle elevations in summer-warm southeastern Europe suggests that this species does not require cold climate *per se*. It rather benefits

from high light availability and soil conditions associated with continental climate (Fig. 2).

Blysmus rufus. – *Blysmus rufus* is currently distributed in three distinct regions: (i) the Atlantic and Baltic Sea coast in northern and northwestern Europe (the Netherlands, Scotland, Denmark, Scandinavia, Baltic Countries, NW Russia); (ii) central Asian, strongly continental mountains and (iii) North American sea coasts (Meusel *et al.* 1965). Along the sea coast, it occupies dune slacks (Hofstra 1996) and salt-marshes, whereas in central Asia (Altai and Trans-Altai region) it occupies saline meadows on clayey soils (von Wehrden *et al.* 2006; e.g. *Trichophorum pumilum* halophytic fen grasslands, Dítě *et al.* 2013).

In the Altai *B. rufus* mostly grows in saline grasslands dominated by *Halerpestes salsuginosa* and *Glaux maritima*, and open fens with a well-developed bryophyte layer. It was recorded in river floodplains of the Chuya basin and Ukok plateau, and in the Menka and Chuya river valleys, where it frequently co-occurred with *Trichophorum pumilum* and *Carex microglochis*. An important environmental factor for *B. rufus* is high pH and high mineral or salt content. This environmental feature is common for European sea-coasts and also for central Asian alluvial meadows and fens where it is supported by salinization because of low summer precipitation.

In Eurasia the two modern centres of distribution may represent refugia from a once more continuous full-glacial range, as supported by fossil seeds found in Lateglacial sediments far from modern occurrences in southwestern Slovakia (Borská lowland; Hájková *et al.* 2015b). Here, numerous *Blysmus* sp. seeds were found along with the seeds of *Triglochin maritima*. We hypothesize that during the glacials, *Blysmus rufus* may have occupied saline alluvial meadows and fens supplied by calcium- or sulphate-rich groundwater, i.e. the same habitats as it occupies currently in central Asia (Table 2).

Krascheninnikovia ceratoides. – *Krascheninnikovia ceratoides* is a circumpolar species with a large distribution range including mainly continental parts of Eurasia and North America (Holmgren 2003). Its North American subspecies (subsp. *lanata*) occurs in the intermountain region of the USA, whereas the type subspecies has a large Eurasian distribution range including southern Siberia, central and southwestern Asia, eastern, central and western Europe, and reaching also to the Sinai Peninsula and the Atlas Mts of northern Africa (Uotila 2011). In Europe, it is scattered throughout southern Russia and southern Ukraine, and also occurs in Romanian Transylvania (Bădărău *et al.* 2002; Kovács 2011), Macedonia, Hungary, Lower Austria (Jalas & Suominen 1980) and the southeastern Czech Republic (now vanished; Tomšovic

1990). The westernmost populations are found in the northeastern Iberian Peninsula (Pérez-Collazos & Catalán 2007).

In Europe it has a similar ecology to *Agropyron cristatum* s. lat. and *Kochia prostrata* (Niklfeld 1964; Bădărașu et al. 2002; Kovács 2011), being confined to very dry open grasslands. In the Altai this low shrub occurs especially in desert steppes of the Chuya basin, but is also found elsewhere in dry steppes where it shares very similar habitat preferences to, but is much rarer than, *Agropyron cristatum* and *Kochia prostrata* (Table 2).

Carex microglochîn. – *Carex microglochîn* is one of the few *Carex* species with a bipolar distribution, occurring in the northern part of the Northern Hemisphere and in the Andean and Patagonian regions of South America (Wheeler & Guaglianone 2003). In Eurasia, it is almost continuously distributed in the southern part of central and eastern Siberia, from the Altai eastwards. It also occurs as disjunct populations in the Caucasus and eastern Himalayas. In Europe, it is a typical arcto-alpine species and is found in the alpine zone of the Alps, northern Scandinavia, Iceland and the northern part of the British Isles (Meusel et al. 1965), where it occupies springs, fens, stream and lake margins, and in humid regions, also rock crevices.

In the Altai *C. microglochîn* grows predominantly in open calcareous fens and wet saline grasslands with high soil pH (above 7.0) and high conductivity (300–2000 $\mu\text{S cm}^{-1}$), mostly together with *Blysmus rufus* and *Trichophorum pumilum*. It was also recorded rarely in tundra grasslands (Ukok plateau). Climatic conditions are similar for all three of these species, i.e. strongly continental climate with mean January temperature about $-19\text{ }^{\circ}\text{C}$ and an annual precipitation of $<250\text{ mm}$ (Figs 3, 4). These factors, together with disturbances associated with dry, open continental landscapes, may further weaken competition from other wetland plants including bryophytes that may compete with vascular plant seedlings.

These climatic parameters suggest that in glacial Europe *C. microglochîn* may have been able to live not only in the mountains, but also at lower altitudes in regions with a cold and dry continental climate. Although suitable habitats, such as calcareous fens and saline grasslands (Table 2, Fig. 2), probably occurred in the region, direct fossil evidence for the presence of this species is missing. In modern Europe it is limited to cold and wet areas, with the mean July temperature optimum of about $11\text{ }^{\circ}\text{C}$ documented from Norway (Saetersdal & Birks 1997) being even lower than that found in the Altai (about $14\text{ }^{\circ}\text{C}$).

Trichophorum pumilum. – *Trichophorum pumilum* (syn. *Baeoethyron pumilum*) in Europe is considered an arcto-alpine species that also inhabits lower latitude/

elevation travertine sites (i.e. with tufa formation). It occurs in the alpine belt of the Western and Southern Alps, in submontane travertines in the Western Carpathians (Slovakia) and in two regions of Norway, one north of the Arctic Circle and one in the mountains located more southwards (Dítě et al. 2013). The more continuous distribution starts in Iran (Naqinezhad et al. 2009) and continues through the central Asian mountains (Tien-Shan, Himalaya, Altai) and southwestern Siberia to Mongolia (Minayeva et al. 2005). The species ranges across the Rocky Mountains in western North America, with a disjunct eastern occurrence along the Gulf of St. Lawrence in Quebec.

In the Altai *T. pumilum* occupies mostly wet saline grasslands and, less frequently, open fens or tundra grasslands. We recorded this species in the Chuya basin, Menka river valley and the northern Kurai range. In central Europe, *T. pumilum* is confined to calcium-rich fens of the *Caricion davallianae* alliance, characterized by low competition from other vascular plants, whereas in Norway it occurs in low-productive tundra (Dítě et al. 2013). The floristic composition of the Western Carpathian travertine fens exhibits considerable similarity to that of Altaian saline grasslands owing to a high representation of halophytic and sub-halophytic species such as *Glaux maritima* and *Triglochîn maritima*. By contrast, populations in the Alps and in Norway contain fewer (sub)halophytic and many more arcto-alpine species (Dítě et al. 2013).

Records of fossil *T. pumilum* seeds from the full-glacial period in Belgium ($\sim 700\text{ km}$ from the nearest extant populations in the Alps; Haest et al. 1986) and from the Lateglacial/early Holocene transition in Slovakia (outside the recent distribution range; Dítě et al. 2013) suggest that the species was more widespread in Europe during the last glacial period, occupying not only travertine swards, fens and tundra, but also saline grasslands or river banks. In the Western Carpathians it tends to be concentrated in ancient calcareous fens, originating in the Lateglacial or Early Holocene, but is absent from younger fens (Hájek et al. 2011).

Carex capillaris. – *Carex capillaris* exhibits a boreal-circumpolar distribution and is considered as an arcto-alpine species in Europe. It occurs in the alpine and sub-alpine belts of the Pyrenees, Alps, Carpathians and Caucasus, and rarely in the Dinaric Mountains. Generally, its distribution is rather continuous across the boreal and sub-arctic zones of the Northern Hemisphere, but its individual populations are sometimes separated by large distances (Hultén & Fries 1986; Stevanović et al. 2009). There is a fairly continuous distribution range in Scandinavia and northeastern Europe.

In Europe the species occurs in wet calcareous habitats (springs, fens or tundra) under cold climate at both high altitudes and high latitudes (Dierssen &

Dierssen 1985; Moen *et al.* 2012). At lower altitudes of temperate Europe it is confined to relict habitats, such as Western Carpathian calcareous fens (Dítě & Pukajová 2004) or extremely species-rich wooded meadows in Estonia (Kull & Zobel 1991). In North America it is largely limited to cool, humid calcareous habitats where it is characteristic of sites supporting glacial relicts along the Great Lakes (Voss 1972).

In the Altai the ecological affinities of *C. capillaris* are rather similar: it was recorded in open wet woodlands dominated by *Larix sibirica*, *Picea obovata* and tree willows (Kuraj basin, Dzhazator river valley), tundra grasslands with *Dryas oxyodonta*, tundra scrub with *Betula rotundifolia* and wet grasslands with *Filipendula ulmaria*.

Fossil records of *C. capillaris* are very rare in Europe and they come only from the sites of its current occurrence (e.g. middle Holocene in the Alps; Jančová & Rybníček 1988). Nevertheless, based on its recent distribution pattern and analogy with central Asia, we hypothesize that this species may also have occurred at lower altitudes of the European Pleistocene landscape.

Agropyron cristatum s. lat. – *Agropyron cristatum* is a morphologically extremely variable species with a large Eurasian distribution range, including the southern half of Europe, southern Siberia, large parts of central Asia and northeastern China, the Caucasus and extending to Morocco (Meusel & Jäger 1992; Tzvelev 1976). Across its entire distribution range, this species is usually divided into numerous subspecies (e.g. Tzvelev 1976), which are sometimes given species rank (e.g. Baikov 2005).

Especially in the forest-steppe regions of eastern central Europe, *A. cristatum* is traditionally considered to be a relict species of the Pleistocene cold loess steppe, as are *Kochia prostrata* and *Krascheninnikovia ceratoides* with which it often co-occurs (Wendelberger 1954; Niklfeld 1964), usually in open dry grasslands on loess slopes (Zólyomi 1958; Niklfeld 1964; Dihoru & Donita 1970; Chytrý 2009).

The habitat affinities of *A. cristatum* in the Altai (Table 2) support the hypothesis of its glacial relict status in temperate Europe. It is confined to the driest habitats of this area (short-grass steppes), where it often co-occurs with *Kochia prostrata* and occasionally *Krascheninnikovia ceratoides*. These interspecific associations can also be found over a broader region of central Asia (Hilbig 1995; Korolyuk 2002). In the Altai *A. cristatum* is most common in the dry intermountain Kuraj and Chuya basins in the southeast, but also occurs elsewhere on dry, usually south-facing steppe slopes. Occasionally it can be also found in short steppic scrub with *Caragana pygmaea* and other species of *Caragana* and *Spiraea*, or in open, herb-rich larch forests, but usually in landscapes dominated by dry to typical steppe.

Allium strictum. – *Allium strictum* is a widely distributed species known from the southern part of Siberia, the adjacent parts of central Asia and the Russian Far East, including the southern part of the Kamchatka peninsula. Its continuous distribution range reaches Europe in the middle Volga basin. Further west it exhibits a disjunct distribution occurring in the valleys of the western and eastern Alps, in central Germany, southwestern Poland (now extirpated; Kaźmierczakowa & Zarzycki 2001), on the Baltic island of Öland and in the Russian part of Karelia (Meusel *et al.* 1965). It is further known from about 30 sites in central and northern Bohemia in the Czech Republic (Martinovský 1969), from a single locality in the Western Carpathians in Slovakia as well as from a handful of sites in western Ukraine (Krahulec *et al.* 2006). All of these European occurrences have been considered as relicts of cold glacial steppes (Martinovský 1969; Krahulec *et al.* 2006).

The European sites are situated from the lowlands up to elevations of about 2500 m a.s.l. in the Swiss canton of Valais. The Alpine populations are found mainly in the continental valleys of the western and central Alps, where it grows with dry-grassland species such as *Koeleria macrantha* (syn. *K. cristata*) and *Phleum phleoides* (Vierhapper 1919). Many of these species have large Eurasian or even circumpolar distribution ranges. In Bohemia, it occurs in short-grass steppes with *Festuca valesiaca* and *Carex humilis* and on dry rock outcrops with *Festuca pallens* (Toman 1981), usually on base-rich volcanic or metamorphic bedrock and in areas with dry continental climate.

In the Altai *A. strictum* occurs in various types of moderately dry to mesic grasslands, ranging from typical steppe through meadow steppe to tundra grassland (Table 2). These grasslands are usually dominated by sedges (*Carex humilis* and *C. pediformis*), grasses (*Helictotrichon altaicum*) or *Iris ruthenica*. It is also found in steppic scrub with various species of *Caragana*, *Cotoneaster*, *Rosa* and *Spiraea*, and in herb-rich larch forests that contain grassland species.

Kochia prostrata. – *Kochia prostrata* is a small procumbent shrub with a Eurasian distribution range (Schubert *et al.* 1981). It is almost continuously distributed in southern Siberia and southwestern and central Asia. In Europe it occurs as scattered populations between the central Iberian Peninsula in the west and the lower Volga River in the east (Jalas & Suominen 1980). It is known also from Morocco and Algeria in northwestern Africa (Uotila 2011).

In Europe it often co-occurs with *Agropyron cristatum* s. lat. (Zólyomi 1958; Chytrý 2009) in communities considered to be Pleistocene cold-steppe relicts (Wendelberger 1954; Niklfeld 1964). In the Altai the habitat range occupied by *K. prostrata* is very similar to that of *A. cristatum* s. lat., although it is hardly ever found

in meadow steppe, steppe scrub or in open woodland. These species often grow together in dry steppes. The constancy of the interspecific association of these two species between the core area of their distribution in central Asia and scattered occurrences in Europe supports the hypothesis of the relict status of the European populations.

Artemisia laciniata. – *Artemisia laciniata* has a large distribution range covering the southern half of Siberia, parts of the Russian Far East, Mongolia and northeastern provinces of China (Jäger 1987; Meusel & Jäger 1992; Krasnoborov 1997). It is also reported from the Yukon Territory and Alaska (Shultz 2006) but the taxonomic identity of the North American populations is not reliably resolved. In Europe *A. laciniata* occurs in the Don basin and in eastern Austria on the eastern shores of Lake Neusiedl. Several populations also occurred near Staßfurt and Artern in central Germany but all went extinct in the late 19th century (Jäger 1987). In that area populations were confined to saline soils, thereby avoiding competition. At these sites it was less frequent than the co-occurring *A. rupestris*.

In the Altai *A. laciniata* is a species of forest-steppe landscapes, where its main habitat is species-rich meadow (tall-herb, closed) steppe with *Carex humilis*, *Fragaria viridis*, *Galium boreale*, *Geranium pratense* and *Phlomis tuberosa*. It also occurs in open herb-rich forests of *Betula pendula*, *Larix sibirica* and *Pinus sylvestris*, which are adjacent to steppes and contain many steppe species in their herb layer (Table 2). *Artemisia laciniata* also grows in other types of grasslands, scrub and forests.

Relict species in the Pleistocene environments

The distributions of the vascular plant and land-snail species considered in this paper were studied in an area with mean annual temperatures ranging from -6.7 to 3.4 °C (median -2.5 °C) and total annual precipitations of 137 to 593 mm (median 283 mm; Table 1). The analysis of the macroclimatic requirements of the glacial relict species sampled in the southern Siberian continental refugium yielded consistent predictions of the full-glacial central Europe climate derived both from plant and land-snail populations. The results did not substantially change if only characteristic glacial land snails were considered or if the central Asian *Pupilla turcmenica* and Beringian *Vertigo* aff. *genesii* were also included (Table 1). We also observed similar patterns of individual species affinities of the studied vascular plants and snails (Figs 3, 4). In both groups there were species limited to areas with a colder and drier climate (e.g. snails *Columella columella* and *Pupilla loessica*, and plants *Kobresia myosuroides* and *Krascheninnikovia ceratoides*), whereas other species

required a warmer or damper climate (e.g. snails *Pupilla turcmenica* and *P. alpicola*, and plants *Artemisia laciniata* and *Carex capillaris*). For snails, most of these results are in good concordance with those already reported by Horsák et al. (2010) and Hoffmann et al. (2011). In comparison with these two earlier studies, however, the results presented here are based on a much larger data set and, most importantly, they are based on a corrected and improved taxonomic concept of some problematic species developed using extensive molecular examination (Nekola et al. 2015; J.C. Nekola unpublished data). The results presented here thus provide a robust overview of the macroclimatic and habitat affinities of the characteristic European full-glacial species, including those for which very few records were available in Horsák et al. (2010) or were entirely missing in Hoffmann et al. (2011) (*Pupilla alpicola*, *Vertigo parcedentata* and *V. pseudosubstriata*).

The analysis of climatic conditions also indicates that distributional shifts of the studied species during the Pleistocene/Holocene transition were closely related to their climatic tolerances. Snail species that went extinct in Europe are currently confined in the Altai to the areas of the coldest and driest climate (i.e. *Pupilla loessica* and *Vallonia tenuilabris*). By contrast, species that have survived at lower altitudes in central Europe have climatic preferences that are shifted towards warmer and/or wetter conditions (*Pupilla alpicola* and *P. turcmenicalsterrii*). The only exception is *Vertigo pseudosubstriata*, which has vanished from Europe yet occupies sites climatically similar to *P. alpicola* in the Altai. As it was found at only six sites, with most exhibiting strong groundwater influence, the actual climate experienced by these populations may be significantly different from the macroclimate values encountered in this study. Likewise, plant species with the lowest temperature requirements in the Altai tend to be confined to refugial habitats in European mountains (e.g. *Kobresia myosuroides*), whereas those currently confined to warmer areas in Siberia also survive in refugial populations in the European lowlands. However, these lowland populations have been strongly restricted, perhaps mainly because of the spread of competitively stronger species, and many survive in specific habitats with limited competition, such as inland saline grasslands (e.g. *Artemisia laciniata*) or dry loess slopes often affected by erosion (e.g. *Kochia prostrata*).

A basic assumption of our study is that the extant refugial populations in the Altai region occur under climatic conditions that are similar to those characteristic of a considerable part of Eurasia in certain periods of the Pleistocene. We can conclude that the observed climatic requirements of both plants and snails in southern Siberia are in good agreement with the climatic values reconstructed for full-glacial tem-

perate Europe based on both palaeoclimatic modelling and fossil pollen data. Based on a positive degree-day glacier mass-balance model with reduced precipitation of 25–75%, Heyman *et al.* (2013) suggested temperature depressions during the Last Glacial Maximum (LGM; about 18–21 ka BP) of between 8.0 °C and 15 °C for four central European upland regions. However, LGM climate models have generally reconstructed a less severe climate than that inferred from pollen data. For example, Strandberg *et al.* (2011) predicted mean annual temperatures to have been 5–10 °C cooler than today for the ice-free areas of central Europe during the LGM. Jost *et al.* (2005) predicted the differences from the present temperature of the coldest month to be around 10 °C and ~350 mm for the total annual precipitation using various climatic models. By contrast, based on pollen data Peyron *et al.* (1998) derived a mean annual temperature for 18 ka BP of 12±3 °C cooler than today for the northern–western zone above the Pyrenees–Alps line, and total annual precipitation of 60±20% lower than today. This was confirmed by Jost *et al.* (2005) based on an updated modern pollen calibration data set. These new data suggested a slightly less cold climate than reconstructed before, but still considerably colder than today for the mean temperature of the coldest month.

Likewise, the habitat requirements of modern populations of the studied species in southern Siberia support the current concept of the Pleistocene loess-steppe environments developed on the basis of the fossil records (e.g. Ložek 2000; Horsák *et al.* 2010; Magyari *et al.* 2014a,b). Both snail and plant assemblages characteristic of the full-glacial environment include species preferring both dry steppe and tundra conditions (Table 2). Additionally, both in Europe and central Asia, many of these full-glacial snails and plants are currently confined to wet habitats, such as alkaline fens and wet grasslands. For some snail species this finding can explain their rare occurrence in loess deposits. Some (e.g. *Columella columella* and *Vertigo parcedentata*) currently establish abundant populations in fens and wet woodlands. In the European glacial landscapes they may have partly survived in small fens, wetlands or woodland patches, although steppe-tundra environments probably formed the landscape matrix over large areas especially in the coldest phases (e.g. Willis & van Andel 2004; Kuneš *et al.* 2008; Magyari *et al.* 2014a, b). Snails, in particular, may have been partly dependent upon shelters provided by tree stands (Horsák *et al.* 2010) as they do not have any specific cryoprotective chemicals (Riddle 1983). We can also consider a protective role of snow cover preventing topsoil from freezing; however, this was probably less important under the dry full-glacial climate than it is today. By contrast, most herbaceous plant species considered as glacial relicts are typical of treeless habitats, which suggests that herbaceous plants may be more limited by

summer than winter temperatures and that they are not so dependent upon the availability of shelters to survive cold periods. However, as the three temperature characteristics (Table 1) assessed for the Altai populations were strongly intercorrelated and we obtained almost identical patterns for all studied snail and plant species, we present the results for individual species only in relation to mean January temperature.

The data derived from the Altai glacial snail populations might be very useful for improving calibration of modern data sets by developing transfer functions for the reconstruction of glacial climate (Rousseau 1991; Moine *et al.* 2002). The reconstructed glacial temperatures derived from modern snail species distributions across western and central Europe were considered to be milder than what would be expected based on other methods (Moine *et al.* 2002). Likewise, in a comparison with our data, the existing transfer functions produced temperatures about 10–15 °C warmer for the coldest month, but were almost identical for the warmest month (see Rousseau 1991; Moine *et al.* 2002). This can be explained by the lack of modern data in the calibration data sets for many characteristic species of loess faunas, especially those that have become extinct in western and central Europe. Their modern climatic affinities in the Altai clearly show that they are limited to the areas of colder climate as opposed to the species that are still common in Europe.

Conclusions

Our results show that climatic affinities of modern refugial populations of both land snails characteristic of central European loess sediments and presumably glacial-relict plant species are in good concordance with climatic scenarios derived from fossil pollen data and climate models. The plausibility of these conclusions is supported by the observed pattern of differences in climatic affinities of individual species, which closely matches the variation in their distributional shifts at the Pleistocene/Holocene transition. In both taxa there were species limited to areas with colder and drier macroclimates (e.g. snails *Columella columella* and *Pupilla loessica*, and plants *Kobresia myosuroides* and *Krascheninnikovia ceratoides*), whereas other species preferred areas of warmer or moister macroclimate (e.g. snails *Pupilla turcomenica* and *P. alpicola*, and plants *Artemisia laciniata* and *Carex capillaris*). However, in such areas individual species may be confined to either moist or dry habitats regardless of the macroclimatic conditions. For example, *Pupilla turcomenica* prefers dry habitats in areas of warm and moist macroclimate whereas some wetland plant species prefer mires and river shores in areas of cold and dry macroclimate.

This study also highlights the importance of wet habitats as refugia in the generally dry full-glacial lowland landscape. All of these findings suggest that the

habitat requirements of southern Siberian populations of land snails and vascular plants can provide important and realistic insights for reconstructions of Eurasian, especially central European, glacial environments. Such observations from modern analogues may be very useful for explaining some questionable palaeoecological interpretations of several loess species as discussed in detail above.

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