

Thirteen years on the hunt for *Buxbaumia viridis* in the Czech Republic: still on the tip of the iceberg?

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Abstract

Rare epixylic moss *Buxbaumia viridis*, which is one of the “Annex II” species of the European “Habitat directive”, has been recorded at 124 localities in the Czech Republic in course of the last 13 years. Most of them were discovered in the last five years following a dedicated search at both historical sites of occurrence and new localities with putatively suitable habitat conditions. The recent and historical area of occupancy and extent of occurrence are not obviously different, although most of the recent localities are concentrated in the Western Carpathians and the Hrubý Jeseník Mts. Surprisingly, only 38% of the localities are located in natural forest habitats, of which herb-rich and acidophilous beech forests were among the most commonly inhabited ones. The rest of occurrences were recorded in non-natural forests (habitats strongly influenced or created by man), particularly the coniferous forest plantations. Sufficient amount of decaying wood of the advanced decay stages, as well as sufficient and constant humidity are crucial prerequisites for the occurrence of *B. viridis* in both types of forests. True epixylic moss *Herzogiella seligeri* and the liverwort *Chiloscyphus profundus* were recorded as the most common associated species, while the rest of commonly co-occurring species were facultatively epixylic, ground or ubiquitous bryophytes; other specialized and rare epixylic mosses or liverworts were only rarely recorded. We also designed a potential distribution model for *B. viridis* based on the distribution of habitats most commonly occupied by the studied moss. Despite the simplicity of the model, its close match with the recent distribution in the Western Carpathians, the Hrubý Jeseník Mts. and Šumava Mts. supports its relevance for the real distribution of *B. viridis*.

Keywords: *Buxbaumia viridis*; Czech Republic; epixylic bryophyte; the “Habitat directive”; threatened bryophyte

Introduction

Although the Central European landscape is extensively forested, most of these forests are strongly impacted by human activity. In the Czech Republic, the area of forest has been reported to account for about 35% but only a third of them (about 10% of the country) are considered to have near-natural composition [1]. Nature-like old-growth forests became extremely rare and heavily fragmented in whole Europe [2]. The degradation and fragmentation of natural forests poses a significant threat to biodiversity, as shown in several comparative studies [3,4]. One of the key factors affecting the biodiversity in managed production forests is the complete removal of wood during harvesting [5,6].

Decaying wood in different stages of decay is a substratum for many invertebrates, fungi, lichens and bryophytes. The threatened nature of epixylic bryophytes has been reflected in the red lists of most European countries [2,7].

A “flagship species” of rare and endangered epixylic mosses is *Buxbaumia viridis*, which received Europe-wide attention as one of the “Annex II” species of the “Habitat directive” [8]. It is a tiny and inconspicuous moss, which can be traced only in its sporophytic stage due to the extremely reduced gametophyte, and thus makes its recording hard even for an experienced bryologist. Its dioicy, resulting in low fertilization rate together with low establishment and poor competitive abilities of the minute gametophyte have been speculated to be among the main reasons for the rarity of *B. viridis* [9]. In addition, the species is sensitive to desiccation of its substratum and the insufficient air humidity or low precipitation during the summer months restrict spore production and germination [9–11].

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The occurrence of *B. viridis* is generally restricted to decaying wood, especially in advanced phases of decay [12]. Its detailed ecological requirements have however only been investigated in a few studies [9,10,13], focused mainly on substratum preference. The species is assumed to grow mainly in old-growth (primeval) forests [13].

We have summarized the information about the current occurrences of *B. viridis* in the Czech Republic, which has accumulated over the last thirteen years (2001–2013) and compared the recent and historical distribution pattern. The ecological information noted by the recorders, together with data from habitat mapping were used to develop a model predicting its distribution over the whole area of the country.

Material and methods

Buxbaumia viridis has been mapped by the Nature Conservation Agency of the Czech Republic since 2001. Positively mapped localities (i.e. localities with *B. viridis*) were visited at least once (see Appendix S1; number of visits is dependent on the availability of sites, the number of surveyor and on the budget for the respective year). The mapping was usually carried out during autumn season, because sporophytes of *B. viridis* were easily visible. Presence of dead wood, forest type, and forest age were considered as main features for selection of areas. In addition, the vast majority of historical localities [13–15] were included in the survey. In the case of the positive discovery at a locality, neighboring logs (typically within ca. 500 m) were particularly thoroughly searched for additional occurrences (microlocalities). At each microlocality, the number of capsules was recorded together with substratum data (the identity of decaying wood where detectable, decay degree) and co-occurring species. The decay degree was measured using a semi-quantitative scale modified from Söderström [16] (Tab. 1). Co-occurring species were defined as those occurring within 15 cm from the capsules of *B. viridis*; the nomenclature of bryophytes follows the current checklist [17]. Bryophytes were divided into four ecological groups: epiphytes (species commonly found on living trees), ground flora (most often recorded on the ground), true epixylic species (exclusively found on rotting wood) and facultative epixylic species (rotting

wood is only sub-optimal substratum). The assignation of the species to these groups followed other studies [18,19] and own experience.

Localities were defined as one or more logs of *B. viridis* within the radius of 500 m. Except for a few exceptions (Appendix S1), only one habitat type occurred at one locality. For each locality, mean altitude, and for each microlocality distance from the nearest watercourse were assessed from topographic maps. The distance from watercourse was classified into 4 categories: (i) up to 10 m; (ii) 11–100 m; (iii) 101–500 m; (iv) >500 m, i.e. no watercourse.

Another type of data assigned to localities was the habitat information. These data were extracted from the geographic information system (GIS) layer of the habitat mapping of the Czech Republic [20]. The habitats were classified according to habitat catalogue [21]. This classification utilizes primarily the formation–vegetation (physiognomic) approach and, secondarily, the floristic approach. The habitats of supposedly higher importance for nature conservation are termed natural habitats. In contrast, the non-natural habitats are those of presumably lower importance for biodiversity or nature conservation and are strongly influenced or created by humans [21]. In addition, syntopic combinations (mosaics) of natural and non-natural habitats can occur. If one of the habitats from the mosaic was non-natural, then the entire mosaic was considered as a non-natural habitat. In the areas of supposedly low frequency of natural habitats, only the natural habitats were recorded and mapped (so-called contextual mapping; [22]), whereas the non-natural habitats were not mapped and were merged in the resulting GIS layer in a single category, labelled “–1”.

For the analysis of distribution, we defined the area of occupancy as the number of the occupied grid squares of the Central European floristic grid [23], with the squares 5×3 geographical minutes. Extent of occurrence is defined as the area contained within the shortest continuous imaginary boundary, which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a species [24]. The distance of the farthest points was set to be 40 km [25]. The area of the occupied grid squares and extent of occurrence were calculated using ArcGis ver. 9 [26].

We combined the GIS layer of habitat mapping [20] and the Corine land cover layer [27] with our results of habitat association frequency and altitudinal distribution of *B. viridis* for the construction of the map of its potential distribution. The Corine land cover refers to the European programme establishing a computerized inventory on land cover of the 27 European Union member countries and other European countries, at an original scale of 1:100 000, using 44 classes with five main categories – artificial surfaces, agricultural areas, forest and other semi-natural areas, wetlands, and water bodies. Forests are subdivided into three categories – broad-leaved, coniferous, and mixed forests. Most frequently occupied habitats (i.e., habitats of interest, habitats in which the occurrence of *B. viridis* was more frequent than five times, see “Results”) and their mosaics (only mosaics wherein the representation of habitats of interest was higher than 50%) within altitudes 300–1100 m a.s.l. were included in the model. The potential distribution map was constructed as the relative proportion of habitat area (only habitats of interest)

Tab. 1 Scale for identification of decay degree [16].

Decay degree	Description of decay degree
1	freshly fallen log, hard, whole, bark intact, branches present
2	log solid, wood hard, more than 50% of bark present
3	some patches of soft wood, more than 50% of bark missing
4	wood softening, outline retained, bark missing
5	log outline slightly deformed
6	pieces of soft wood, log outline still distinguishable
7	only log core remains
8	log outline indeterminable, humification 100%, no evidence of hard wood

per each square. For the non-natural habitats merged in the category “-1” (one of the habitats of interest) in the layer of the habitat mapping, the information from the Corine land cover layer was used to select coniferous and broad leaved-coniferous forests. Only these two types of “-1” habitats were used in the modeling of potential distribution of *B. viridis*. All other “-1” habitats were regarded as completely uninhabitable for *B. viridis*.

The general linear model, calculated by R version 2.12 [28], was used to test the influence of the altitude, habitat type (natural vs. non-natural), habitat unit, degree of decay, and distance from watercourse on the sporophyte production, measured as the mean number of capsules per each locality. The mean number of sporophytes per each locality was log-transformed prior to analysis to improve normality.

Results

Historical and recent distribution

Buxbaumia viridis has to date been recorded on 167 localities in the Czech Republic (Fig. 1, Tab. 2, Appendix S1). One hundred twenty four localities (and 192 microlocalities) were recorded in the recent 13 years (2001–2013), of which 89 localities were newly found occurrences. Of the 78 historical localities (recorded before 2001 [13–15]), 35 were checked with positive results, while at 21 localities *B. viridis* was not re-found and 22 historical records were not verified due to insufficient capacities, inaccurate localization etc. Since 2001, 242 sites were explored in total (i.e., both revision of historical localities and survey of newly selected ones), *B. viridis* was not found at 118 of them (Fig. 2).

Although the number of recent localities is higher than the number of historical localities, the area and extent of occurrence of historical localities reached higher values

(Tab. 2). Altitudinal distribution of the localities spanned 250–1200 m, of which most were recorded at the altitudes between 600–900 m a.s.l. (Fig. 3). 42% of all microlocalities (N = 192) were situated within 10 m from a watercourse, 32% microlocalities within 11–100 m from a watercourse, 23% microlocalities within 101–500 m from a watercourse and only 4 microlocalities were farther than 500 m from watercourse (Fig. 4).

Habitat requirements and association, co-occurring species

The recorded substratum of *B. viridis* was primarily the decaying wood of conifers in late decay phases (degree 5, 6, 7 or 8; Fig. 5). Of the 148 cases (microlocalities), when the substratum could be determined, 88% were conifers (mainly *Picea abies* and *Abies alba*) and 12% were broad leaved trees, mainly beech (*Fagus sylvatica*; 8%), 1–2 microlocalities were

Tab. 2 The area of occupancy (AOO) and the extent of occurrence (EOO) for recent and historical localities were summarized.

Recent localitis	N	AOO	EOO (km ²)
	124	74	4445
Historical localitis	N	AOO	EOO (km ²)
	78	66	4359

The grid squares are defined by the project “Kartierung der Flora Mitteleuropas” (KFME), with the squares of 5' longitude and 3' latitude.

Recent and historical localities, N = 167

Recent localities (2001-2013), N = 124

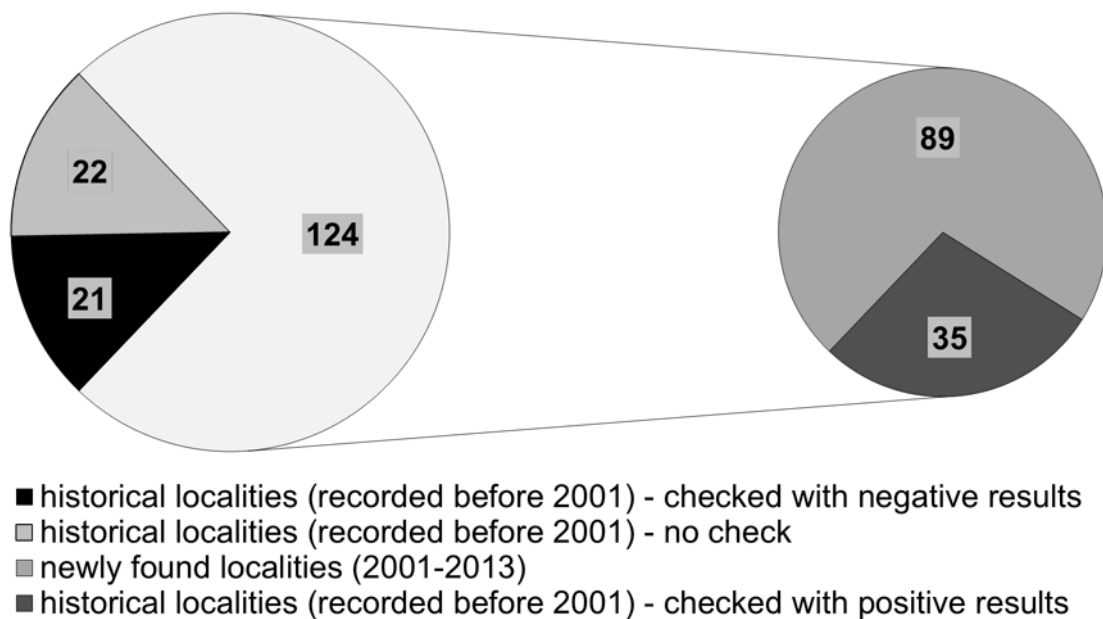


Fig. 1 The number of historical and recent localities.

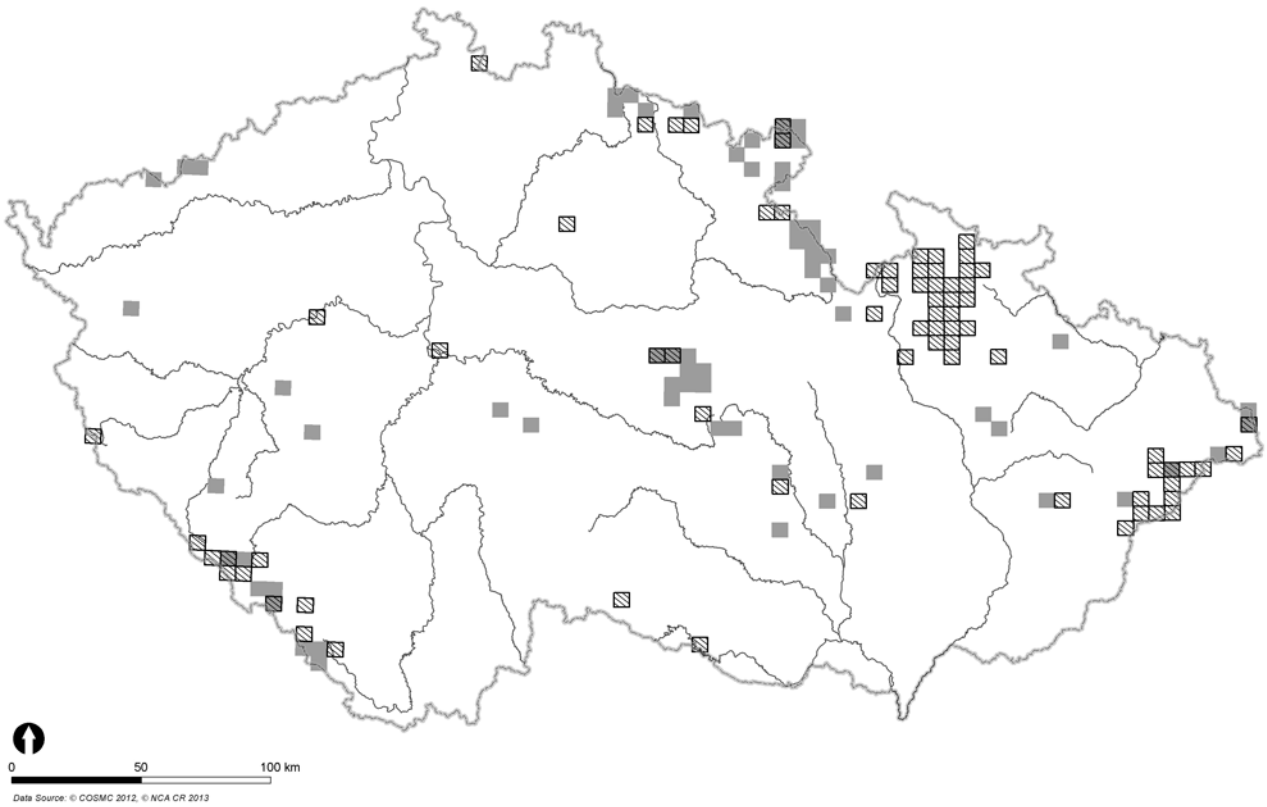


Fig. 2 Map of explored area. Hatched squares show positively explored area; grey squares are negatively explored area. The grid squares are defined by the project “Kartierung der Flora Mitteleuropas” (KFME), with the squares of 5' longitude and 3' latitude.

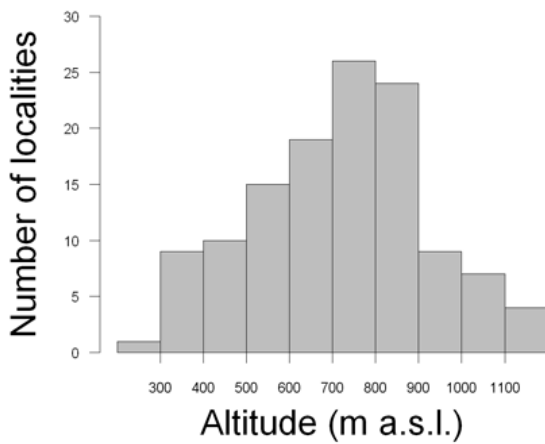


Fig. 3 Altitudinal distribution for recent localities of *B. viridis* from the Czech Republic; $N = 124$.

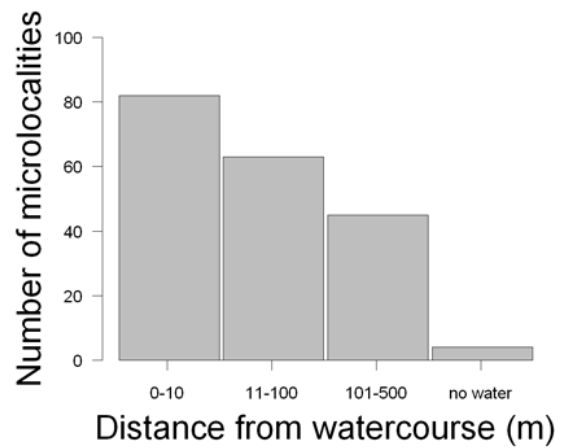


Fig. 4 Distance of *B. viridis* microlocalities from a watercourse; $N = 192$.

recorded for alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*) and birch (*Betula pendula*).

The co-occurring species and their frequency at recent microlocalities are summarized in **Tab. 3**. Altogether, 68 species were recorded (24 liverworts and 44 mosses), of which the most common (growing at more than 40% of microlocalities) were liverwort *Chiloscyphus profundus* and mosses *Herzogiella seligeri*, *Rhizomnium punctatum*, *Dicranum scoparium* and *Tetraphis pellucida*. Forest ground

species dominated among co-occurring species (40 species), whereas only 9 species were classified as true epixylic species and 17 as facultative epixylic species, 3 as the epiphytes. Nevertheless, the most common accompanying species (see above) were true or facultative epixylic species.

The mean number of sporophytes per one microlocality varied from 1 to 108 capsules (mean = 8, median = 3), most microlocalities (80%) and localities (70%) had only up to 10 sporophytes. However, number of sporophytes

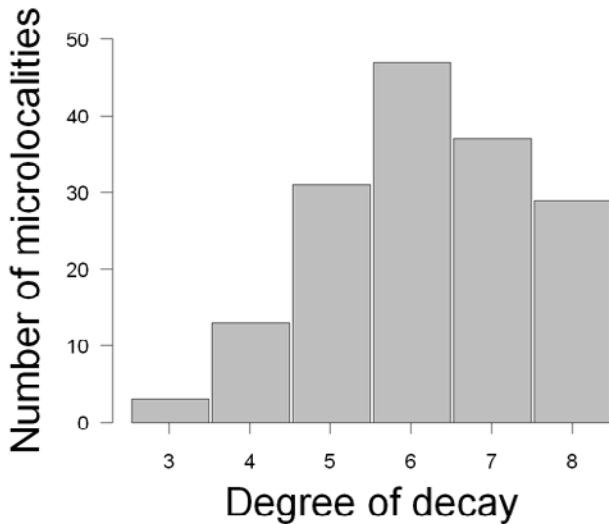


Fig. 5 Frequency of different decay stages of logs (microlocalities) with presence of *B. viridis*; $N = 160$ (modified from Söderström [16] – (3) some patches of soft wood, more than 50% of bark missing; (4) wood softening, outline retained, bark missing; (5) log outline slightly deformed; (6) pieces of soft wood, log outline still distinguishable; (7) only log core remains; (8) log outline indeterminable, humification 100%, no evidence of hard wood).

on microlocalities varied among years, e.g. at the locality Halenkov (195 sporophytes in 2001, 6 sporophytes in 2011), Senice – Val. Kyčera (7 sporophytes in 2002, 64 sporophytes in 2011), Vrchovištní pot. (94 sporophytes in 2001, 14 sporophytes in 2009). The numbers for all localities are listed in the [Appendix S1](#). The average number of sporophytes per locality showed no relation to altitude ($F = 2.3924$, $P = 0.1254$), habitat type ($F = 0.0432$, $P = 0.8357$), habitat unit ($F = 1.6006$, $P = 0.1463$), decay degree ($F = 3.4437$, $P = 0.0667$), or watercourse ($F = 2.2432$, $P = 0.1377$). It seems that variation among years is an important predictor of persistence of *B. viridis* on locality. However, our data do not allow us this type of analysis because we have not accumulated sufficient amount of repeated observations from each locality.

Only 38% of recent localities were situated in 6 habitats units and 17 subunits, which are classified as natural according to habitat mapping GIS layer ([Tab. 4](#)). The remaining localities were recorded in 3 units and 8 subunits of habitats classified as non-natural. The most common natural habitats were beech forests, particularly herb-rich and acidophilous beech forests, the most common non-natural habitats were non-specified habitats of contextual mapping and habitats strongly influenced or created by man, particularly the forest plantations of coniferous trees.

Potential distribution map

The potential distribution model is shown in [Fig. 6](#). The model and recent distribution show a close match mainly in the Western Carpathians and the Hrubý Jeseník Mts., where there are frequent records of *B. viridis* as well as the

Tab. 3 Co-occurring species at microlocalities of *B. viridis*.

Species	% of co-occurring species (N = 169)	Ecological category
Liverworts		
<i>Chiloscyphus profundus</i>	56	TX
<i>Cephalozia bicuspidata</i>	31	FX
<i>Lepidozia reptans</i>	27	TX
<i>Blepharostoma trichophyllum</i>	16	FX
<i>Plagiochila porelloides</i>	11	G
<i>Scapania nemorea</i>	8	FX
Mosses		
<i>Herzogiella seligeri</i>	70	TX
<i>Rhizomnium punctatum</i>	50	FX
<i>Dicranum scoparium</i>	45	FX
<i>Tetraphis pellucida</i>	40	TX
<i>Dicranum montanum</i>	28	E
<i>Hypnum cupressiforme</i>	21	FX
<i>Sanionia uncinata</i>	17	FX
<i>Plagiothecium curvifolium</i>	12	G
<i>Dicranella heretomalla</i>	12	G
<i>Polytrichum formosum</i>	12	G
<i>Pohlia nutans</i>	11	G
<i>Atrichum undulatum</i>	9	G
<i>Dicranodontium denudatum</i>	7	TX
<i>Plagiomnium affine</i>	6	G
<i>Plagiothecium laetum</i>	6	G
<i>Sciuro-hypnum reflexum</i>	6	G

Bryophytes with low frequency (less than 5%). Liverworts: *Bazania trilobata* (ecological category: G), *Calypogeia azurea* (G), *C. integristipula* (G), *Crossocalyx hellerianus* (TX), *Chiloscyphus coadunatus* (G), *Ch. cuspidatus* (G), *Diplophyllum obtusifolium* (G), *Lioclada lanceolata* (FX), *Lophozia ascendens* (TX), *Lophozia ventricosa* (FX), *Marchantia polymorpha* (G), *Nowellia curvifolia* (TX), *Orthocaulis attenuatus* (FX), *Ptilidium pulcherrimum* (E), *Riccardia latifrons* (TX), *Riccardia palmata* (TX), *Schistochilopsis incisa* (FX), *Tritomaria exsectiformis* (FX). Mosses: *Aulacomnium androgynum* (FX), *Brachythecium rivulare* (G), *B. rutabulum* (G), *B. salebrosum* (FX), *B. velutinum* (FX), *Bryum moravicum* (E), *Buxbaumia aphylla* (G), *Cirriphyllum piliferum* (G), *Dicranella subulata* (G), *Dichodontium pellucidum* (G), *Eurhynchium angustirete* (G), *Hylocomium splendens* (G), *Mnium hornum* (G), *M. spinosum* (G), *Plagiomnium cuspidatum* (FX), *P. undulatum* (G), *Plagiothecium curvifolium* (G), *P. nemorale* (G), *P. succulentum* (G), *Pleurozium schreberi* (G), *Pogonatum urnigerum* (G), *Polytrichum juniperinum* (G), *P. longisetum* (G), *Rhynchostegium riparioides* (G), *Rhytidiadelphus loreus* (G), *Sciuro-hypnum curtum* (G), *Sphagnum girgensohnii* (G), *Thuidium tamariscinum* (G). Ecological categories: E – epiphyte, FX – facultative epixylic species, G – ground species, TX – true epixylic species and.

high modeled probability of its occurrence (cf. [Fig. 2](#) and [Fig. 6](#)). The high probability of occurrence according to the model is also reflected in at least several recent records of *B. viridis* in Moravian Karst, Giant Mts. and Šumava Mts. On the other hand, the relatively high modeled probability of occurrence contrasts with only two positive recent records

Tab. 4 Representation of habitats on recent localities of *Buxbaumia viridis* ($N = 121$).

Forest habitat	N	Habitat unit	N	Habitat subunit	N	
Natural	46	Alluvial forests (L2)	2	Ash-alder alluvial forests (L2.2)	2	
		Oak-hornbeam forests (L3)	2	Hercynian oak-hornbeam forests (L3.1)	2	
		Ravine forests (L4)	3	Ravine forests (L4)	3	
		Beech forests (L5)	24	Herb-rich beech forests (L5.1)	12	
					Montane sycamore-beech forests (L5.2)	3
					Acidophilous beech forests (L5.4)	9
		Spruce forests (L9)	4	Montane <i>Calamagrostis</i> spruce forests (L9.1)	2	
	Bog and waterlogged spruce forests (L9.2)			1		
	Montane <i>Athyrium</i> spruce forests (L9.3)			1		
		Mosaic	11	Ash-alder alluvial forests (L2.2) + ravine forests (L4)	1	
	Ravine forests (L4) + chasmophytic vegetation of siliceous cliffs and boulder screes (S1.2)			2		
	Ravine forests (L4) + chasmophytic vegetation of calcareous cliffs and boulder screes (S1.1)			1		
	Herb-rich beech forests (L5.1) + chasmophytic vegetation of siliceous cliffs and boulder screes (S1.2)			2		
	Herb-rich beech forests (L5.1) + ravine forests (L4)			2		
	Herb-rich beech forests (L5.1) + chasmophytic vegetation of calcareous cliffs and boulder screes (S1.1)			1		
	Acidophilous beech forests (L5.4) + herb-rich beech forests (L5.1)			1		
Herb-rich beech forests (L5.1) + forest springs without tufa formation (R1.4)	1					
Non-natural	75	Contextual mapping (-1)	41	Contextual mapping (-1)	41	
		Habitats strongly influenced or created by man (X)	27	Anthropogenic areas with sparse vegetation (X6)	1	
				Forest plantations of coniferous trees (X9A)	22	
				Forest clearings (X10)	4	
		Mosaic	7	Ash-alder alluvial forests (L2.2) + forest plantations of coniferous trees (X9A)	3	
	Forest plantations of coniferous trees (X9A) + herb-rich beech forests (L5.1)			2		
	Forest plantations of coniferous trees (X9A) + forest clearings (X10)			1		
	Forest clearings (X10) + forest springs without tufa formation (R1.4)			1		

Mainly microlocalities of one locality belonged to same habitat type. Only a few microlocalities of three localities differed in habitat type (for more details see [Appendix S1](#)), this localities were not included. Most frequented habitat subunits (habitats of interest) are highlighted.

in the Orlické hory Mts., although we paid an adequate effort to the recent focused search for the species (cf. [Fig. 2](#) and [Fig. 6](#)). The military area Brdy remains among regions with the high-modeled probability of occurrence and inadequate recent exploration.

Discussion

Historical and recent distribution

The considerable amount of recent localities, especially in the Hrubý Jeseník in the last five years, cannot be interpreted in terms of the recent spread of the species. Rather, we could see the increasing intensity of the exploration, together perhaps with the increasingly better search strategy and knowledge of ecology, resulting in the more focused search of the surveyors. In addition, *Buxbaumia viridis* was re-found at nearly a half of the historical localities (44%), which convincingly shows that the species may persist at the localities

for a long time, provided that sufficient amount of suitable deadwood is retained, as most of the historical localities date back to or precede the 1950s. Even though, *B. viridis* may be still under-recorded, as the rate of its potentially suitable habitats, visible only in sporophyte stage to the number of surveyors, is still far too high. On the other hand, the survey density and success rate in finding is probably highest in the Czech Republic in comparison with neighboring countries. About 95 recent localities have been found in significantly larger Germany [29] and 85 were reported from Austria [30], and only 15 localities were recorded in Slovakia [31]. In neighboring Poland, the current state of the population is less known. The species was reported from tens of localities over a wide geographic range, discovered mainly in the 19th century [32]. Most occurrences were reported from the Western Carpathians, as well as in the Sudety Mts. and the Sudety foothills [32]. Nevertheless, even in Poland, the trend of recent discoveries of new localities has been observed [33–36].

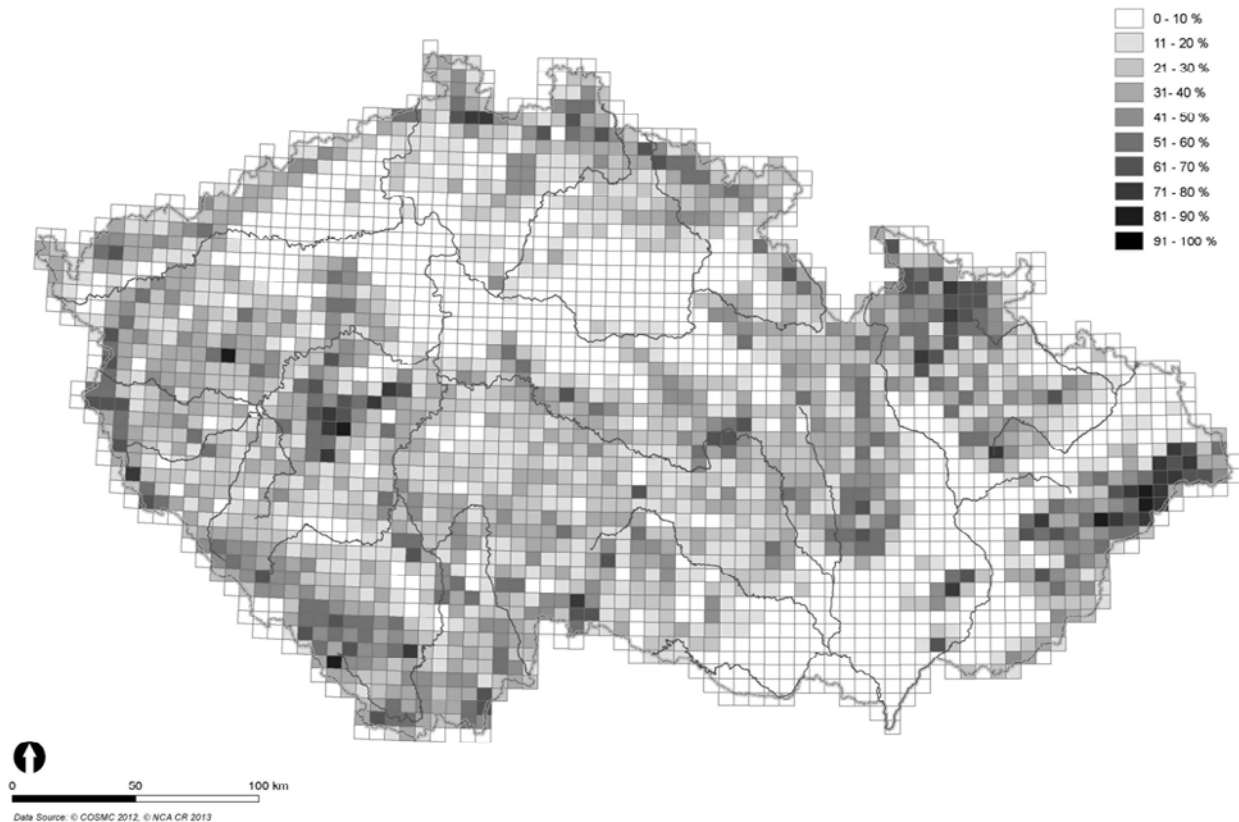


Fig. 6 Potential distribution map of *B. viridis*, the relative proportion of habitat area (only habitats of interest) per each square are given. The grid squares are defined by the project “Kartierung der Flora Mitteleuropas” (KFME), with the squares of 5' longitude and 3' latitude.

Most of the recent localities are situated in the Western Carpathians and the Hrubý Jeseník Mts., while the historical localities were distributed more evenly in the Czech Republic. However, the recent and historical area of occupancy and extent of occurrence are not obviously different. The highest density of recent occurrences in the mountains of the northeastern part of Czech Republic agrees well with our model of potential distribution (Fig. 6). The reasons for this pattern might include the highest proportion of forests [37], ideal span of altitude, and generally more humid conditions, resulting from high precipitation averages [38] and favorable geomorphology. At the same time, the Western Carpathians and the Hrubý Jeseník Mts. are the best-explored areas for the species in the recent period (Fig. 2), in contrast to the historical state. Other well-researched mountain regions of Czech Republic (Orlické hory Mts., Giant Mts.) demonstrably support a much smaller number of recent localities (Fig. 2), which implies that the Western Carpathians and the Hrubý Jeseník Mts. indeed represent the core area for the occurrence of *B. viridis* in the Czech Republic. In addition, many new records in the Šumava Mts. during the two last years of focused survey suggest that the real situation here might be closer to that of Western Carpathians and the Hrubý Jeseník Mts. than previously thought. However, additional survey in the Šumava Mts. is needed to confirm this trend.

Habitat requirements and co-occurring species

The most important abiotic factor, which affects the occurrence of *B. viridis* is probably the humidity. The insufficient

moisture was speculated to hamper the sporophyte production by the inhibition of gametangia and fertilization, or death of the protonema [9]. *B. viridis* also prefers the wood in advanced phases of decay, with high and fairly constant water content. Indeed, the majority of sites were located within 100 m from a stream. The exact pattern of the yearly course of air humidity at the sites, which is probably crucial for the successful establishment of gametophytes and development of sporophytes, is nevertheless much more difficult to trace. Our data unfortunately do not allow any scholarly analysis in this way, particularly because the GIS layer used for the retrieval of watercourses might not have included smaller streams, which nevertheless provide the sufficient source of humidity for the development of *Buxbaumia sporophytes*.

Epixylic bryophytes do not seem to be restricted to specific wood species [3,9]. This was confirmed for *B. viridis*, although Spruce logs were the most frequently occupied substratum. This may be due to the better holding capacity of brown-rot fungi that grow in conifer wood [9,18].

B. viridis tends to occur with rather common moss species. It prefers mosses to liverworts, and only two of the most frequently recorded mosses (*Herzogiella seligeri*, *Tetraphis pellucida*) are rather specifically associated with dead wood (true epixylic mosses) in the Czech Republic. True epixylic liverworts are generally good indicators of the high air-humidity, being moisture-demanding or intolerable of prolonged drought periods. However, *B. viridis* rarely if ever grows associated with such liverworts (*Crossocalyx hellerianus*, *Lophozia ascendens*, *Nowellia curvifolia*), which seems

to be contradictory to the general demand on air humidity discussed above. Protonematal growth of *B. viridis* is very slow (0.5–3 mm after 70 days in cultivation) and does not seem to expand rapidly to the empty space [10]. Therefore, *B. viridis* is probably not successful in competitive interaction with bryophytes during the juvenile stage of the life cycle. The pleurocarpous mosses, which are commonly associated with the sporophytes of *B. viridis* (*Herzogiella seligeri*, *Hypnum cupressiforme*, *Sanionia uncinata*) may provide shadier and damper shelter for germination and protonematal growth of *B. viridis* than tiny liverworts.

Habitat association and potential distribution

B. viridis is generally considered to be an indicator species of old-growth (primeval) forests (e.g. [13,39]). Nevertheless, only 38% of the Czech localities are situated in natural forest habitats, while the rest is situated in managed forests, most

typically in spruce plantations. It seems that the crucial factor is not habitat association (type of forest) but probably suitable humidity, typically near a watercourse with a sufficient amount of decayed wood. These conditions seem to be crucial for the occurrence of *B. viridis*. However, it is exactly these factors, which are difficult to retrieve, analyze and include to the distribution model. The microclimatic humidity is influenced by topography and substratum characteristics of the logs. The amount of dead wood is not specified in any of the existing databases (cf. habitat mapping [20] and Czech national phytosociological database – ČNFD [40]). Although only the frequency of the most commonly occupied habitat (which is definitely also linked to certain extent to these parameters) was included to the model, its match with the recent distribution shows that the model may be used as a basis for focused search for the new localities of *B. viridis*.

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Authors' contributions

The following declarations about authors' contributions to the research have been made: responsible for coordination of monitoring *Buxbaumia viridis* (since 2008), field work, data and GIS analysis, paper writing and manuscript preparation: EH; GIS analysis: JV; field work, manuscript preparation: EN, MZ, VP; coordination of monitoring *Buxbaumia viridis* (2000–2007), field work: RL; field work, paper writing and manuscript preparation: JK.

Supplementary material

The following supplementary material for this article is available online at <http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/aspb.2014.015/0>:

1. Appendix S1: historical and recent records of *Buxbaumia viridis* in the Czech Republic.

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