

SPIDER (ARANEAE) COMMUNITIES OF SCREE SLOPES IN THE CZECH REPUBLIC

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ABSTRACT. We assessed the effects of environmental factors on spider communities in screes (sloping mass of coarse rock fragments) of the Czech Republic, based on catches from 325 pitfall traps, exposed for 177–670 days, from 1984–2000. Bootstrap resampling was applied to test for fuzziness of the partitions in cluster analysis of the samples. Two distinct spider communities were identified. The first one was confined to sites where ice is formed and persists until late summer or over the whole year. This community consists of numerous relict spiders, such as *Bathypantes simillimus buchari* Růžička 1988, *Diplocentria bidentata* (Emerton 1882) and *Leptyphantes tripartitus* Miller & Svatoň 1978, possibly persisting in these cold screes from the early postglacial period. The other community included all other sites, irrespective of their environmental characteristics. Monte Carlo simulations were used to test the significance of environmental factors and their interactions on the studied communities. Ice formation near the traps and position of the traps within individual screes were the most significant factors, followed by the depth of the traps within the scree, diameter of stones forming the scree, and altitude. A marginally significant effect was found for organic content in the scree matter, whereas presence of trees and phytogeographical districts appeared non-significant. Our analyses support the view that spiders inhabiting cold screes in Central Europe belong to a unique relict community of species requiring cold and stable microclimate.

Keywords: Scree slopes, environmental factors, ice formation, CCA, Monte Carlo simulations

At middle elevations scree slopes (or talus, an accumulation of coarse rock debris that rests against the base of an inland cliff; Allaby & Allaby 2003) represent common terrain forms in larger parts of Europe. Most stone accumulations result from frost weathering of primarily compact rocks. These screes are widespread especially in the subarctic and in mountains in mid-latitudes, where a periglacial climate (i.e., climate of areas adjacent to a glacier or ice sheet) prevailing in the recent geological past promoted their development. Screes situated at middle elevations have attracted the attention of ecologists only recently, perhaps due to logistic constraints (difficult access, a permanent danger of falling stones, landslides, etc.). Relatively small cavities situated deeply in the scree are usually covered by unstable layers of stones, making non-destructive studies rather difficult or almost impossible. Further, the low densities of most invertebrates colonizing the inner parts of screes make short-term studies inefficient. In spite of these difficulties, current ecological research

showed that some of the screes host peculiar and surprisingly species-rich fauna of invertebrates. Recent ecological studies demonstrated that the screes represent island-like ecosystems, supporting species which do not occur in the surrounding areas (Möseler & Molenda 1999; Kubát 2000). Repeated field observations supported by microclimatic measurements have shown that some screes function as large coolers, accumulating cold air that persists in some parts of the screes over the whole season. The thermic regime of the screes is often extremely conservative, largely independent of temperature fluctuations above-ground, both within and between years. At the bottom of some screes ice is formed, sometimes persisting there over the whole year, even if temperatures above-ground are higher by 30 °C or even more (Gude et al. 2003). Therefore, the stability of the temperature regime with extremely cold temperatures throughout the year and permanently high humidity enables persistence of a unique community of invertebrates, including

several representatives of arctic fauna which retreated from other habitats in Central Europe more than 10,000 years ago.

The research focused on the fauna of invertebrates in screes of the Czech Republic was considerably intensified after modified pitfall traps were developed (Růžička 1982, 1988b). These traps were exposed by the senior author for several months up to two years in most important scree localities in the country over the course of the last two decades. Numerous surprising findings have been reported, based on this research, including twelve species of spiders, mites and diplopods new to the Czech Republic (Růžička 1988b, 1994, 2000, 2002; Růžička et al. 1989; Růžička & Antuš 1998; Růžička & Hajer 1996; Zacharda 1993) and five species/subspecies new to science (Růžička 1988a; Zacharda 2000a, b, c). The results of the studies carried out on nearly 66 localities revealed also a considerable heterogeneity of spider communities inhabiting the screes. While some localities host numerous relict species (see Discussion), other sites are relatively poor in biogeographically and ecologically interesting spiders. Also, a considerable variation was observed within individual localities, with great differences between individual parts of the screes. These observations resulted in several ecological questions that we address in this paper: 1) What are the environmental factors responsible for the observed variation in species composition of spider assemblages in the screes? 2) Is the occurrence of relict species in screes correlated with some environmental factors? 3) Is there a sharp boundary between spider communities of cold and warm sites within individual screes?

To answer these questions we compiled all available records of spiders from screes of the Czech Republic, obtained by pitfall traps exposed for a longer time, and added available information on environmental factors, either measured or estimated in other ways at sites where the spiders were collected. This resulted in a relatively large and complete dataset which we used in the analysis.

METHODS

Study area and localities.—The Czech Republic is situated in the temperate zone of Europe between 48° 33' and 51° 03' N, and 12° 05' and 18° 51' E. Major parts of the

Czech Republic belong to the Proterozoic and Palaeozoic Bohemian Massif, only the easternmost part is pervaded by the Tertiary mountain system of the western Carpathians. The Bohemian Massif was long ago transformed by erosion into a levelled terrain, which was, during the Alpine formation of mountains, disrupted by faults, fractures in rock strata; elevated crustal blocks formed mountain regions (particularly border mountains), and the volcanic region of České Středohoří Mts. in the north of the Czech Republic was formed. The system of deeply cut river valleys was formed during the Tertiary and, especially, during the Quaternary (Ložek 1988). Due to its geology and geomorphology, the territory of the Czech Republic is rich in various boulder accumulations (Růžička 1993).

Material was collected from 66 localities distributed all over the Czech Republic (Fig. 1). Elevations of the localities ranged from 270–1550 m a.s.l. The investigated screes are formed by andesite, basalt, conglomerate, limestone, phonolite, quartzite, sandstone, granite and other kinds of rock. The height of scree fields from the foot to the top varied between 10 and 250 m, slope angles ranged between 20° and 40°.

Sampling.—The animals were usually trapped in modified pitfall traps made of rigid plastic (Růžička 1982, 1988b). The traps consisted of a board (20 x 25 cm), which forms an artificial horizontal surface (note that a flat horizontal soil surface is not present in scree slopes) and a can inserted in the centre of the board. Traditional pitfall traps (simple cans) were also used. The cans contained a mixture of 7% formaldehyde and 10% glycerol with a few drops of a surfactant. The traps were placed among the stones. Field research was conducted from 1984–2000. In total, 325 traps were installed, most of them (85%) for more than 300 days.

The catch, especially from deeper scree layers, is often poor in species. To obtain more representative samples, we combined catches from traps placed at the same position along the scree slope in individual localities. This resulted in 128 samples.

Environmental characteristics.—In total, eight environmental characteristics were registered: elevation (m a.s.l.); scree type (1 = bare scree slopes, 2 = scree slopes partly

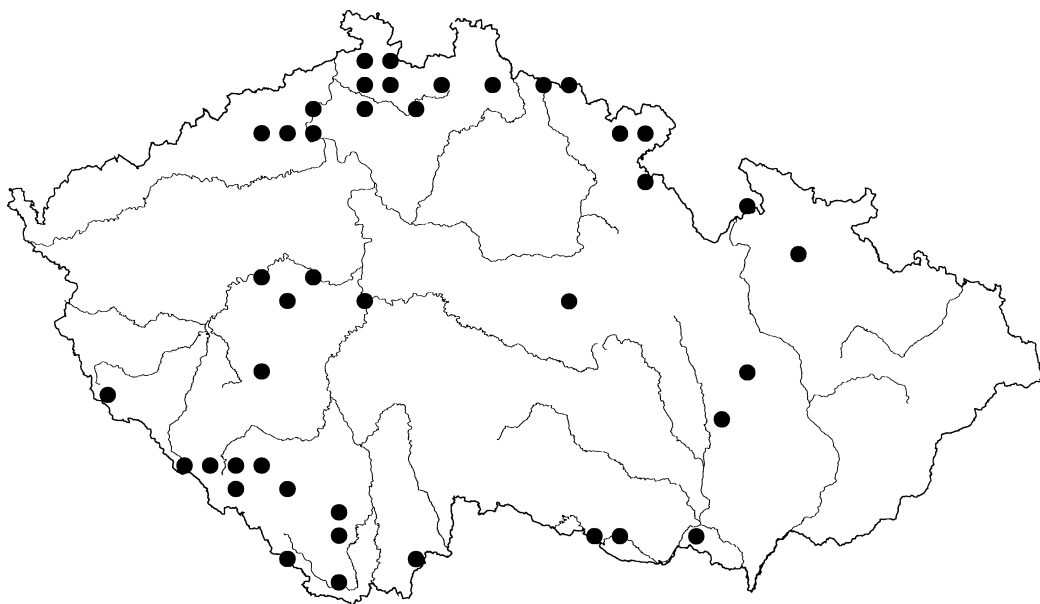


Figure 1.—Location of the studied screens on a grid map of the Czech Republic. The circles represent one or several localities used in the analysis.

overgrown by solitary trees, 3 = scree forests, corresponding to a gradient from bare to forest screes); position of pitfall traps along the temperature gradient in scree field (1 = lower margin of the scree, 2 = middle part, and 3 = upper margin of the scree); ice formation near the trap (1 = no ice formation, 2 = temporal ice inside scree, melting in summer, 3 = permanent ice forming permafrost-like conditions); typical size of stones in the scree (diameter ranging from 0.1–10 m); depth below the surface in which the trap was installed (ranged from 0–5.0 m); substrate around the trap (1 = bare stones, 2 = soil, 3 = detritus, 4 = mosses, ranges from sterile to organic substrate); phytogeographical district (1 = thermo-, 2 = meso-, 3 = oreophyticum, characterized by vegetation on a broader scale, Slavík 1984).

In addition, three covariables were used: type of trap (1 = a pot, which was a low efficiency trap; 2 = a pot sunken into a board, which was considered a high efficiency trap); number of traps at a site (ranging from 1–11); number of days during which the trap was exposed.

Data analysis.—In the numerical analyses we always used the whole data set, i.e., all localities and all species. The input data were log-transformed prior to analysis. Detrended

Canonical Correspondence Analysis (DCA) was used to estimate species turnover along the main direction of variability. After that CCA (Canonical Correspondence Analysis) implemented into the CANOCO program (ter Braak & Šmilauer 1998) was performed to test the effects of individual variables and their interactions on species composition. Monte Carlo simulations with 10,000 permutations were calculated to assess the significance of individual environmental factors and their interactions. In these analyses the factors which were not used as explanatory variables were defined as covariables, to remove their effects on the results and to obtain a net effect of individual environmental variables. Using this approach we could perform tests that are counterparts to ANOVA but for multivariate data.

Spider communities were classified by a cluster analysis based on Ward's method, using Euclidean distances for quantitative data (Jongman et al. 1995, p. 178), calculated for log-transformed catches, using the Syn-tax program by Podani (2001). The sharpness of the resulting classification was tested using a bootstrap resampling, in which stability of partition at a given level was tested by resampling the original data, according to Pillar

(1999). The outcome of this testing indicates whether groups in the partition reappear more often in resampling data than expected on a random basis.

Nomenclature follows the catalogue of spiders of the Czech Republic (Buchar & Růžička 2002). Species characteristics were also taken from this source. Voucher specimens are deposited in the collection of V. Růžička.

RESULTS

Site characteristics.—The strongest significant correlation between pairs of the eight environmental characteristics was found between elevation and phytogeographical district ($r = 0.70$). This reflects the crucial role of elevation in the distribution of plant communities at a broader scale. The position of the traps was strongly negatively correlated with the incidence of ice at the traps ($r = -0.49$), implying that traps situated at the lower margin of the screes were often surrounded by permanent ice whereas traps placed at the upper margin were free of ice. As expected, bare scree slopes were usually built of large boulders whereas forested screes developed on gravel screes ($r = 0.40$). Further, scree sites with large amounts of organic matter and covered by mosses usually developed in warm regions ($r = -0.32$), at lower elevations ($r = -0.34$) and at the lower margin of the screes ($r = -0.35$).

Ice formation was negatively correlated with elevation ($r = -0.20$). Even if elevations of the sites (270–1550 m) spanned the range of elevations in the Czech Republic almost completely, surprisingly the screes with ice formation were found at rather low elevations; the screes with permanent ice filling were situated at 350–650 m a.s.l., the screes with temporal ice filling at 270–700 m a.s.l. The ice was found more often in sterile screes without organic matter and deeper in the scree than in screes with organic matter and near traps situated closely to the scree surface ($r = 0.26$ and $r = -0.21$, respectively). All these correlations were significant at $P < 0.05$.

Species composition.—In total, 1047 spiders were captured, belonging to 176 species of 22 families. Based on our knowledge on ecological demands of all spider species in the Czech Republic (Buchar & Růžička 2002), the following sets of species can be identified among the captured spiders:

1. Species occurring exclusively in bare scree slopes (and in adjacent underground spaces) and in scree forests: *Acantholycosa norvegica* (Thorell 1872), *Bathypantes simillimus buchari* Růžička 1988, *Clubiona alpicola* Kulczyński 1882, *Comaroma simoni* Bertkau 1889, *Diplocentria bidentata* (Emerton 1882), *Kratochviliella bicapitata* Miller 1938, *Lepthyphantes notabilis* Kulczyński 1887, *Lepthyphantes improbulus* Simon 1929, *Lepthyphantes zimmermanni* Bertkau 1890, *Liocranum rutilans* (Thorell 1875), *Meta menardi* (Latreille 1804), *Micrargus apertus* (O. P.-Cambridge 1871), *Neon levis* (Simon 1871), *Pholcomma gibbum* (Westring 1851), *Porrhomma myops* Simon 1884, *Porrhomma rosenhaueri* (L. Koch 1872), *Rugathodes bellicosus* (Simon 1873), *Saaristoa firma* (O. P.-Cambridge 1905), *Trogloneta granulum* Simon 1922, *Wubanoidea uralensis* (Pakhorukov 1981).

2. Species of scree slopes, occurring also in other habitats (in brackets): *Lepthyphantes leprosus* (Ohlert 1865), *Liocranum rupicola* (Walckenaer 1830), *Nesticus cellulanus* (Clerck 1757), *Pholcus opilionoides* (Schrank 1781), *Sitticus pubescens* (Fabricius 1775) (synanthropic), *Ceratinella major* Kulczyński 1894, *Megalepthyphantes collinus* (L. Koch 1872), *Tegenaria silvestris* L. Koch 1872 (forests), *Lepthyphantes tripartitus* Miller & Svatoň 1978, *Theonoe minutissima* (O. P.-Cambridge 1879) (peat bogs), *Agraecina striata* (Kulczyński 1882) (lowland forests), *Walckenaeria capito* (Westring 1861) (rock steppes), *Cryphoeca silvicola* (C.L. Koch 1834) (spruce forests), *Porrhomma egeria* Simon 1884 (caves and subalpine belt).

The cluster analysis of samples revealed two distinct groups, indicating that two clearly separated spider communities can be identified in the screes (Fig. 2). The bootstrap resampling showed a partitioning at this level. For lower levels, i.e. when considering partitioning to a higher number of clusters, we obtained non-significant results. Accordingly, all clusters except for those labelled in Fig. 2 A and B should be interpreted as fuzzy, not distinctly separated from each other. All ten samples from sites at which permanent ice was observed and most samples from sites at which temporal ice formation was registered were included in cluster A. The other cluster, B, included all other localities.

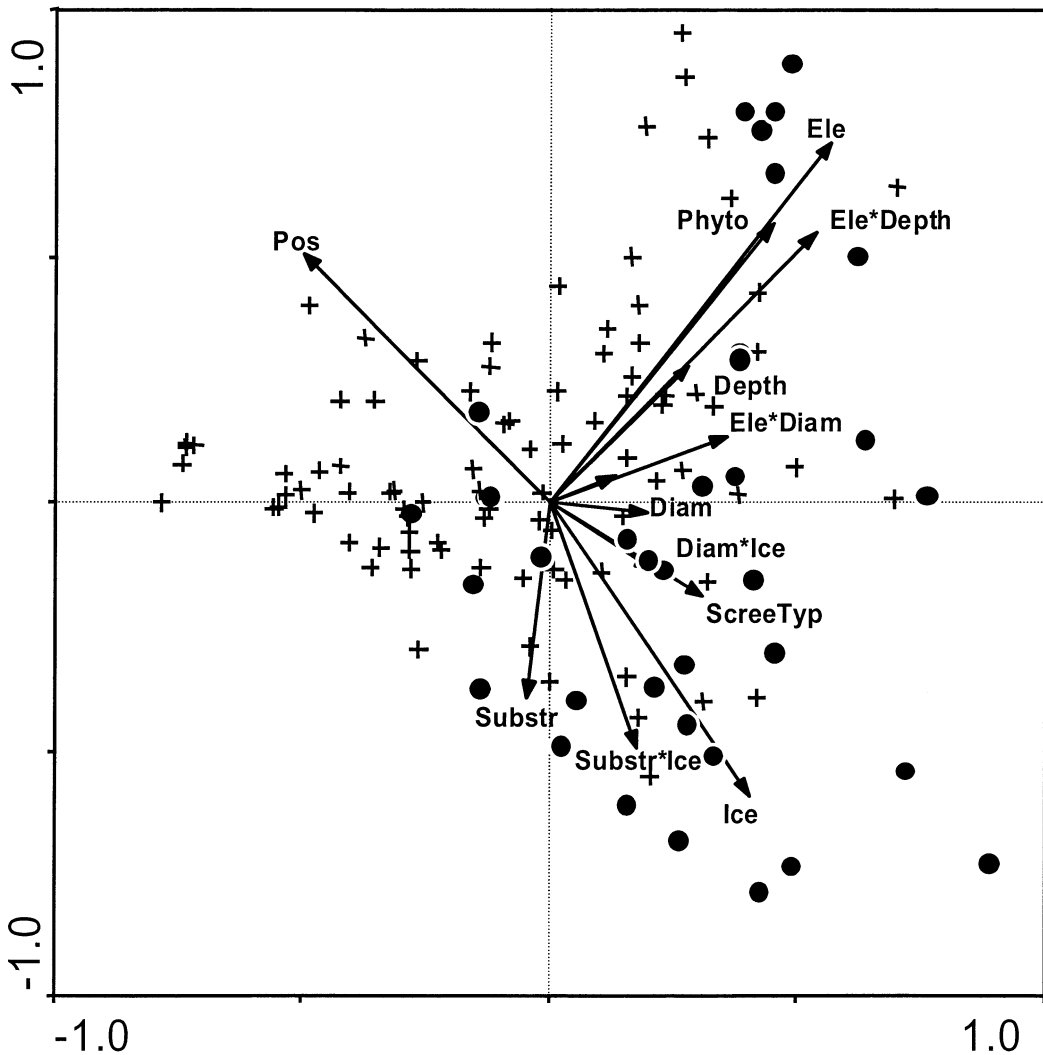


Figure 3.—CCA ordination of samples. Arrows indicate the effect of environmental variables. Full circles = samples belonging to A cluster in Fig. 2, crosses = samples belonging to B cluster. ELE: elevation; ICE: ice formation near the trap; DEPTH: depth below the surface, in which the trap was installed; POS: position of pitfall trap along the temperature gradient in scree field; DIAM: typical size of stones; SUBSTR: substrate around the trap; PHYTO: phytogeographical district; SCREETYP: from bare scree to scree forest.

relatively high number of samples scattered over the whole Czech Republic enabled a more detailed analysis of the effect of environmental factors on individual species.

Analyses of the relationship between environmental variables and the number of captured spiders of individual species (linear regression) showed that species found mainly at higher elevations included *Clubiona alpicola* (only above 700 m a.s.l.), *Wubanoidea uralensis* (only above 930 m), *Bathypantes sim-*

illimus, and *Walckenaeria capito*. Several species were caught mainly at lower elevations: *Lepthyphantes improbulus* (up to 400 m a.s.l.), *Pholcus opilionoides* (up to 750 m), *Liocranum rupicola* (up to 800 m) and *Pholcomma gibbum*.

Metellina merianae occurred primarily in scree forests; *Acantholycosa norvegica*, *Lepthyphantes notabilis*, *Clubiona alpicola* were recorded exclusively on bare, open scree slopes.

Table 1.—Results of the CCA analyses applied to log abundances of spiders caught in pitfall traps. *r*: species-environment correlation on the first axis, *var*: percentage of species variability explained by the first ordination axis. *F*: the *F*-ratio statistics for the test on the trace. *P*: corresponding probability value obtained by the Monte Carlo permutation test. The variables not used as explanatory variables in individual analyses, were used as covariables. Type of the trap, number of traps at a site and number of days for which the trap was exposed were used as covariables in all analyses. *ELE*: elevation; *ICE*: ice formation near the trap; *DEPTH*: depth below the surface, in which the trap was installed; *POSITION*: position of pitfall trap along the temperature gradient in scree field; *DIAM*: typical size of stones; *SUBSTR*: substrate around the trap; *PHYTO*: phytogeographical district; *SCREETYP*: from bare scree to scree forest.

Explanatory variables	<i>r</i>	<i>var</i>	<i>F</i>	<i>P</i>
<i>ELE</i>	0.812	1.5	1.67	0.0017
<i>ICE</i>	0.828	1.7	1.84	0.0001
<i>DEPTH</i>	0.833	1.4	1.54	0.0003
<i>POSITION</i>	0.803	1.7	1.87	0.0001
<i>DIAM</i>	0.809	1.4	1.59	0.0089
<i>SUBSTR</i>	0.8	1.2	1.3	0.0497
<i>PHYTO</i>	0.732	0.9	1.03	0.3920
<i>SCREETYP</i>	0.767	0.9	0.95	0.5951
<i>ELE</i> × <i>DIAM</i>	0.778	1.3	1.47	0.0215
<i>DIAM</i> × <i>ICE</i>	0.843	1.4	1.54	0.0185
<i>SUBSTR</i> × <i>ICE</i>	0.847	1.3	1.42	0.0192
<i>ELE</i> × <i>DEPTH</i>	0.809	1.3	1.38	0.0323
<i>SUBSTR</i> × <i>DEPTH</i>	0.81	1.2	1.3	0.0396
<i>PHYTO</i> × <i>SUBSTR</i>	0.774	1.1	1.23	0.1060
<i>SCREETYP</i> × <i>SUBSTR</i>	0.783	1	1.07	0.3015

Lepthyphantes notabilis and *Pholcus opilionoides* colonized mainly upper scree margins; *Lepthyphantes tripartitus* and *Diplocentria bidentata* occurred mainly at lower margins.

The dependence on ice formation is sharp in some spiders: *Rugathodes bellicosus*, *Lepthyphantes notabilis*, *Tegenaria silvestris*, *Nesticus cellulanus*, *Pholcomma gibbum*, *Meta menardi*, *Acantholycosa norvegica*, *Lio-cranum rupicola*, *Pholcus opilionoides* avoided sites with ice formation, whereas *Lepthyphantes tripartitus*, *Diplocentria bidentata* and *Bathypantes simillimus buchari* at lower elevations were confined to these sites.

Diplocentria bidentata and *Lepthyphantes tripartitus* occurred together at sites where ice is formed. Along the gradient of substrate type, *L. tripartitus* preferred more detritus-rich sites, whereas *D. bidentata* colonised more mossy habitats. *Diplocentria bidentata* tended to occur at the surface, whereas *L. tripartitus* occurred in deeper layers. These trends were univocally supported by the separate sieving of moss and detritus on Klíč Mt. on 12th October 1999: 28 specimens of *L. tripartitus* and 6 specimens of *D. bidentata* were collected by detritus sieving, whereas 66 specimens of *D.*

bidentata and 1 specimen of *L. tripartitus* were collected by moss sieving.

Orb weavers *Metellina merianae* and *Meta menardi* preferred spaces among larger stones; in contrast, *Lepthyphantes notabilis*, *Pholcomma gibbum*, *Acantholycosa norvegica* were more abundant at sites with smaller stones.

The species occurring mainly at the scree surface included *Acantholycosa norvegica*, *Diplocentria bidentata*, whereas *Porrhomma myops*, *Rugathodes bellicosus*, *Meta menardi*, *Nesticus cellulanus*, *Wubanooides uralensis* were found mainly in the depth of the screes.

Finally, species found mainly at the surface of bare stones included *Lepthyphantes notabilis*, *Clubiona alpicola*, *Rugathodes bellicosus*, *Meta menardi*, *Theonoe minutissima*, and *Wubanooides uralensis*.

DISCUSSION

Balch (1900) was possibly the first who documented ice formation in scree slopes at middle (but not at higher) elevations. We showed that ice is regularly formed in screes also from 270–700 m. According to Gude et al. (2003) lower parts of scree slopes are intensively cooled during short periods of winter frost. Cold air penetrates inside the screes

only during periods with no (or limited) snow cover. Long-term data from three south Bohemian meteorological stations support this hypothesis. They indicate a negative relationship between the number of frost days without snow cover and altitude: there are 23 frost days without snow per year in České Budějovice at 389 m, 19 such days at Kašperské Hory (737 m) and only 10 frost days without snow per year on Churáňov at 1,118 m a.s.l. Mountain scree slopes do not markedly cool in winter, because frost air cannot penetrate the scree slopes through the snow cover.

Spatial heterogeneity of invertebrates in scree slopes was studied by Molenda 1989; Růžička et al. 1995; V. Růžička 1990, 1996, 2002; J. Růžička 1996. The position of a site along the scree slope was designated as the main factor influencing species distribution by Brabec (1973) in his pioneer study. We found that the effects of position of the trap on the scree slope and ice formation are strongly significant. Ice formation is a principal factor and ice is usually formed on the lower margin of scree slopes. However, concave slope forms can be formed by various slope denudation processes also in the middle part of a scree slope (Demek et al. 1975; Růžička 1999c). In such cases, ice can be formed also in the middle part of a scree slope.

Elevation patterns in spiders and mites of screes also have been documented by Růžička & Zacharda (1994) who focused on scree habitats in our highest mountains in the Krkonoše National Park, and by V. Růžička (1996), who studied spiders in screes at low elevations of the Podyjí National Park.

Spatial distribution of spiders in screes was studied by Růžička 1999a, 2002 and Růžička et al. 1995. Temperature is a key factor responsible for the presence or absence of species in individual parts along the slope. The dependence of *L. tripartitus* on detritus explains the fact, that this species colonizes the whole profile of the lower margin of the screes, from the surface to the depth of about one meter, whereas *D. bidentata*, which is restricted to moss cushions, cannot colonize deeper layers.

Land surfaces at higher latitudes in the northern hemisphere support a range of forest, scrub, tundra and peatland communities at the present day that may collectively be called the "coldland complex". Physiognomically and

floristically similar communities also occur at higher elevations of mountains further south (Tallis 1991). Current disjunct distribution of some spider species is a result of their withdrawal from Central Europe caused by changing climatic conditions in the Pleistocene. Twenty-seven spider species of the Czech arachnofauna exhibit boreo-montane type of geographical distribution (Růžička in prep.). They occur in higher latitudes and have disjunct, island-like populations in Central Europe. The present findings indicate that some scree spiders in Central Europe could be regarded as relicts of former climatic periods ("glacial relicts"). Four of these species occur exclusively in scree slopes (Buchar & Růžička 2002).

Having a distribution center in Siberia/North Asia, *Wubanooides uralensis* and *Acantholycosa norvegica* occur only in several localities in Central Europe (Schikora 2004; Marusik et al. 2003), independent of ice formation. *Bathypantes simillimus* shows about the same general distributional pattern. In contrast, *Diplocentria bidentata* has a Holarctic distribution. In Scotland, northern England and Wales it occurs locally with a low abundance in highlands (Harvey et al. 2002). In Central Europe it is known only from the peat bogs in Harz, Germany, situated at the highest elevations (Wiehle 1965); in the Czech Republic on hilltops in the Krkonoše Mountains (2 specimens) and on lower margin of frozen scree slopes (243 specimens). The occurrence of the latter two species is closely tied to ice formation in scree slopes. The same is true for the Central European mountain species *Lepthyphantes tripartitus*. The occurrence of the three species at lower elevations is closely tied to the present periglacial temperature regime in frozen scree slopes, and the presence of these species indicates the palaeoregional character of these habitats (Zacharda et al. in press), i.e. island-like habitats inhabited by populations of formerly more widespread species (Nekola 1999).

Deep layers of screes represent shallow subterranean spaces, in which gradual adaptation to the stable environment of deep subterranean spaces takes place (Růžička 1999b). Species, which preferentially colonise deep scree layers, exhibit leg elongation, depigmentation, body diminishing, and eye reduction (Růžička 1988a, 1990, 1998; Schikora 2004).

We found some of these species on several localities (*R. bellicosus*, *B. s. buchari*); on the other hand, the occurrence of *Porrhomma myops* and *Comaroma simoni* is known from one locality only. The reason for their rarity (a special combination of environmental factors vs. our inability to penetrate more deep in scree?) remains unknown.

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LITERATURE CITED

- Allaby, A. & M. Allaby. 2003. Oxford Dictionary of Earth Sciences. Oxford University Press, Oxford, 608 pp.
- Balch, E.S. 1900. Glaciers or freezing caverns. Allen, Lane & Scott, Philadelphia, 377 pp.
- Brabec, E. 1973. The ecology of stony debris in the České Středohoří Mt.—a second approximation. Thesis, Charles University, Praha, 95 pp. (in Czech).
- Buchar, J. & V. Růžička. 2002. Catalogue of spiders of the Czech Republic. Peres, Praha, 351 pp.
- Demek, J., J. Pašek, & J. Rybár. 1975. The principles of erosion-denudation slope processes. *Studia geographica* 51:195–204 (in Czech).
- Gude, M., S. Dietrich, R. Mäusbacher, C. Hauck, R. Molenda, V. Růžička & M. Zacharda. 2003. Probable occurrence of sporadic permafrost in non-alpine scree slopes in central Europe. Pp. 331–336. In Proceedings of the 8th International Conference on Permafrost. (M. Phillips, S. M. Springman & L. U. Arenson, eds.). Lisse (NL).
- Harvey, P.R., D.R. Nellist & M. G. Telfer. 2002. Provisional atlas of British spiders (Arachnida, Araneae). Biological Records Centre, Huntingdon, 406 pp.
- Jongman, R.H., C.J.F. ter Braak, & O.F.R. van Tongeren. 1995. Data analysis in community and landscape ecology. Wageningen, Pudoc, 299 pp.
- Kubát, K. (ed.). 2000. Stony Debris Ecosystems. *Acta Universitatis Purkynianae, Biologica* 4, 204 pp.
- Ložek, V. 1988. Inorganic nature in relation to flora and vegetation. Pp. 31–35, 156–157. In *Květena České socialistické republiky* [The flora of the Czech Socialist Republic]. (S. Hejny & B. Slavík, eds.). Academia, Praha, (in Czech, English summary).
- Marusik, Y.M., G.N. Azarkina & S. Koponen. 2003. A survey of East Palaearctic Lycosidae (Aranei). II. Genus *Acantholycosa* F. Dahl, 1908 and related new genera. *Arthropoda Selecta* 12(2):101–148.
- Molenda, R. 1989. Käfer in kaltluftzeugenden Blockhladen—ökologische Untersuchungen an einem stark bewetterten Spaltenökosystem. 4 Rundschreiben der Arbeitsgemeinschaft Rheinischer Koleopterologen. Pp. 103–111.
- Möseler, B.M. & R. Molenda. (eds.). 1999. Lebensraum Blockhlade. *Decheniana-Beihefte* 37. 170 pp.
- Nekola, J.C. 1999. Paleorefugia and neorefugia: the influence of colonization history on community pattern and process. *Ecology* 80:2459–2473.
- Pillar, V.D. 1999. How sharp are classifications? *Ecology* 80:2508–2516.
- Podani, L. 2001. *Syn-Tax 2000. User's Manual*. Scientia, Budapest.
- Růžička, J. 1996. The beetles (Insecta: Coleoptera) in rock debris of the Plešivec hill (northern Bohemia, České středohoří Protected Landscape Area). *Klapalekiana* 32:229–235 (in Czech, English summary).
- Růžička, V. 1982. Modifications to improve the efficiency of pitfall traps. *Newsletter of the British Arachnological Society* 34:2–4.
- Růžička, V. 1988a. Problems of *Bathypantes eumenis* and its occurrence in Czechoslovakia (Araneae, Linyphiidae). *Věstník Československé společnosti zoologické* 52:149–155.
- Růžička, V. 1988b. The longtimely exposed rock debris pitfalls. *Věstník Československé společnosti zoologické* 52:238–240.
- Růžička, V. 1990. Spider (Araneae) communities of rock debris on a typical hillside in the České Středohoří Mts. (North Bohemia). *Acta Entomologica Bohemoslovaca* 86[1989]:419–431.
- Růžička, V. 1993. Structure and ecology of invertebrate communities of stony debris in Czech Republic. Research project. *Bulletin de la Société neuchâteloise des Sciences naturelles* 116(1):209–214.
- Růžička, V. 1994. Spiders in south Bohemian stony debris. *Acta Universitatis Purkynianae, Biologica* 1[1993]:9–18.
- Růžička, V. 1996. Species composition and site distribution of spiders (Araneae) in a gneiss massif in the Dyje river valley. *Revue suisse de Zoologie*, vol. hors série:561–569.
- Růžička, V. 1998. The subterranean forms of *Lepthyphantes improbulus*, *Theonoe minutissima* and *Theridion bellicosum* (Araneae: Linyphiidae, Theridiidae). Pp. 101–105. In Proceedings of the 17th European Colloquium of Arachnology. (P.

- A. Selden, ed.). British Arachnological Society, Burnham Beeches, Bucks.
- Růžička, V. 1999a. Spiders (Araneae) of scree slopes in the Moravian Karst. *Acta Musei Moraviae, Scientiae biologicae* (Brno) 84:205–210.
- Růžička, V. 1999b. The first steps in subterranean evolution of spiders (Araneae) in Central Europe. *Journal of Natural History* 33:255–265.
- Růžička, V. 1999c. The freezing scree slopes and their arachnofauna. Pp. 141–147. *In Lebensraum Blockhlade*. (B. M. Möselers & R. Molenda, eds.). Decheniana-Beihefte 37.
- Růžička, V. 2000. *Porrhomma myops* and *Porrhomma egeria* in the Czech Republic. *Acta Universitatis Purkynianae, Biologica* 4:149–150.
- Růžička, V. 2002. Spatial distribution of spiders (Araneae) on scree slopes in Křivoklátsko and Moravský Kras Protected Landscape Areas. *Acta Societatis Zoologicae Bohemicae* 66:321–328.
- Růžička, V. & P. Antuš. 1998. Spiders in stony debris in central Bohemia. *Acta Universitatis Purkynianae, Biologica* 2:19–29.
- Růžička, V., J. Boháč, O. Srovátka & L. Klimeš. 1989. Invertebrates from rock debris in north Bohemia (Araneae, Opiliones, Coleoptera, Diptera). *Sborník Severočeského Muzea—Přírodní Vědy, Liberec* 17:25–36 (in Czech, English summary).
- Růžička, V. & J. Hajer. 1996. Spiders (Araneae) of stony debris in North Bohemia. *Arachnologische Mitteilungen* 12:46–56.
- Růžička, V., J. Hajer & M. Zacharda. 1995. Arachnid population patterns in underground cavities of a stony debris field (Araneae, Opiliones, Pseudoscorpionidea, Acari: Prostigmata, Rhagidiidae). *Pedobiologia* 39:42–51.
- Růžička, V. & M. Zacharda. 1994. Arthropods of stony debris in the Krkonoše Mountains, Czech Republic. *Arctic and Alpine Research* 26:332–338.
- Shikora, H.-B. 2004. *Wubanoidea uralensis* (Pakhorukov 1981)—Geographic variation, mating behaviour, postembryonic development and description of a new subspecies (Araneae, Linyphiidae). Pp. 327–341. *In Diversität und Biologie von Webspinnen, Skorpionen und anderen Spinnentieren*. (K. Thaler ed.). *Denisia* 12.
- Slavík, B. 1984. *Grundlegende Phytochorotypen der Tschechischen Sozialistischen Republik*. *Preslia* 56:241–265.
- Tallis, J.H. 1991. *Plant Community History*. Chapman and Hall, London.
- ter Braak, C.J.F. & P. Šmilauer. 1998. CANOCO reference manual and users guide to “Canoco for Windows” software for canonical community ordination, version 4. Microcomputer Power, Ithaca.
- Wiehle, H. 1965. Die Spinnenfauna des Harzes. *Natur und Museum* 95(4):133–142.
- Zacharda, M. 1993. Glacial relict Rhagidiidae (Acari: Prostigmata) from superficial underground enclosures in the Krkonoše Mountains, Czechoslovakia. *Journal of Natural History* 27:47–61.
- Zacharda, M. 2000a. New and little-known species of Rhagidiidae from talus ecosystems, in the Czech Republic and Austria. *Journal of Zoology, London* 251:105–118.
- Zacharda, M. 2000b. New species of the rhagidiid genus *Foveacheles* (Acari: Prostigmata: Eupodoidea) with a lyrifissure-like structure of the chelicerae. *Journal of Natural History* 34:247–265.
- Zacharda, M. 2000c. New species of the genus *Troglocheles* (Acari: Prostigmata: Rhagidiidae) from Oetztaler Alps, Tyrol, with a key to adult species of the genus. *Journal of Natural History* 34:463–478.
- Zacharda, M., M. Gude, S. Krause, C. Hauck, R. Molenda & V. Růžička. In press. The Relict Mite *Rhagidia gelida* (Acari, Rhagidiidae) as Biological Cryoindicator of Periglacial Microclimate in European Highland Scree. *Arctic, Antarctic and Alpine Research*.

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