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Periglacial microclimate in low-altitude scree slopes supports relict biodiversity

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Air circulation through talus slopes creates unique microclimates, with some of the most interesting being low-elevation mid-latitude scree in areas with frequent snow-free $< 0°C$ (e.g. "black frost") days that allow for development of year-round ice accumulations. Here, we document this phenomenon on Kamenec Hill in North Bohemia (Czech Republic) located at an altitude of 330 m above sea level, where mean annual temperatures $< 0°C$ are maintained in a narrow strip along the slope's lower margin. This microhabitat, as well as interstitial spaces between scree blocks elsewhere on this slope, supports an important assemblage of boreal and arctic bryophytes, pteridophytes and arthropods that are disjunct from their normal ranges far to the north. This freezing scree slope represents a classic example of a palaeorefugium that significantly contributes to protection and maintenance of regional landscape biodiversity.

Keywords: scree; periglacial microclimate; habitat islands; arthropods; palaeorefuge

Introduction

Stony accumulations (screes and taluses) represent common habitats in subarctic and arctic regions that also occur further south in bedrock-dominated landscapes. In non-boreal landscapes such sites are usually limited to steep slopes associated with hills and river valleys, and often owe their origin to late-Pleistocene periglacial processes. In the modern landscape these sites often exist as open habitat islands surrounded by a densely forested matrix (Růžička 1990).

Airflow through the interstitial spaces between talus blocks has allowed development of unique microclimates in central Europe with year-round ice persisting more than 1000 m below the present lower limit of alpine permafrost (Zacharda et al. 2007). The basic conditions for subterranean ice formation were formulated by Balch (1900: 148, 149): " . . . two things are necessary: the first is cold, the second is water. Subterranean ice formations are always found in parts of the world where, during part of the year at least, the temperatures of the surrounding country fall below freezing

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point." Růžička (1999: 143) additionally pointed out for freezing scree slopes that "Cold air must flow . . . to the lower part [of the slope]." However, there is a prerequisite: voids must be present for cold air to penetrate and pass through. In this respect, screes and caves differ greatly: the former consists of many small voids, whereas the latter possess a few large voids.

Although the physical and biological conditions within and under snow-pack is increasingly well-known (Halfpenny and Ozanne 1989; Marchand 1996; Delaloye et al. 2010) less has been determined about the conditions found in isolated, mid-latitude permafrost deposits. The Czech Republic occupies a key biogeographical position to analyse the biota of such habitats. During the last glaciation, a narrow ice-free corridor occurred between the Northern and Alpine glaciers (Ehlers and Gibbard 2004), which allowed boreal plants and animals to colonize the landscape. Populations of these species still persist in this region not only in island-like scree slopes (Růžička and Zacharda 1994; Růžička 2011) but also in subalpine and alpine zones, mountain forests and peatlands (Tallis, 1991; Hájková, forthcoming).

In this paper we concentrate on an ice-forming scree slope in northern Bohemia. Two main questions are addressed: (1) what factors enable ice formation in low elevation scree slopes, and (2) how are guilds of plants and animals influenced by underground ice formation?

Materials and methods

Study site

The study site is located in the České Středohoří Mountains Protected Landscape Area in northern Bohemia, 50.706° N, 14.354° E, at an altitude of 330–390 m above sea level (a.s.l.). The area's climate is temperate with mean annual air temperature of 6–8°C and average January and July mean air temperatures of – 3°C and 16°C, respectively. Precipitation measured from nearby meteorological stations totals 600–750 mm with maximum snow depths in January of 20–35 cm. The region is underlain by Cretaceous sediments consisting of marlite, claystone and sandstone, through which volcanic basalts and phonolites penetrated during the Tertiary. Between the towns of Benešov nad Ploučnicí and Česká Lípa, the Ploučnice River forms a canyon that cuts through both flood basalts and sandstone, with an ice-forming basalt scree located on the north-facing slope of Kamenec Hill. This scree slope is approximately 150 m wide, with an elongated shallow depression in its centre (Figure 1). Scree thickness is estimated to be 10 m (Gude et al. 2003). The scree is surrounded by a deciduous forest on the sides and top, and with spruce along the lower margin.

Regional climate and persistent subterranean ice deposits

The altitude and presence/absence of permanent subterranean ice deposits from all registered caves in Slovakia was obtained from Bella (1995). These data were also recorded from the 66 arachnologically investigated scree slopes in the Czech Republic (Růžička and Klimeš 2005). Average annual temperature and number of black frost days (i.e. days without snow cover and mean daily temperature $\leq$ 0°C) were obtained from 30-year climate records at three meteorological stations of different elevations located in the nearby Šumava Mountains and associated piedmont (Figure 2).

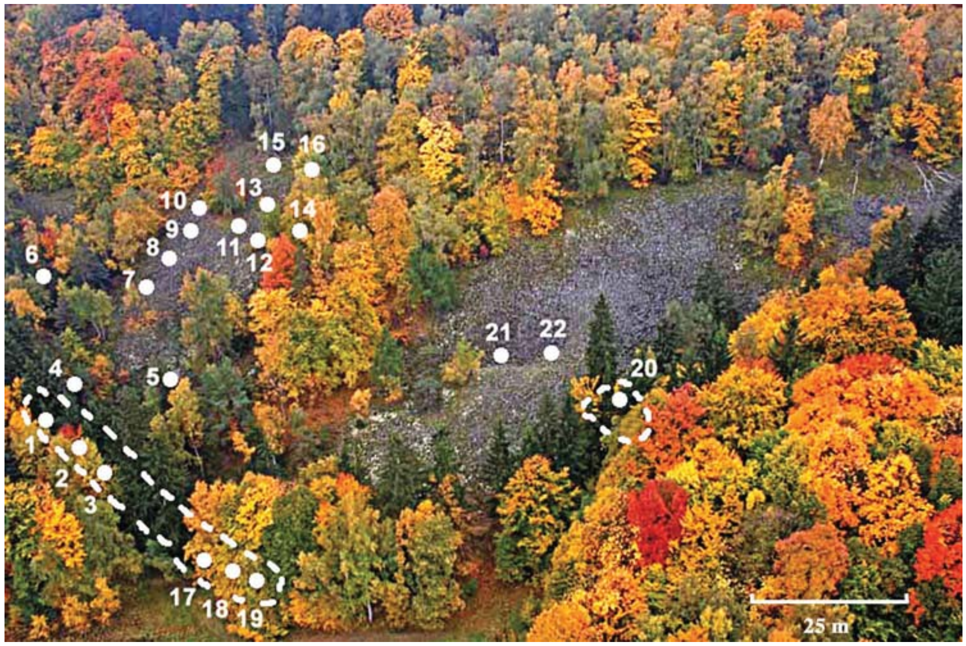


Figure 1. Aerial photograph of Kamenec hill, autumnal aspect. The locations of pitfall traps are marked by full circles. Dashed line indicates the area with periglacial microclimate. Photo: L. Jenka.

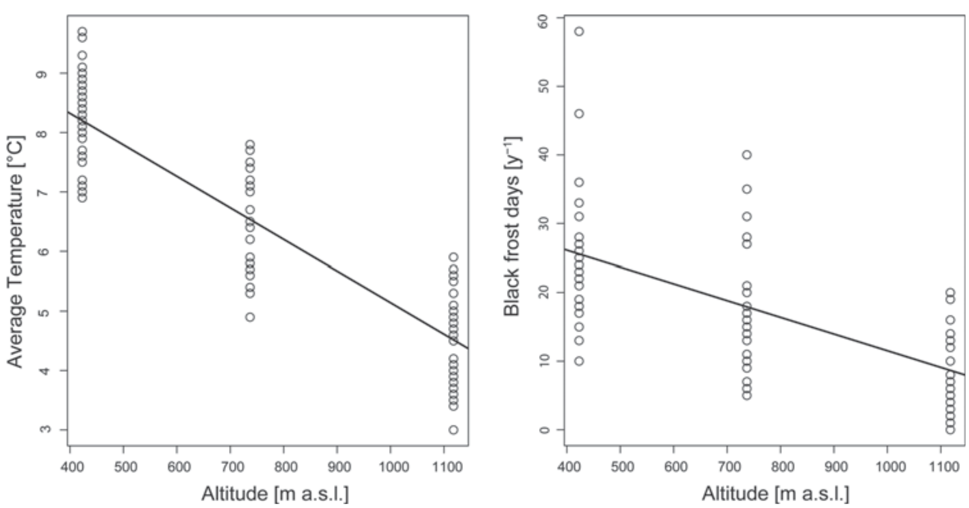


Figure 2. Relation of average annual temperature (A), and the annual number of black frost days (B) for three meteorological stations: Strakonice (423 m a.s.l.), Kašperské Hory (737 m a.s.l.) and Churáňov (1118 m a.s.l.). From 1976 to 2005. $F_{1,29} = 487.49$, $P < 10^{-16}$; and $F_{1,29} = 65.6$, $P \leq 10^{-8}$, respectively.

Kamenec scree temperature measurements

Data-loggers (Model TGU-0050, Gemini Data Loggers Ltd., Chichester, UK) with internal thermistors (accuracy ± 0.2°C) were used to measure temperature every 3 hours. The loggers were left in place for 5 years (2004–2008), with data being downloaded yearly using the GEMINI LOGGER MANAGER, ver. 2.3, software. Ambient air temperature was measured by one shaded logger hanging about 2.5 m above the scree surface at the foot of the scree slope. Two data loggers measured internal ground temperature in subsurface voids with ice formation near traps No. 2 and No. 18 at depths of 50–70 cm. One logger was placed at a depth of *c*. 80 cm in the central part of the scree, near trap No. 8 (Figure 1).

To obtain data on substrate surface temperature in the basal part of the talus on a hot sunny summer day, temperature of soil surface was measured at 65-cm intervals along two 20-m-long transects using a handheld temperature probe (Fisher Scientific (subdivision of Thermo Fisher Scientific), Pardubice, Czech Republic. MMA electronic thermometer, accuracy ± 1.5%) between 12.00 and 14.00 h on 22 August 2001. The two transects were oriented along and perpendicular to the elevational contour of the slope, encompassing a 400-m^2 extent and intersecting the region with the coldest air flux (Zacharda et al. 2005).

Bryophyte and pteridophyte sampling

From 1988 to 1990 bryophytes and pteridophytes were recorded from 139 sample sites spread across the entire scree field. Flowering vascular plants were excluded from analysis because of their scarcity at the site. The samples were placed to fully capture the ecological gradients over the whole talus. Sample plots ranged from 100 cm^2 to 1600 cm^2 with size being set to ensure homogeneous environments and to encounter an approximately equal number of ramets. As a result, samples were smaller in fissures and holes, which possess strong environmental gradients over short distances and support smaller-statured species, whereas samples placed on stone tops were larger because of shorter environmental gradients and the larger species stature. All bryophytes were recorded from each sample, with the cover of each species being estimated using the Frey (1933) scale. Although most bryophyte identifications were made in the field, vouchers were taken from the genera *Grimmia*, *Polytrichum*, *Lophozia* and *Scapania* and species-level identifications were determined in the laboratory using a standard dissecting microscope.

Arthropod sampling

Arthropods were sampled via pitfall traps made of rigid plastic (Růžička 1982). The traps consisted of a board (20 × 25 cm), which forms an artificial horizontal surface, and a can (13 cm high and 10.5 cm in diameter) inserted in the centre of the board. They contained a mixture of 7% formalin and 10% glycerol, plus a few drops of detergent. Twenty-two traps were deployed from June 1993 to July 1995 to cover the full range of distances from underground ice formation on the scree field (Figure 1). Traps were emptied at monthly intervals. Small arthropod individuals were also collected using a small aspirator containing 70% ethanol as a preservative. The whole catch was processed in the laboratory, examined under a standard light microscope and identified to species.

Data analysis

Differences in the elevation of ice caves and ice-retaining screes were tested using a Welch two-sample *t*-test. The effect of altitude upon average temperature and the number of black frost days was tested with a mixed linear model (Pinheiro and Bates 2000) with random effects of location and year.

Bryophyte/pteridophyte species % composition was related to a four-level factor representing location on the scree slope: NI (Near Ice), plots < 5 m from underground ice accumulations; MP (Middle Part), SP (Side Part) and UM (Upper Margin). Abundance data were log-transformed to normalize distributions, and then ordinated using the unimodal constrained method in Canonical Correspondence Analysis (ter Braak 1986). The significance of sample location on composition was determined using a Monte Carlo permutation test. The best-fit species centroids were also plotted into the ordination diagram.

Arthropod species % composition was linked to a two-level factor related to distance from underground ice: plots < 5 m or > 5 m from an ice source. The distance of 5 m was chosen based on the above microclimatic measurements. Abundance data were again log-transformed to normalize distributions. Using a Monte Carlo permutation test, Redundancy Analysis (Rao 1973) was performed on the pooled species table, as well as separately on each taxonomic group, to determine how much variance was explained by proximity to ice.

The different choice of constrained ordination methods for the bryophyte/pteridophyte data versus arthropod data is based on their different β-diversity as evaluated by a trial run of Detrended Correspondence Analysis (see Lepš and Šmilauer 2003: 169–171).

All multivariate statistical analyses were performed using CANOCO FOR WINDOWS version 4.5 (ter Braak and Šmilauer 2002). The mixed linear model was fitted with package *nlme* and *t*-test with the function *t.test*, both using R PROGRAM version 2.8 (R Development Core Team 2008).

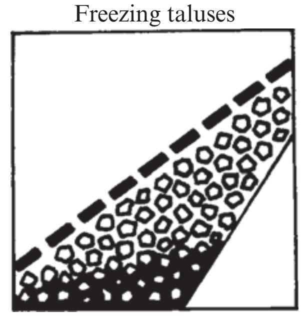
We evaluated the presence of species with ranges disjunct from the boreal zone, i.e. those taxa with (sub)arctic–(sub)alpine or boreo-montane ranges (Tallis 1991). Disjunct ranges were found among bryophytes (Düll 1983, 1984, 1985), spiders (Buchar and Růžička 2002) and mites (Zacharda et al. 2005). The presence of montane species was also noted.

Results

Mid-latitude subterranean ice deposits and associated temperature anomalies

In total, 5474 caves are registered in Slovakia at altitudes of 142–2080 m a.s.l, and 66 are known to accumulate ice deposits seasonally (Bella 1995). In the Czech Republic, 66 arachnologically investigated scree slopes ranged in elevation from 270 to 1550 m a.s.l. but ice formation is known from only seven (Růžička and Klimeš 2005). The ice caves are predominantly located at high altitudes (mean 1225 m) whereas ice-retaining scree slopes are predominantly located at low altitudes (mean 381 m) (Table 1). This difference is highly significant ($t_{47} = 13.4$, $P < 10^{-15}$). Additionally, both the average annual temperature and the number of black frost days are highly significantly and negatively correlated with altitude ($F_{1,29} = 487.5$, $P < 1.0\text{e-}6$ and $F_{1,29} = 65.6$, $P < 1.0\text{e-}6$, respectively) (Figure 2).

Table 1. Characteristics of underground ice formation in freezing caves and freezing taluses.

	Freezing caves	Freezing taluses
		
Entry of cold air into underground	Through one large cave entrance (the 'hole' type)	Through numerous small interspaces among stones (the 'sieve' type)
Mean annual temperature near the places with ice formation in Dobšinská ice cave (Bella 2007), and in scree talus on Klíč Mt and Kamenec hill (Zacharda et al. 2007)	from – 1.0 to – 0.4°C	from – 1.6 to – 0.1°C
Altitude (m above sea level) of ice caves in Slovakia (Bella 1995) and freezing taluses in Czech Republic (Růžička & Klimeš 2005)	503–1996 m (mean 1225 m)	270–540 m (mean 381 m)
Mean annual temperature in the neighbourhood of the ice caves and freezing taluses at mean altitude	2–4°C	7–8°C
Prevailing regimen of air circulation	static	dynamic

Ice formation is drawn in black. Bold line represents the type of entry of the cold air into underground.

At the Kamenec Hill scree, temperature profiles from the lower slope margin differ profoundly from ambient atmosphere (Figure 3). In an area of about 100 m^2 at the base of the scree slope, the soil surface temperature never exceeded + 10°C, and in the coldest area surface soil temperature was only + 1.5°C during hot summer days. These low temperatures are maintained by local cool air outflows from fissures between bedrock blocks. However, ground temperatures up to + 19°C were noted on hot summer days from adjacent microsites with direct exposure to sunlight and no cold air seepage.

From spring to autumn in the middle and upper parts of the slope, the internal scree temperature fluctuated in accordance with the ambient air temperature but with reduced diurnal variations. However, from September until the end of November episodic exhalations of warm air occurred, particularly on days having low ambient air temperature. Because of this warm air advection, areas within the upper part of the slope remained frost-free throughout the year.

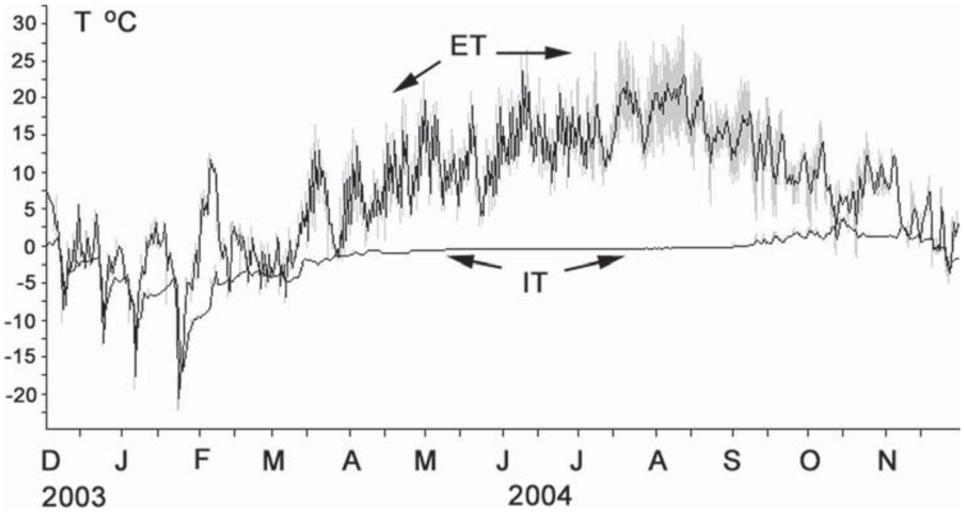


Figure 3. Temperature variations (°C) in the Kamenec scree slope from the beginning of December 2003 to the end of November 2004. ET, external ambient air temperature; IT, internal air temperature on lower margin of the scree slope near trap No. 2.

Bryophytes and Pteridophytes

Ninety-two bryophyte and ten pteridophyte species were encountered. Thirty-five of these are largely confined to European mountains. *Anastrophyllum saxicola*, *Andreaea rupestris*, *Diplophylum taxifolium*, *Gymnomitrion concinnatum*, *Gymnomitrion corallioides*, *Lophozia sudetica*, *Polytrichum alpinum*, *Racomitrium fasciculare* and *Racomitrium lanuginosum* have isolated populations in the Kamenec Hill, and the populations of *Cryprogramma crispa* and *Gymnomitrion* spp. represent the lowest known elevational limits for the Czech Republic and Central Europe, respectively.

Although only a relatively small amount of compositional variation (3.4%) is explained by sample location, this effect is highly significant ($P = 0.002$). Near Ice plots were the most divergent, with *Andreaea rupestris*, *Diplophylum taxifolium*, *Gymnomitrion corallioides*, *Lophozia sudetica* and *Polytrichum alpinum* occurring exclusively in these locations (Figure 4). In contrast, *Anastrophyllum saxicola*, *Gymnomitrion concinnatum*, *Racomitrium fasciculare* and *Racomitrium lanuginosum* never occurred near ice.

Arthropods

Sampled arthropods comprised spiders (Araneae: 751 specimens, 99 species), rhagidiid mites (Acari, Rhagidiidae: 1679 specimens, 7 species), harvestmen (Opiliones: 574 specimens, 10 species), beetles (Coleoptera: 1067 specimens, 155 species), millipedes (Diplopoda: 182 specimens, 15 species) and woodlice (Oniscoidea: 430 specimens, 7 species). Seventeen spider species and the beetle *Pterostichus negligens* are typical of European mountains, with the Kamenec Hill representing the lowermost limit of their elevational distribution in the Czech Republic.

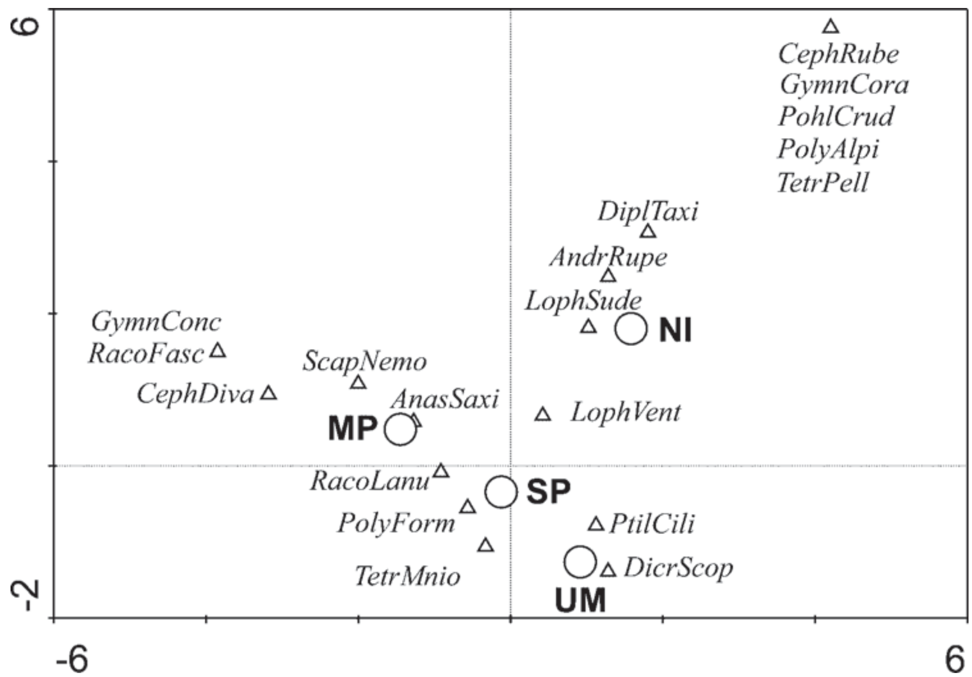


Figure 4. Ordination diagram of Canonical Correspondence Analysis, displaying first two axes constrained by the sample location category (3.4% of total variation explained, $P = 0.002$). NI, near ice, plots < 5 m from the places with underground ice formation; MP, middle part; SP, side part; and UM, upper margin. Sixteen bryophyte species best explained by the location are shown: *AnasSaxi*, *Anastrophyllum saxicola* (Schrad.) R. M. Schust.; *AndrRupe*, *Andreaea rupestris* Hedw.; *CephDiva*, *Cephaloziella divaricata* (Sm.) Schiffn.; *CephRube*, *Cephaloziella rubella* (Nees) Warnst.; *DicrScop*, *Dicranum scoparium* Hedw.; *DiplTaxi*, *Diplophyllum taxifolium* (Wahlenb.) Dumort.; *LophSude*, *Lophozia sudetica* (Nees ex Hueneber) Grolle; *LophVent*, *Lophozia ventricosa* (Dicks.) Dumort.; *PohlCrud*, *Pohlia cruda* (Hedw.) Lindb.; *PolyAlpi*, *Polytrichum alpinum* Hedw.; *PolyForm*, *Polytrichum formosum* Hedw.; *PtilCili*, *Ptilidium ciliare* (L.) Hampe; *RacoFasc*, *Racomitrium fasciculare* (Hedw.) Brid.; *RacoLanu*, *Racomitrium lanuginosum* (Hedw.) Brid.; *ScapNemo*, *Scapania nemorea* (L.) Grolle; *TetrPell*, *Tetraphis pellucida* Hedw.

Some spider and rhagidiid mite populations exhibit extreme disjunctions from Northern European populations. For instance, the main distribution of the predatory mite *Rhagidia gelida* is circumpolar and mostly north of the Arctic Circle. The spiders *Acantholycosa norvegica*, *Bathyphantes eumenis*, *Diplocentria bidentata*, *Semljicola faustus* and *Wubanoides uralensis* have their main ranges in Siberia. For the spider *Wubanoides uralensis* the Kamenec Hill is the lowest known elevation site in Europe.

Proximity to ice deposits is a strong predictor of the arthropod composition, explaining nearly 23% of the total variation (Figure 5). For instance, the occurrence of *Rhagidia gelida*, *Bathyphantes eumenis*, *Diplocentria bidentata* and *Semljicola faustus* is intimately tied to ice reservoirs. Direct observations of active *Rhagidia gelida* confirmed this result, and individuals were limited to bare and moist block walls or fissures between blocks and adjacent moss pads immediately adjacent to ice deposits.

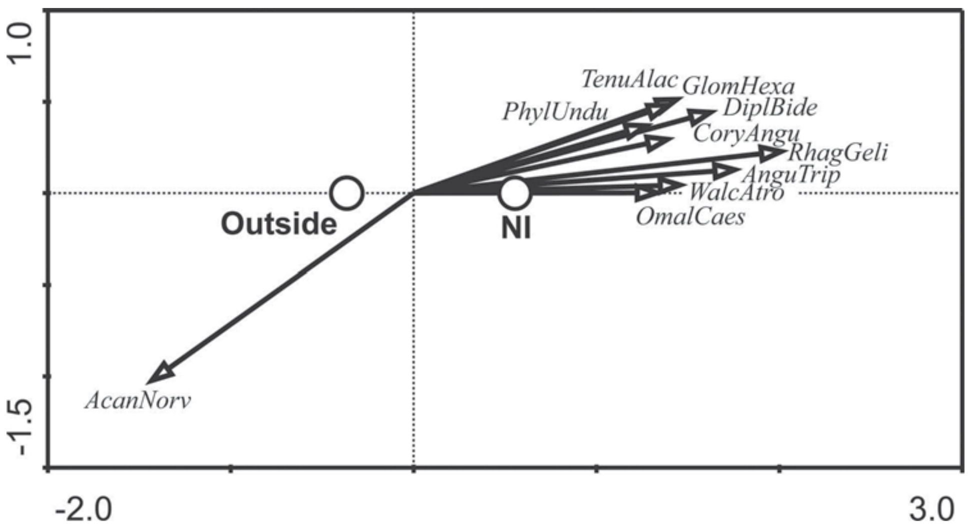


Figure 5. Ordination diagram of the Redundancy Analysis method on the dataset with all arthropods. The first (horizontal) axis defined by the proximity to ice formation places explains 22.7% of the total variation in species data, while the second (vertical) axis explains another 18.5% of the variation, unrelated to the tested factor. NI, near ice, plots < 5 m from the places with underground ice formation; Outside, all remaining plots. Ten species best fitted by the proximity of ice-formation places are shown: Acari: *RhagGeli*, *Rhagidia gelida* Thorell, 1872; Araneae: *AcanNorv*, *Acantholycosa norvegica* (Thorell, 1872); *AnguTrip*, *Anguliphantes tripartitus* (Miller and Svatoň, 1978); *DiplBide*, *Diplocentria bidentata* (Emerton, 1882); *TenuAlac*, *Tenuiphantes alacris* (Blackwall, 1853); *WalcAtro*, *Walckenaeria atrotibialis* (O. P.-Cambridge, 1878); Coleoptera: *CoryAngu*, *Coryphium angusticolle* Stephens, 1834; *OmalCaes*, *Omalium caesum* Gravenhost, 1806; *PhylUndu*, *Phyllotreta undulata* Kutschera, 1860; Diplopoda: *GlomHexa*, *Glomeris hexasticha* Brandt, 1833.

In contrast, *Acantholycosa norvegica* and *Wubanoides uralensis* never occurred near ice deposits.

Table 2 summarizes the strength and significance of the proximity to ice deposits in the composition of particular taxonomic groups. When strength values approach the value one, as is the case for the Rhagidiidae and Araneae, proximity to ice deposits represents the single most important factor determining composition. For Coleoptera and Diplopoda this factor is also relatively important, whereas in Oniscoidea it has a relatively weak, although significant, impact on composition. Distance to ice deposits had no effect upon Opiliones composition.

Discussion

Underground ice deposits in temperate latitudes

In temperate latitudes, the two main natural habitats in which subterranean ice formations can be found throughout the year are talus slopes and caves. Although freezing caves are generally found at fairly high altitudes (approx. 1100–1800 m), freezing taluses occur at much lower altitudes (approx. 300–500 m). Why?

Table 2. Summary of the relations between composition of individual species groups and the sample placement near the area with underground ice formation.

Group	Relation strength	*P*
Araneae	0.80	0.001
Rhagidiidae	0.92	0.001
Coleoptera	0.47	0.002
Diplopoda	0.39	0.013
Oniscoidea	0.20	0.037
Opiliones	0.10	n.s.
All species	0.86	0.001

The "Relation strength" column compares the amount of variation explained by the factor of sample placement with that obtained on the first axis of principal componenets analysis; the *P* column refers to the Monte Carlo permutation test of significance of this relation.

This pattern is related to the different architecture of voids in caves and scree slopes in conjunction with the inverse correlation between the number of black frost days and elevation. Ishikawa (2003) noted that ground cooling before the onset of seasonal snow cover was a critical factor determining the presence or absence of mid-latitude permafrost deposits. At high altitudes cold air is able to enter cave systems because their large entrances are usually not snow covered. In contrast, thick snow cover forms an insulating blanket between the cold winter atmosphere and sub-nivean spaces in screes (Aitchison 1978). As a result, soil, bedrock and also subterranean voids in screes do not freeze at high elevations. At low elevations with thin or no snow cover, cold air is able to penetrate into scree voids. Consequently, during the winter, scree blocks are chilled below freezing on black frost days. When melt water and rainwater penetrate subsurface voids in the spring, they freeze on contact with the chilled bedrock. The resultant subterranean ice-mass slowly melts during the summer, causing continuous seepage of cold air on the lower slope margin. Only for a few weeks in the autumn does the temperature of air flux increase above zero.

Although ice reservoirs in caves have limited or no ability to influence surface habitats, in screes there is continual seepage of cold air from the entire bottom of the slope because ice deposits are separated from surface habitats by only a thin, permeable veneer of stones, soil and vegetation. As a result, microsites with a mean annual temperature near 0°C are maintained far south of regional climates sharing this characteristic. In Eurasia the 0°C isotherm runs thousands of kilometres north of Kamenec Hill from the northern margin of Scandinavia, across the Ural Mountains through Siberia, passing along the south side of Lake Baikal. Screes with ice reservoirs therefore represent habitat islands of periglacial microclimate in lower latitudes.

Plant and animal biodiversity

Air circulation in the talus forms a mosaic of microspaces offering a broad array of microclimates (Růžička et al. 1995). We documented 15 species of bryophytes, spiders, and a mite which have isolated populations at Kamenec Hill. Only some are cold-adapted (or "cryophilic") species (Růžička 2011): eight species are closely tied to underground ice deposits, but the remaining seven are not. The boreal spider *Wubanoides uralensis* and Alpine spiders *Rugathodes bellicosus* and *Lepthyphantes notabilis*, for instance, inhabit the middle of the Kamenec Hill scree slope. Their persistence appears to depend on a complicated (and unknown) mosaic of factors including stone orientation, degree of insolation, local humidity gradients, presence of microspaces with moderate winter microclimate. However, their presence on these sites contributes significantly to local biodiversity (Růžička and Zacharda 2010).

Habitat

In Central Europe, freezing talus slopes have developed on a number of bedrock types such as basalt, andesite, sandstone and limestone (Růžička 1999; Zacharda et al. 2007). All of these sites are characterized by deep rock rubble with only sporadic soil development and a sparse vegetation of bryophytes and lichens. As at Kamenec Hill, air and soil temperatures in specific microsites rarely exceed 8°C in summer, with mean annual temperatures in their basal parts being near 0°C. These sites also support relict bryophytes, mites and spiders. For example, *Bathyphantes eumenis buchari* Růžička, 1988, and *Wubanoides uralensis lithodytes* Schikora, 2004, represent subspecies that are limited to these habitats and possess troglomorphic morphological adaptations such as elongated appendages (Růžička 1988; Schikora 2004).

Temperate latitude, mid-low elevation ice-chilled habitats are not confined to central Europe. In North America, comparable ice-maintaining screes are generally referred to as Talus Glaciers or Felsenmeers (Wisconsin's endangered resources 2012). Examples of such habitats in the Appalachian Mountains include the Ice Caves at White Rocks National Recreation Area in southern Vermont and Ice Mountain in eastern West Virginia. The latter site (elevation 210 m a.s.l.) represents a massive scree slope consisting of Devonian Oriskany Sandstone with ice reservoirs and cold air seepage at its base (Core 1975). As on the Kamenec Hill, this site supports a wide array of plant and animal species with disjunct distributions from the northern taiga.

Algific talus slopes at low elevations (e.g. 300 m a.s.l.) in the Upper Midwestern USA also provide similar habitat conditions, as well as numerous highly disjunct and endemic plant (angiosperms, pteridophytes and bryophytes) and animal (springtails, land snails, mites) populations that appear to represent relict populations from the late Wisconsinian (Frest 1991; Nekola 1999). However, the mechanisms that lead to underground ice formations in these sites are considerably different. In algific talus slopes ice is held in fissure caves within carbonate bedrock units. Cold air is able to penetrate into these fissures from upland sinks during the winter, and escapes during the summer by passing horizontally through bedrock colluvium. Although there may be some local storage of ice in near-surface colluvium, the bulk is retained in bedrock up to 0.5 km from the hillslope surface. As a result, cold air drainage in algific talus slopes is not limited to slope bases – in fact numerous sites are perched above 20-m vertical cliffs – and do not require the presence of an unvegetated zone immediately upslope.

At temperate latitudes in Eurasia, as well as North America, microclimatic buffering by cold air seepage from freezing screes and algific talus slopes supports populations of numerous boreal species that would not otherwise be able to persist within the regional landscape. These habitats therefore significantly contribute to microclimatic and biological diversity of landscape, and should be targeted for conservation.

Acknowledgements

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