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ABSTRACT

Field studies in Hungary during the last six years have led to the discovery of 82 localities and 2145 sporophytes of *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl., i.e. 41 times more localities and 143 times more sporophytes than reported in the previous census carried out up to 2014. The recent occurrences of the species known at that time (two localities with four stands and 15 sporophytes) were found exclusively on decaying wood in old growth forests. However, in the light of 20th century herbarium data from Hungary and new observations in Central Europe, our survey was extended to include the soil of acidophytic, young and middle-aged, managed and disturbed forests, and the new populations were mainly found in these types of habitats, almost exclusively on acidic soil. Details of population size, habitat and substrate preference, and environmental conditions at the newly found stands are reported in this paper. If these unusual preferences (i.e. acidic soil in managed, acidophytic beech forests) are not confined to Hungary, the total population size of this Natura 2000 species listed in annex II of the Habitat Directive might be severely underestimated in Europe.

KEYWORDS
Acidic soil,
acidophytic forests,
Buxbaumia aphylla Hedw.,
disturbed habitats,
ecology,
management,
old growth forest,
substrate preference.

RÉSUMÉ

Buxbaumia viridis *(Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. à prédominance terricole en Hongrie et trouvée dans les forêts aménagées.*

Les études sur le terrain menées en Hongrie au cours des six dernières années ont permis de découvrir 82 localités et 2145 sporophytes de *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl., c'est-à-dire 41 fois plus de localités et 143 fois plus de sporophytes qu'au dernier recensement effectué jusqu'en 2014. Les occurrences récentes précédemment connues de l'espèce (deux localités avec quatre peuplements et 15 sporophytes) ont été trouvées exclusivement sur du bois en décomposition dans des forêts anciennes. Cependant, d'après les données des spécimens hongrois dans l'herbier au XXe siècle et les nouvelles observations réalisées en Europe centrale, notre étude a été étendue aux sols de forêts à caractère acidophytique, jeunes et d'âges moyens, gérées et perturbées, et les nouvelles populations se trouvaient principalement dans ces types d'habitats, presque exclusivement sur des sols acides. La taille de la population, l'habitat et la préférence du substrat ainsi que les conditions environnementales des peuplements récemment découverts sont ici précisément décrits. Si ces préférences inhabituelles (sol acide dans les hêtraies aménagées à substrat acide) ne se limitent pas à la Hongrie, la taille de la population de cette espèce Natura 2000 inscrite dans l'annexe II de la Directive Habitat pourrait être fortement sous-estimée en Europe.

MOTS CLÉS
Sol acide,
forêts à substrat acide,
Buxbaumia aphylla Hedw.,
habitats perturbés,
écologie,
aménagement,
forêt ancienne,
préférence de substrat.

INTRODUCTION

The bryological literature on *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. apparently agrees on its habitat: the species is characterized as colonizing dead wood (usually conifers, mainly *Picea abies* (L.) H. Karst.), in an advanced state of decay. It is typically found in stands of the alliance Nowellion curvifoliae Phil. 1965, but very rarely also occurs on soil. The rotting wood that it colonizes is usually found in montane and boreal regions, in sites with high air humidity, especially stands of old beech (*Fagus sylvatica* L.) or conifer forests, often in ravines, where human impact is absent (Orbán & Vajda 1983; Hill & Preston 1998; Dierssen 2001; Plášek 2004; Smith 2004; Schofield 2007; Amphlett 2010; Papp *et al.* 2014; Goia & Gafta 2018). Based on this paradigm, it was primarily this type of habitat that was targeted during earlier investigations in the 21st century in Hungary, although the previously known seven populations were mostly found on acidic soil (Boros 1968; Erzberger *et. al.* 2018). The two existing populations occurring on decaying wood in beech forests, partly on limestone, were very small, with 15 sporophytes on 4 beech logs (Papp *et al.* 2014).

According to the literature (Plášek 2004, Fudali *et al.* 2015, Spitale & Mair 2015), the main habitat types of *B. viridis* became increasingly scarce worldwide during the 20th century, and therefore the species was considered threatened in Europe. It is listed in annex II of the EC Habitats and Species Directive and in appendix I of the Bern Convention (Council of Europe 1993). Consequently, *B. viridis* is treated as a threatened species in previous Red Lists for Europe (ECCB 1995: Vulnerable) and Hungary (Papp *et al.* 2010: Endangered). However, in the latest European Red List (Hodgetts *et al.* 2019) it is considered as Least Concern (LC).

The aims of this study are to clarify the distribution and population size of *B. viridis* in Hungary; to examine its altitudinal range, habitat and substrate preference, the age of the occupied forests and the extent of any potential disturbance; and to identify the most important fine-scale indicators of the species in order to increase the chance of its being found during further surveys.

MATERIAL AND METHODS

From 2014 to 2019 systematic surveys were carried out in Hungary, in each year from mid-autumn to early summer, when the capsules of *B. viridis* are most noticeable. The field work was conducted in the seven historical localities (Boros 1968; Erzberger *et al.* 2018) and in other landscape areas where similar habitats occur. Based on 20th century herbarium data from Hungary and new observations in Europe (e.g. Taylor 2010; Holá *et al.* 2014; Jasík & Potocky 2016), the targeted habitats were acidophytic communities – mainly beech (*Fagus sylvatica*) forests and oak (*Quercus petraea* agg.) forests and spruce (*Picea abies*) plantations – and ravine forests, including young and middle-aged, disturbed stands, in the colline and (sub)montane regions of Hungary. The visited sites were selected according to the habitat distribution maps of Bölöni *et al.* (2008, 2011) and our own field experience, but some promising microhabitats based on our previous knowledge were also found accidentally during unrelated field work, and checked with positive results (e.g. ruderal lowland forest on acidic sand). The habitats were classified into national (ÁNÉR: Bölöni *et al.* 2011) and also international habitat categories (EUNIS: European Environment Agency 2020, Natura 2000: Haraszthy 2014; European Commission DG Environment 2017). Information about the forest management units, officially called subcompartments (age, date and type of last usage) were obtained from the National Food Chain Safety Office, Forestry Directorate (NÉBIH 2020) and Mecsekerdő Zrt. Forests older than 120 years are considered as old-growth forests (WWF 2016).

In a geographic context, we distinguish landscape areas (geographic regions) and localities, i.e. forest subcompartments occupied by *B. viridis* and defined according to the Forestry Directorate (Tobisch & Kottek 2013; NÉBIH 2020). Subcompartment is the unit of forest planning in Hungary, since site conditions and tree layer composition are more or less homogeneous within each of them and they are usually managed by the same silvicultural tools (Tobisch & Kottek 2013). Although, some of them are very close to each other, so the concept of locality used in this paper is probably narrower than in traditional botanical terminology. Since the extent of subterranean protonema is unknown, counting 'gametophyte individuals' is problematic, so we simply report the number of *B. viridis* sporophytes and stands (1 m^2-sized plots located around the capsules on soil, or individual pieces of wood if this was the substrate). Since there were usually multiple stands within a locality, the central coordinates (centroids) of each locality (calculated by averaging the measured coordinates of the constituent stands of *B. viridis*) and the average distance of stands from the corresponding centroids are given. To calculate the distance between locality centroids and abiotic objects (settlements, buildings, roads), Google Maps (n. d.) was used.

In almost every newly discovered stand, phytosociological relevés (according to Lájer *et al.* 2008) were also taken at a scale of 1 m^2, placed around the sporophytes. We recorded the identities of vascular plants and bryophytes, GPS coordinates (in WGS84 projection), altitude, substrate type (soil or decaying organic matter, e.g. peaty cushions of other mosses, rotting fronds of ferns and decaying wood using the decay phases defined by Holá *et al.* 2014). If it was difficult to distinguish soil from the final stages of decaying wood, we examined the substrate carefully searching for some remnants of wood and inserting a thin stick into the ground to check the substrate consistency. The cover values of moss layer, bare surfaces and organic debris (e.g. leaf-litter, remnants of dead plants) were also estimated. Considering their legal protection and Natura 2000 status, the capsules of *B. viridis* identified in the field were not collected but documented by photos in each stand.

The amount of decaying wood was not recorded, since decaying wood (especially well-decayed, large logs) was almost absent at most of the localities, and we were aware from our former experience that *B. viridis* preferred soil as a substrate in Hungary even when there was appropriate decayed wood in the neighbourhood.

For identification of bryophytes, the keys of Orbán & Vajda (1983) and Smith (2004) were used. The ecological tolerances of the species were determined according to Orbán (1984), Horváth *et al.* (1995), Dierssen (2001) and Ellenberg & Leuschner (2010). Nomenclature follows Index Fungorum (2020) for lichens, Söderström *et al.* (2016) for liverworts, Hill *et al.* (2006) for mosses and Király (2009) for vascular plants. The newly collected specimens of cryptogamic species were deposited in the Herbarium of the University of Pécs (JPU), the Herbarium of the Botanical Museum and Botanic Garden, Berlin (B) and the Bryophyte Collection of the Hungarian Natural History Museum, Budapest (BP).

RESULTS

Number of landscape areas, localities, stands and sporophytes

Between 2014 and 2019, *B. viridis* was detected in 18 landscape areas, and at 82 localities in Hungary (Appendix 1, Fig. 1). Among the seven historical localities (documented before 1970), three were checked with positive results, while in four the species was not re-found at the original site, but new stands were recorded in the neighbouring forests.

300 stands with 2145 sporophytes were detected in total (Appendix 1), occurring in small patches (about 4-8 capsules per relevé), but the largest stand (found on soil) numbered more than 200 well-developed capsules within 1 m^2.

Characteristics of forest subcompartments (altitude, habitat, disturbance, age)

The altitudinal distribution of the localities spanned 144-819 m, of which most (76%) were recorded in the colline zone, at altitudes between 201-500 m a.s.l. (Appendix 1).

The localities of *B. viridis* occurred principally in acidophytic communities: in *Fagus sylvatica* (69.5%) and *Quercus petraea* agg. forests (6.1%) (Fig. 2), or in the transitional zone of these vegetation types (9.8%). Occasionally, it was detected in *Picea abies* plantations (8.5%), but it was also found in the following additional habitats: Pannonian-Balcanic *Quercus cerris*-*Quercus petraea* woodlands (2.4%), mixed forest of slopes and screes (1.2%), coniferous plantation mixed with native deciduous trees (1.2%), and *Pinus sylvestris* L. plantation with *Robinia pseudoacacia* L. (1.2%) (Appendix 1, Table 1).

At least 19.5% of these woodlands had been disturbed by different types of forest management in the previous five years, e.g. clearing, sanitary logging, thinning, preparatory logging, and in one case drastic final removal cut (Table 2). The forests with *B. viridis* were usually located within the peri-urban zone, close to places frequented by humans (e.g. settlements, tourist houses, foresters' lodges, paved roads), and therefore exposed to potential several anthropogenic impacts (Fig. 3).

78% of the occupied forest subcompartments were younger than 120 years (so not old-growth forests), and 12% of them were not more than 40 years old; the median value of their age was 87 years. The youngest forest stand was only 23 and the oldest 172 years old (Table 3).

Substrate preference

Only a small proportion of the *B. viridis* stands were detected on decaying matter (35 stands, 11.7%), including decaying beech (7 stands) and conifer wood (23 stands), peaty cushions of *Leucobryum* Hampe (white-moss) (4 stands) and rotten fronds of ferns (1 stand). The decayed wood was always in an advanced stage of decay (degree 6, 7 or 8), sometimes not more than a few cm in diameter. The majority of the stands were terricolous (265 stands, 88.3%) (Appendix 1; Fig. 1; 4), occurring on acidic (moder or mull-moder) soil rich in organic matter, and a small stand was also found on an abandoned ants' nest in a young, planted spruce forest.

Table 1. — Habitat types of *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. localities.

No. of localities	EUNIS	ÁNÉR	Natura 2000
5	G1.871 Woodrush oak forests	L4a Closed acidofrequent oak forests	–
57	G1.611 Medio-European collinar woodrush beech forests	K7a Acidofrequent beech forests	9110 Luzulo-Fagetum beech forests
8	transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests	transition of L4a and K7a	–
2	G1.7696, G1.768 Balkano-Anatolian thermophilous oak forests	L2a Pannonian-Balcanic *Quercus cerris-Quercus petraea* woodlands	91M0 Pannonian-Balkanic turkey oak sessile-oak forests
7	G3.F21 Exotic spruce, fir, larch, douglas fir, deodar plantations	S5 Plantations of other conifers	–
1	G1.A45 Thermophilous Alpine and peri-Alpine mixed Tilia forests	LY2 Mixed forests of slopes and screes	9180* Tilio-Acerion forest of slopes, screes and ravines
1	G3.F22 Exotic pine plantations	S4 Scots and black pine plantations	–
1	G4.F Mixed forestry plantations	RDa Coniferuos forests and plantations mixed with native deciduous tree species	–

Table 2. — Date and type of the most recent forest management activities in the forest subcompartments occupied by *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. N/A: not available.

	1980-1984	1985-1989	1990-1994	1995-1999	2000-2004	2005-2009	2010-2014	2015-2019	N/A
Clearing	–	–	–	–	–	1	1	3	–
Sanitary logging	–	–	–	1	1	3	4	2	–
Increment thinning	–	–	1	–	–	4	1	4	–
Selective thinning	–	1	–	–	2	–	2	2	–
Selective logging	–	–	–	–	–	–	2	2	1
Preparatory logging	–	–	–	–	–	4	2	2	–
Final removal cut	–	–	–	–	–	–	–	1	–
Clearcutting	1	–	–	–	–	–	–	–	–
Other	–	–	–	–	–	–	1	–	–
N/A	1	1	1	3	6	–	–	–	21

Fine-scale conditions (slope, exposition, coverage, co-occurring species)

The measured stands were detected mostly on steep (> 30°), north- (34%), northwest- (30%) or northeast-facing (16%) slopes, mainly on bare patches of ground (e.g. banks of trails, bases of trees). In the 1 m^2 plots the cover values for the moss layer were usually smaller than the extent of bare surfaces and the coverage of organic debris; the sporophytes of *B. viridis* developed mainly on the bare patches.

The frequent (frequency > 50%) co-occurring taxa of *B. viridis* (herbs: *Luzula luzuloides* (Lam.) Dandy et Wilmott; bryophytes: *Dicranella heteromalla* (Hedw.) D.Mohr, *Dicranum scoparium* Hedw., *Hypnum cupressiforme* Hedw., *Lophocolea heterophylla* (Schrad.) Dumort., *Polytrichastrum formosum* (Hedw.) G.L.Sm.; lichens: *Cladonia* P.Browne spp.) were typically acidophilic and terricolous plants – except *L. heterophylla*, which usually prefers decaying wood, but we found it more frequently on soil. These species are usually widespread in moist and shady acidophytic habitats, but several nationally rare and/or redlisted mosses and liverworts (Papp *et al.* 2010) were also found among the associated taxa. As an example, we found *Buxbaumia aphylla* Hedw. at 50 Hungarian localities (61% of all its recent localities) in the immediate vicinity of *B. viridis*, in 28 cases in the same relevé (min. distance between them: < 1 mm). Mosses that are expanding their range – e.g. *Campylopus flexuosus* (Hedw.) Brid. – or are invasive – i.e. *Campylopus introflexus* (Hedw.) Brid. – were present too in some localities and grew close to *Buxbaumia* Hedw. species, especially in South Transdanubia (Mecsek Mts, East-Inner Somogy) (cf. Szűcs *et al.* 2014; Csiky *et al.* 2015; Alegro *et al.* 2018).

DISCUSSION

Increased number of *B. viridis* occurrences

Although *B. viridis* was thought to be one of the rarest threatened mosses in Hungary, it proved to be comparatively frequent in appropriate habitats. During our surveys over the period 2014–2019, the number of recent localities of *B. viridis* increased 41 times from 2 to 82 compared to the period 1970-2014, and the recently recorded number of sporophytes increased 143 times from 15 to 2145 in Hungary. This increase is probably a consequence of intensive, systematic surveys, as in other European countries, e.g. Croatia (Alegro *et al.* 2014), Czech Republic (Holá *et al.* 2014), Italy (Spitale & Mair 2015) and Slovakia (Jasík & Potocky 2016).

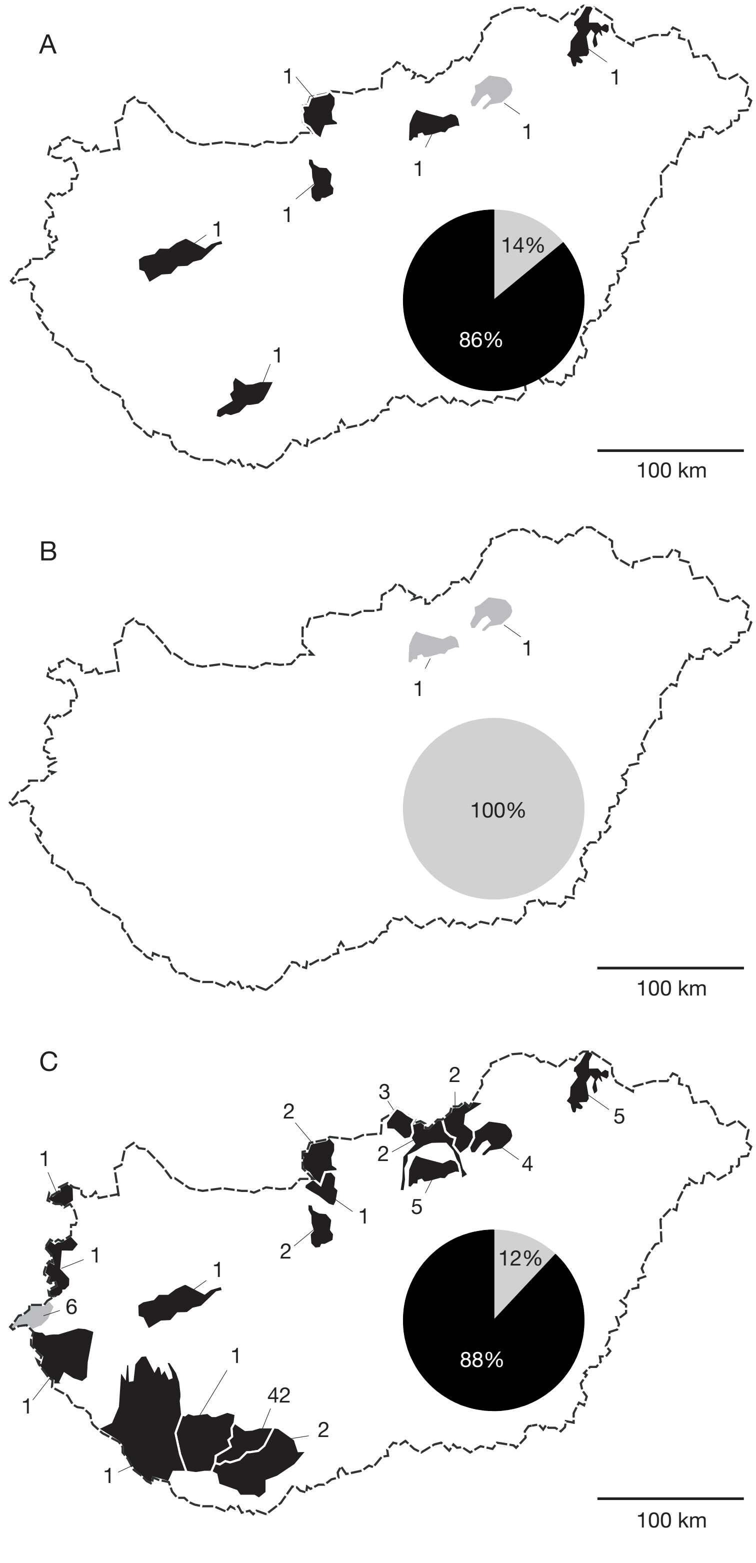

FIG. 1. — Distribution of *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. in three periods (**A**, 1900-1970; **B**, 1970-2014; **C**, 2014-2019) according to landscape areas in Hungary. Numbers of the localities are given. Landscape areas with epixylic dominance are highlighted in grey. Pie charts represent the country-wide ratio of epixylic (**grey**) and terricolous (**black**) sporophytes.

Characteristics of forest subcompartments

B. viridis was found in all the main altitudinal zones (i.e. lowland, colline and montane). Although it is considered typically a montane species (e.g. Hill & Preston 1998; Dierssen 2001), our results do not show a preference for this zone; however, this may be due to the fact that montane areas (above 500 m a.s.l.) are very rare in Hungary (< 1% of the country surface) (Gábris *et al.* 2018). The smallest numbers of *B. viridis*

FIG. 2. — Typical habitat of *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl.: young, acidophytic beech forest.

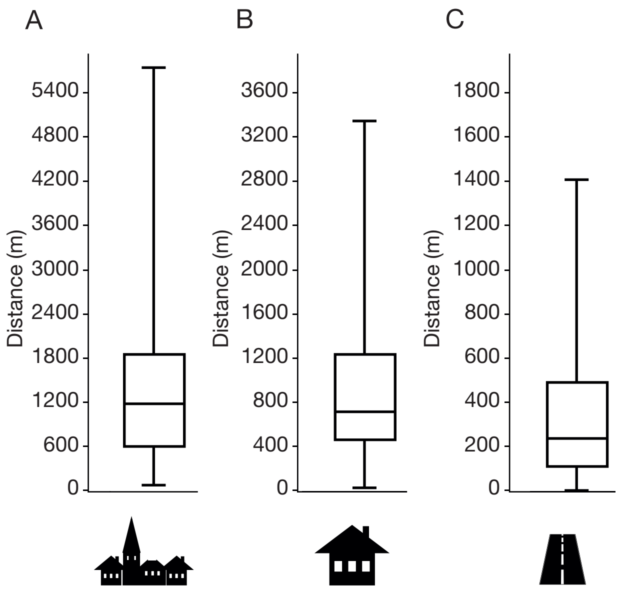

FIG. 3. — Distance of *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. localities from settlements (**A**, average: 1370 m, median: 1168 m, min.: 79 m, max.: 5752 m), frequently used buildings (including buildings scattered in the forests) (**B**, average: 908 m, median: 706 m, min.: 27 m, max.: 3352 m) and paved roads (**C**, average: 326 m, median: 236 m, min.: 1 m, max.: 1409 m).

were found in the extended lowlands (more than 80% of the country area), but this is not surprising, given the low amount of precipitation and lack of appropriate forests (Borhidi *et al.* 2012; Bihari *et al.* 2018; Gábris *et al.* 2018). The number of localities in the colline zone was striking. Several other studies also report the presence of *B. viridis* in this zone (e.g. Plášek 2004; Holá *et al.* 2014; Jasík & Potocky 2016), but the majority of their finds were in the submontane-montane region.

TABLE 3. — Age of the forest subcompartments occupied by *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. (average: 89 years, median: 87 years, min.: 23 years, max.: 172 years). N/A: not available.

Age of the forests (years)	No. of localities	No. of sporophytes
20-40	10	590
41-60	6	98
61-80	17	348
81-100	18	472
101-120	13	224
121-140	13	356
141-160	3	28
161-180	1	17
N/A	1	12

The observation that *B. viridis* is a montane species and prefers beech, spruce and ravine forests is based on the fact that these habitats usually provide a humid microclimate, which is necessary for the ontogeny of *B. viridis* (Holá *et al.* 2014). However, acidophytic beech forests could also offer sufficient habitat and humidity, although at a finer (microclimatic) scale. The poor herb layer and the slow decomposition of leaf litter favours the growth of bryophytes (Thauront & Stallegger 2008), and the extensive moss layer influences the microclimate, since thick bryophyte cushions/carpets are able to store water, preventing the temporary drying of soil and therefore hygrophytic plants in their surroundings (Boros 1943; Vanderpoorten & Goffinet 2009).

Although fallen trees within *Luzulo-Fagetum* forests would constitute a potential habitat for epixylic bryophytes, the wood almost never reaches an advanced stage of decay in Europe, since these forests are managed and dead or decaying wood is frequently removed for reasons of sanitation and tidiness (Thauront & Stallegger 2008). These activities are not favourable for epixylic *B. viridis*; its previously described preference for undisturbed, old woodlands (Dierssen 2001; Papp *et al.* 2014) probably originates in the fact that these habitats are relatively rich in dead, decayed wood (Faliński 1978) – but for terricolous populations this is not a limiting factor.

Given that 95% of the total forest area is used for wood production and old-growth forests are very rare and small in extent in Hungary (WWF 2016), it is not surprising that the species, which was searched for in these forests, was considered so rare in the country (cf. Papp *et al.* 2014). According to our experience *B. viridis* occasionally does also occur in them, but was found more often in young or middle-aged and disturbed stands, as several former studies performed outside the Carpathian Basin also confirm (Anonymous 1996; Hajek 2010; Plášek & Novozámská 2011; Holá *et al.* 2014; Jasík & Potocky 2016; Horvat *et al.* 2017).

UNIQUE SUBSTRATE PREFERENCE

The occurrence of *B. viridis* on soil has in fact been reported in several parts of the Northern Hemisphere (Boros 1968; Orbán & Vajda 1983; Anonymous 1996; Dierssen 2001; Wiklund 2002; Smith 2004; Taylor 2010). Surprisingly, Warnstorf (1903-1906) mentions the species as mainly growing on soil rich in humus in deciduous forests in Brandenburg, Northern Germany (which is one of the most arid parts of this country [Deutscher Wetterdienst 2018]), with just occasional occurrences on decaying wood – as in Hungary. The ants' nest as an appropriate substrate was also not unprecedented as it was first detected in Scotland (Taylor 2010). Our surveys in the Papuk Mts (Croatia), on the margin of the Pannonian Biogeographical region (cf. Fekete *et al.* 2016) also confirm the preference for acidic soil, since several stands of *B. viridis* were observed in similar conditions to those in Hungary (unpublished data).

It seems that the absence or low amount of decaying woody matter is not the only factor responsible for the preference for soil in Hungary. Due to its location (surrounded by high mountains: the Alps, Dinarides and the Carpathians), macroclimate (sub-continental) and relief (basin), zonally humid, mesic beech and conifer forests (i.e. the mountain forest belt, which is considered to be the typical habitat of *B. viridis*) are not present regionally or are very small in extent in this country (Borhidi 1961; Bölöni *et al.* 2011; Borhidi *et al.* 2012; Fekete *et al.* 2014). Since the semi-arid forest-steppe zone and the zone of closed oak forests are predominant (Borhidi 1961), microclimatic circumstances may play a more important role in the distribution of *B. viridis* than macroclimate in Hungary, especially in the lowlands and the colline region. In terms of microclimate, it is noteworthy that well-decayed logs generally have higher water holding capacity than soil (Wiklund 2003; Wiklund & Rydin 2004), however the moss cover on the sampled places are usually not regarded. Considering that humidity decreases upwards from the ground (Geiger 1965), and emergent decayed logs have a relatively large surface area compared to their mass, in some case they probably dry out more rapidly than the extensive soil layer thickly covered with mosses, which can hold moisture for a long time. Beside moisture, pH and nutrient content also effect on *B. viridis*. The species can germinate at lower pH if water availability is high, whereas it needs higher pH at dryer environments (Wiklund & Rydin 2004). Since the soil is rather acidic at the preferred habitats in Hungary (Thauront & Stallegger 2008; Bölöni *et al.* 2011), that is an open question, whether the soil is really wetter than decaying wood in these habitats or whether other factors stand in the background – e.g. litter from deciduous trees may increase the pH and P concentration, which also could compensate the unfavourably low pH (Wiklund 2003). Supposing that a climate-dependent substrate preference factually exists, it might explain some strange situations as well: the predominantly terricolous populations found in a rather arid part of Germany (Warnstorf 1903-1906; Deutscher Wetterdienst 2018) and the preference of logs on the western slopes of the Cascades and extremely decayed logs (that appear to have 'melted' into the soil) on the eastern slopes in the US (Harpel 2003). In the latter, the climate is much drier due to the rain-shadow effect (Siler *et al.* 2013).

In the recent Hungarian literature and in most of the Hungarian handbooks (cf. Boros 1953, 1968; Orbán & Vajda 1983; Papp *et al.* 2014) habitat and substrate preferences were not described accurately in the context of local Hungarian conditions, therefore earlier surveys in the country usually failed to refind formerly known stands or to find new ones. Even when searched for, it is much harder to detect the sporophytes on soil than on dead wood, since the target area is less clearly defined and the recognition of suitable microsites needs much experience. The chance of accidentally detecting terricolous stands of *B. viridis* is very low.

Fig. 4. — A large terricolous stand of *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl.

We are convinced that with systematic studies targeting suitable substrates (e.g. acidic, moder or mull-moder soil rich in organic matter, which is typical of *Luzulo-Fagetum* forests in Europe [Thauront & Stallegger 2008]) further occurrences of *B. viridis* will be found in the margin of the Pannonian Biogeographical region and in the Carpathians (e.g. Papuk Mts in Croatia; Cerová vrchovina, Štiavnické vrchy, Slovenské Rudohorie, Zemplínske vrchy, Vihorlat in Slovakia; Apuseni Mts in Romania) (cf. Ronikier 2011; Fekete *et al.* 2016).

Fine-scale indicators

The potential growth sites within an appropriate habitat are best recognized from the fine-scale conditions: steepness of slope, orientation to the north and the presence of bare patches interspersed in the moss carpet. Since *B. viridis* is a poor competitor and probably not successful in competitive interaction with other mosses and herbs (cf. Wiklund 2002; Taylor & Taylor 2007; Holá *et al.* 2014; Spitale & Mair 2015), it usually needs bare patches for its development, especially during the juvenile stage of its life cycle. However, the presence of frequent and conspicuous co-occurring species around the bare patches is also a useful indicator of *B. viridis* (e.g. the blueish-grey thalli of *Cladonia* lichens).

Although the habitat preference of *Buxbaumia aphylla* was thought to differ from that of *B. viridis* (cf. Orbán & Vajda

1983; Dierssen 2001; Smith 2004), the two species were frequently found together on acidic soil. Our field work in the Papuk Mts (Croatia) also confirms that they often occur together (unpublished data). *Buxbaumia aphylla* is listed as Vulnerable (VU) in the national Red List (Papp *et al.* 2010), but it proved to be locally widespread in appropriate acidophytic communities on soil (Deme *et al.* 2017). Unaware that the two species prefer the same substrate, Papp & Ódor (2006) questioned the correct identification of historical specimens of *B. viridis* collected from soil and erroneously revised them as *B. aphylla* (cf. Erzberger *et al.* 2018).

Both of the *Buxbaumia* species are presumably threatened by mosses that are expanding their range (*Campylopus flexuosus*) or are invasive (*C. introflexus*), and are spreading rapidly in the relevant habitats (Szűcs *et al.* 2014; Csiky *et al.* 2015; Alegro *et al.* 2018), especially in South Transdanubia, where the most extensive populations of *Buxbaumia* species were found. By forming dense carpets and covering bare surfaces effectively, these disturbance-tolerant mosses could displace *Buxbaumia* species from suitable habitats.

CONCLUSIONS

According to our results, previous knowledge about the distribution, habitat, substrate preference and disturbance-tolerance of *B. viridis* in Hungary (Boros 1953, 1968; Orbán & Vajda 1983; Papp *et al.* 2014) seems to be far removed from reality.

Since the species was found more frequently in disturbed forests than previously, it would be worth examining the effects of human activities on the populations. In lack of empirical studies, it can only be assumed that minor anthropogenic (e.g. limited trampling by tourists on the banks of trails, mushroom picking) and natural disturbances (e.g. trampling of ungulates, soil erosion at tree bases due to the flowing rain) might have a positive impact on *B. viridis* by creating bare surfaces on the ground appropriate for poor competitors, since the fine-scale mechanical disturbances loosen the dense, compact moss carpet or thick layer of leaf-litter (Holá *et al.* 2014; Ódor 2016). Forest management would also produce a suitable substrate (trunks and logs) for several epixylic bryophytes (e.g. *B. viridis* generally in Europe) and threatened saproxylic species, if the wood were not removed (Hajek 2010; BISE 2020).

There is also an important question to be answered, what lies behind the unusual substrate preference of *B. viridis* in Hungary: substrate shift at the edge of its area (where sufficient moisture is not provided by the macroclimate) or the underestimation of terricolous populations due to the misconceptions about the ecology of the species.

Anyway, if *B. viridis* prefers acidic soil in less humid (e.g. subcontinental) conditions, considering the effects of global climate change (Samaniego *et al.* 2018), this behaviour could become more widespread in the future than previously (not only in Hungary but outside of it as well).

Independently from climate change, it should be tested by further research, whether this preference is limited to certain parts of the continent (e.g. the Carpathian Basin), or whether surveying the soil surface in acidic woodlands of Europe would result in the detection of significantly more *B. viridis* stands. *Luzulo-Fagetum* beech forests are one of the most widespread vegetation types in central and northern Europe. According to some surveys, the estimated surface of *Luzulo-Fagetum* beech forests in Hungary is 1300 ha (Bölöni *et al.* 2011), which is 0.24% of the total surface of this habitat type in the 15 European countries that were measured/included (cf. Thauront & Stallegger 2008). This means that if a suspected substrate preference for acidic moder or mull-moder soil types in beech forests by *B. viridis* is not restricted to Hungary, and has been overlooked in other countries before, the population size of this bryophyte species listed in annex II of the Habitat Directive might be severely underestimated in Europe.

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REFERENCES

ALEGRO A., PAPP B., SZURDOKI E., ŠEGOTA V. & ŠAPIĆ I. 2014. — Contributions to the bryophyte flora of Croatia III. Plitvička jezera National Park and adjacent areas. *Studia Botanica Hungarica* 45: 49-65. https://doi.org/10.17110/StudBot.2014.45.49

ALEGRO A., ŠEGOTA V., PAPP B., DEME J., KOVÁCS D., PURGER D. & CSIKY J. 2018. — The invasive moss *Campylopus introflexus* (Hedw.) Brid. (Bryophyta) spreads further into South-Eastern Europe. *Cryptogamie, Bryologie* 39 (3): 331-341. https://doi.org/10.7872/cryb/v39.iss3.2018.331

AMPHLETT A. 2010. — *Buxbaumia viridis*, *in* ATHERTON I., BOSANQUET S. D. S. & LAWLEY M. (eds), *Mosses and Liverworts of Britain and Ireland – a Field Guide.* British Bryological Society, Plymouth, 337 p.

ANONYMOUS 1996. — Draft Management Recommendations for

Green bug moss *Buxbaumia viridis* (DC.) Moug. & Nestl. https://www.blm.gov/or/plans/surveyandmanage/MR/Bryophytes/buvi.pdf. Accessed on 23 March 2020.
Bihari Z., Babolcsai Gy., Bartholy J., Ferenczi Z., Gerhátné Kerényi J., Haszpra L., Homokiné Ujváry K., Kovács T., Lakatos M., Németh Á., Pongrácz R., Putsay M., Szabó P. & Szépszó G. 2018. — Climate [Éghajlat (in Hungarian)], *in* Kocsis K. (editor-in-chief), *National Atlas of Hungary: Natural environment* [*Magyarország nemzeti atlasza: természeti környezet*]. Magyar Tudományos Akadémia, Csillagászati és Földtudományi Kutatóközpont, Földrajztudományi Intézet, Budapest: 58-69. (in Hungarian).
BISE (Biodiversity Information System for Europe) 2020. — Saproxylic Beetles. https://biodiversity.europa.eu/topics/species/saproxylic-beetles. Accessed on 23 March 2020.
Bölöni J., Molnár Zs., Bíró M. & Horváth F. 2008. — Distribution of the (semi-)natural habitats in Hungary II. Woodlands and shrublands. *Acta Botanica Hungarica* 50: 107-148.
Bölöni J., Molnár Zs. & Kun A. (eds) 2011. — *Habitats of Hungary. Descriptions and Identification Keys of Vegetation Types of Hungary* [*Magyarország élőhelyei. A hazai vegetációtípusok leírása és határozója*.] MTA ÖBKI, Vácrátót, 441 p. (in Hungarian).
Borhidi A. 1961. — Climate diagrams and climate map of Hungary (Klimadiagramme und klimazonale Karte Ungarns [in German]). *Annales Universitatis Scientarium Budapestiensis, Sectio Biologica* 4: 21-50.
Borhidi A., Kevey B. & Lendvai G. 2012. — *Plant Communities of Hungary*. Akadémiai Kiadó, Budapest, 544 p.
Boros Á. 1943. — The mosses in nature and in human life [A mohok a természetben és az ember életében.] *Természettudományi Közlöny* 75 (2): 33-46. (in Hungarian)
Boros Á. 1953. — *Bryophytes of Hungary [Magyarország mohái (in Hungarian)]*. Akadémiai Kiadó, Budapest, 360 p.
Boros Á. 1968. — *Bryogeography and Bryoflora of Hungary* [*Bryogeographie und Bryoflora Ungarns*]. Akadémiai Kiadó, Budapest, 466 p. (in German).
Council of Europe 1993. — Bern Convention. Recommendation No. 40 on the elaboration of conservation or recovery plans for species in Appendix I to the convention.
Csiky J., Erzberger P., Kovács D. & Deme J. 2015. — *Campylopus flexuosus* (Hedw.) Brid. in the Western Mecsek Mts. (South Transdanubia, Hungary) [*Campylopus flexuosus* (Hedw.) Brid. a Nyugat-Mecsekben]. *Kitaibelia* 20 (1): 28-37. (in Hungarian). http://doi.org/10.17542/kit.20.28
Deme J., Erzberger P., Kovács D., Baráth K., Lantos I., Magos G., Nagy J., Nagy K., Nagy Z., Németh Cs., Ódor P., Papp B., Tóth I. Zs. & Csiky J. 2017. — Distribution and habitat preference of *Buxbaumia* Hedw. species in Hungary. *Acta Biologica Plantarum Agriensis* 5 (1): 32. https://doi.org/10.21406/abpa.2017.5.1.32
Deutscher Wetterdienst. 2018. — Climatological maps of Germany. Aridity Index, 1961-1990. https://www.dwd.de/EN/ourservices/klimakartendeutschland/klimakartendeutschland.html. Accessed on 23 March 2020.
Dierssen K. 2001. — *Distribution, Ecological Amplitude and Phytosociological Characterization of European Bryophytes.* Cramer, Berlin, 289 p.
ECCB (European Committee for Conservation of Bryophytes) 1995. — *Red Data Book of European Bryophytes*. Trondheim, 291 p.
Ellenberg H. & Leuschner Ch. 2010. — *Vegetation of Central Europe with the Alps: in Ecological, Dynamic and Historical View* [*Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht*], 6th ed. Ulmer, Stuttgart. (in German). https://doi.org/10.1111/j.1654-1103.2012.01443.x
Erzberger P., Németh Cs., Deme J. & Csiky J. 2018. — Stomatal anatomy allows clarification of historical collections of *Buxbaumia* Hedw. species in Hungary. *Studia Botanica Hungarica* 49 (1): 71-82. https://doi.org/10.17110/StudBot.2018.49.1.71
European Commission DG Environment 2017. — Interpretation Manual of European Union Habitats. http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf. Accessed on 23 March 2020.
European Environment Agency 2020. — Habitat types search. https://eunis.eea.europa.eu/habitats.jsp Accessed on 23 March 2020.
Faliński J. B. 1978. — Uprooted trees, their distribution and influence on the primeval forest biotope. *Vegetatio* 38: 175-183. https://doi.org/10.1007/BF00123268
Fekete G., Király G. & Molnár Zs. 2016. — Delineation of the Pannonian vegetation region. *Community Ecology* 17: 114-124. https://doi.org/10.1556/168.2016.17.1.14
Fekete G., Molnár Zs., Magyari E., Somodi I. & Varga Z. 2014. — A new framework for understanding Pannonian vegetation pattern: regularities, deviations and uniqueness. *Community Ecology* 15: 12-26. https://doi.org/10.1556/ComEc.15.2014.1.2
Fudali E., Zubel R., Stebel A., Rusińska A., Górski P., Vončina G., Rosadziński S., Cykowska B., Staniaszek-Kik M., Wierzcholska S., Wolski G. J., Wojterska M., Wilhelm M., Paciorek T. & Piwowarski B. 2015. — Contribution to the bryoflora of Roztocze National Park (SE Poland). Bryophytes of the Świerszcz river valley. *Steciana* 19 (1): 39-54. https://doi.org/10.12657/steciana.019.006
Gábris Gy., Pécsi M., Schweitzer F. & Telbisz T. 2018. — Relief (Domborzat [in Hungarian]), *in* Kocsis K. (editor-in-chief), *National Atlas of Hungary: Natural Environment* [*Magyarország nemzeti atlasza: természeti környezet*]. Magyar Tudományos Akadémia, Csillagászati és Földtudományi Kutatóközpont, Földrajztudományi Intézet, Budapest: 42-57. (in Hungarian).
Geiger R. 1965. — *The Climate Near the Ground.* Harvard University Press, Cambridge (MA). https://doi.org/10.1002/qj.49709339529
Goia I. & Gafta D. 2018. — Beech versus spruce deadwood as forest microhabitat: does it make any difference to bryophytes? *Plant Biosystems – An International Journal Dealing with all Aspects of Plant Biology*. https://doi.org/10.1080/11263504.2018.1448011
Google Maps n. d. — https://www.google.com/maps/. Accessed on 23 March 2020.
Hajek B. 2010. — Distribution, environmental requirements and phenology of rare moss *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. in Trójmiejski Landscape Park (N Poland) [Rozmieszczenie, wymagania środowiskowe oraz fenologia rzadkiego mchu *Buxbaumia viridis* (Moug. ex Lam., DC.) Brid. ex Moug., Nestl. w Trojmiejskim Parku Krajobrazowym (in Polish)]. *Acta Botanica Cassubica* 7-9: 161-175.
Haraszthy L. (ed.) 2014. — *Natura 2000 Species and Habitats in Hungary [Natura 2000 fajok és élőhelyek Magyarországon].* Pro Vértes Közalapítvány, Csákvár. (in Hungarian).
Harpel J. 2003. — *Buxbaumia viridis* (DC.) Moung. & Nestl. https://www.dnr.wa.gov/publications/amp_nh_buxvir.pdf. Accessed on 23 March 2020.
Hill M. O., Bell N., Bruggeman-Nannenga M. A., Brugués M., Cano M. J., Enroth J., Flatberg K. I., Frahm J.-P., Gallego M. T., Garilleti R., Guerra J., Hedenäs L., Holyoak D. T., Hyvönen J., Ignatov M. S., Lara F., Mazimpaka V., Muñoz J. & Söderström L. 2006. — An annotated checklist of the mosses of Europe and Macaronesia. *Journal of Bryology* 28 (3): 198-267. https://doi.org/10.1179/174328206X119998
Hill M. O. & Preston C. D. 1998. — The geographical relationships of British and Irish bryophytes. *Journal of Bryology* 20 (1): 127-226. https://doi.org/10.1179/jbr.1998.20.1.127
Hodgetts N., Cálix M., Englefield E., Fettes N., García Criado M., Patin L., Nieto A., Bergamini A., Bisang I., Baisheva E., Campisi P., Cogoni A., Hallingbäck T., Konstantinova N., Lockhart N., Sabovljevic M., Schnyder N., Schröck C., Sérgio C., Sim Sim M., Vrba J., Ferreira C. C., Afonina O., Blockeel T., Blom H., Caspari S., Gabriel R., Garcia C., Garilleti R., González Mancebo J., Goldberg I.,

Hedenäs L., Holyoak D., Hugonnot V., Huttunen S., Ignatov M., Ignatova E., Infante M., Juutinen R., Kiebacher T., Köckinger H., Kučera J., Lönnell N., Lüth M., Martins A., Maslovsky O., Papp B., Porley R., Rothero G., Söderström L., Ştefănuţ S., Syrjänen K., Untereiner A., Váňa J., Vanderpoorten A., Vellak K., Aleffi M., Bates J., Bell N., Brugués M., Cronberg N., Denyer J., Duckett J., During H. J., Enroth J., Fedosov V., Flatberg K.-I., Ganeva A., Gorski P., Gunnarsson U., Hassel K., Hespanhol H., Hill M., Hodd R., Hylander K., Ingerpuu N., Laaka-Lindberg S., Lara F., Mazimpaka V., Mežaka A., Müller F., Orgaz J. D., Patiño J., Pilkington S., Puche F., Ros R. M., Rumsey F., Segarra-Moragues J. G., Seneca A., Stebel A., Virtanen R., Weibull H., Wilbraham J. & Żarnowiec J. 2019. — *A Miniature World in Decline: European Red List of Mosses, Liverworts and Hornworts.* Brussels, Belgium: IUCN, 88 p.

Holá E., Vrba J., Linhartová R., Novozámská E., Zmrhalová M., Plášek V. & Kučera J. 2014. — Thirteen years on the hunt for *Buxbaumia viridis* in the Czech Republic: still on the tip of the iceberg? *Acta Societatis Botanicorum Poloniae* 83 (2): 137-145. https://doi.org/10.5586/asbp.2014.015

Horvat V., Heras P., García-Mijangos I. & Biurrun I. 2017. — Intensive forest management affects bryophyte diversity in the western Pyrenean silver fir-beech forests. *Biological Conservation* 215: 81-91. https://doi.org/10.1016/j.biocon.2017.09.007

Horváth F., Dobolyi Z. K., Morschhauser T., Lőkös L., Karas L. & Szerdahelyi T. 1995. — *Hungarian Flora Database 1.2.* [*Flóra adatbázis 1.2.*]. MTA Ökológiai és Botanikai Kutatóintézete és MTM Növénytár, Vácrátót. (in Hungarian).

Index Fungorum 2020. — http://www.indexfungorum.org/ Accessed on 23 March 2020.

Jasík M. & Potocký P. 2016. — Analysis of the recent distribution of *Buxbaumia viridis* in central Slovakia [Analýza aktuálního výskytu *Buxbaumia viridis* na stredn om Slovensku]. *Bryonora* 58: 1-17. (in Slovak).

Király G. (ed.) 2009. — *New Hungarian Herbal. The Vascular Plants of Hungary. Identification key* [*Új magyar füvészkönyv. Magyarország hajtásos növényei. Határozókulcsok*]. Aggteleki Nemzeti Park Igazgatóság, Jósvafő, 616 p. (in Hungarian).

Lájer K., Botta-Dukát Z., Csiky J., Horváth F., Szmorad F., Bagi I., Dobolyi Z. K., Hahn I., Kovács J. A. & Rédei T. 2008. — Hungarian Phytosociological database (COENODATREF): sampling methodology, nomenclature and its actual stage. *Annali di Botanica nuova series* 7: 197-201. https://doi.org/10.4462/annbotrm-9083

NÉBIH 2020. — Erdőtérkép. https://erdoterkep.nebih.gov.hu/. Accessed on 23 March 2020.

Ódor P. 2016. — Effects of forest management on the biodiversity of bryophytes and lichens [Erdőgazdálkodás hatása az erdei moha- és zuzmóközösség biodiverzitására], *in* Korda M. (ed.), *Effect of forest management on the biodiversity of forests* [*Az erdőgazdálkodás hatása az erdők biológiai sokféleségére*]. Duna-Ipoly Nemzeti Park Igazgatóság, Budapest: 57-70. (in Hungarian).

Orbán S. 1984. — Life strategies and T. W. R. values of Hungarian bryophytes [A magyarországi mohák stratégiái és T. W. R. értékei]. *Acta Academiae Paedagogicae Agriensis, Nova Series Tom.* 17: 755-765. (in Hungarian)

Orbán S. & Vajda L. 1983. — *Manual of the Bryophyte Flora of Hungary* [*Magyarország mohaflórájának kézikönyve*]. Akadémiai Kiadó, Budapest. (in Hungarian).

Papp B., Erzberger P., Ódor P., Hock Zs. Szövényi P., Szurdoki E. & Tóth Z. 2010. — Updated checklist and red list of Hungarian bryophytes. *Studia Botanica Hungarica* 41: 31-59.

Papp B. & Ódor P. 2006. — *Green shield-moss (Buxbaumia viridis)* [*Zöld koboldmoha (Buxbaumia viridis)*]. Környezetvédelmi és Vízügyi Minisztérium, Természetvédelmi Hivatal, Budapest. (in Hungarian).

Papp B., Ódor P. & Szurdoki E. 2014. — Green shield-moss [Zöld koboldmoha], *in* Haraszty L. (ed.), Natura 2000 *Species and Habitats in Hungary* [Natura 2000 *fajok és élőhelyek Magyarországon*]. Pro Vértes Közalapítvány, Csákvár, 25-27. (in Hungarian).

Plášek V. 2004. — The Moss *Buxbaumia viridis* (Bryopsida, Buxbaumiaceae) in the Czech part of the Western Carpathians - distribution and ecology, *in* Stebel A. & Ochyra R. (eds), *Bryological studies in the Western Carpathians.* Sorus, Poznań, 37-44.

Plášek V. & Novozámská E. 2011. — Historical and recent occurrence of epixylous moss *Buxbaumia viridis* in the Javorníky Mts. and the Vsetínské vrchy hills (western Carpathians). Časopis Slezského Zemského Muzea, *Opava (A)* 60: 185-189. https://doi.org/10.2478/v10210-011-0020-9

Ronikier M. 2011. — Biogeography of high-mountain plants in the Carpathians: An emerging phylogeographical perspective. *Taxon* 60 (2): 373-389. https://doi.org/10.1002/tax.602008

Samaniego L., Thober S., Kumar R., Wanders N., Rakovec O., Pan M., Zink M., Sheffield J., Wood E. F. & Marx A. 2018. — Anthropogenic warming exacerbates European soil moisture droughts. *Nature Climate Change* 8: 421-426. https://doi.org/10.1038/s41558-018-0138-5

Schofield W. B. 2007. — *Buxbaumiaceae* Schwägrichen, *in* Flora of North America Editorial Committee (eds), *Flora of North America*. Oxford University Press, New York, Oxford 27: 118-120.

Siler N., Roe G. & Durran D. 2013. — On the Dynamical Causes of Variability in the Rain-Shadow Effect: A Case Study of the Washington Cascades. *Journal of Hydrometeorology* 14: 122-139. https://doi.org/10.1175/JHM-D-12-045.1

Smith A. J. E. 2004. — *The Moss Flora of Britain and Ireland,* second ed. Cambridge University Press, Cambridge, 1026 p. https://doi.org/10.1017/CBO9780511541858

Söderström L., Hagborg A., von Konrat M., Bartholomew-Began S., Bell D., Briscoe L., Brown E., Cargill D. C., Costa D. P., Crandall-Stotler B. J., Cooper E. D., Dauphin G., Engel J. J., Feldberg K., Glenny D., Gradstein S. R., He X., Heinrichs J., Hentschel J., Ilkiu-Borges A. L., Katagiri T., Konstantinova N. A., Larraín J., Long D. G., Nebel M., Pócs T., Felisa Puche F., Reiner-Drehwald E., Renner M. A. M., Sass-Gyarmati A., Schäfer-Verwimp A., Segarra-Moragues J. G., Stotler R. E., Sukkharak P., Thiers B. M., Uribe J., Váňa J., Villarreal J. C., Wigginton M., Zhang L. & Zhu R.-L. 2016. — World checklist of hornworts and liverworts. *PhytoKeys* 59: 1-828.

Spitale D. & Mair P. 2015. — Predicting the distribution of a rare species of moss: The case of *Buxbaumia viridis* (Bryopsida, Buxbaumiaceae). *Plant Biosystems* 151 (1): 1-11. https://doi.org/10.1080/11263504.2015.1056858

Szűcs P., Csiky J. & Papp B. 2014. — Distribution of *Campylopus introflexus* (Hedw.) Brid. in Hungary [A neofiton *Campylopus introflexus* (Hedw.) Brid. elterjedése Magyarországon]. *Kitaibelia* 19: 212-219. (in Hungarian).

Taylor S. 2010. — *Buxbaumia viridis* in Abernethy Forest and other sites in northern Scotland. *Field Bryology* 100: 9-14.

Taylor S. & Taylor J. 2007. — Firwood Cottage, Nethybridge. http://firwoodcottage.blogspot.hu/2007/12/. Accessed on 23 March 2020.

Thauront M. & Stallegger M. 2008. — Management of Natura 2000 habitats, *Luzulo-Fagetum* beech forests, 9110. European Commission. http://ec.europa.eu/environment/nature/natura2000/management/habitats/pdf/9110_Luzulo-fagetum_beech_forests.pdf. Accessed on 23 March 2020.

Tobisch T. & Kottek P. 2013. — Forestry-related Databases of the Hungarian Forestry Directorate. https://portal.nebih.gov.hu/documents/10182/862096/Forestry_related_databases.pdf/3ff92716-2301-4894-a724-72fafca9d4fc. Accessed on 23 March 2020.

Vanderpoorten A. & Goffinet B. 2009. — *Introduction to Bryophytes.* Cambridge University Press, Cambridge (reprinted 2010). https://doi.org/10.1017/CBO9780511626838

Warnstorf C. 1903-1906. — *Cryptogam flora of Margraviate of Brandenburg: Liverworts and Peat mosses, Mosses* [*Kryptogamenflora der Mark Brandenburg: Leber- und Torfmoose, Laubmoose*]. Bornträger, Leipzig, 1160 p. (in German).
Wiklund K. 2002. — Substratum preference, spore output and temporal variation in sporophyte production of the epixylic moss *Buxbaumia viridis*. *Journal of Bryology* 24 (3): 187-195. https://doi.org/10.1179/037366802125001358
Wiklund K. 2003. — Phosphorus concentration and pH in decaying wood affect establishment of the red-listed moss *Buxbaumia viridis*. *Canadian Journal of Botany* 81 (6): 541-549. https://doi.org/10.1139/b03-048
Wiklund K. & Rydin H. 2004. — Ecophysiological constraints on spore establishment in bryophytes. *Functional Ecology* 18: 907-913. https://doi.org/10.1111/j.0269-8463.2004.00906.x
WWF 2016. — Old-growth forests in Hungary in danger. http://wwf.panda.org/?269991/Old-growth-forests-in-Hungary-in-danger. Accessed on 23 March 2020.

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APPENDIX 1. — Occurrences of *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. localities with the EUNIS habitat types and the number of stands. B: beech, C: conifer, F: rotting fern, L: peaty cushions of *Leucobryum* Hampe.

Landscape area	Locality (settlement, code of forest subcompartment)	Centroid coordinates	Average distance of stands from the centroid (m)	Altitude (m a.s.l.)	No. of stands (sporophytes)		EUNIS habitat type
					on soil	on decaying matter, type of decaying matter	
Zemplén Mts	Bózsva, 130 I(90)	48.46511° N, 21.46074° E	2	269	3 (16)		G1.611 Medio-European collinar woodrush beech forests
	Bózsva, 130 C(30)	48.47119° N, 21.45499° E	19	270	3 (8)	1 (1), B	G1.611 Medio-European collinar woodrush beech forests
	Telkibánya, 79 D(40)	48.46933° N, 21.32517° E	0	386		1 (13), C	G1.611 Medio-European collinar woodrush beech forests (with Picea abies)
	Telkibánya, 67 O(150)	48.45957° N, 21.37954° E	54	438		2 (3), B, C	G3.F21 Exotic spruce, fir, larch, douglas fir, deodar plantations (here: spruce)
	Nagyhuta, 143 (D)40	48.42576° N, 21.49656° E	0	318	1 (2)	1 (3), B	G1.611 Medio-European collinar woodrush beech forests
Bükk Mts	Kisgyőr, 68 G(70)	48.02231° N, 20.64691° E	58	403	7 (21)		G1.611 Medio-European collinar woodrush beech forests
	Bükkzsérc, 6 K(110)	48.04898° N, 20.48811° E	2	574	2 (28)		G1.611 Medio-European collinar woodrush beech forests
	Felsőtárkány, 113 H(80)	48.05267° N, 20.47275° E	19	612	4 (17)		G1.611 Medio-European collinar woodrush beech forests
	Felsőtárkány, 104 B(20)	48.05064° N, 20.46527° E	0	672	1 (2)		G1.871 Woodrush oak forests
Heves-Borsod Hills	Hangony, 23 E(50)	48.20363° N, 20.17238° E	2	324	3 (10)		transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests
	Hangony, 22 E(50)	48.20294° N, 20.17999° E	16	264	2 (6)		G1.611 Medio-European collinar woodrush beech forests
Medves Mts	Salgótarján-Zagyvaróna, 453 D(40)	48.13765° N, 19.89610° E	20	413	3 (27)		G1.611 Medio-European collinar woodrush beech forests
	Bárna, 2 B(20)	48.11242° N, 19.91361° E	0	481	1 (4)		G1.611 Medio-European collinar woodrush beech forests
Karancs Mts	Somoskőújfalu, 116 A(10)	48.14285° N, 19.79785° E	10	398	4 (19)		G1.76 Balkano-Anatolian thermophilous oak forests
	Karancsalja, 1 A(10)	48.15243° N, 19.78498° E	0	657	1 (1)		G1.611 Medio-European collinar woodrush beech forests
	Karancslapujtő, 8 A(10)	48.15880° N, 19.77841° E	47	533	6 (29)		G1.611 Medio-European collinar woodrush beech forests
Mátra Mts	Parád, 12 F(60)	47.91033° N, 20.01240° E	0	452	2 (12)		G1.871 Woodrush oak forests
	Parád, 29 E(50)	47.87595° N, 20.01669° E	6	819	2 (12)	1 (1), F	G1.A45 Thermophilous Alpine and peri-Alpine mixed Tilia forests
	Parádsasvár, 26 A(10)	47.91184° N, 19.95274° E	27	636	3 (11)		G1.611 Medio-European collinar woodrush beech forests
	Parádsasvár, 24 A(10)	47.91589° N, 19.94755° E	58	643	4 (30)	1 (1), B	G1.611 Medio-European collinar woodrush beech forests
	Parád, 13 H(80)	47.91214° N, 20.00989° E	50	411	2 (30)		G1.611 Medio-European collinar woodrush beech forests
Börzsöny Mts	Kemence, 57 C(30)	47.96629° N, 18.94194° E	0	667	1 (20)		G1.611 Medio-European collinar woodrush beech forests
	Kemence, 57 D(40)	47.96410° N, 18.94007° E	0	707	1 (8)		G1.611 Medio-European collinar woodrush beech forests
Visegrád Mts	Dömös, 39 E(50)	47.72350° N, 18.89114° E	2	668	2 (5)		G1.611 Medio-European collinar woodrush beech forests
Buda Mts	Budakeszi, 54 D(40)	47.51119° N, 18.90233° E	0	247	1 (12)		G1.871 Woodrush oak forests
	Budakeszi, 55 A(10)	47.51325° N, 18.89827° E	26	258	3 (14)		transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests
Bakony Mts	Sümeg, 137 B(20)	46.92987° N, 17.33905° E	0	173	1 (3)		G1.611 Medio-European collinar woodrush beech forests

Appendix 1. — Continuation

Landscape area	Locality (settlement, code of forest subcompartment)	Centroid coordinates	Average distance of stands from the centroid (m)	Altitude (m a.s.l.)	No. of stands (sporophytes): on soil	No. of stands (sporophytes): on decaying matter, type of decaying matter	EUNIS habitat type
Sopron Mts	Sopron, 128 A(10)	47.65978° N, 16.51461° E	0	401	1 (10)		G1.611 Medio-European collinar woodrush beech forests (with Pinus sylvestris, roadcut)
Kőszeg Mts	Bozsok, 16 A(10)	47.33689° N, 16.47710° E	44	437	2 (13)		G3.F21 Exotic spruce, fir, larch, douglas fir, deodar plantations (here: spruce)
Őrség-Vendvidék	Szakonyfalu, 68 D4(44)	46.89107° N, 16.23515° E	10	315	8 (56)		G1.611 Medio-European collinar woodrush beech forests (with Picea abies)
	Szakonyfalu, 74 B2(22)	46.89592° N, 16.21731° E	2	336		4 (17), C	G4.F Mixed forestry plantations
	Szakonyfalu, 11 A(10)	46.90489° N, 16.22322° E	0	326	1 (2)		G1.611 Medio-European collinar woodrush beech forests
	Kondorfa, 32 A2(12)	46.89320° N, 16.43622° E	2	238		3 (12), C	G3.F21 Exotic spruce, fir, larch, douglas fir, deodar plantations (here: spruce)
	Iváncz, 8 E(50)	46.89588° N, 16.46706° E	39	274		2 (10), C	G3.F21 Exotic spruce, fir, larch, douglas fir, deodar plantations (here: spruce)
	Iváncz, 5 C(30)	46.90759° N, 16.46656° E	0	220		1 (6), C	G3.F21 Exotic spruce, fir, larch, douglas fir, deodar plantations (here: spruce and larch)
Göcsej	Kerkakutas, 8 ÚT1(731)	46.78548° N, 16.55820° E	2	224	2 (12)		G3.F21 Exotic spruce, fir, larch, douglas fir, deodar plantations (here: spruce, roadcut)
East-Inner Somogy	Istvándi, 32 M(130)	46.02161° N, 17.59517° E	0	144	1 (1)		G3.F22 Exotic pine plantations (with Robinia pseudoacacia)
Zselic Hills	Ibafa, 69 B	46.15978° N, 17.97154° E	0	240	1 (14)		G1.611 Medio-European collinar woodrush beech forests
Mecsek Mts	Abaliget, 3 B	46.15059° N, 18.07778° E	27	201	5 (28)	11 (96), C	G3.F21 Exotic spruce, fir, larch, douglas fir, deodar plantations (here: spruce)
	Bakonya, 10 C	46.10505° N, 18.08485° E	11	373	7 (421)		G1.611 Medio-European collinar woodrush beech forests
	Bakonya, 10 A	46.10285° N, 18.07690° E	0	378	1 (1)		G1.611 Medio-European collinar woodrush beech forests
	Kővágótöttös, 24 A(10)	46.10234° N, 18.11223° E	0	405	1 (30)		G1.611 Medio-European collinar woodrush beech forests
	Kővágótöttös, 26 H(80)	46.09295° N, 18.09488° E	11	260	3 (80)		G1.611 Medio-European collinar woodrush beech forests
	Kővágótöttös, 26 I(90)	46.09294° N, 18.09458° E	0	257	1 (12)		G1.611 Medio-European collinar woodrush beech forests
	Kővágótöttös, 23 D(40)	46.09866° N, 18.10290° E	72	314	4 (30)		G1.611 Medio-European collinar woodrush beech forests
	Pécs, 21 C	46.10303° N, 18.15565° E	35	382	4 (20)		G1.611 Medio-European collinar woodrush beech forests
	Pécs, 36 E	46.08532° N, 18.16986° E	12	329	4 (29)		transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests
	Pécs, 34 B	46.08915° N, 18.15682° E	0	456	1 (3)		G1.611 Medio-European collinar woodrush beech forests
	Pécs, 27 A	46.09647° N, 18.17202° E	0	308	1 (1)		G1.611 Medio-European collinar woodrush beech forests (roadcut)
	Pécs, 32 E	46.09675° N, 18.16395° E	8	365	3 (12)		transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests (roadcut)
	Pécs, 32 I	46.09665° N, 18.16844° E	10	319	8 (26)		G1.611 Medio-European collinar woodrush beech forests (roadcut)

Appendix 1. — Continuation

Landscape area	Locality (settlement, code of forest subcompartment)	Centroid coordinates	Average distance of stands from the centroid (m)	Altitude (m a.s.l.)	No. of stands (sporophytes) on soil	No. of stands (sporophytes) on decaying matter, type of decaying matter	EUNIS habitat type
	Pécs, 31 F	46.09536° N, 18.16054° E	16	403	2 (2)		G1.611 Medio-European collinar woodrush beech forests (roadcut)
	Pécs, 200 L(120)	46.08925° N, 18.17886° E	0	250	1 (2)		G1.611 Medio-European collinar woodrush beech forests
	Pécs, 32 G	46.09256° N, 18.17433° E	21	295	21 (114)	4 (14), L	transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests
	Pécs, 32 C	46.09104° N, 18.17595° E	26	312	7 (87)		G1.871 Woodrush oak forests
	Pécs, 32 D	46.09136° N, 18.17687° E	0	272	1 (2)		G1.871 Woodrush oak forests
	Pécs, 78 K	46.10678° N, 18.22706° E	0	309	1 (2)		G1.611 Medio-European collinar woodrush beech forests
	Pécs, 78 L	46.10514° N, 18.22334° E	0	380	1 (17)		G1.611 Medio-European collinar woodrush beech forests (roadcut)
	Pécs, 159 D(40)	46.13385° N, 18.31613° E	20	252	18 (62)		G1.611 Medio-European collinar woodrush beech forests
	Pécs, 156 G(70)	46.14112° N, 18.31116° E	2	280	2 (16)		G1.611 Medio-European collinar woodrush beech forests
	Pécs, 156 I(90)	46.14152° N, 18.31231° E	9	252	8 (11)		G1.611 Medio-European collinar woodrush beech forests
	Pécs, 156 C(30)	46.13839° N, 18.30753° E	0	288	1 (4)		G1.611 Medio-European collinar woodrush beech forests
	Mecseknádasd, 92 F(60)	46.22300° N, 18.44346° E	0	274	1 (1)		G1.611 Medio-European collinar woodrush beech forests
	Mecseknádasd, 90 E(50)	46.21637° N, 18.44355° E	10	399	6 (39)		G1.611 Medio-European collinar woodrush beech forests
	Zengővárkony, 22 A	46.20158° N, 18.43743° E	0	338	1 (9)		G1.611 Medio-European collinar woodrush beech forests
	Zengővárkony, 22 D	46.20211° N, 18.43744° E	0	334	1 (13)		G1.611 Medio-European collinar woodrush beech forests
	Zengővárkony, 22 E	46.20142° N, 18.44294° E	0	308	1 (7)		G1.611 Medio-European collinar woodrush beech forests
	Zengővárkony, 36 B (20)	46.18159° N, 18.42439° E	3	313	2 (5)		transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests
	Zengővárkony, 36 A(10)	46.18266° N, 18.42128° E	18	329	6 (14)		G1.611 Medio-European collinar woodrush beech forests
	Pécsvárad, 54 A(10)	46.18328° N, 18.41862° E	0	328	1 (3)		G1.611 Medio-European collinar woodrush beech forests
	Hosszúhetény, 33 B(20)	46.18350° N, 18.35496° E	0	385	1 (1)		G1.611 Medio-European collinar woodrush beech forests
	Hosszúhetény, 33 D(40)	46.18603° N, 18.36859° E	2	436	5 (25)		transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests
	Hosszúhetény, 35 I(90)	46.18358° N, 18.37163° E	21	523	11 (170)	1 (1), B	G1.611 Medio-European collinar woodrush beech forests
	Hosszúhetény, 26 D	46.17593° N, 18.33302° E	114	544	2 (20)		G1.611 Medio-European collinar woodrush beech forests (roadcut)
	Hosszúhetény, 26 I	46.17713° N, 18.33517° E	0	565	1 (12)		G1.611 Medio-European collinar woodrush beech forests (roadcut)
	Pécsvárad, 19 A	46.18427° N, 18.38301° E	29	501	8 (17)		G1.611 Medio-European collinar woodrush beech forests
	Pécsvárad, 19 F	46.18462° N, 18.38265° E	8	489	2 (4)		G1.611 Medio-European collinar woodrush beech forests
	Pécsvárad, 19 G	46.18227° N, 18.38378° E	31	583	3 (3)		G1.611 Medio-European collinar woodrush beech forests

Appendix 1. — Continuation

Landscape area	Locality (settlement, code of forest subcompartment)	Centroid coordinates	Average distance of stands from the centroid (m)	Altitude (m a.s.l.)	No. of stands (sporophytes) on soil	No. of stands (sporophytes) on decaying matter, type of decaying matter	EUNIS habitat type
	Pécsvárad, 27 B	46.18278° N, 18.39819° E	41	433	12 (41)	1 (9), B	transition of G1.871 Woodrush oak forests and G1.611 Medio-European collinar woodrush beech forests
	Pécsvárad, 24 C	46.18186° N, 18.39600° E	36	464	3 (15)	1 (8), B	G1.611 Medio-European collinar woodrush beech forests
Geresd Hills	Fazekasboda, 13 A(10)	46.13568° N, 18.49441° E	25	188	12 (80)		G1.611 Medio-European collinar woodrush beech forests
	Bátaapáti, 50 A(10)	46.21111° N, 18.60110° E	0	179	1 (4)		G1.76 Balkano-Anatolian thermophilous oak forests