



## Direct evidence of central European forest refugia during the last glacial period based on mollusc fossils



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### ABSTRACT

Although there is evidence from molecular studies for the existence of central European last glacial refugia for temperate species, there is still a great lack of direct fossil records to confirm this theory. Here we bring such evidence in the form of fossil shells from twenty strictly forest land snail species, which were recorded in radiocarbon-dated late glacial or older mollusc assemblages of nine non-interrupted mollusc successions situated in the Western Carpathians, and one in the Bohemian Massif. We proposed that molluscs survived the last glacial period in central Europe in isolated small patches of broadleaf forest, which we unequivocally demonstrate for two sites of last glacial maximum age.

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### Introduction

One of the central paradigms of European paleoecology is the alternation of glacial and interglacial faunas via large-scale migrations, where whole communities shifted southwards to the Mediterranean refuge during glacial periods and northwards during interglacial periods (e.g., De Lattin, 1967). However, it has been called into question during the past two decades by an increasing amount of evidence from central European last glacial refugia for temperate species, sometimes called cryptic refugia because of their small area and difficult detection.

Where then did temperate species survive during the last glacial period? Much coincident as well as contradictory evidence has been discovered. Some authors even consider the Mediterranean region to be an area of paleo-endemism rather than a source for northwards postglacial colonization (Bilton et al., 1998). A review of the current knowledge was given by Schmitt and Varga (2012), which asked in the title of their review whether extra-Mediterranean refugia are the rule or exception during species range shifts. They answer that, in fact, they are a bit of both. Instead of the above-mentioned simple model, a more complicated situation is taking shape, with many small refugia situated both in the Mediterranean and/or far from it having hosted various species during various periods, which then spread to various directions at various times. We know the current situation, but particular phases of this confused process remain largely undescribed.

The majority of evidence for central European last glacial refugia comes from molecular phylogeography, which has been established as a useful tool for this purpose. Current results from many molecular

studies (e.g., Pfenninger et al., 2003; Pincheel et al., 2005; Kotlík et al., 2006; Ursenbacher et al., 2006; Benke et al., 2009) reveal very complex, often taxon-specific, patterns of species range dynamics. But molecular phylogeography provides neither direct evidence of past distributions nor the entire context of the paleoenvironment including the composition of species assemblages. Though some direct evidence exists for pollen and plant remains (e.g., Birks, 2003; Magri et al., 2006; Jankovská and Pokorný, 2008), snails (Ložek, 2006) and mammals (e.g., Horáček, 2006; Sommer and Nadachowski, 2006; Sommer and Zachos, 2009), there is still great work remaining for paleontologists to complete the mosaic of our knowledge on glacial/interglacial species ranges shifts.

Land snails can be used as relatively independent proxy for paleoecological reconstructions because of their close relationships to geological background and microclimatic conditions but not to particular plant species (e.g., Ložek, 1964, 2000; Davies, 2008). Although their shells persisted only in calcium-rich environments, such environments covered a wide spectrum of humidity and elevation and there were usually a large abundance of snails (Ložek, 2000). Unlike pollen, which is commonly used for reconstruction of the paleoenvironment, snail shells can be identified to species level, which is essential if we wish to elucidate shifts in ranges. Moreover, snails are usually fossilized directly in places where they lived or in close surroundings, thus we have direct paleo-faunistic records at our disposal, which is again crucial. Finally, a representative network of sites in the critical area, where cryptic refugia have been indicated to be present based on molecular phylogeography and/or fossil records, is also at our disposal (Ložek, 1964, 1982 and unpublished data).

Here we are interested in the last glacial refugia of temperate forest snail species only, because the existence of broadleaf forests in central Europe during the last glacial period is still not yet broadly accepted (Willis et al., 2000; Carcaillet and Vernet, 2001; Svenning et al., 2008). Therefore, we searched our database of land snails successions situated

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in the Bohemian Massif and Western Carpathians for such lithologically distinct radiocarbon-dated last glacial layers where records of strictly forest species occur. We restricted our dataset to this ecological group of snails only to document broadleaf woodlands as the only habitat where these snails can live. Our aim is to provide evidence of the survival of canopy forest snails in areas considered a few decades ago as harsh glacial wastelands.

**Material and methods**

We selected ten strictly forest mollusc records from more than 300 existing mollusc successions across the Czech Republic and Slovakia from our unpublished database of mollusc Holocene successions. We used only samples with direct radiocarbon dating, from which these snails were separated, rather than using age-estimation models for non-directly dated samples. Radiocarbon analyses were performed in the Center for Applied Isotope Studies of the University of Georgia, USA. Mollusc shells were measured by the AMS (Accelerator Mass Spectrometry) method and calibrated for variable initial <sup>14</sup>C concentration using the OxCal v4.1 calibration program (Bronk Ramsey, 2009). The only material suitable for dating was mollusc shells, which can contain so-called dead carbon sometimes leading to an over-estimation of their age (Goodfriend and Stipp, 1983). To minimize this dating error, we used the amalgam of small species shells for radiocarbon dating because 78% of them do not contain any dead carbon (Pigati et al., 2010). The lithology was further used as a proxy to control that the development of the sediment at each site was undisturbed.

All these mollusc successions were sampled by standard methods (Ložek, 1964), i.e. 8 dm<sup>3</sup> of spatially discrete sediment samples were taken from the central part of each lithologically distinguishable layer within 80-cm-wide excavation pits or open outcrops. Mollusc shells were extracted from the sediments by a combination of floating and sieving. After careful drying, each sample was disaggregated in water and then if necessary also in hydrogen peroxide. Floating shells and their fragments were repeatedly decanted into a 0.5 mm sieve and dried under laboratory conditions. Afterwards, the fraction above the sieve was dried and sorted by sieving into a variable number of fractions based on the type of resulting sediment. Shells were systematically removed from the sediment and identified under a dissection microscope.

Molluscs were determined according to Ložek (1964) and L. Juříčková's and V. Ložek's personal comparative collections of recent and fossil shells. The recorded snails were classified into ten main ecological groups (Ložek, 1964). From these ecological groups we chose only those species that are woodland sensu stricto, and which could not have survived outside of a canopy forest (Ložek's group 1, excluding debatable species *Discus ruderatus*, *Monachoides incarnatus* and *Vertigo pusilla* that sometimes also occur in other than broadleaf forest types). Such species thus indicate not only sparse woodland with light patches or parkland landscape but also specific microclimatic conditions, which can only be present in a true canopy forest. No other commonly used proxy, such as pollen or vertebrate bones, can provide such an indication. Eight of these mollusc successions have been published in various mostly regional journals but lack radiocarbon dating. For mollusc successions and lithology of these profiles see Supplementary Table 1; for detailed information about particular successions and site descriptions, see the papers cited in Table 1; and for complete mollusc successions of the two unpublished profiles see Supplementary Table 2.

**Results**

Altogether, 46 records (three in Bohemian Massif and 43 in the Western Carpathians) of twenty strictly forest mollusc species were found in ten directly radiocarbon-dated mollusc assemblages contained within non-interrupted mollusc fauna successions (Table 2). Two assemblages are of late glacial age, six are older but not as old as the last glacial maximum (LGM) (approximately 13,500–18,500 cal yr BP),

**Table 1**  
Site characteristics and radiocarbon dating of ten localities with last glacial records of forest molluscs.

Situation	Name of the site	Latitude	Longitude	Altitude (m)	Orientation	Precipitation (mm)	July mean temp. (°C)	January mean temp. (°C)	Type of the sediment	Type of relief	Species in assemblage	Non-calibrated age BP	Calibrated age BP	Lab code	Deep (cm)	Published in
Bohemian Karst	Kobylá Quarry, west part	49°54'43"	14°04'43"	460	none	580	17.0	-2.7	Deluvium	Hill	21	11,870 ± 40	11,911–11,544	6435-UGAMS	125–137	Ložek (1989)
Danube lowland	Zlatná, bank of Danube River	47°45'35"	17°58'32"	112	none	532	20.5	-2	Aluvium	Aluvium	34	11,290 ± 30	11,336–11,156	7692-UGAMS	49–90	Unpublished data
Fatra Mts.	Škřitová Valley	49°09'00"	19°10'48"	540	S	880	17.0	-4.5	Tuľa	Foothill	25	11,860 ± 30	11,886–11,540	7711-UGAMS	465–485	Ložek (2009)
Drieňov	Brálle, Malé Kršteňany	48°38'44"	18°27'10"	260	SE	699	18.4	-3.1	Overhang	Slope	16	15,020 ± 40	16,591–16,070	9675-UGAMS	61–85	Darola and Ložek (1982)
Slovenský Raj Mts.	Medvedia Cave	48°56'42"	20°25'20"	740	none	705	15.6	-5.2	Cave	Slope	19	10,300 ± 30	10,426–10,023	7687-UGAMS	195–218	Ložek (2012)
Tatra Mts.	Ohnište, Sokol Hill	48°58'37"	19°41'33"	900	S	1108	13.0	-6.4	Overhang	Slope	24	14,730 ± 40	16,487–15,690	7725-UGAMS	150–204	Unpublished
Hron River Valley	Farkašovo, upper part	48°48'30"	19°24'13"	420	SE	816	18.1	-4.2	Talus accumulation	Foothill	31	17,120 ± 40	18,898–18,156	9662-UGAMS	94–142	Ložek (2006)
	Farkašovo, lower part	48°48'30"	19°24'13"	420	SE	816	18.1	-4.2	Talus accumulation	Foothill	8	28,530 ± 80	31,405–30,488	9663-UGAMS	544–613	Ložek (2006)
Slovakian Karst	Hámorská Cave	48°32'58"	20°24'40"	280	SW	576	19.1	-3.4	Cave	Slope	18	12,420 ± 30	12,997–12,192	7723-UGAMS	293–315	Horaček and Ložek (1993)
	Maštalná Cave	48°32'21"	20°27'40"	600	SE	634	17.6	-4.2	Cave	Foothill	27	9930 ± 30	9643–9292	7691-UGAMS	255–277	Ložek and Horaček (1988)
	Brzořín, bank of Slaná River	48°36'45"	20°29'31"	250	NE	663	18.5	-3.8	Talus accumulation	Foothill	9	31,420 ± 90	34,512–33,331	9673-UGAMS	155–225	Ložek (2006)
Lovinobanská brázda	Velká Ružinská Cave	48°50'11"	21°07'08"	680	SE	792	15.8	-5.3	Cave	Slope	28	11,550 ± 30	11,541–11,330	12528-UGAMS	136–148	Horaček and Ložek (2007)

**Table 2**  
Records of strictly forest land snail species radiocarbon-dated mollusc assemblages of ten Central European refugia from the last glacial period. Records of species are marked in gray.

Recent zoogeography	Species	Bohemian massive	Western Carpathians								
		Kobyła	Zlatná	Brálie	Stankovany	Ohniště	Farkašovo	Medvedia	Mašťalná	Hámorská	Brzotín
Wider European or Central European	<i>Acanthinula aculeata</i>										
	<i>Aegopinella pura</i>										
	<i>Cochlodina laminata</i>										
	<i>Cochlodina orthostoma</i>										
	<i>Isog. isognomostomos</i>										
	<i>Daudebardia rufa</i>										
	<i>Merdigera obscura</i>										
	<i>Ena montana</i>										
	<i>Macrogastra plicatula</i>										
	<i>Helicodonta obvolvata</i>										
	<i>Oxychillius depressus</i>										
	<i>Petasina unidentata</i>										
	<i>Platyla polita</i>										
	<i>Ruthenica filograna</i>										
	<i>Sphyradium doliolum</i>										
<i>Vitrea diaphana</i>											
Carpathian	<i>Macrogastra latestriata</i>										
	<i>Faustina faustina</i>										
	<i>Faustina rossmaessleri</i>										
	<i>Vitrea transsylvanica</i>										

one complete succession was dated to the LGM sensu Clark et al. (2009) to the time span app. 18,500–31,000 cal yr BP, and one is slightly older (appx. 33,900 cal yr BP). These ten sites are situated in areas that we proposed to be the last glacial refugia for some strictly forest snail species. Nine sites are situated in the Western Carpathians: Malá and Velká Fatra Mts., Nížké Tatry Mts., Hron River valley, Lovinobanská brázda furrow, Slovenský raj Mts., and Slovakian Karst (Fig. 1). As discussed below, the refugium in the Bohemian Karst (within the Bohemian Massif) remains questionable. For detailed characteristics of the sites and radiocarbon data see Table 1.

Sixteen species have recent wider European or approximately central European distribution ranges, one of them has a Carpathian–Baltic range, and three are Carpathian endemics (according to Kerney et al., 1983), and so their last glacial refugia are situated inside the area of their recent distribution ranges. The total proportion of forest species, not only strictly forest, but also semi-opened woodland, damp and alluvial woodland, in a particular mollusc assemblages is rather high (from 64% in the Velká Ružinská Cave to 25% in the Brálie successions). The highest proportions of woodland species in a particular area were found in the Slovakian Karst successions (Hámorská and Mašťalná Caves and Brzotín, with 56% of woodland species even during the LGM); the proportion of forest species in the Bohemian Massif successions is lower but not negligible (Fig. 1, Table 3).

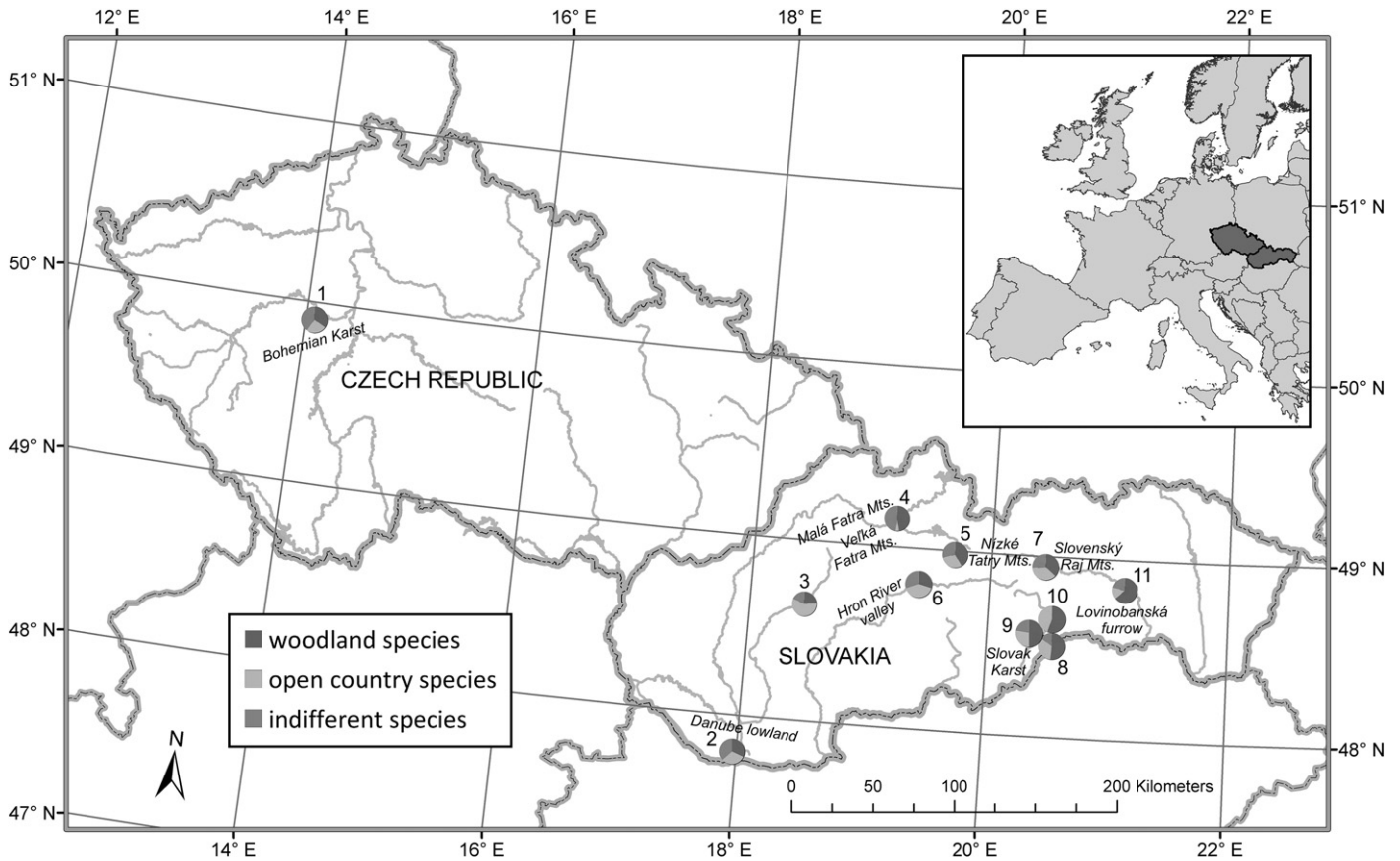
## Discussion

### The Western Carpathians contained last glacial refugia for some canopy forest snails

Both molecular and/or fossil evidence support the idea of the occurrence of taiga-like (Jankovská and Pokorný, 2008) and even some broadleaf (Willis and van Andel, 2004) forests in the Western Carpathians during the LGM. Moreover, one of the central European refugia for beech has been proposed in this area (Magri et al., 2006; Magri, 2008), and modeling of nemoral trees surviving during the LGM also suppose the occurrence there of *Alnus glutinosa*, *Tilia cordata*, *Ulmus glabra* and *U. laevis* (Svenning et al., 2008). The woodland mammal *Clethrionomys glareolus* survived the entire last glacial period in

such habitats (Kotlík et al., 2006). The canopy forest of the above-mentioned trees represents suitable habitat for all snail species found from this area, as is also true of beech forests (Table 2). Of course we do not consider the range of any of the snail species found as being completely continuous; rather, we are inclined to the idea of multiple microrefugia (Rull, 2009). We must also take into account that the area of possible forest refugia was usually reduced to the lower foothill zone, since in addition to the upper timber line at about 600 m elevation a lower timber line also existed at the upper boundary of the loess steppe at 300–350 m, which covered most of the lowlands hill countries. However, every snail species probably has its specific population and biogeographic history. Only a few forest species could probably survive in the gallery forests along larger rivers within the loess zone, for instance *Ena montana* in the Zlatná site near the Danube River.

The Carpathian endemic species *Faustina faustina* perhaps survived in substantial parts of its recent range. Eight records from different parts of the Western Carpathians and different intervals during the late glacial period support this suggestion. The westernmost part of its range, situated recently up to the Western Sudetes foothills (Bohemian Massif), has been colonized recently. We have no fossil records of this species from Bohemia. Thus, the range of this species probably shifted eastward during the last glacial period, but some populations which occurred in the Carpathians remained in place. Surprisingly, the mid- and southwestern-European species *Helicodonta obvolvata* had a last glacial refugia in the Western Carpathians. Although multiple refugia of this species have been confirmed, combining our records from the Western Carpathians and records from Mediterranean refugia in the Apennine peninsula (Girod, 2011) and Provence (Magnin, 1991), the question arises if some other refugia may also have been situated in the Alps and/or in other lower French mountains. Both Western Carpathian (our data) and Mediterranean refugia (see below) have been confirmed for another six forest species. *Cochlodina laminata* survived the last glacial period in the Apennine peninsula (Girod, 2011), Provence (Magnin, 1991) and probably in Susak Island in the Adriatic Sea (Štamol and Poje, 1998), *Ruthenica filograna* in the Trieste Karst (Girod, 2011), *Macrogastra plicatula* probably in Susak (Štamol and Poje, 1998), and *Acanthinula aculeata*, *Merdigera obscura* and *Sphyradium doliolum* in Provence (Magnin, 1991).



**Fig. 1.** The situation of all successions with proportional diagrams of woodland, open country and indifferent species sensu Ložek (1964). Sites: 1 – Kobyla Quarry, west part; 2 – Zlatná na Ostrove, bank of the Danube River; 3 – Brálie, Malé Kršteňany; 4 – Stankovany, Škútová Valley; 5 – Ohnište, Sokol Hill; 6 – Farkašovo; 7 – Medvedia Cave; 8 – Maštaľná Cave; 9 – Hámsorská Cave; 10 – Brzotín, bank of the Slaná River; 11 – Veľká Ružinská Cave.

Sixteen (maybe more) forest species of recent Central European distribution range (Table 2) probably survived the last glacial period at suitable sites in the Western Carpathians and then spread eastwards and/or northwards. While climate is generally the more important factor for species spread, accessibility is particularly important for species such as land snails with limited long-distance dispersal ability (Normand et al., 2011). Although the majority of species found occupied their recent range during the climatic optimum of the Holocene (e.g., Ložek, 1964), some of them spread more slowly (e.g., *Helicodonta obvolvata*), while some never colonized particular areas with primeval agricultural settlements (Juříčková et al., 2013a,b). Elucidating the exact direction of spread for particular forest species needs further research.

In our study, the most surprising habitat used for surviving the last glacial period is undoubtedly Ohnište-Sokol. This rock shelter is situated 900 m above sea level, which seems too high to be appropriate as a refugium of forest species, but the review by Schmitt (2009) highlights the importance of high mountains for species biogeography. Maybe such sites exposed to sunshine could be more resistant to frost than sites situated in valleys and susceptible to cold-weather inversions.

The survival of woodland snail species during the LGM in the Western Carpathians was previously proposed by Ložek (2006), based on two non-radiocarbon-dated mollusc successions. However, the contexts of mollusc assemblages, with the glacial index species *Vallonia tenuilabris* occurring together with strictly forest species, clearly indicated last glacial refugia. For definitive proof of this relative dating, we radiocarbon-dated the first and last layer of the Farkašovo succession (Ložek, 2006), which is situated in the center of the Western Carpathians, and layer 6 of the Brzotín profile situated in the southern foothills near the Panonian steppe area. The Farkašovo succession was dated as falling with the LGM (app. 20,500–33,000 cal yr BP), while the Brzotín profile is somewhat older

(app. 33,900 cal yr BP). These data represent undisputable proof of the survival of several strictly forest species in the Western Carpathians during the LGM. *Faustina faustina* and *Oxychilus depressus* occurred continuously throughout the LGM in Farkašovo, while the other strictly woodland species *Helicodonta obvolvata*, *Isognomostoma isognomostomos* and *Vitrea diaphana* occurred in particular layers of this succession. There were also other strictly woodland species likely present, but with uncertain identification. *F. faustina*, *H. obvolvata* and *I. isognomostomos* were also continuously found at Brzotín. Both sites provide abundant LGM forest faunas.

All other sites studied here are poorer in fossil remains and younger than the LGM, and thus provide just indications corroborating the results from the Farkašovo and Brzotín sites. We consider the evidence from these two sites to be sufficient proof of the existence of broadleaf forests in the Western Carpathian during the LGM. On the other hand, their extent, the reciprocal distance of forest islands and the approximate number are still in question. We can only speculate about relatively small islands in sheltered sites of southward orientation, which are hardly detectable in the pollen spectra but are sufficient for the survival of forest snails. We imagine a similar model for forest snails to that proposed by Bennett (1985) for North American *Fagus grandiflora* and Magri (2008) for European *Fagus sylvatica*, where post-glacial forest re-establishment was not actually a re-colonization, but rather a process of increasing degree of occupancy.

*Were there also last glacial refugia for forest snails in the Bohemian Massif? Probably, yes*

Unfortunately, as opposed to the favorable calcareous areas of the Western Carpathians, the foothill belt of the Bohemian Massif does



**Table 3**  
Lists of species found in the radiocarbon-dated mollusc assemblages. Sites: 1 – Kobyła Quarry, west part; 2 – Zlatná na Ostrove, bank of the Danube River; 3 – Brálie, Malé Kršteňany; 4 – Stankovany, Škútová Valley; 5 – Ohnište, Sokol Hill; 6 – Farkašovo, layers 4–11 (Ložek, 2006); 7 – Medvedia Cave; 8 – MaštaĽná Cave; 9 – Hámorská Cave; 10 – Brzotín, bank of the Slaná River; 11 – Vělká Ružinská Cave.

Ecologic and biostratigraphic characteristics		List of species	1	2	3	4	5	6	7	8	9	10	11		
A	1	!	<i>Acanthinula aculeata</i>	+			+			+					
		!	<i>Aegopinella pura</i>	+			+				+			+	
		!	<i>Cochlodina laminata</i>	+		+									
		!	<i>Cochlodina orthostoma</i>					+						+	
		(G)	<i>Discus ruderatus</i>	+	+		+	+	+	+		+		+	
		!!	<i>Drobacia banatica</i>										+		
		!	<i>Ena montana</i>		+		+								
		(!)	<i>Faustina faustina</i>				+	+	+	+	+	+	+	+	+
		!	<i>Faustina rosmaessleri</i>							+					
		!	<i>Helicodonta obvolvata</i>							+			+	+	
		!	<i>Isognomostoma isognomostomos</i>					+	+	+				+	
		!	<i>Macrogastra latestriata</i>												+
		!	<i>Macrogastra plicatula</i>												+
		!	<i>Monachoides incarnatus</i>	+						+					+
		(G)	<i>Oxychilus depressus</i>							+	+	+			+
		!	<i>Petasina unidentata unidentata</i>						+						+
	!	<i>Platyla polita</i>					+				+			+	
	!	<i>Ruthenica filograna</i>									+			+	
	!	<i>Sphyradium doliolum</i>								+	+			+	
	(!)	<i>Vertigo pusilla</i>	+	+		+				+		+			
	!	<i>Vitrea diaphana</i>							+	+	+				
	!	<i>Vitrea transylvanica</i>					+								
	2	!	<i>Aegopinella minor</i>			+		+		+	+				
		!	<i>Alinda biplicata</i>			+					+				
		(+)	<i>Arianta arbustorum</i>		+		+		+				+	+	
		!	<i>Cepaea hortensis</i>		+										
		(G)	<i>Cochlodina cerata cerata</i>					+	+		+	+	+	+	
		!	<i>Discus rotundatus</i>								+			+	
		(!)	<i>Fruticola fruticum</i>		+					+				+	
		!	<i>Helix pomatia</i>			+					+				
		(G)	<i>Semilimax kotulae</i>	+				+				+		+	
		(+)	<i>Vitrea crystallina</i>				+	+	+			+	+	+	
(G)		<i>Clausilia pumila</i>								+					
(G)		<i>Monachoides vicinus</i>					+								
G		<i>Perforatella bidentata</i>				+									
(+)		<i>Vestia turgida</i>										+	+		
B		4	M	<i>Ceciliooides acicula</i>						+					
			!!	<i>Cepaea vindobonensis</i>			+				+				
	(+)		<i>Granaria frumentum</i>		+	+					+	+			
	+		<i>Helicopsis striata</i>	+											
	(G)		<i>Chondrina clienta</i>					+		+	+	+		+	
	(G)		<i>Chondrina tatra</i>					+		+	+				
	(+)		<i>Chondrula tridens</i>		+	+			+			+			
	M		<i>Oxychilus inopinatus</i>			+									
	+	<i>Pupilla sterrii</i>					+	+	+						
	(+)	<i>Pupilla triplicata</i>						+							
	(G)	<i>Pyramidula pusilla</i>					+		+	+			+		
	!!	<i>Truncatellina claustralis</i>									+				
	5	++	<i>Columella columella</i>	+											
		(!)	<i>Euomphalia strigella</i>			+		+	+	+	+	+		+	
		G	<i>Faustina cingulella</i>					+	+						
		+	<i>Pupilla muscorum</i>		+				+						
(!)		<i>Truncatellina cylindrica</i>		+	+				+	+					
(+)		<i>Vallonia costata</i>	+	+	+	+	+	+	+	+	+		+		
G		<i>Vallonia pulchella</i>	+	+	+										
++		<i>Vallonia tenuilabris</i>						+							
(G)	<i>Vertigo pygmaea</i>		+												
C	6	(!)	<i>Cochlicopa lubricella</i>	+	+	+									
		(+)	<i>Clausilia dubia</i>		+	+		+	+			+	+		
	7	(+)	<i>Cochlicopa lubrica</i>	+	+		+		+				+		
		(+)	<i>Euconulus fulvus</i>	+	+			+	+	+				+	
		!	<i>Helicigona laticida</i>									+			
		!	<i>Laciniaria plicata</i>									+		+	
		(+)	<i>Orcula dolium</i>	+		+	+	+	+	+	+	+		+	
		(+)	<i>Perpolita hammonis</i>	+	+			+		+					
		(+)	<i>Plicasteria lubomirskii</i>				+								
		(+)	<i>Punctum pygmaeum</i>	+	+			+	+						
		+	<i>Trochulus hispidus</i>												
		+	<i>Trochulus sericeus</i>	+											
+	<i>Trochulus striolatus danubialis</i>		+												
G	<i>Vertigo alpestris</i>	+					+	+	+		+				

Table 3 (continued)

Ecologic and biostratigraphic characteristics		List of species	1	2	3	4	5	6	7	8	9	10	11	
8	(G)	<i>Vitrea contracta</i>			+			+		+		+		
	(G)	<i>Vitrina pellucida</i>	+											
	!	<i>Carychium tridentatum</i>	+			+				+	+		+	
	(!)	<i>Columella edentula</i>					+						+	
	+	<i>Succinella oblonga</i>		+		+		+						
	!	<i>Trochulus villosulus</i>				+								
	(G)	<i>Vertigo substriata</i>				+								
	D	G	<i>Carychium minimum</i>				+							
		(+)	<i>Oxyloma elegans</i>		+									
		(+)	<i>Pseudotrichia rubiginosa</i>		+									
10	(+)	<i>Succinea putris</i>		+										
	(+)	<i>Zonitoides nitidus</i>		+		+								
	(+)	<i>Anisus spirorbis</i>		+										
	(+)	<i>Aplexa hypnorum</i>		+										
		<i>Bithynia troschelii</i>		+										
	(G)	<i>Bythinella austriaca</i>				+		+						
	(+)	<i>Galba truncatula</i>		+		+								
	G	<i>Gyraulus acronicus</i>		+										
	(+)	<i>Pisidium casertanum</i>				+								
	(+)	<i>Planorbis planorbis</i>		+										
	<i>Segmentina nitida</i>		+											
	<i>Valvata cristata</i>		+											
	<i>Valvata macrostoma</i>		+											

Ecological characteristics: Main ecological groups: A – woodland (in general); B – open country; C – woodland/open country; D – wetlands and aquatic habitats. Ecological groups: 1 – woodland (*sensu stricto*); 2 – woodland, partly semi-opened habitats; 3 – damp woodland; 4 – xeric open habitat; 5 – open habitats in general (moist meadows to steppes); 6 – predominantly dry; 7 – mesic or various; 8 – predominantly damp; 9 – wetlands, banks; 10 – aquatic habitats.

Biostratigraphic characteristics: + – characteristic loess species; ++ – index loess species; (+) – local or occasional loess species; ! – species of warm phases; (!) – eurythermic species of warm phases; !! – index species of warm phases; G – species surviving glacial out of loess zone; (G) – ditto, as relics; M – modern (postglacial) immigrants.

Presence in layers: 1 – number of individuals; ?1 – only an approximate determination; (!) – allochthonous (reworked) shells. Semi-quantitative estimate of species abundances (Tabs S3, S5, S9): M – mass occurrence (thousands of individuals); H – high abundance (hundreds of individuals); X – intermediate abundance (tens of individuals); L – low abundance (5–10 specimens); R – rare occurrence (1–4 specimens).

not provide suitable conditions for the fossilization of mollusc shells because of acidic sediments and soils. We thus depend on sites from lower altitudes, mostly at the outskirts of the loess steppe where the survival of forests is hardly imaginable. While the Western Carpathian last glacial refugia of broadleaf forests have been already hinted, the idea of last glacial refugia for strictly forest species situated in the Bohemian Karst seems to be a little scandalous (see the modeling of nemoral tree species by Stewart et al., 2010).

Even though the occurrence of *Alnus glutinosa* has been documented in Central Bohemia during the LGM (Jankovská and Pokorný, 2008), the survival of a canopy forest in the Bohemian Karst inhabited by three strictly forest snail species, where the total proportion of forest species is 35%, seems highly unlikely. It must be emphasized that like other forest species found (see Table 3), these three species are quite resistant to survive in various forest environments, as seen in their wide recent ranges from Scandinavia to the Mediterranean (Kerney et al., 1983). But the Bohemian Karst is probably the best sampled area in the world from the point of view of Quaternary mollusc succession. More than 70 mollusc successions have been studied situated in an area of only 130 km<sup>2</sup> (Ložek, 1964, 1982 and unpublished data). Only one of them has given evidence of the survival of forest species during the late glacial period and none during the LGM. So for now we are hesitant to consider the Bohemian Karst as containing last glacial refugia, although there is evidence of the survival of some forest species during warmer glacial periods, with radiocarbon dating fitting the onset of Allerød interstadial period (app. 13,500 cal yr BP). Further radiocarbon data of the large amount of material from this area could clarify this suspicion.

Thus in answer to our question of whether last glacial refugia existed for forest species in the Bohemian Massif: probably yes, but more likely in the form of very scattered, remote microrefugia *sensu* Rull (2009) of uncertain persistence.

## Conclusions

- We demonstrate the survival during the LGM of six strictly forest snail species in two Western Carpathian sites, with eight younger sites corroborating these findings.
- Another fourteen strictly forest species survived during later periods than the LGM in the Western Carpathians.
- We have only late glacial records of strictly forest species from the Bohemian Massif.
- Our data confirm the theory of cryptic refugia of broadleaf forests in the Western Carpathians.
- The extent, reciprocal distance, approximate number of these refugia and details of the species' spread from them still remain in question.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yqres.2014.01.015>.

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