Journal of Bryology (2005) **27:** 35–46

Diversity of bryophytes on treeless cliffs and talus slopes in a forested central European landscape

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SUMMARY

The bryophyte flora and its environmental correlates were studied on 28 treeless cliffs and 18 treeless talus slopes in forested river valleys of the southern Czech Republic. The diversity of bryophyte assemblages was assessed through species richness and spectra of distribution-range types, growth forms and life strategies, using analysis of covariance. Species richness of cliffs increased with their area but this was not the case for talus slopes, where a high microtopographic heterogeneity appeared to be the key factor governing diversity. No habitat island effects were detected for cliffs; there were no differences between isolated cliffs and cliffs found in the neighbourhood of other cliffs or talus slopes. Island effects were not studied for talus slopes as they were nearly always found in clusters with cliffs and other talus slopes. Talus slopes were characterized by a strong effect of the ecotone between forest and open talus, with ecotonal vegetation being more diverse than the central part of talus slopes. However, no ecotone effect was found on cliffs. The effect of potential irradiation, used as a proxy for moisture availability, was weak on cliffs but strong on talus slopes where more insolated slopes had lower diversity, more temperate and fewer boreal species, a predominance of short turf or cushion-like mosses over large bryophytes and a higher proportion of the colonist strategy, as opposed to perennial stayers and long-lived shuttle species. On cliffs, base-rich rocks had higher total species richness but a lower proportion of hepatics, fewer suboceanic and more submediterranean species, and more small turf or cushion-like mosses. The effect of base status was not assessed for talus slopes as they were all formed from acidic rocks. These results demonstrate that cliffs and talus slopes in the same area are quite different habitats and each is characterized by distinctive environmental conditions.

KEYWORDS: Area effect, calcicole–calcifuge, Czech Republic, distribution range, ecotone, growth form, habitat island, irradiation, isolation, life strategy, species richness.

INTRODUCTION

Saxicolous and terricolous bryophytes present a group of organisms with specific physiological and ecological adaptations, which make them successful in various terrestrial habitats (Bates, 2000; Frahm, 2001). Several studies have shown that species diversity of the assemblages of these bryophytes depends, among other factors, on latitude (Cox & Larson, 1993), habitat insolation (Hedderson & Brassard, 1990), microtopographic heterogeneity (Kimmerer & Driscoll, 2000; Kubešová, 2000) or successional age of substratum (Pharo & Vitt, 2000; Hedderson, Letts & Payne, 2003). However, it is important to note that the responses of bryophyte diversity to environmental gradients may differ from the responses of vascular plants to the same gradients (McCune & Antos, 1981; Cox & Larson, 1993).

In temperate or boreal forested landscapes, local centres of saxicolous bryophyte diversity occur on habitat islands such as rock outcrops, cliffs, talus (scree) slopes or erratic boulders. In central Europe there have been several studies of bryophyte vegetation on treeless cliffs (Jurko & Peciar, 1963; Zittová-Kurková, 1984) or talus slopes (Lüth, 1990; Halfmann 1991; Hachtel, Weddeling & Möseler, 1999; Weddeling & Hachtel, 2000; Kubešová, 2000; Němcová, 2001), most of them focusing on description of local vegetation differentiation or vegetation–environment relationships, but rarely concerned with diversity patterns.

Arguably, these treeless ecosystems embedded in forested landscapes provide an alternative situation for testing the robustness of the basic tenets of the theory of island biogeography (MacArthur & Wilson, 1967), namely the positive relationship of species richness to habitat area and

DOI: 10.1179/174328205X40563

Received 22 March 2004. Revision accepted 3 September 2004

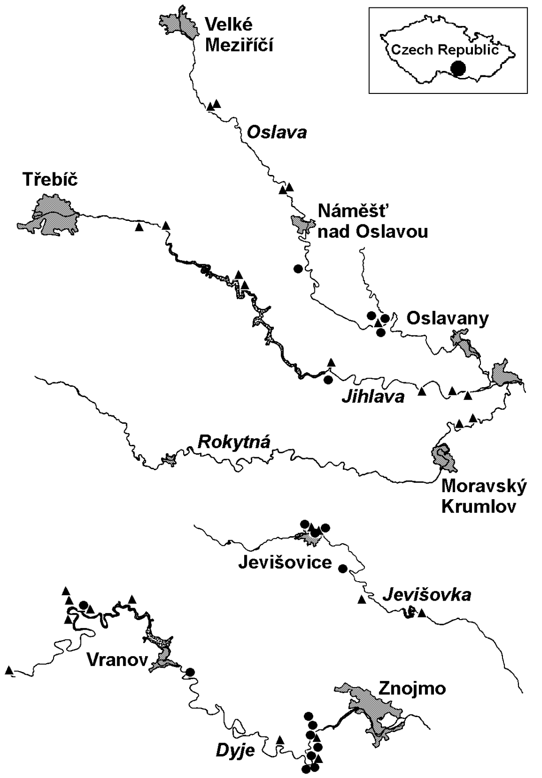

Figure 1. Map of the study area with locations of cliffs (triangles) and talus slopes (circles).

the negative relationship to the degree of habitat isolation. Unlike true islands, terrestrial habitat islands often include a well-developed ecotone, a transitional area between the habitat island and the surrounding habitat that forms the landscape matrix. Ecotones are known to harbour a high diversity as they support species of both adjacent habitat types (van der Maarel, 1990; Łuczaj & Sadowska, 1997), and may consequently increase the total species richness of the terrestrial habitat islands.

Most diversity studies focus on species richness, which is only one of many facets of diversity. Equally suitable measures of diversity can be defined in terms of the number of plant 'functional types', e.g. growth forms, life strategies (During, 1992) or phytogeographical groups (Duell, 1983, 1984, 1985). As these groups usually possess specific environmental relationships (Frahm, 2001), they can provide insights into diversity relationships in addition to those offered by simple species numbers.

In the present paper, we analyse various measures of bryophyte diversity in a system of isolated treeless cliffs and talus slopes that form terrestrial habitat islands in a forested landscape of the southern Czech Republic. Our aim is to test: (1) the predictions of the theory of island biogeography, i.e. the effects of habitat island size and isolation upon bryophyte diversity; (2) the effect of ecotone; (3) the effects of other environmental factors that may control bryophyte diversity, namely irradiation and base status of the substratum.

Materials and Methods

Study sites

Data were collected on 28 treeless cliffs and 18 treeless talus slopes in otherwise forested valleys of the Dyje, Jevišovka, Jihlava and Oslava rivers in southwestern Moravia, Czech Republic (Fig. 1). The valleys are 60–230 m deep, at altitudes ranging between *ca* 200 m on the bottoms and 450 m at the upper edges. The forests in the river valleys are mostly natural oak–hornbeam forests (phytosociological alliance *Carpinion*), hornbeam–lime–maple ravine forests (*Tilio-Acerion*), acidophilous oak forests (*Genisto germanicae-Quercion*) and thermophilous oak forests (*Quercion petraeae*); also locally patches of pine forest occur on rock outcrops (*Dicrano-Pinion*) (Chytrý & Vicherek, 1995, 1996). The treeless cliffs and talus slopes with their rich flora of bryophytes and lichens, and sparse vegetation of vascular plants form isolated habitat islands in the forested landscape matrix (Chytrý, 1993). The bryophyte flora of the cliffs and talus slopes studied has been described in separate papers (Hradílek & Novotný, 1998; Hradílek, 2000; Kubešová, 2003a, b).

The treeless cliffs studied were 4–5000 m^2 in extent, with inclinations ranging between 14 and 90° from the horizontal. The cliffs are formed of rocks of differing base status, including acidic (mica schist, gneiss, granulite, granodiorite or granite), ultramafic (serpentine) and calcareous (marble, Permo-Carboniferous calcareous conglomerate) types. The cliff faces are bare, but shallow layers of fine soil are patchily developed on their rock terraces.

The talus slopes studied are 100–7000 m^2 in extent, with inclinations from 27 to 54°. They are all formed of acidic rocks such as gneiss, granulite, granodiorite or granite. They originated by peri-glacial freeze-and-thaw cycles in the Pleistocene (Brzák, 2000) and current rockfall episodes are extremely rare. Occasional stone movement occurs only in the upper parts of some slopes, but most stones are large (diameters 20–300 cm) and fairly stable. Vegetation disturbance is therefore insignificant. Treeless talus slopes have almost no soil because organic particles fall through the large spaces between the boulders. Only on the tops of large, flat boulders, is a shallow soil layer occasionally formed. In the hollows between the boulders, organic debris is trapped in some places, particularly in marginal parts of the open talus slopes near to the adjacent forest.

Most of the cliffs and all the talus slopes are situated in a moderately warm region, with the mean temperature in January between −2 and −4°C, in July between 17 and 19°C, and with precipitation in the growing season (April–September) ranging between 350 and 450 mm and in the winter season (October–March) between 200 and 300 mm. Five cliffs were located in a warm region with the mean temperature in January between −2 and −3°C, in July between 18 and 19°C, and with the precipitation in the growing season of 350–400 mm and in the winter season of 200–300 mm (Quitt, 1975). These macroclimatic characteristics, however, can be strongly modified by the valley topoclimate (Chytrý & Tichý, 1998).

Bryophyte diversity data

Preliminary field observations showed that the bryophyte flora differs between the ecotonal part of each treeless locality and its central part (Kubešová, 2000). Therefore sampling was performed separately in the ecotone and the open central part, with the ecotone being defined as the area shaded by trees of the adjacent forest. On talus slopes, the ecotone was richer in accumulated tree litter and had a higher cover of vascular plants (usually up to 40%), while on the cliffs the differences between ecotone and the open central part were not so striking. In five small cliffs where the ecotone and the open central part could not be distinguished, the whole cliff was assigned to one of these two categories.

In each site, the presence of bryophyte species was recorded separately for the open central part and the ecotone. For the analysis of bryophyte diversity, we used total species numbers, but we also classified the species into distribution-range types, growth forms and life-strategy types (see the Appendix).

The classification into distribution range types was according to Duell (1983, 1984, 1985).

Growth forms were defined on the basis of plant architecture, without direct consideration of its ecological relevance. The growth-form system of During (1992) was used. This emphasizes the distinctions between erect acrocarpous, cushion-like acrocarpous and pleurocarpous bryophytes, and between small and large bryophytes. For the analysis of the number of growth forms, all growth forms as defined by During (1992, table 1.1) were used, while for the analysis of proportional representations, rare categories were merged with similar ones, resulting in a classification into (1) low acrocarpous, (2) tall acrocarpous, (3) low pleurocarpous (mats) and (4) tall pleurocarpous (wefts, dendroids) bryophytes.

Life-strategy categories were taken from Dierßen (2001) who used a system proposed by During (1992). Unlike the growth-form systems, life-strategy systems emphasize subjectively selected plant traits that are assumed to be the most important adaptations to different environments. During (1992) emphasized the life span of a species, as an adaptation to substrata of varying longevity, and number and size of spores, which determine the ability of species to spread to new habitat patches. For analysis of percentage proportions of individual life strategies in this paper, we merged rare categories with similar common ones and recognized colonists (short life span, numerous light spores), perennial stayers (long life span, numerous light spores), short-lived shuttle (short life span, few large spores) and long-lived shuttle (long life span, few large spores).

Species nomenclature follows Kučera & Váňa (2003).

Environmental data

The following environmental data were compiled for each site.

Area. The area of the treeless cliffs or talus slopes was extremely difficult to measure exactly in the topographically complex terrain, therefore it was estimated on the following ordinal scale: 1, <30 m^2, 2, 30–100 m^2, 3, 101–1000 m^2, 4, 1001–3000 m^2, 5, >3000 m^2. The median area was 2 for cliffs and 3 for talus slopes.

Isolation. The isolation of each cliff was calculated as the mean distance from the three nearest open cliffs or talus slopes, including localities that were not surveyed. Mean isolation was 2.7 km. For talus slopes, this variable was not calculated as they were nearly always clustered with cliffs or other talus slopes.

Table 1. *Descriptive statistics for bryophyte diversity variables on cliffs and talus slopes. Letters C and P in brackets next to the variable names indicate that the variable is either a count or a percentage, respectively.*

	Cliffs (mean ±SD)	Talus slopes (mean ± SD)
Total species richness (C)	13.4 ± 5.4	21.2 ± 7.0
Species richness of hepatics (P)	14.1 ± 10.1	15.5 ± 7.1
Distribution range types (C)	3.1 ± 1.1	3.7 ± 0.9
Growth forms (C)	5.4 ± 1.3	7.2 ± 1.2
Life strategies (C)	4.9 ± 1.1	5.9 ± 0.9
Boreal species (P)	31.0 ± 17.0	54.3 ± 11.5
Submediterranean species (P)	2.1 ± 5.3	–
Suboceanic species (P)	2.9 ± 5.8	2.3 ± 2.7
Temperate species (P)	61.5 ± 19.5	41.6 ± 9.8
Low acrocarpous species (P)	46.4 ± 20.0	27.8 ± 10.4
Tall acrocarpous species (P)	13.6 ± 9.8	19.5 ± 5.5
Low pleurocarpous species (P)	27.9 ± 14.0	34.3 ± 8.9
Tall pleurocarpous species (P)	5.4 ± 6.3	9.9 ± 7.0
Colonist species (P)	46.7 ± 17.2	30.0 ± 9.7
Perennial stayer species (P)	41.1 ± 15.7	57.0 ± 11.4
Short-lived shuttle species (P)	1.6 ± 3.3	–
Long-lived shuttle species (P)	10.2 ± 8.3	11.8 ± 4.8

Irradiation. The potential direct solar irradiation was calculated on the basis of slope inclination and aspect and summed over 7 days of the year (21 December, 21 January, 21 February, 21 March, 21 April, 21 May, 21 June), using a computer program for calculation of relative values of potential direct radiation by Tomáš Herben (http://botany.natur.cuni.cz/cz/studium/pot_radiace.php). The calculated numbers represent relative values. The mean value was 33±13 (standard deviation) for cliffs and 29±13 for taluses.

Base status. For cliffs, base status of the rock was defined as either base poor (mica schist, gneiss, granulite, granodiorite or granite; 21 sites) or base rich (calcareous conglomerate, limestone or serpentine; seven sites). Talus slopes were only formed of base-poor rocks.

Data analysis

Relationships between bryophyte diversity variables and environmental variables were analysed with general linear models using the STATISTICA version 6 program (www.statsoft.com).

Dependent variables were counts (number of species, numbers of distribution-range types, growth forms and life strategies) and proportions (proportion of hepatics and proportions of individual distribution-range types, growth forms and life strategies). To obtain appropriate transformations of dependent variables, count data were square-root-transformed (after adding 0.5 to each value) and proportions were angular transformed, using the function $p' = \arcsin(\sqrt{P})$, where p is a proportion ranging from 0 to 1. Appropriateness of the transformations was checked by plotting standardized residuals against fitted values.

First, we calculated gross effects of each environmental variable, using models in which only that particular variable was used as a predictor. Second, we calculated multiple regression models (analysis of covariance) for each diversity variable, using stepwise forward selection of predictor variables. Additional predictor variables were added in each step if they significantly improved the existing model (F test, $p<0.05$).

RESULTS

Descriptive statistics of the bryophyte diversity variables are summarized in Table 1. Predictor variables showed a very similar response both in the analyses of their gross effects and in stepwise multiple regression models. This similarity indicates low correlations between the predictor variables, which means that each predictor describes a distinct facet of the bryophyte-environment relationship. Therefore we present only the results of the multiple regression models (Tables 2, 3).

Total species richness of cliffs increased with area and was higher on base-rich rocks. On talus slopes, total species richness was lower on well-irradiated slopes but increased in ecotone areas between the open talus and adjacent forest. The proportion of hepatics was lower on base-rich rocks.

Diversity of functional groups (number of distribution-range types, growth forms and life strategies) on cliffs could not be explained by the predictor variables. On talus slopes, all of the functional groups were richer in ecotones and the former two tended to be poorer on well-irradiated slopes.

Among the distribution-range types on cliffs, the two rare range types, submediterranean and suboceanic, both responded to base status of the rock, the former positively and the latter negatively. Species of suboceanic distribution were also confined to shaded sites. On talus slopes the two most frequent range types had a complementary pattern, with boreal species preferring shaded and temperate species well-irradiated sites. Submediterranean species were not found on talus slopes at all.

Among growth forms, low acrocarpous bryophytes were positively related to base-rich cliffs, tall acrocarpous bryophytes were more frequent on small, shaded and acidic cliffs, and pleurocarpous mats were more frequent on larger cliffs. On talus slopes, low acrocarpous bryophytes were positively related to well-lit sites and to larger localities, while tall pleurocarps were related to shaded sites and ecotone areas.

Life strategies were mainly related to irradiation. Long-lived perennial stayers were found more frequently in shaded sites, both on cliffs and talus slopes, and on larger cliffs. The long-lived shuttle category included more species on well-insolated and acidic cliffs and short-lived colonists were better represented on well-insolated talus slopes. Short-lived shuttle species were absent from talus slopes.

DISCUSSION

Cliffs, talus slopes and island biogeography of bryophytes

The theory of island biogeography (MacArthur & Wilson, 1967) predicts that larger islands are richer in species due to lower rates of extinction, whereas more isolated islands are poorer owing to lower rates of immigration. It is difficult, however, to separate possible island effects on species richness from the effects of a larger number of microhabitats in larger areas. The results of our study, i.e. the positive relationship between species richness and area for cliffs, and no relationship for talus slopes, is presumably mediated through microhabitat heterogeneity. While the number of microhabitats on cliffs may strongly depend on cliff size, it is possibly not the case for talus slopes, where fine-scale microtopographic heterogeneity creates a high number of microhabitats even in a small area (Kubešová, 2000). A similar pattern was documented by Kimmerer & Driscoll (2000) who found that bryophyte species richness was positively related to microtopographic and substratum diversity of isolated boulders but was independent of boulder size. Evidence for a poor effect of habitat area on bryophyte species richness was provided by Haig, Matthes & Larson (2000), who did not find any relationship between bryophyte species richness and the total area of the fragmented limestone cliffs.

In most of the previous studies, species richness of bryophytes was found to be independent of the degree of isolation of both true islands (Menzel & Passow-Schindhelm, 1990; Dirkse, Bouman & Losada-Lima, 1993; Frahm *et al.*, 1996) and habitat islands (Kimmerer & Driscoll, 2000). The lack of relationship between bryophyte species richness and habitat isolation was confirmed for cliffs in our study (it was not analysed for talus slopes, which are rarely isolated in the study area). The most probable explanation is an easy dispersibility of light diaspores of bryophytes, both spores and vegetative propagules (Tan & Pócs, 2000). In addition, habitat islands for such ubiquitous organisms as some bryophytes are rarely the perfectly isolated entities afforded by true islands, and their species composition can strongly depend on propagule input from the dominant habitat of the landscape matrix, i.e. forest, which shares several species with open rocky habitats. This is the reason why even shuttle species, which have larger spores with a restricted long-distance dispersal, did not show any relationship to habitat isolation. A majority of the shuttle species found on the studied rocky habitats were epixylic or forest-floor species, e.g. *Atrichum undulatum, Frullania dilatata, Ptilidium ciliare* and *Radula complanata*. However, some specialists of rocky habitats with shuttle life strategy may be restricted by the island effect, e.g. rare hepatics *Frullania inflata* and *Mannia fragrans*, which were found in single sites on rather isolated cliffs.

The ecotone effect

There was a strong ecotone effect found on the talus slopes, resulting in a higher species richness and a higher diversity of distribution range types, growth forms and life strategies in the ecotone than in the open central part. The bare boulders in the central part of talus slopes create a stressful environment, dominated by crustose lichens, but also colonized by few bryophyte species. On the other hand, closed deciduous forest adjacent to the talus slopes provides fewer habitats for saxicolous and terricolous bryophytes owing to accumulation of a distinct layer of leaf litter. Thus the ecotone creates a habitat with limited negative effects of both stress and litter accumulation and favours high bryophyte diversity.

In the ecotone, as opposed to the central open part, high nutrient enrichment from leachates originating from canopy throughfall may positively affect growth of bryophytes, as documented in the classical studies by Tamm (1953). Although most of these nutrients are probably washed out into large underground spaces among boulders, a considerable proportion of them can be intercepted on flat surfaces of large blocks. Litter from tree leaves, trapped in the spaces among the boulders, and accumulated in the ecotone, can possibly also be exploited as a source of nutrients by ground bryophytes (Rincón, 1988). Water is another resource which is probably more abundant in the ecotone than in the open central part due to higher air humidity in the shelter of the tree canopy. Kubešová (2000) demonstrated this pattern by an analysis of bryophyte indicator values for moisture on a transect across two talus slopes of the study area. Increased availability of nutrients and water results in a higher representation of tall pleurocarpous mosses (e.g. *Antitrichia curtipendula, Hedwigia ciliata, Hylocomium splendens, Pleurozium schreberi, Rhytidiadelphus triquetrus*) and possibly also in a higher overall diversity of bryophytes in the ecotone.

Another factor influencing the higher bryophyte diversity of the talus slope ecotone is its higher substratum diversity, which is enhanced by the occurrence of fine woody debris such as pieces of tree branches. Pieces of wood or bark are colonized by epixylic bryophytes (most frequently by *Platygyrium repens* and rarely by *Chiloscyphus profundus, Herzogiella seligeri, Tetraphis pellucida*) and, in the advanced stages of decay, also by facultatively epixylic species of ground bryophyte flora.

Besides the effect of forest edge, the high diversity of bryophyte communities at the margins of talus slopes can also result from specific microclimatic features of this environment. On several talus slopes of central Europe, the development of local air circulation systems has been described (Wunder & Möseler, 1996; Gude & Molenda, 2000). In summer, cold air exits at the talus toe, causing condensation of water vapour and favouring rich bryophyte communities (Hachtel *et al.*, 1999; Němcová, 2001). The best examples of these circulation systems are found on basalt taluses, where isodiametric stone blocks provide sufficient space for air movement. On non-basalt taluses of our study area, air movement can be occasionally observed at the base of some larger talus slopes but its effect is limited, probably due to the large size and elongated or flat shape of some blocks which provide an obstacle to air movement.

Although all measures of diversity were higher in the ecotone than in the open central part of talus slopes, interestingly, no differences were found in the proportions of distribution-range types, growth forms or life strategies, except for a higher proportion of tall acrocarpous species in the ecotone. Probably a high microhabitat heterogeneity of talus slopes helped these ‘functional types‘ to establish in both parts of the talus slopes. In the central part of the studied talus slopes, most bryophytes were found in less exposed sites such as below boulder overhangs, in joints between boulders and on flat top surfaces of large boulders, which retained some environmental features of the ecotone (Kubešová, 2000).

Unlike on talus slopes, no effect of ecotone was detected for cliffs. This is probably due to poor accumulation of litter, nutrients and water in cliff ecotones, and owing to steep slopes and lack of microtopographic features that would support litter accumulation.

Table 2. *Models for cliff habitats resulting from stepwise multiple regression. Standardized regression (beta) coefficients are shown, with corresponding significance level (***$p<0.001$, **$p<0.01$, *$p<0.05$, n.s. – not significant). The letters C and P in brackets next to the response variable names indicate that the variable is either count or proportion, respectively. R^2, coefficient of determination for the particular model, F, test statistic value for the model, p, significance level of the model.*

	Area	Isolation	Irradiation	Ecotone	Base-rich	R^2	F	p
Total species richness (C)	0.32**	n.s.	n.s.	n.s.	0.43***	0.39	5.6	<0.001
Species richness of hepatics (P)	n.s.	n.s.	0.28*	n.s.	−0.37**	0.22	2.5	0.044
Distribution-range types (C)	n.s.	n.s.	n.s.	n.s.	n.s.			
Growth forms (C)	n.s.	n.s.	n.s.	n.s.	n.s.			
Life strategies (C)	n.s.	n.s.	n.s.	n.s.	n.s.			
Boreal species (P)	n.s.	n.s.	n.s.	n.s.	n.s.			
Submediterranean species (P)	n.s.	n.s.	n.s.	n.s.	0.65***	0.47	7.9	<0.001
Suboceanic species (P)	n.s.	n.s.	−0.47***	n.s.	−0.35**	0.39	5.8	<0.001
Temperate species (P)	n.s.	n.s.	n.s.	n.s.	n.s.			
Low acrocarpous species (P)	n.s.	n.s.	n.s.	n.s.	0.43**	0.26	3.2	0.015
Tall acrocarpous species (P)	−0.40***	n.s.	−0.42***	n.s.	−0.42***	0.56	11.4	<0.001
Low pleurocarpous species (P)	0.39**	n.s.	n.s.	n.s.	n.s.	0.27	3.3	0.013
Tall pleurocarpous species (P)	n.s.	n.s.	n.s.	n.s.	n.s.			
Colonist species (P)	n.s.	n.s.	n.s.	n.s.	n.s.			
Perennial stayer species (P)	0.26**	n.s.	−0.35**	n.s.	n.s.	0.29	3.8	0.006
Short-lived shuttle species (P)	n.s.	n.s.	n.s.	n.s.	n.s.			
Long-lived shuttle species (P)	n.s.	n.s.	0.36**	n.s.	−0.28*	0.22	2.6	0.039

Irradiation, moisture and bryophyte diversity

As the localities studied were all treeless, potential direct solar irradiation should be considered as proxy variable for moisture rather than for light availability. This interpretation is consistent with the fact that irradiation was never a significant predictor of diversity measures on cliffs, which are rather dry on both north- and south-facing slopes, except during short periods after rain events. Taluses have a better capacity of water retention, particularly due to their less steep slopes, a higher degree of wind protection from the adjacent forest, and a cool air reservoir in the interstitials between boulders, which promotes condensation of water vapour as it approaches the warmer talus surface. Therefore a distinct gradient of moisture availability occurs between northern and southern aspects of talus slopes (Hachtel *et al.*, 1999).

North-facing talus slopes supported higher diversities than south-facing slopes in terms of species richness, numbers of distribution range types and numbers of growth forms. More species-rich bryophyte vegetation on the northern aspect was also reported from other talus slopes of central Europe, e.g. in eastern Belgium (Hachtel *et al.*, 1999) and in northern Bohemia (Němcová, 2001). Boreal species were more common on north-facing and temperate species on south-facing slopes, which corresponds to the pattern reported by Weddeling & Hachtel (2000) for bryophytes on Belgian talus slopes. The pattern of north-facing slopes supporting higher diversity was also found for vascular plants on the talus slopes of the study area (Chytrý, 1993) and is consistent with the pattern of higher diversity encountered in the ecotone. Both patterns support an interpretation of northern aspects and ecotonal positions as habitats with sufficient moisture availability.

As poikilohydric plants, bryophytes possess desiccation-evasive vegetative shoots which make them perfectly adapted to dry rocky habitats. Due to their ability to take up water over the whole shoot surface, they may be quite efficient in water intercept from dewfall. These adaptations are advantageous on stressful substrata where competition by faster-growing species is exluded (Grime, Rincón & Wickerson, 1990; Bates, 2000). However, different bryophyte species vary strongly in their drought tolerance. While a restricted group of epilithic mosses can dry out and recover to full turgor relatively quickly after rain events, forest-floor mosses dry out and recover rather slowly (Tuba, Proctor & Csintalan, 1998; Proctor, 2000). These forest-floor mosses, belonging to the large pleurocarpous growth form, showed clear affinities to less insolated habitats on the studied talus slopes. More insolated talus slopes, on the other hand, supported low acrocarpous mosses in which desiccation is limited due to positive interactions between neighbouring shoots in dense cushions or turfs (van der Hoeven & During, 1997). The dichotomy between these two types of bryophytes may result from competitive exclusion of short-living acrocarpous mosses by pleurocarpous mosses on the more humid north-facing slope.

Insolated and shaded slopes also differed in representation of life strategies. Perennial stayers, i.e. long-lived species with numerous small spores (a category mostly overlapping with the growth form of large pleurocarpous mosses discussed above), showed a significant affinity to less insolated habitats both on cliffs and talus slopes. Other studies repeatedly confirmed that this group of bryophytes was supported by stable environments with a high moisture availability (Gonzáles-Mancebo & Hernández-García, 1996; Kürschner & Parolly, 1999; Kürschner, Frey & Parolly, 1999).

By contrast, colonists were more frequent on well-insolated talus slopes, but had no relationship to insolation on cliffs. This life strategy is typical of rock surfaces and

Table 3. *Models for talus-slope habitats resulting from stepwise multiple regression. Standardized regression (beta) coefficients are shown, with corresponding significance level (***$p<0.001$, **$p<0.01$, *$p<0.05$, n.s. – not significant). R^2, coefficient of determination for the particular model, F, test statistic value for the model, p, significance level of the model. Letters C and P in brackets next to the response variable names indicate that the variable is either count or proportion, respectively. The proportion of submediterranean and short-lived shuttle species was not analysed due to absence of these groups on talus slopes.*

	Area	Irradiation	Ecotone	R^2	*F*	*P*
Total species richness (C)	n.s.	−0.32*	0.67***	0.56	13.5	<0.001
Species richness of hepatics (P)	n.s.	n.s.	n.s.			
Distribution-range types (C)	n.s.	−0.37**	0.57***	0.48	10.1	<0.001
Growth forms (C)	n.s.	−0.38**	0.55***	0.48	9.8	<0.001
Life strategies (C)	n.s.	n.s.	0.50**	0.31	4.8	0.007
Boreal species (P)	n.s.	−0.59***	n.s.	0.36	6.1	0.002
Suboceanic species (P)	n.s.	n.s.	n.s.			
Temperate species (P)	n.s.	0.60***	n.s.	0.35	5.7	0.003
Low acrocarpous species (P)	0.30*	0.59***	n.s.	0.43	8.1	<0.001
Tall acrocarpous species (P)	n.s.	n.s.	n.s.			
Low pleurocarpous species (P)	n.s.	n.s.	n.s.			
Tall pleurocarpous species (P)	n.s.	−0.71***	0.32*	0.58	14.7	<0.001
Colonist species (P)	n.s.	0.53**	n.s.	0.32	5.1	0.005
Perennial stayer species (P)	n.s.	−0.48**	n.s.	0.25	3.6	0.025
Long-lived shuttle species (P)	n.s.	n.s.	n.s.			

other dry habitats, where the short life span, caused by drought-dependent mortality, is compensated by a high production of small spores (Kürschner, 1994; Frey & Kürschner, 1995; Gonzáles-Mancebo & Hernández-García, 1996; Kürschner & Parolly, 1999).

Long-lived shuttle species, i.e. those with few large spores, were less common on shaded than sun-exposed cliffs but did not show such pattern on talus slopes. The high proportion of this group on sun-exposed cliffs is due to coexistence of xerophytic and heliophilous species (*Encalypta vulgaris, Frullania inflata* and *Mannia fragrans*) with non-xerophytic species such as *Lejeunea cavifolia* and *Mnium stellare* that grow in crevices. These species are typical of south-facing cliffs but do not occur on south-facing talus slopes.

Calcifuge and calcicole bryophyte diversity

As in vascular plants, the distinction between calcicole and calcifuge bryophytes is an important dichotomy in regional bryophyte floras (Nagano, 1969; Bates, 1995). In our case, the relationship of bryophytes to basic or acidic substrata was only studied on cliffs, because all talus slopes were formed of acidic rocks. Tall acrocarpous mosses were more frequently found on acidic rocks, while low acrocarpous mosses were more common on basic rocks. Possibly this is a consequence of adaptation of tall species to more productive, deeper soils, which are often superficially acidified by leaching. Therefore they tend to be calcifuges. The group of small acrocarpous mosses tolerates a broader pH range, but due to competition with pleurocarpous and tall acrocarpous mosses is restricted to base-rich rocks. Pleurocarpous bryophytes were found to be independent of the rock base status, most probably due to their poorer contact with the substratum, resulting from their creeping habit and formation of an underlying layer of accumulated litter in some places. An interesting result of the present study is the higher proportion of hepatics on acidic cliffs, which could be considered as evidence for niche conservatism of a phylogenetic lineage (Prinzing *et al*., 2001); however, attempts to generalize this pattern seem to be premature due to the low number (15) of hepatics recorded on the cliffs and possible confounding effects of other factors.

The tendency of submediterranean and subatlantic species to be found on base-rich and base-poor substrates, respectively, reflects the preponderance of calcareous rocks in the submediterranean mountain ranges and the widespread occurrence of acidic, leached soils in oceanic parts of Europe. The same pattern was documented for vascular plants in the study area (Chytrý, 1995).

The fact that total species richness of bryophytes was higher on base-rich than on acidic cliffs is consistent with similar patterns found in some vascular plant communities of central Europe (Chytrý, Tichý & Roleček, 2003; Schuster & Diekmann, 2003) or in peatland bryophyte communites, except the most basic ones (Vitt, Li & Belland, 1995; Hájková & Hájek, 2003). On the regional scale in central Europe, Ellenberg *et al.* (1992) recognized more calcicole than calcifuge bryophytes (631 species with ‘basic’ indicator values 6–9 versus 517 species with ‘acidic’ values 1–4). This pattern, however, is much less pronounced than the predominance of calcicoles among the vascular plants (1748 versus 449 species). Here, the predominance of calcicoles was hypothesized to result from historical and evolutionary processes in the Pleistocene, when landscapes of the present northern temperate and boreal zone were dominated by rejuvenated base-rich soils (Pärtel, 2002; Chytrý *et al*, 2003; Ewald, 2003). For bryophytes, as a more ancient evolutionary lineage, such an explanation may not hold true. There are also alternative explanations of the higher species richness on base-rich cliffs, in particular a higher habitat heterogeneity of these cliffs due to a mosaic of base-rich rock surfaces and acidified rock ledges, whose pH drops as organic matter accumulates and calcium is leached from the developing initial soil. Obviously, the issue of calcicole–calcifuge diversity in terricolous and saxicolous bryophytes still needs to be studied more in order to recognize basic patterns.

Acknowledgements

This study was supported through the project MSM 0021622416.

Taxonomic Additions and Changes: Nil.

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APPENDIX

A list of recorded species

Species names are followed by (1) chorological type; (2) growth form (D, dendroid; LC, large cushion; OT, open turf; P, pendant; RM, rough mat; SC, short cushion; SM, smooth mat; ST, short turf; T, tail; TM, thalloid mat; TT, tall turf; W, weft (merged categories used for the analyses of proportions are given in brackets)); (3) life strategies (C, colonists; CP, pioneer colonists; F, fugitives; L, long-lived shuttles; P, perennials; PC, competitive perennials; PS, stress-tolerant perennials; S, short-lived shuttles (merged categories used for the analyses of proportions are given in brackets)).

Liverworts

Bazzania trilobata: subboreal, RM (low pleurocarpous), PC (perennial stayers)

Cephaloziella divaricata: temperate, ST (low acrocarpous), C (colonists)

Chiloscyphus coadunatus: temperate, W (tall pleurocarpous), PC (perennial stayers)

C. minor: temperate, RM (low pleurocarpous), C (colonists)

C. profundus: temperate, RM (low pleurocarpous), C (colonists)

Frullania dilatata: temperate, SM (low pleurocarpous), L (long-lived shuttle)

F. inflata: relictual–submediterranean–montane, SM (low pleurocarpous), L (long-lived shuttle)

Jamesoniella autumnalis: subboreal–montane, RM (low pleurocarpous), C (colonists)

Lejeunea cavifolia: suboceanic–montane, SM (low pleurocarpous), L (long-lived shuttle)

Lophozia barbata: subboreal–montane, RM (low pleurocarpous), PS (perennial stayers)

L. excisa: boreal–montane, RM (low pleurocarpous), C (colonists)

L. hatcheri: boreal–montane, RM (low pleurocarpous), C (colonists)

L. longidens: boreal–montane, RM (low pleurocarpous), C (colonists)

L. ventricosa: boreal, RM (low pleurocarpous), C (colonists)

Mannia fragrans: submediterranean, TM (low pleurocarpous), L (long-lived shuttle)

Metzgeria furcata: temperate, TM (low pleurocarpous), P (perennial stayers)

Plagiochila porelloides: subboreal–montane, RM (low pleurocarpous), PS (perennial stayers)

Porella platyphylla: temperate, RM (low pleurocarpous), PS (perennial stayers)

Ptilidium ciliare: boreal, RM (low pleurocarpous), L (long-lived shuttle)

P. pulcherrimum: boreal, RM (low pleurocarpous), S (short-lived shuttle)

Radula complanata: temperate, SM (low pleurocarpous), L (long-lived shuttle)

Mosses

Amblystegium serpens: temperate, RM (low pleurocarpous), P (perennial stayers)

Anomodon attenuatus: subcontinental–(montane), W (tall pleurocarpous), P (perennial stayers)

A. longifolius: boreal–montane, RM (low pleurocarpous) & D (tall pleurocarpous), P (perennial stayers)

A. viticulosus: temperate, RM (low pleurocarpous), P (perennial stayers)

Antitrichia curtipendula: suboceanic, RM (low pleurocarpous), L (long-lived shuttle)

Atrichum undulatum: temperate, TT (tall acrocarpous), S (short-lived shuttle)

Aulacomnium androgynum: temperate, ST (low acrocarpous), C (colonists)

Barbula unguiculata: temperate, ST (low acrocarpous), C (colonists)

Bartramia pomiformis: boreal–(montane), LC (tall acrocarpous), L (long-lived shuttle)

Brachythecium albicans: subboreal, RM (low pleurocarpous), P (perennial stayers)

B. laetum: subcontinental–submediterranean–dealpine, RM (low pleurocarpous), P (perennial stayers)

B. populeum: temperate, RM (low pleurocarpous), P (perennial stayers)

B. rutabulum: temperate, RM (low pleurocarpous), C (colonists)

B. salebrosum: subboreal, RM (low pleurocarpous), C (colonists)

B. velutinum: temperate, RM (low pleurocarpous), P (perennial stayers)

Bryoerythrophyllum recurvirostrum: temperate-montane, ST (low acrocarpous), C (colonists)

Bryum argenteum: temperate, ST (low acrocarpous), C (colonists)

B. caespiticium: temperate, ST (low acrocarpous), C (colonists)

B. capillare: temperate, ST (low acrocarpous), C (colonists)

B. imbricatum: temperate, ST (low acrocarpous), S (short-lived shuttle)

B. laevifilum: -, ST (low acrocarpous), C (colonists)

Buxbaumia aphylla: boreal, OT (-), F (-)

Ceratodon purpureus: temperate, ST (low acrocarpous), C (colonists)

Cirriphyllum tommasinii: temperate-montane, RM (low pleurocarpous), P (perennial stayers)

Cynodontium polycarpon: boreal–montane, ST (low acrocarpous), C (colonists)

Dicranella heteromalla: temperate, ST (low acrocarpous), C (colonists)

Dicranoweisia cirrata: suboceanic, ST (low acrocarpous), C (colonists)

Dicranum fulvum: temperate–montane, TT (tall acrocarpous), C (colonists)

D. montanum: subboreal, ST (low acrocarpous), PC (perennial stayers)

D. polysetum: boreal, TT (tall acrocarpous), PC (perennial stayers)

D. scoparium: subboreal, LC (tall acrocarpous), PC (perennial stayers)

Didymodon acutus: submediterranean, ST (low acrocarpous), C (colonists)

D. fallax: temperate, ST (low acrocarpous), C (colonists)

D. rigidulus: temperate, ST (low acrocarpous), C (colonists)

Ditrichum flexicaule: subboreal–(montane), ST (low acrocarpous), C (colonists)

Encalypta streptocarpa: subboreal—(montane), ST (low acrocarpous), P (perennial stayers)

E. vulgaris: submediterranean, ST (low acrocarpous), L (long-lived shuttle)

Eurhynchium angustirete: subcontinental, W (tall pleurocarpous), P (perennial stayers)

E. striatulum: submediterranean–suboceanic–montane/dealpine, W (tall pleurocarpous), P (perennial stayers)

Fissidens dubius: temperate–montane, ST (low acrocarpous), P (perennial stayers)

Grimmia laevigata: submediterranean–suboceanic–montane, SC (low acrocarpous), C (colonists) & L (long-lived shuttle)

G. ovalis: subboreal–montane, SC (low acrocarpous), C (colonists)

G. pulvinata: temperate, SC (low acrocarpous), C (colonists)

G. trichophylla: temperate—(montane), SC (low acrocarpous), PC (perennial stayers)

Gyroweisia tenuis: submediterranean–suboceanic–montane, SC (low acrocarpous), C (colonists)

Hedwigia ciliata: subboreal-(montane), T (–), L (long-lived shuttle)

Herzogiella seligeri: subboreal, RM (low pleurocarpous), PS (perennial stayers)

Homalia trichomanoides: temperate, W (tall pleurocarpous), PS (perennial stayers)

Homalothecium lutescens: temperate, RM (low pleurocarpous), P (perennial stayers)

H. sericeum: temperate, RM (low pleurocarpous), P (perennial stayers)

Homomallium incurvatum: subboreal–montane, RM (low pleurocarpous), C (colonists)

Hylocomium splendens: subboreal, W (tall pleurocarpous), PC (perennial stayers)

Hypnum cupressiforme: temperate, RM (low pleurocarpous), PS (perennial stayers)

Isothecium alopecuroides: temperate, D (tall pleurocarpous), PS (perennial stayers)

I. myosuroides: suboceanic, D (tall pleurocarpous), PS (perennial stayers)

Leskea polycarpa: temperate, RM (low pleurocarpous), P (perennial stayers)

Leucodon sciuroides: temperate, T (-), L (long-lived shuttle),
Neckera besseri: subcontinental–montane, RM (low pleurocarpous), PS (perennial stayers)

Orthotrichum affine: temperate, SC (low acrocarpous), C (colonists)

O. anomalum: temperate, SC (low acrocarpous), C (colonists)

O. cupulatum: temperate–(montane), SC (low acrocarpous), C (colonists)

Paraleucobryum longifolium: boreal–montane, LC (tall acrocarpous), P (perennial stayers)

Plagiomnium affine: temperate, RM (low pleurocarpous), PC (perennial stayers)

P. cuspidatum: subboreal, RM (low pleurocarpous), PC (perennial stayers)

P. undulatum: temperate, W (tall pleurocarpous), PC (perennial stayers)

Plagiothecium cavifolium: boreal–(montane), RM (low pleurocarpous), PS (perennial stayers)

P. curvifolium: boreal, RM (low pleurocarpous), PS (perennial stayers)

P. denticulatum: subboreal, RM (low pleurocarpous), PC (perennial stayers)

P. laetum: boreal, RM (low pleurocarpous), PS (perennial stayers)

P. nemorale: temperate, RM (low pleurocarpous) & P (perennial stayers)

P. succulentum: suboceanic, RM (low pleurocarpous), PC (perennial stayers)

Platygyrium repens: subcontinental, RM (low pleurocarpous), PS (perennial stayers)

Pleurozium schreberi: subboreal, W (tall pleurocarpous), PC (perennial stayers)

Pohlia cruda: temperate–montane, ST (low acrocarpous), C (colonists)

P. nutans: subboreal, ST (low acrocarpous), C (colonists)

P. wahlenbergii: subboreal, ST (low acrocarpous), PC (perennial stayers)

Polytrichastrum cf. *longisetum*: boreal, TT (tall acrocarpous), PC (perennial stayers)

P. formosum: temperate, TT (tall acrocarpous), PC (perennial stayers)

Polytrichum commune: subboreal, TT (tall acrocarpous), PC (perennial stayers)

P. juniperinum: temperate, TT (tall acrocarpous), PS (perennial stayers)

P. piliferum: temperate, TT (tall acrocarpous), PS (perennial stayers)

Pseudoleskeella nervosa: boreal-montane, RM (low pleurocarpous), PS (perennial stayers)

Pseudotaxiphyllum elegans: suboceanic, RM (low pleurocarpous), C (colonists)

Pterigynandrum filiforme: boreal–montane, RM (low pleurocarpous), PS (perennial stayers)

Racomitrium canescens: boreal, TT (tall acrocarpous), C (colonists)

R. elongatum: boreal, TT (tall acrocarpous), C (colonists)

R. lanuginosum: boreal–montane, TT (tall acrocarpous), PS (perennial stayers) & D (-)

R. microcarpon: boreal–montane, TT (tall acrocarpous), C (colonists)

Rhabdoweisia fugax: boreal–montane, LC (tall acrocarpous), C (colonists)

Rhynchostegium confertum: submediterranean-oceanic, RM (low pleurocarpous), P (perennial stayers)

R. murale: temperate, RM (low pleurocarpous), P (perennial stayers)

Rhytidiadelphus triquetrus: subboreal, W (tall pleurocarpous), PC (perennial stayers)

Rhytidium rugosum: subboreal–(montane), RM (low pleurocarpous), PC (perennial stayers)

Schistidium apocarpum: temperate, SC (low acrocarpous), C (colonists)

S. crassipilum: – SC (low acrocarpous), C (colonists)

Schistostega pennata: suboceanic–montane, ST (low acrocarpous), C (colonists)

Scleropodium purum: temperate, W (tall pleurocarpous) & RM (low pleurocarpous), P (perennial stayers)

Syntrichia intermedia: submediterranean–montane, ST (low acrocarpous), C (colonists)

S. ruralis: temperate, ST (low acrocarpous), C (colonists)

Tetraphis pellucida: temperate, ST (low acrocarpous), C (colonists)

Thuidium abietinum: boreal, RM (low pleurocarpous), P (perennial stayers)

T. recognitum: suboceanic–montane, W (tall pleurocarpous), PS (perennial stayers)

Tortella inclinata: temperate, ST (low acrocarpous), C (colonists)

T. tortuosa: boreal–montane, ST (low acrocarpous), PS (perennial stayers)

Tortula muralis: temperate, SC (low acrocarpous), C (colonists)

T. subulata: subboreal–(montane), ST (low acrocarpous), C (colonists)

Trichostomum crispulum: temperate–montane, ST (low acrocarpous), C (colonists)

Weissia condensa: submediterranean–montane, ST (low acrocarpous), C (colonists)