

Domenico Puntillo & Michele Puntillo

Monitoring of *Buxbaumia viridis* (*Buxbaumiaceae*, *Bryophyta*) in Calabria (southern Italy) with some historical and ecological notes**Abstract**

Puntillo, D. & Puntillo, M.: Monitoring of *Buxbaumia viridis* (*Buxbaumiaceae*, *Bryophyta*) in Calabria (southern Italy) with historical overview and some ecological notes. — *Borziana* 5: 5-39. 2024 — ISSN: 2724-5020 online.

A random monitoring of *Buxbaumia viridis* was carried out throughout the territory of the Calabria region by exploring river courses, rivulets, river escarpments, forests with long ecological continuity to assess the species abundance and ecological characteristics. The species has been found at 94 sites with a total 1027 capsule-inclusive sporophytes and 286 capsule-free setae, 2 sites with both protonema and vegetative propagules and one site with only the protonema. Historical overview and ecological evaluation of the species are given.

Key words: *Buxbaumia viridis*, Distribution, Ecology, Protonemal propagules, Historical overview, Mediterranean.

Introduction

The genus *Buxbaumia* (vernacular name: Bug moss, Bug-on-a-stick Moss, Elf-cap Moss, Humpbacked Elves, Green Schield-moss, Aladdin's lamp) includes 12 species distributed in the northern hemisphere (Crosby & al. 2000; Goffinet & al. 2008). In Europe and Italy, the only known species of the genus are *B. aphylla* and *B. viridis* (Hill & al. 2006). The latter is a small annual, acrocarpous, dioecious, epixylix moss (Figs. 1, 2), highly specialized and atypical because characterized by a persistent protonema over a number of years, microscopic gametophyte developing an annual perishable sporophyte with a large distinctive capsule.

This species has a boreal-mountain distribution preferring primeval forests, with long ecological continuity, and decaying tree trunks and stumps, especially conifers, in the undergrowth, on which it grows.

In Europe is legally protected (Annex I of the Bern Convention, Annex II of the "Habitat-Fauna-Flora" directive). First included in the European Red List of Bryophytes (Schumacher & Martiny 1995) in the group of endangered species (Critically Endangered



Fig. 1. Old sporophytes (brown) of *Buxbaumia viridis* (DC.) Moug. & Nestl. from the previous year mixed with new ones (green); (Sila Grande, Moccone, 03/03/2021).

category – CR, B1 + B2 ab) of the Red List of Italian mosses (Cortini Pedrotti & Aleffi 1992, Aleffi 2008, Rossi & al. 2013) it is recognized as protected at national level by the decree of the Ministry of the Environment in Italy. Recently, due to the numerous new findings in Europe it has been moved to the of Least Concern (LC) group species in the new European Red List (Hodgetts & al. 2019). The species requires protection in areas designated as *Natura 2000* protected area (Plášek in Stebel 2004). For this reason their current distribution and ecology are being studied intensively in all countries involved in this program.

Wiklund (2002) suggests that the rarity of *B. viridis*, is caused by its small size, dioicity, short-life, sensitivity to substrate drying, low probability to find free spots, and low competitiveness of its microgametophyte cannot compete with larger bryophytes.

Wiklund (2003) and Duckett & al. (2004) added a very slow growth of the protonemata compared to other moss species; finally Korhonen & al (2006) added the influence of canopy closure to the forest floor microclimate and light condition.

The aim of this work is to overcome gaps in the biology and distribution of this species in the Mediterranean area and to describe the *B. viridis* population in the Calabria region in terms of its abundance and spatial distribution and altitudinal range, habitat and substrate preference, via searching capsule-inclusive sporophytes, capsule-free setae, protonema and propagules.

The data are provisional and therefore not exhaustive as monitoring will continue in the near future by searching new populations, also taking into account the predictive models used by Číhal & al. (2020), Guisan & al. (2006), Holá & al. (2014), Spitale & Mair (2015) and Strazzaboschi (2017) for a better estimation of habitat and distribution of this moss.

Methodology

Since this preliminary investigation aimed at covering a wide territory, it was not possible to adopt the official grids (10 x 10 km) referred to the European Projection System (LAEA5210-ETRS89) imposed by the European Agency for the Environment (EEA). Thus, we preferred to adopt a random monitoring according to the different habitats of the



Fig. 2. *Buxbaumia viridis* (DC.) Moug. & Nestl. sporophytes after sporification, mixed with *Herzogiella seligeri* (Brid.) Z. Iwats. moss (Monte Gariglione, 02/08/2020).

species (streams, river valleys, slopes of small watercourses or forests undergrowth with long ecological continuity), though it induced greater energy effort.

The microsities are located at an altitude between 861 and 1756 meters a.s.l. The average annual rainfall in the studied areas (12 weather selected stations) is approximately 1530 mm by year with an average of 106 rainy days (12 selected stations). In summer (June, July and August) the amount of precipitation is around 3.3 mm per day. The average annual temperature (7 selected stations) is around 10 °C while in the summer (June, July and August) is around 18 °C (ARPACAL 2024, historical data. Fig. 3). The strong solar radiation and the consequent evapotranspiration of the summer months is compensated by the high humidity of the microsities. The 8 macro arias of the 94 microsities are indicated in Fig. 4.

Given the protection granted to the species, only a few specimens of sporophytes and logs with protonema and propagules were collected and preserved in the Herbarium of the Botanical Garden (CLU). Old capsules from the previous year were not included in the count.

The species nomenclature follows the Checklist of the Bryophytes of Italy (Aleffi & al. 2020) and The Information System on Italian Lichens (Nimis & Martello 2020) for Lichens.

Phytoclimate and vegetation

Both the climate and the vegetation of the areas studied are varied in relation to the orographic diversity, altitude and exposure of the slopes.

The Sila plateau is the largest in Europe with an average altitude of 1200 m. a.s.l. and occupies the central area of Calabria. The bioclimate mostly belongs to the Supra-temperate Submediterranean type (according to Rivas-Martinez & Loidi Arregui, 1999), with harsh and snowy winters.

The high mountain reliefs are colonized by beech forests included in the alliance *Geranio versicoloris-Fagetum sylvaticae* Gentile 1970: *Asyneumato-Fagetum sylvaticae*

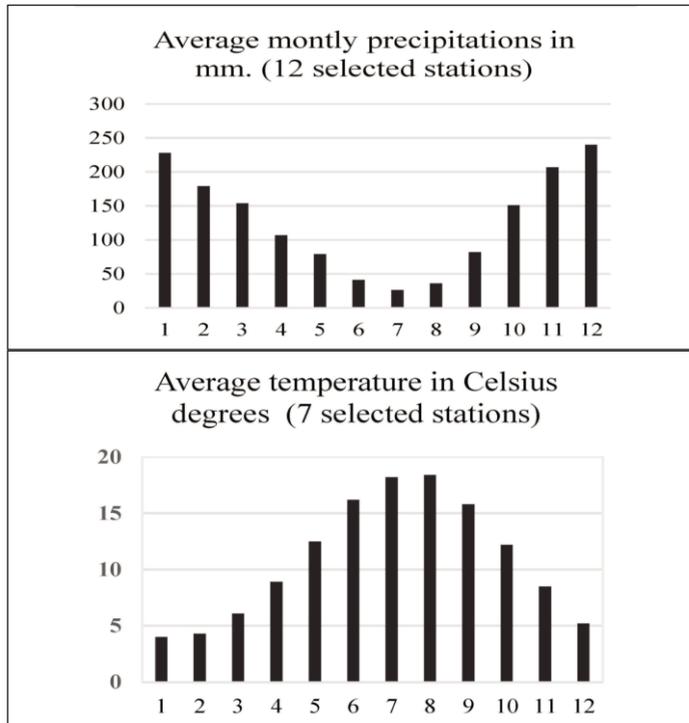


Fig. 3. Annual average precipitation and temperature.

Gentile 1970 (= *Ranunculo brutii-Fagetum sylvaticae* Bonin 1967) and its variant with *Abies alba* at the upper belt, locally replaced by *Aceri lobelii-Fagetum sylvaticae* Aita, Corbetta & Orsino 1984, and the *Anemono apenninae-Fagetum sylvaticae* (Gentile 1969) Brullo 1984 at lower altitudes.

The sunny slopes exposed to the East and South are covered by vegetation belonging to the *Hypochoerido-Pinetum calabricae* Bonin ex Brullo Scelsi e Spampinato 2001: pine forests were favoured by forestry activity and today occupy also territories potentially characterized by beech forests. In these large areas, 76 of the 94 microsites were observed.

The same vegetation was found on the Aspromonte massif where only 8 microsites were observed.

Only two stations have been observed on the slope of the western Pollino massif also attributable at *Asyneumato-Fagetum sylvaticae* and *Anemono apenninae-Fagetum sylvaticae*.

In the Serre plateau, with a supra-temperate supramediterranean hyperhumid bioclimate, characterized by abundant rainfall as well as hidden rainfall (frequent days of fog), the remaining eight sites were observed in the monospecific forests of *Abies alba* (*Monotropo-Abietetum apenninae* Brullo, Scelsi et Spampinato 2001).

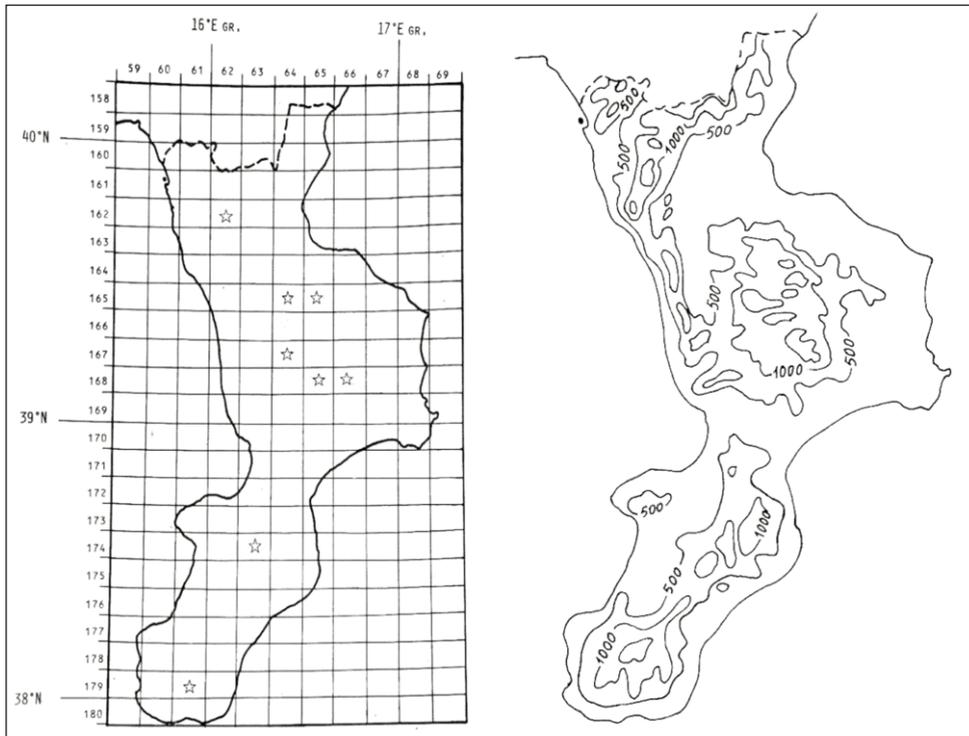


Fig. 4. Map of the 8 macro areas relating to the 94 microsites shown on the left according to MTB (Messtischblatt) quadrant grid of the Floristic Cartography Project of Central Europe (the grid unit “base area” rectangles have an area of 11 x 14 km) + Isohypse map shows rugged morphology of the Calabrian territory (to the right).

The majority of the sites (84) fall within steep impluvia with small watercourses (rivulets, streams) or in the immediate vicinity. Only one macro-area hosts the species in the undergrowth away from river courses (Bosco di Santa Maria) on the Serre plateau. Here the species grows on fir stumps.

Overview of literature data on taxonomy, ecology, phenology, Italian distribution and growth cycle of *Buxbaumia viridis* (DC.) Moug. & Nestl.

A - Historical overview and taxonomy

The first scientist who realized this small organism was an undescribed species of a moss was Buxbaum (1728). He reported this organism as ‘*Muscus capillaceus aphyllus, capitulo crasso, bivalvi*’ collected along the banks of the Volga River near Astracan (southern European Russia). Buxbaum would have liked to dedicate it to his father: ‘*As proof of this, I would have*

liked to dedicate the name to my father but the fox came to mind, who was mocked by others because he asked for grapes not for himself, but for his sick mother' (Buxbaum 1728).

Other botanists who studied this moss were: Micheli (1729) with this description: '*Muscus nanus tuberosa radice foliis iuniperinis tenuissime serrates, capitulo magno ovato ventricoso calyptra tomentosa D. Montius*'; Dillenius (1741) who reported Buxbaum's description and added a drawing taken from a single specimen sent to him by the Italian botanist Giuseppe Monti.

Later on, Haller (1742) was the first to call this moss *Buxbaumia* dedicating it to its discoverer, but he put it among mushrooms.

Then, Fabricius (1743) placed the species among mosses with the name of *Hippopodium* [from greek ἵππος hippos, lat. *equus* (horse) and ποῦς, pou lat. *pes* (foot)] due to the presumed similarity of the capsule with the hoof of a horse. Gleditsch (1753) included it in the mushrooms in the genus *Stemonites* (sic!). Furthermore, Antonius Roland Martin (1757) discussed a thesis dedicated to *Buxbaumia*, Linnaeus as supervisor. On the cover of the dissertation a drawing of this species is reported. The thesis was re-published in the Linnaean series of *Amoenitates Academicae* (Linnaeus 1760) where a table with different stages of the capsules is reported. Later, in another thesis of Hoelzel (1758), supervisor D. Casimir Christoph Schmidel, the new name of *Buxbaumia caulescens* was introduced with this diagnosis '*Buxbaumia bulbo villis tecto*'. Schmidel himself (1783) relocated the species to the mosses: '*Buxbaumia esse verum Muscum Muscum sui generis*'.

The valid name of the genus, with *aphylla* as type species, was given by Hedwig (1801) in the *Species Muscorum Frondosorum* because this date is the starting point for the nomenclature of all mosses (except *Sphagnaceae* L.), as decreed by the Fifteenth International Botanical Congress (Yokohama, August-September 1993) validated by the International Code of Botanical Nomenclature, Tokyo Code, 1994, art. 13, Musci.

The first to collect the congener *viridis* was Mougeot (Mougeot & Nestler 1823) in the Vosges Mountains. The holotype was preserved in the herbarium and his description was published in the *Stirpes Cryptogamae Vogeso-Rhenanae* lineages, with the number 724, and collected in the woods near Bruyères (Hoff & al. 1995). While the first who validly described the species was De Candolle (1815) with the epithet *Buxbaumia aphylla* β *viridis*. Finally, Bridel (1826) assigned this moss the new name of *Buxbaumia indusiata* but Price & Ellis (2015) highlighted it as '*nomen illegitimum et superfluum*'. These authors (2015) designed as lectotype: 'No. 30. *Buxbaumia aphylla* var *viridis* in viis cavis sylvarum, et ad ligna putrida iadem locis circa Bruyerium aestate. M. Mougeot. 1814' (G, G00053982). The specimen is annotated '*Buxbaumia aphylla* b *viridis* DC. suppl. n. 1323. *Buxbaumia indusiata* Brid. ipso teste (a. P. DC.)'.

B - Ecology

Eastwood (1939) believed *Buxbaumia* was able to absorb organic substances from humus or adjacent green mosses just directly. However, at present we know that these mosses are unable to do that. Kuijt (1969) and Weber (1993) hypothesize that these species should be parasitic, although often described as achlorophyllous and thus myco-heterotrophic (Leake 1994, 2005; Bidartondo 2005). Nevertheless, despite 'reduced habit',

all *Buxbaumia* species contain chlorophyll. As already highlighted by Imhof & al. (2013), the heterotrophy of this moss has been a subject of discussion for a long time. No association was found between rhizoids and gametophors of *Buxbaumia* and the abundant fungal hyphae on the rotten wood (Duckett & al. 2004). Thus, the notion of partial saprotrophism in *Buxbaumia* no longer seems credible. Although numerous fungi have been recorded growing on both mosses and liverworts (Hansruedi 1988), symbioses have only been demonstrated in liverworts and hornworts.

The presence of rhizoids provided with anastomoses and clamp-like connections (Goebel 1892b, fig. 13), which make them similar to fungal hyphae, suggests a heterotrophic pathway (Haberlandt 1886). This last author stressed their similarity to hyphae because of their frequent anastomoses, which is not characteristic for mosses rhizoids.

The immature stages of sporophytes showing a green-colored capsule (presence of chloroplasts) suggest an autotrophic pathway but nowadays no detailed information are available about mycorrhizal, endophytic or parasitic interactions, which could explain the strange habit of these mosses. Therefore, more in-depth studies are needed that can better reveal the trophic nature of this moss.

Since capsules of *Buxbaumia viridis* have a special protective layer on their surface, i.e. a thick, hydrophobic and impermeable cuticle (Koch et al. 2009) it was believed, that no fungal infections could attack them in their early stages of development. Recently, Gyosheva & Natcheva (2022) found parasitized sporophytes by the fungus *Cladosporium herbarum* (Capnodiales, Dothideomycetes). In this case, sporophytes appear deformed, dark brown, withered and mummified. However, only two (out of 120) sporophytes were attacked by parasites, which did not pose any danger to the populations of this species.

B. viridis is an ephemeral (its cycle lasts less than one year) and a fugitive species (Dierssen 2001): it often disappears from a locality without any apparent cause and then reappears many years later in the same place. According to Boulay (1872), the species was common in the Vosges in 1866 but it became very rare in 1870 and 1871, ‘certainly due to the aridity’. It forms “patch-tracking” metapopulations (Thomas 1994; Snäll & al. 2003). ‘If new patches are not colonized before the occupied patches disappear, the species will be lost from the site’ (Wiklund & Rydin 2004).

B. viridis is stenoic because has a very narrow substrate receptivity, being attached to dead wood in a decaying stage retaining water; it has first been thought as saprolignicolous, but, as many other epixylic bryophytes, does not appear to be restricted to specific woods (Andersson & Hyttborn, 1991). Indeed, it was recorded on decaying wood of various phorophytes: *Acer*, *Abies*, *Alnus*, *Betula*, *Fagus*, *Picea*, *Pinus*, *Thuja*, *Prunus* and *Sorbus* (Taylor 2010); *Juniperus* and *Quercus* (Taylor 2012); *Pinus*, *Prunus*, *Ulmus glabra* (Möller 1923, Hassel & Gaarder 1999); *Betula*, *Populus*, *Salix* (Wiklund 2002). It also grows on anthills (wood ant nest) or even on live tree bark of Alder (Taylor 2010) and rarely on soil (saturated with dead wood debris?), as the congener *aphylla* (Deme & al. 2020, Taylor 2010). Two well-formed capsules were found at a height of 4.9 m on a tree (*Salix caprea*) before felling.

Unexpectedly, it seems able to survive on a site after extreme and rare events, such as a woodland flood (Agnew & Rao, 2016). Recently, it was reported also in dry habitats, such as humus-bearing granite rocks (Hugonnot & al. 2023).

Relevant ecological variables explaining the occurrence of the species are rainfall, canopy closure, amount of necromass in a late state of decay, watercourses (Spitale & Mair 2015) and altitude (Chmura & al. 2002). A dense overstory maintains a stable forest floor microclimate and light (Korhonen & al. 2006; Anonymous 1996). As a species apparently linked to well-preserved forest stands with large accumulations of bulky and coarse woody debris, it has been suggested that *B. viridis* is an indicator of long ecological continuity of woods. The decrease and fragmentation of primeval forests cause a threat to bryophytes and therefore also to *B. viridis*. Finally, it is sometimes considered as an umbrella species (confering protection to other species that occur along with it).

This moss is included within the bryophytes association *Lophocoleo heterophyllae-Buxbaumietum viridis* Vadam 1982 (pioneer, post-pioneer to nomadic montane association of debarked softwood stumps and rotting wood chips in a high-humidity environment) under the order *Nowellion curvifoliae* Philippi 1965 and under the class of *Lepidozio-Lophocoletea heterophyllae* v. Hübenschmann 1976 (pioneers communities, post-pioneers to nomads, sapro-lignicolous to saxico-humicolous and acidophilic humo-saxicoles).

C - Phenology

Data on phenology are scarce and offer conflicting information. According to Plášek in Stebel (2004) and Papp & al. (2014) the sporophytes emerge in summer and autumn. By contrast, according to Wiklund (2002), Callaghan & Taylor (2017) and Wolf (2015), the sporophytes grow during the autumn or winter. Deme & Csiky (2021) state that sporophytes start growing in autumn and develop rapidly reaching maturity in summer. However, first freezing and then drought could arrest the development of the sporophyte (Dierssen 2001, Wiklund 2002).

The sporophyte is visible all year around in its different gametophyte stages. Callaghan & Taylor (2017) cite eight developmental stages of the sporophyte. First stage: the calyptra emerges from a female gametophyte without a visible seta (Fig. 5). Second stage: elongation of the seta (Fig. 6). Third stage: the seta is fully grown and a small swelling is visible just below the calyptra (Fig. 7). Fourth stage: development of the capsule. Fifth stage: the capsule is fully developed but contains immature spores (Fig. 1). Sixth stage: maturity of the spores becoming brownish with intact operculum. Seventh stage: the fall of the operculum and detachment of the dorsal cuticle of the capsule (Fig. 8). Eighth stage: emptying of mature spores from the capsule. From the second stage up to the fifth the capsule is green while from the sixth stage onwards is brown.

The mortality rate of sporophytes in *B. viridis* is very high. It has been reported a mortality of 30-60% in Spain (Infante & Heras 2018) and of 62-89% in Scotland (Rothero 2008) due to desiccation, freezing, chewing, rarely also to fungal infections (Gyosheva & Natcheva 2022). Excessive droughts negatively affect the maturation of sporophyte by drying them out prematurely and reducing their spore production; 'only 20% of spores in *B. viridis* germinated after 12 days' dry storage'. All spores die after 48 days' dry storage (Wiklund & Rydin 2004).

Green capsules are preyed (Fig. 9) upon by small animals in spring (Infante & Heras 2018), especially ants and slugs (genus *Arion*, Férussac 1819). Mice are also potential



Fig. 5. Very young sporophytes with apical calyptra and with basal leaflet, seta still not visible (Sila Grande, Bosco Apitetto, 15.10.2023; 8 x magnification).

predators (Kropik & al. 2020). As it happens with the congener *aphylla*, the capsules can be preyed also by adults of fungus gnats (*Mycetophilidae*) (Müller 2012).

On the one hand, moderate grazing of sporophytes by animals, could actually be a dispersion vector for bryophytes as *Buxbaumia*, since not all spores are digested; on the other hand, excessive grazing should be interpreted in a negative way when the sporophytes are consumed in an early phase, i.e. before the maturation of the spores (Infante & Heras 2018).

Also freezing before winter causes high mortality among immature sporophytes, as observed for the congener *aphylla* (Hancock & Brassard 1974), and conditions of high temperature and low rainfall can also decrease sporophytes survival in spring (Wiklund & Rydin 2004).

The high number of spores per capsule (Wiklund 2002), the perennial protonema and the production of vegetative propagules (Wolf 2015) can compensate for the low number of sporophytes produced in some years due to predation or due to long periods of drought.

D – Italian distribution

The species falls within the Eurosiberian region (Pedrotti 1996). In Italy (Aleffi 2008) it is known for the Aosta Valley in Val di Cogne (Schumacker & al. 1999), Piedmont in Val Sangone (Aleffi & al. 2004a), Lombardy in Val Porcellizza (Pfeffer 1871), Trentino-Alto Adige in Welsperg Wood (Aleffi & al. 2004b), Veneto in Bosco Montello and Cansiglio (Saccardo 1872) and near Revolto (Massalongo 1896), Friuli-Venezia Giulia near Tarvisio



Fig. 6. Very young sporophytes with apical calyptra and with basal leaflet, partial emerged seta (Sila Grande, Bosco Apitetto, 15.10.2023; 8 x magnification).

(Sguazzin 2004, 2005), Emilia Romagna in the Modenese and Reggiano areas (Fiori 1886), Tuscany in the Boscolungo and near Camaldoli (Bottini 1887), Lazio at M. Terminillo (Aleffi 2006 pers. obs.), Abruzzo in the National Park (Mastracci & Düll 1991), Campania in the Matese region (Castaldo 1968), Calabria in the Aspromonte National Park (Aleffi & al. 2001) and in the Pollino National Park (Aleffi & Puntillo 1998).

The species was known for a long time from this last region; it was collected by Reynier and brought back by Bridel (1826), Bruch & Schimper (1837), De Notaris (1869). Giordano (1879) also reports a collection by Thomas made in Serra San Bruno (Vibo Valentia) [*Ad truncos vetustos*, (Thomas in Herb. Tenoreano), *et eodem* in Schmpr. Syn. Musc. et Bryol. Europ. Citata. Satis Rara!].

***E - Buxbaumia viridis* growth cycle**

The development of a gametophyte in *B. viridis* was for the first time described by Goebel (1892a) and later by Dening (1928). It is microscopic and not visible to the naked eye but only under the lens of a powerful stereomicroscope. The moss is only visible when the sporophyte appears. The retention of juvenile features into adulthood is considered neoteny (Grandstein & Wilson 2008 = pedomorphosis, Gould 1977) '*generally interpreted as a short-cut in the life cycle, allowing for rapid maturation and reproduction in unstable, impermanent habitats*' (Grandstein & Wilson 2008). In this case, neoteny permits the species to avoid some life cycle stages: the leafy gametophyte.



Fig 7. Young sporophyte with apical calyptra and basal part of the stem covered by leaflets (Sila Grande, Valle dell’Inferno, 12/10/2020).; 4 x magnification.

Buxbaumia, would be ‘*the simplest primitive moss*’, ‘*the simplest form of moss ... in which the sexual organs are directly born, with or without an involucre, on a filamentous protonema*’ (Goebel 1892b), ‘*the simplest moss plants we know*’ (Goebel 1905), and ‘*ancient type of Moss which still retains a number of primitive characters*’ (Goebel 1892b).

Being the species dioecious, both female and male gametophytes are formed on the richly branched and anastomosed filamentous persistent and epixylic protonema (applied tightly to the wood fibers.), which can reach several square centimeters in optimal condi-



Fig. 8. Mature capsules with the presence of “*indusium*”. Spores not yet expelled (Sila Grande, Vallone Cavaliere, 18/06/2023); 1 x magnifications.

tions (Dening 1928). The protonema is equipped with colorless and occasionally branched rhizoids, 15 μm in diameter wide, with oblique transverse walls, and numerous elongate and conspicuously large chloroplasts (Duckett & al. 2004). These are recognizable along the outside wall of the filaments. It has also tick vacuolated cell walls with uniform texture, average width ca. 0.7 μm . Ribosomes, endoplasmatic reticulum, and mitochondria are presents. Plasmodesmata (700-750 \AA) enter and pass though the cross walls, and are lined to the plasmalemma, which is continuous from cell to cell (Mueller, 1972). The protonema is very slow growing in culture, taking several months to reach a diameter of 1 cm (Duckett & al. 2004).

The first to discover female and male vegetative protonemal propagules (Figs. 10, 11) in *Buxbaumia aphylla* was Dening (1928). In *B. viridis* they were observed for the first time in culture by Wiklund (2002) and in the field by Wolf (2015) and Guillet & al. (2021), although their formation is very common in the dioecious mosses (Correns 1899, quoted in Frahm 2001). We observed and photographed them for the first time in Italy.

These male and female propagules in *B. viridis* are multicellular, obloid, with a prominent warty ornamentation, and their size varies between 40 μm and 70 μm in length. They form brownish (chocolate), large and highly distinctive glomeruli that are relatively easily recognizable in the field with the aid of a magnifying glass. When metabolic protonema activity resumes, they become green-brown or even golden yellow (Hugonnot & al. 2023).



Fig. 9. Partially grazed capsule (Sila Grande, Vallone Cavaliere, 18/06/2023;); 2.8 x magnification.

B. viridis is apparently a unique case in bryophytes, possessing a morphologically distinct, independent, and persistent protonemal stage (Guillet & al. 2021).

These asexuale propagules can live independently, that is, they can live separately from the sporophyte but it has not been demonstrated if they can originate from germination of spores or from other propagules (Guillet & al. 2021).

Furthermore, the sterile protonema with propagules and the sporophytes can occupy two distinct ecological niches. Protonemata with propagules were found at lower altitudes in broad-leaved woods on wood in a less advanced state of decay, while the fertile ones at higher altitudes in *Abieti-Fagetum* on a well decayed wood (Guillet & al. 2021).

Recently, also Hugonnot & al. (2023) reported that the distribution of the gametophyte (protonemata and propagules) has a much wider distribution than the sporophyte. In

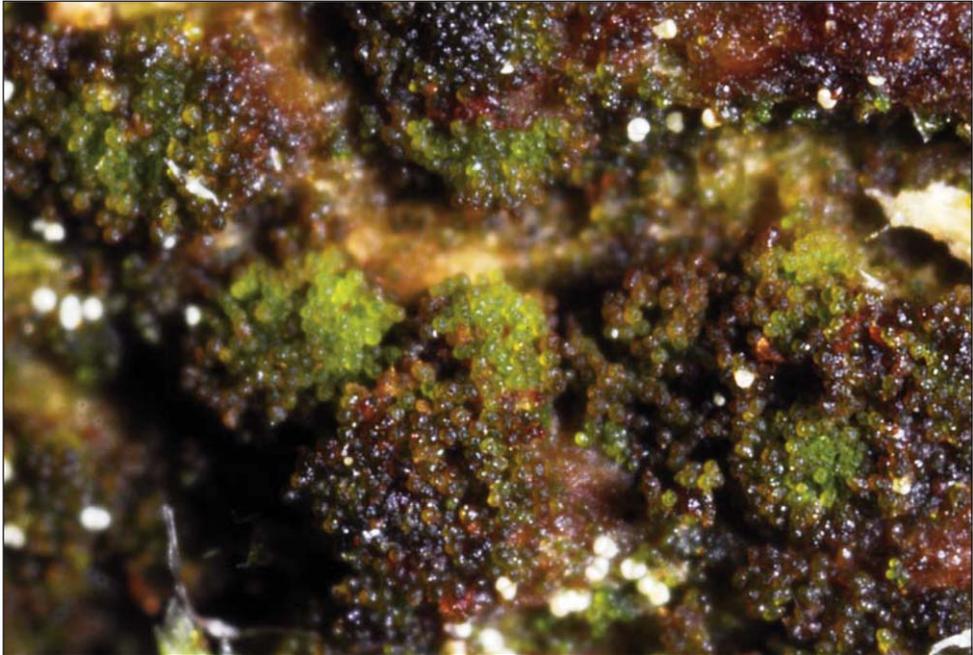


Fig. 10. Golden yellow, green-brown protonema propagules (photo, 8.5 x magnification), Sila Piccola (Pietrascritta, 24/06/2023).

France, gametophytic populations would also be widespread in the flat areas of the Mediterranean region up to the lower altitude of 10 meters and observed on various types of substrates as bark of dead or living trees, rough humus, dying mosses and acid rock (Hugonnot & al. 2023), but always without sporophytes. These authors subjected three gametophytic populations to molecular sequencing, unequivocally confirming their belonging to *Buxbaumia viridis* (data not yet published). As we said, the vegetative propagules are easily recognizable in the field because they appear as a granular chocolate-colored mass, while the protonema assumes the form of a whitish (in the dry state) greenish (in the wet state) film, strongly adhering to the fibers of the wood (Fig. 12). It is possible to observe together sporophyte, vegetative propagules and protonema or both sporophyte and protonema or only protonema or only vegetative propagules (Fig. 12).

Since the species is stenoic, sexual reproduction is difficult. This occurs when both male and female spores germinated and produce both protonemata with sex organs close to each other because only in the presence of water the spermatozoa can actively travel at only a very short distance and so swim to the egg to allow fertilization (up to about 1.5 cm, Frahm 2001). Consequently, female and male plants must grow very close together to produce a new organism. Vegetative propagules, although much heavier than spores, are also dispersed by animals (zoochory) and by storms (anemocory), and produce new moss plants more easily (Wolf 2015). Chmielewski & Eppley (2019) have long demonstrated that forest passerines are vector of viable bryophyte propagules at considerable distances.



Fig. 11. Protonema propagules seen under a biological optical microscope (Sila Piccola, Pietrascritta, 24/06/2023; photo 400 x magnification).

Dening (1928) showed that the propagules of *Buxbaumia* are considerably more resistant to drought than the cells of the protonema. Then they sprout again even after a long period of drought, and thus a protonema can develop again. These vegetative diaspores are of great importance for the conservation of the species in warm areas after repeated periods of drought (Wolf 2015). The species could survive during periods of unfavorable conditions by forming these brood cells that can germinate after long dry periods (Goode & al. 1993) and would save *B. viridis* populations from extinction in years with low rainfall and/or with periods of long drought.

The male gametophyte, 100 μm (90 μm to about 150 μm) in size, is reduced to only one leaflet surrounding the antheridium, placed on the protonema as a short lateral branch (Limpricht 1895). It is also equipped with small colorless branched rhizoids, 15 μm in diameter, with oblique transverse walls and a network of erect and wavy chloronematic filaments frequently provided with anastomosis (Goebel 1892b).

The female gametophyte (300 to 700 μm) has 6-8 leaflets (max up to 13), small, ovoid, ovate-lanceolate or palmate, ciliated, green only at the base and without ribs (ecostate) that envelop 3-4 archegonia (Brown 1819). Once fertilization has occurred a secondary protonema occurs on the marginal cells of the edges of the female gametophyte. Rhizoids form on the epidermis.

Young leaflets are predominantly water-white and hardly brown coloured (Figs. 5-13). Older ones are predominantly brown (Fig. 13) and surround the basal part of the stem (Fig.



Fig. 12. Top left, three grazed capsule-free setae from the previous year's sporification; top right, current young sporophytes with apical calyptra; bottom right, the vegetative propagules; bottom left, the protonema (whitish green film) of the current year (Sila Grande, Bosco Apitetto, 15.10.2023).

5). '*Buxbaumia* has not apical cells to the leaves but only a cell-grouping more or less resembling that of leaves of the *Hepaticae*' (Goebel 1905).

The leaflet margins are crenulated to indented, by protruding cell ends. In both male and female gametophytes, the chlorophyll content of the cells is very different. The cells in the area of the stem have chlorophyll, but when the gametophytes hidden in crevices have little or no chlorophyll in contrast with specimens growing in open situation (Wolf 2015).

The fully-grown sporophyte of *B. viridis* varies in length from 7 to 25 mm (Möller, 1923). The seta is warty-papillose, from sub-erect to erect, 0.5-0.8 mm long, and support a large ellipsoidal and asymmetrical capsule. The capsules have a less flattened upper surface, greenish-yellow in color, yellow-brown when ripe, bright (due to the presence of a cuticle), waxy, and provided with the outer layer slit longitudinally and rolled on the surface superior after the sporosis (named *indusium* = shirt, dress, tunic), which tears and detaches (Fig. 8).

Capsules have a tick impermeable and hydrophobic cuticle (Koch & al. 2009), and internally provided with a columella, which extends up to the conical, obtuse, operculum, supporting the sporogenic sac, which almost completely fills the cavity of the sporogonium. The operculum 0.7-1.2 mm long, is covered with a small prematurely deciduous thimble-shaped and weakly mucronate calyptra (Figs. 6, 7), made up of the haploid neck tissue of the archegonia that in most sporophytes disappear by the end of October.

A scanning electron microscope (SEM) study showed that the peeling of the cuticle of ripe capsules extends to the complete epidermis, covered with epicuticular wax crystals in different morphologies. The shape of the wax crystals indicates the presence of massive layers of wax with small plates and granules embedded and superimposed on top (Koch & al. 2009).

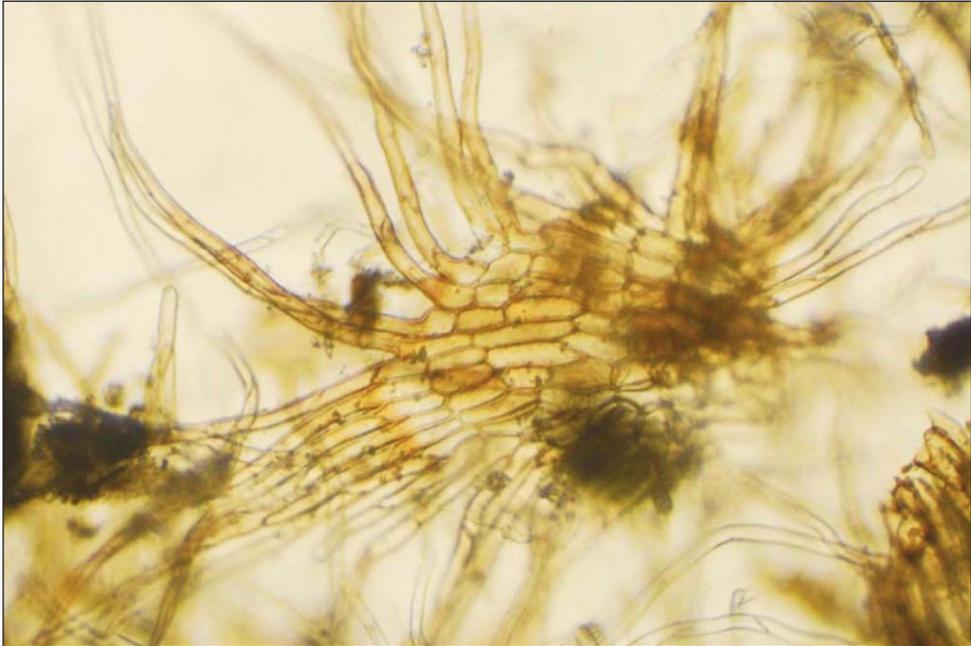


Fig. 13. Leaflet of *B. viridis*; 40 x magnification.

The capsule is provided with very shallowly immersed stomata (phaneropores) surrounded by two guard cells. The stomata are restricted to a narrow zone at the junction of the capsule neck to the seta (Erzberger & al. 2018).

The capsule (sporangium) is persistent and produces a high number of small papillose spores: 6.0 million in average. More precisely, the spore production per capsule ranges from 1.4 to 9.0 million, with an average value of 6.0 and a median of 6.3 million (Wiklund 2002) correlated to capsule size. This huge number of small spores of ca. 11.9 μm in diameter (Boros & Járαι-Komlódi 1975) allows effective dispersion to long distances (Löbel & Rydin 2009), and generally fosters dispersal by wind. *Buxbaumia viridis* spores germinate rapidly but, unfortunately, are viable for only a few weeks (Wiklund & Rydin 2004). The spores of *Buxbaumia viridis* died after only 48 h of dry storage (Wiklund & Rydin, 2004).

The peristome is arthrodontous diplolepidous (double peristoma); exostomy with three concentric series of strongly papillose teeth, the internal 0.5-0.6 mm long, the external ones shorter; less developed endostomy 0.8-0.0 mm long, papillose.

Philibert (Taylor 1962) regarded the peristome of *B. viridis* as representing the primitive condition that links the arthrodontous and nematodontous ones (Edwards in Schuster 1984). Dixon (1932) regarded the order *Buxbaumiales* as probably an ‘archic’ type, which has survived in something like its primeval form. Edwards in Schuster (1984) provided many details for early stages of peristome development in *Buxbaumia*, and speculates that the formula of *B. viridis* is 8:4:4; he concludes that *Buxbaumia* is a ‘living fossil’ representing a group of ancestral mosses to both the nematodontous and arthrodontous. Goebel

(1905) maintained that the reduction of the *Buxbaumia* gametophyte should be considered as a primitive character, while Castaldo (1972-1973) argued that the reason why this archaic group survived by preserving the gametophyte in such a 'primitive' form must be sought in its particular saprotrophic nutrition. Recently, Ignatov & al. (2018), in a detailed study of the peristome, hypothesized its development revealing differences from all other peristomic mosses, thus concluding that a peristomial formula is missing, and that the capsule structure 'does not represent an archaic type, but seems to be extremely specialized'.

Results

In the monitoring periods (years from 2020 to 2023) it has been detected in 94 microsites (Fig. 4; Tab. 1) into 8 macro-areas where 1027 capsule-inclusive sporophytes and 286 capsule-free setae were observed, plus 2 sites with only protonema and vegetative propagules and one site with only the protonema. Due to the difficulty of recognizing both protonema and propagules in the field, if there are no capsules nearby, a long experience was necessary: the former as a whitish film (in the dry state) and greenish (in the wet state), the latter as a chocolate-coloured granular warty mass (Fig. 10). To confirm this, however, it was necessary to examine under the microscope small pieces of trunk taken in the field.

The number of sporophytes observed ranged between 1 and 83 on a single log (Tab. 1). The highest number of sporophytes per log was observed at higher altitudes, the lowest at lower.

B. viridis, has been recorded all year around except for the snowy season, on wood of various phorophytes. The most common host trees species are *Pinus nigra* J. F. Arnold subsp. *laricio* Palib ex Maire, followed by *Abies alba* Mill., *Fagus sylvatica* L. and *Alnus glutinosa* (L.) Gaertn. Collections on logs of *Pinus* and *Abies*, with very few exceptions, was carried out in mixed forests with *Fagus sylvatica*. In the monophytic *Pinus* forests standing on steep sunny south-facing slopes or drier soils at lower altitudes, the species grows on patches of wood out of water but on partially submerged trunks, in small leeward river courses, in the undergrowth to compensate for excessive evapotranspiration of these microsites.

The species also rarely grows in a few or isolated individuals occurring on acidic soil rich in organic matter (*moder* or *mull-moder*), on rivulet slopes in the undergrowth, mixed with other bryophytes, such as *Calypogeia fissa* (L.) Raddi, *Fuscocephaloziopsis lunulifolia* Váňa & L. Söderstr. and *Lophozia ventricosa* (Dicks.) Dumort.

On decaying wood it has been collected both in patches lacking other bryophytes or mixed with the following: *Aulacomnium androgynum* (Hedw.) Schwägr., *Fuscocephaloziopsis lunulifolia* Váňa & L. Söderstr., *Dicranella heteromalla* (Hedw.) Schimp., *Dicranum tauricum* Sappégin, *Diphyscium foliosum* (Hedw.) D. Mohr, *Kindbergia praelonga* (Hedw.) Ochyra, *Herzogiella seligeri* (Brid.) Z. Iwats, *Hypnum cupressiforme* Hedw., *Isoetecium myosuroides* Brid., *Lophocolea heterophylla* (Schrad.) Dumort., *Nowellia curvifolia* Dicks.) Mitt., *Pterigynandrum filiforme* Hedw., *Rhizomnium punctatum* (Hedw.) T.J.Kop., *Riccardia palmata* (Hedw.) Carruth and with the lichen *Protopannaria pezizoides* (Weber) P.M. Jorg. & S. Ekman and the green alga *Trentepohlia* sp. (Tab. 1).

B. viridis in Calabria has a fragmented distribution, mainly linked to small river courses or along the very humid impluvia that run through the mountains. Only at high altitudes, it also grows in the undergrowth of forests. These sites may become future outposts from

Tab. 1. Localities, UTM coordinates, number of sporophytes, number of capsule-free setae, altitude, exposure, phorophytes substrate, associated bryophytes and observation date.

Localities	Coord.	Nr. Caps.	Caps. free setae	Alt. a.s.l.	Exp.	Phorophytes and associated species of Bryophytes	Dates
Sila Grande, Vallone Neto-Fallistro	625111 – 4352746	12	5	1494	E	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes.	04/10/2020
Sila Grande, Fiumarella di Montecristo	621440 – 4346386	20	3	1312	W	On rotting wood of <i>Fagus sylvatica</i> . <i>Dicranella heteromalla</i> , <i>Rhizomnium punctatum</i>	07/10/2020
Sila Grande, Camigliatello Silano	624636 – 4355261	4	1	1284	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	10/10/2020
Sila Grande, Camigliatello Silano	624699 – 4355274	15	2	1299	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	10/10/2020
Sila Grande, Camigliatello Silano	624735 – 4355291	7	1	1300	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	10/10/2020
Sila Grande, Vallone dell'Inferno	628076 – 4351917	5	3	1474	W	On rotting wood of <i>Pinus laricio</i> . <i>Rhizomnium punctatum</i> , <i>Lophocolea heterophylla</i> , <i>Herzogiella seligeri</i>	12/10/2020
Sila Grande, Valle del Fiume Neto	623933 – 4352298	14	2	1633	NE	On rotting wood of <i>Fagus sylvatica</i> . <i>Nowelia curvifolia</i> , <i>Lophocolea heterophylla</i>	14/10/2020
Parco Nazionale del Pollino, Fiumarella di Rossale	588506 – 4404168	3	2	1235	W	On rotting wood of <i>Fagus sylvatica</i> . <i>Rhizomnium punctatum</i> <i>Lophocolea heterophylla</i> , <i>Herzogiella seligeri</i>	26/10/2020
Sila Grande, Fontana del Colonnello	624323 – 4350050	1	1	1697	N	River escarpment. <i>Calyptogeia fissa</i> , <i>Fuscocephaloziopsis lunulifolia</i> , <i>Lophozia ventricosa</i>	31/10/2020
Sila Grande, Fontana del Colonnello	624276 – 4350118	1	1	1697	N	River escarpment. <i>Diphyscium foliosum</i>	31/10/2020
Sila Grande, Fontana del Colonnello	624428 – 4350371	22	3	1676	N	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes.	31/10/2020
Sila Grande, Fontana del Colonnello	624181 – 4349904	12	4	1737	N	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes.	31/10/2020
Parco Regionale delle Serre (Serra S. Bruno), Bosco Archiforo	617027 – 4267247	3	2	1122	NW	On rotting wood of <i>Abies alba</i> . <i>Kindbergia praelonga</i> , <i>Hypnum cupressiforme</i>	28/02/2021
Parco Regionale delle Serre, Bosco Archiforo	617064 – 4267263	7	1	1134	NW	On rotting wood of <i>Abies alba</i> . <i>Isoetecium myuroides</i>	28/02/2021
Parco Regionale delle Serre, Bosco Archiforo	616939 – 4267308	5	2	1093	NW	On rotting wood of <i>Abies alba</i> . <i>Hypnum cupressiforme</i> , <i>Isoetecium myuroides</i>	28/02/2021
Parco Regionale delle Serre, Bosco di S. Maria	614003 – 4267443	2	2	878	N	On rotting wood of <i>Pinus laricio</i> . <i>Abies alba</i> . Patches free of other bryophytes.	28/02/2021

Table 1. continued.

Parco Regionale delle Serre, Bosco di S. Maria	614176 – 4267803	5	3	861	N	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	28/02/2021
Sila Grande, Vallone Tasso	622272 – 4354457	7	3	1404	E	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes.	03/03/2021
Sila Grande, Vallone Tasso	622218 – 4354464	31	6	1404	E	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes.	03/03/2021
Sila Grande, Vallone Tasso	622065 – 4354264	32	5	1434	E	On rotting wood of <i>Pinus laricio</i> . <i>Rhizomnium punctatum</i>	03/03/2021
Sila Grande, Vallone Tasso	622008 – 4354207	64	3	1449	E	On rotting wood of <i>Pinus laricio</i> . <i>Pinus laricio</i> .	03/03/2021
Sila Grande, Vallone Tasso	622012 – 4354199	5	2	1450	E	On rotting wood of <i>Pinus laricio</i> . <i>Pinus laricio</i> .	03/03/2021
Sila Grande, Vallone Tasso	621995 – 4354186	68	5	1446	E	On rotting wood of <i>Pinus laricio</i> .	03/03/2021
Sila Grande. Sbanditi	637723 – 4361224	14	3	1345	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	16/05/2021
Sila Grande. Sbanditi	637721 – 4361219	14	4	1346	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	16/05/2021
Sila Grande. Sbanditi	637719 – 4361212	39	6	1347	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	16/05/2021
Sila Grande. Sbanditi	637720 – 4361203	22	3	1347	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	16/05/2021
Sila Grande. Sbanditi	637719 – 4361197	5	2	1348	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	16/05/2021
Sila Grande. Sbanditi	637716 – 4361190	1	3	1350	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	16/05/2021
Sila Grande, Vallone Fossiata	636736 – 4362212	8	3	1298	S	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	16/05/2021
Sila Grande, Vallone Fossiata	636753 – 4362348	5	1	1286	S	On rotting wood of <i>Abies alba</i> . <i>Herzogiella seligeri</i> , <i>Rhizomnium punctatum</i>	16/05/2021
Sila Grande, Vallone Fossiata	636812 – 4362613	9	2	1297	S	On rotting wood of <i>Abies alba</i> . <i>Nowellia curvifolia</i> , <i>Lophocolea heterophylla</i> , <i>Rhizomnium punctatum</i> , <i>Dicranella heteromalla</i>	16/05/2021
Sila Grande, Vallone Fossiata	636811 – 4363520	30	5	1301	S	On rotting wood of <i>Abies alba</i> . <i>Nowellia curvifolia</i> , <i>Dicranella heteromalla</i> , <i>Rhizomnium punctatum</i> , <i>Lophocolea heterophylla</i> , <i>Aulocomnium androgynum</i>	16/05/2021

Table 1. continued.

Sila Grande, Vallone Fossiateda	636777 – 4363723	24	3	1362	S	On rotting wood of <i>Abies alba</i> . <i>Nowellia curvifolia</i> , <i>Lophocolea heterophylla</i> , <i>Riccardia palmata</i>	16/05/2021
Sila Grande, Vall. Fossiateda-Gallopane	636529 – 4364120	5	1	1400	E	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	16/05/2021
Sila Grande. Fossiateda – Sbanditi	637713 – 4361181	15	5	1352	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	16/05/2021
Sila Grande, Vallone Fossiateda- Gallopane	636484 – 4364130	2	1	1409	E	On rotting wood of <i>Abies alba</i> . <i>Rhizomnium punctatum</i> , <i>Herzogiella seligeri</i> , <i>Lophocolea heterophylla</i>	16/05/2021
Sila Grande, Vallone Fossiateda- Gallopane	636439 – 4364115	2	2	1413	E	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	16/05/2021
Sila Grande, Bosco Gallopane	636435 – 4363943	1	1	1471	E	On wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	16/05/2021
Parco Nazionale del Pollino, Cozzo del Pellegrino	588840 – 4399897	12 9 7	3 2 1	1641	E	On rotting wood of <i>Fagus sylvatica</i> , <i>Dicranella heteromalla</i>	25/06/1991 07/05/2000 30/05/2021
Parco Regionale delle Serre, Rosarella	626355 – 4268266	6	1	914	W	On stump of <i>Abies alba</i> . Patches free of other bryophytes.	19/06/2021
Parco Regionale delle Serre, Bosco di S. Maria	613805 – 4266521	2	1	1008	N	On stump of <i>Abies alba</i> . Patches free of other bryophytes.	26/06/2021
Parco Regionale delle Serre, Bosco di S. Maria	613806 – 4266341	6	3	1019	N	On stump of <i>Abies alba</i> . <i>Herzogiella seligeri</i>	26/06/2021
Sila Grande, Vallone Sette Acque	624525 – 4355063	7	2	1286	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	29/07/2021
Sila Grande, Vallone Sette Acque	624355 – 4354835	2	2	1305	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	29/07/2021
Sila Grande, Vallone Sette Acque	624220 – 4354641	15	4	1317	NE	On rotting wood of <i>Pinus laricio</i> . <i>Rhizomnium punctatum</i>	29/07/2021
Sila Grande, Vallone Sette Acque	623999 – 4354338	8	0	1348	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	29/07/2021
Sila Piccola, Macchia dell’Orso	642924 – 4332821	12	2	1641	S	On rotting wood of <i>Fagus sylvatica</i> . <i>Herzogiella seligeri</i>	05/08/2021
Sila Piccola, Macchia dell’Orso	642915 – 4332853	15	1	1644	S	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes	05/08/2021
Sila Piccola, Macchia dell’Orso	642893 – 4332865	83	11	1646	S	On rotting wood of <i>Fagus sylvatica</i> . <i>Herzogiella seligeri</i>	05/08/2021
Sila Piccola, Macchia dell’Orso	642873 – 4332889	4	1	1647	S	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes	05/08/2021

Table 1. continued.

Sila Piccola, Macchia dell'Orso	642859 – 4332911	6	2	1650	S	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes	05/08/2021
Sila Piccola, Macchia dell'Orso	642934 – 4332886	5	2	1645	S	On rotting wood of <i>Fagus sylvatica</i> . <i>Lophocolea heterophylla</i> , <i>Rhizomnium punctatum</i>	05/08/2021
Sila Piccola, Monte Gariglione	641591 – 4333135	1	1	1716	N	On rotting wood of <i>Pinus laricio</i> . <i>Pterigynandrum filiforme</i>	05/08/2021
Sila Piccola, Fosso di Circilla	637284 – 4337327	3	0	1317	N	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	07/08/2021
Vallone del Tassito	639600 – 4338807	2	0	1306	N	On rotting wood of <i>Fagus sylvatica</i> . Patches free of other bryophytes.	16/08/2021
Sila Grande, Fiumarella Monte Curcio	622155 – 4353539	6	2	1464	E	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	28/08/2021
Sila Grande, Fiumarella Monte Curcio	622022 – 4353269	10	3	1480	E	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	28/08/2021
Sila Grande, Fiumarella Monte Curcio	621908 – 4352869	20	4	1526	E	On rotting wood of <i>Pinus laricio</i> . <i>Rhizomnium punctatum</i>	28/08/2021
Sila Piccola, Monte Gariglione, Pietra Scritta	643542 – 4133440	6	71	1755	N	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes	31/08/2021
Parco Nazionale Aspromonte, Valle Torrente Listi	574181 – 4221974	4	2	1435	SE	On rotting wood of <i>Abies alba</i> . <i>Lophocolea heterophylla</i> , <i>Dicranella heteromalla</i>	18/09/2021
Parco Nazionale Aspromonte, Valle Torrente Listi	574277 – 4222003	6	3	1445	SE	On rotting wood of <i>Abies alba</i> . <i>Lophocolea heterophylla</i>	18/09/2021
Parco Nazionale Aspromonte, Valle Torrente Listi	574329 – 4221982	12	2	1447	SE	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	18/09/2021
Parco Nazionale Aspromonte, Valle Torrente Listi	579311 – 4220146	6	3	1467	SE	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	18/09/2021
Aspromonte. Valle Torrente Listi	574692 – 4221921	8	1	1470	SE	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	18/09/2021
Parco Nazionale Aspromonte, Valle Torrente Listi	574671 – 4221901	5	3	1468	SE	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	18/09/2021
Parco Nazionale Aspromonte, Valle Fiume Menta	579126 – 4220012	6	2	1360	E	On rotting wood of <i>Abies alba</i> . <i>Herzogiella seligeri</i> , <i>Pterigynandrum filiforme</i> , <i>Lophocolea heterophylla</i> and the lichen <i>Protopannaria pezizoides</i> .	18/09/2021
Parco Nazionale Aspromonte, Valle Fiume Menta	579078 – 4220016	5	1	1360	E	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes.	18/09/2021
Sila Grande, Vallone Moccone	622020 – 4354652	1	0	1395	E	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	07/10/2021

Table 1. continued.

Sila Grande, Vallone Moccone	621876 – 4354332	4	8	1445	E	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	08/10/2022
Sila Grande, Sbanditi	637728 – 4361244	67	12	1340	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes.	24/04/2023
Sila Grande, Sbanditi	637728 – 4361246	2	0	1340	NE	On stump of <i>Abies alba</i> . Patches free of other bryophytes.	24/04/2023
Sila Grande, Cupone	634135 – 4360709	1	0	1214	N	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	03/05/2023
Sila Grande, Campeggio	623340 – 4354289	5	2	1419	NW	On rotting wood of <i>Pinus laricio</i> . <i>Herzogiella seligeri</i> , <i>Lophocolea</i> <i>heterophylla</i> , <i>Trentepohlia</i> sp.	11/06/2023
Sila Grande, Campeggio	623269 – 4354448	7	3	1395	NW	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	11/06/2023
Sila Grande, Campeggio	623182 – 4354556	2	0	1377	NW	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	11/06/2023
Sila Grande, Campeggio	623380 – 4354212	2	1	1426	NW	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	14/06/2023
Sila Grande, Vallone Cavaliere	621625 – 4355125	2	0	1368	NE	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	18/06/2023
Sila Grande, Vallone Cavaliere	621639 – 4354957	6	2	1415	NE	On rotting wood of <i>Pinus laricio</i> . <i>Herzogiella seligeri</i> , <i>Lophocolea</i> <i>heterophylla</i> , <i>Rhizomnium</i> <i>punctatum</i> .	18/06/2023
Sila Piccola, Pietrascritta	643546 – 4333471	only protonema with propagules	-	1753	S	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes	24/06/2023
Sila Piccola, Pietrascritta	643551 – 4333459	1	-	1756	S	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes	24/06/2023
Sila Grande, Fiumarella Curcio	622415 – 4353714	10	4	1480	N	On rotting wood of <i>Pinus laricio</i> . <i>Lophocolea heterophylla</i> , <i>Rhizomnium punctatum</i> .	25/07/2023
Sila Grande, Pisciaturò	622442 – 4353906	only protonema with propagules	-	1437	SW	On rotting wood of <i>Pinus laricio</i> . <i>Lophocolea heterophylla</i> , <i>Rhizomnium punctatum</i> .	25/07/2023
Sila Grande, Nocelle	633640 – 4344409	only protonema without propagules	-	1380	N	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	22/08/2023
Sila Grande, Valle del Cavaliere	626518 – 4348249	2	1	1566	SE	On rotting wood of <i>Pinus laricio</i> . <i>Lophocolea heterophylla</i> , <i>Riccardia palmata</i> , <i>Aulacomnium</i> <i>androgyneum</i> .	27/08/2023
Sila Grande, Serra Magnaudo	627504 – 4348425	2	-	1522	SW	On rotting wood of <i>Pinus laricio</i> . <i>Herzogiella seligeri</i> , <i>Rhizomnium</i> <i>punctatum</i> .	27/08/2023

Table 1. continued.

Sila Grande, Serra Magnaudo	627496 – 4348367	3	1	1512	SW	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	27/08/2023
Sila Grande, Serra Magnaudo	628014 – 4348077	2	2	1497	SW	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	27/08/2023
Sila Grande, Serra Magnaudo	628316 – 4347934	3	-	1480	SW	On rotting wood of <i>Pinus laricio</i> . Patches free of other bryophytes	27/08/2023
Sila Grande, Serra Magnaudo	628696 – 4347363	1	-	1440	SW	On rotting wood of <i>Alnus glutinosa</i> . <i>Rhizomnium punctatum</i> .	27/08/2023
Sila Grande, Bosco Apitetto	61991 – 435248	43	4	1465	W	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes	15/10/2023
Sila Grande, Bosco Apitetto	619900 – 4352489	17	3	1459	W	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes	15/10/2023
Sila Grande, Bosco Apitetto	619884 – 4352488	3	-	1453	W	On rotting wood of <i>Abies alba</i> . Patches free of other bryophytes	15/10/2023
Sila Piccola, Monte Femminamorta	644204 – 4330245	1	-	1686	NE	On rotting wood of <i>Abies alba</i> . <i>Herzogiella seligeri</i> . <i>Dicranum tauricum</i> , <i>Pterigynandrum filiforme</i>	16/11/2023

which the species can radiate in case of marginalization in these areas. In the lowest sites it was observed in forests with oceanic climate, with high amounts of rainwater and occult precipitations (frequent foggy days) always either in the rivulet beds, on rivers escarpments, streams and rivulets or on mossy stumps with high water retention.

Following Söderström's (1988a, 1988b) decomposition stages of the logs ranging from 1 to 8, most individuals were observed on wood in stages 8 (when the wood is easily penetrated by a knife blade). At the site of Cozzo del Pellegrino (Tab. 1) in the year 1991 the log was quite hard and the sporophytes had grown inside a longitudinal crevice, so they were all aligned in a single row.

The growth of sporophytes frequently begin between the end of September and the beginning of October, but they are just visible and not fully formed (Figs. 6, 7). Most capsules are visible by mid-December but they are still immature and very green (Fig. 14).

The capsules remain green between the end of April and the end of June, while sporulation takes place at the end of June when they are now yellow-brown. However, sporophytes with almost mature capsules were observed already in October. Vice versa in two sites (Serre Vibonesi and Cozzo del Pellegrino) the capsules had not yet reached maturity on 19 June and on 29, respectively (Tab. 1). Most capsules are dehiscent in July but many contain a spore residue until the end of August. The greatest number of sporophytes occurs at the end of autumn but it starts to decrease until summer due to frost and grazing. The old empty capsules are visible in early October mixed with the new ones (Fig. 15).



Fig. 14. Immature sporophytes with the calyptra now lost (Sila Grande, Fallistro, 04/10/2020); 1 x magnifications.

According to Wiklund (2002) and Deme & al. (2020), the species grows on short-lived substrates. However, in one site (Cozzo del Pellegrino, Pollino National Park) the species has been monitored for a long time: it has been found on the same log for 30 years and continues to bear fruit regularly every year, but gradually in smaller amounts due to the reduction of wood mass now partially covered by litter forest. This station would either contradict the hypothesis that the species is fugitive (Dierssen 2001) or would represent an exception to the rule.

Contrary to what was observed in France (Guillet & al. 2021) and northern Italy (Spitale & al. 2015) where stations are mainly located according to northern exposure, in Calabria they are located mainly toward North-East or according to eastern exposure without significant differences. Even the sites exposed toward North and South are similar (Fig. 16). Even altitude does not appear to be a predictor for Calabria, as hypothesized by Chmura & al. (2022) for Poland, too.

In agreement with Holá & al. (2014), it can be said that the most important ecological factors for this species are the continuous turnover of a large quantity of dead wood available with different degrees of decay, its state of decomposition, the high humidity, the altitude and the opening of the canopy. Indeed, the most frequent observations concern the rivers banks or the riverbed itself with the presence of rotting fallen trees. Field observations have shown that there is no correlation between this moss occurrence and the volume of logs because the species was found on small broken branches as well as on very large logs (see Ruete & al. 2012a), but as hypothesized by Spitale & al. (2015), the amount of necromass increases the probability of its detection. Using niche-based models to improve the sampling of rare species, such as *B. viridis* (Guisan & al. 2006), seems more predictive because it considers a higher number of environmental variables.



Fig. 15. Young sporophyte from the current year (left) and old sporophyte from the previous year (Sila Grande, Valle dell'Inferno, 12/10/2020); 1.3 x magnification.

'The law of the relative constancy of the ecological factors' (Walter & Straka 1970) suggests that the sets of all abiotic factors as rainfall, edaphic humidity, atmospheric moisture, fog, temperature, exposure, shading, light, altitude, geomorphology (micro-topography), wind and pH of the logs, are important, that in all micro-niches these factors do not undergo very large variations over the year. A strong change in just one of these factors modifies the ecological niche. The wind, both cold and hot, that sweeps away the atmospheric moisture of the undergrowth. The low rainfall, and the relative high temperatures in the summer months (June, July and August) are counterbalanced by the high humidity of the water-courses that are always found in leeward impluvia with steep slopes. The cold temperatures of the winter months are mitigated by the snow cover, which partially protects the capsules from freezing. Shading and lighting have a one-to-one correspondence with the coverage of the forest canopy (more or less closed) which influences the degree of the humidity of the undergrowth. Logs decomposition may be nutritionally beneficial to

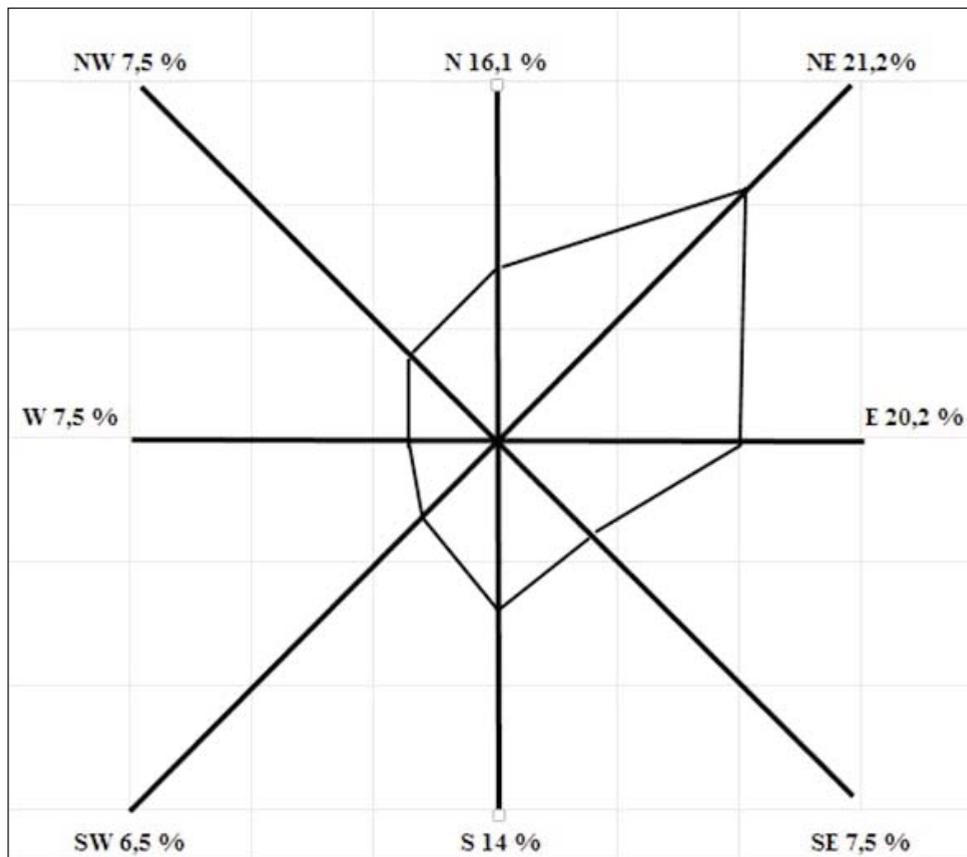


Fig. 16. Relative frequency of occurrence of *B. viridis* sporophytes in relation to surface aspect.

epixylic mosses as *B. viridis*. As highlighted by Wiklund (2003), the site for germination and establishment of this moss is either a substrate with continuously high moisture or a substrate with lower moisture but with increased pH and (or) P content. In addition to phosphorus, coarse woody debris (CWD) often has greater availability of sugars (Karppanen & al. 2008), nitrogen (Fukasawa & al. 2008), base cations (Gruba & Zwydak 2010). At the same time, being a humidity condenser (Proctor & Tuba 2002) by absorbing rain water and percolation water on sloping soil, CWD is useful in periods of water stress. In contrast, fine woody debris (FWD) dries quickly and therefore decays slowly.

B. viridis is linked to forests with long ecological continuity and is considered an indicator for air quality (Hallingbäck 1992; Plášek 2001). In fact, until now, in Calabria it seems to be relegated exclusively to protected areas (Pollino National Park, Sila National Park, Aspromonte National Park and Serre Natural Park). In the Sila plateau it is found, especially in the old areas, the so-called 'camere chiuse' (closed chamber), forests where the removal of wood by private individuals was prohibited and reserved to the Navy which managed them exclusively for the use of wood for the construction of naval equipment.

Habitat persistence and availability are key factors for metapopulation dynamics. It is essential for the conservation of the species where there is a continuous turnover of suitable substrates over time: a constant availability of logs in a late stage of degradation and large patches of log free from other bryophytes so they can occupy and colonize these sites for several consecutive years. Indeed, the other bryophytes are implacable competitors; only very few sporophytes were found mixed with gametophytes of other bryophytes, making them much more difficult to detect. Other bryophytes were not usually found in patches occupied by *B. viridis* but only close to them.

Since many decades are necessary to degrade the logs of the forest floor (Söderström 1988b; Hytteborn & Packham 1987; Hytteborn, & al. 1991), it is essential to leave *in situ* all dead trees until degradation is complete (Hytteborn & al. 1991). As highlighted by Paillet & al. (2010) and Spitalè & al. (2015), the availability of a large amount of necromass guarantees the turnover of the biodiversity of epixylic organisms, including *B. viridis*.

Although the survival of this saproxylic species is not only dependent on the quantity, but also on the quality of deadwood (Lachat & al. 2013). This increases the probability of the moss occurring on wood in various decay stages.

Although in Calabria its sporophyte spatial distribution is underestimated and misrepresented and despite these numerous findings, the species is in a serious danger of rarefaction due to the lack of suitable substrates, to forests fragmentation and, above all, due to the climatic changes (global warming), which could relegate it to progressively higher altitudes with its total disappearance at lower altitudes. Ruete & al. (2012b) hypothesize even with a scenario of low emissions, over 65% risk of population halving.

Thinning and clear-cutting modify the environment of the undergrowth by increasing the entry of light, rain, wind and extreme temperatures, thus favoring drying stress. The recent silvicultural activities that include the removal of all woody mass, including small branches to obtain pellets and biogas depriving the soil of the substrate on which the species can settle. In such woods, the chance of finding sporophytes drops drastically, to close to zero.

For the conservation of this species is therefore necessary that the policy makers implement a forestry policy aimed at the conversion of unmixed and even-aged forests into mixed and uneven-aged forests management (see Schall & al. 2018). Is also of fundamental importance leaving overripe and decaying dead trees *in situ* because they are essential for the life of numerous organisms, including xylophagous invertebrates, fungi, lichens and epixylic bryophytes, such as *Buxbaumia viridis* (in the sporophytic form) to avoid their rarefaction or extinction.

Finally, in the light of the recent findings of autonomous gametophytes at even at low altitudes on various substrates (Hugonnot & al. 2023), it is appropriate to extend the monitoring to these altitudes to establish the real distribution of the species and whether in these areas, during highly rainy years, the gametophytes (protonemata and propagules) could produce sporophytes or not.

Furthermore, it is also necessary to make resources and experienced personnel available to continue the search for species included in the red lists, in order to conserve this and other endangered or rarefied species by continuing to monitor them over the years otherwise its protection will become only a chimera, a mirage.

Acknowledgements

The monitoring of *Buxbaumia viridis* was promoted and financed by the Calabria Region and entrusted to the Department of Biology, Ecology and Earth Science (DiBEST) of University of Calabria as part of the Project “POR Calabria 2014/2020 azione 65A1 - Monitoraggio Siti Rete Natura 2000”. Many thanks to Dr. Giovanni Sicoli (Department of Biology, Ecology and Earth Sciences, The University of Calabria) for English revision and to Dr. Carmen Gangale (Ministry of the Environment and Energy Security, DG for European and International Activity) for the useful suggestions on phytoclimate and vegetation.

References

- Agnew, J. & Rao, S. 2016: *Buxbaumia viridis* hot-spot survives severe flooding. – *Field Bryol.* **115**: 19-21.
- Aleffi, M. 2008: *Buxbaumia viridis* (Lam. & DC.) Moug. & Nestl. – *Inform. Bot. Ital.* **40(1)**: 135-136.
- Aleffi, M., Barbo, M., Bertani, G., Bonini, I., Buffa, G., Carratello, A., Cogoni, A., Flore, F., Miserere, L., Perego, S., Piovano, S., Puntillo, D., Schumacker, R. & Sguazzin, F., 2004a: Contributo alla conoscenza briologica della Valle Stura di Demonte (Alpi Occidentali, Piemonte, Italia). – *Boll. Mus. Reg. Sci. Nat. Torino* **21(1)**: 227-248.
- Aleffi, M., Bonini, I., Carratello, A., Cogoni, A., Cortini Pedrotti, C., Miserere, L., Prezzavento, A. D., Privitera, M., Puntillo, D. & Sguazzin F., 2001: Contributo alla Flora Briologica dell’Aspromonte (Calabria). – *Inform. Bot. Ital.* **33(1)**: 17-25.
- Aleffi, M., Puntillo, D. 1998: Contributo alla conoscenza della flora briologica della Calabria. – *Webbia* **53(1)**: 181-190.
- Aleffi, M., Schumacker, T. & Tacchi, R. 2004b: Contributo alla conoscenza della flora briologica del Trentino: il Bosco Welsperg (Parco Naturale Paneveggio-Pale di S. Martino), con una nota sulla *Radula visianica* C. Massal. – *Braun-Blanquetia* **34(1)**: 87-94.
- Aleffi, M., Tacchi, R. & Poponesi, S. 2020: New Checklist of the Bryophytes of Italy. – *Cryptogam. Bryol.* **41(13)**: 147-195. <https://doi.org/10.5252/cryptogamie-bryologie.2020v41a13>.
- Andersson, L. I. & Hytteborn, H., 1991: Bryophytes and decaying wood – a comparison between managed and natural forest. – *Holarct. Ecol.* **14(2)**: 121-130.
- Anonymous, 1996: Draft Management Recommendations for Green bug moss *Buxbaumia viridis* (DC.) Moug. & Nestl. – Oregon.
- ARPACAL 2024: Centro Funzionale Multirischi, Historical Data. – <https://www.cfd.calabria.it/index.php/dati-stazioni/dati-storici> [accessed 5/1/2024]
- Bidartondo, M. I. 2005: The evolutionary ecology of myco-heterotrophy. – *New Phytol.* **167(2)**: 335-352. <https://doi.org/10.1111/j.1469-8137.2005.01429.x>.
- Boros, Á. & Járαι-Komlódi, M. 1975: An atlas of recent European moss spores. – Budapest.
- Bottini, A., 1887: Appunti di briologia toscana. – *Malpighia* **1**: 383-390.
- Boulay, M. 1872: Flore Cryptogmiquie de l’Est. Muscinées (Mousses, Sphaignes, Hépatiques). – Paris.
- Bridel, S. E. 1826: *Bryologia Universa*. – Leipzig.
- Brown, R. 1819: Characters and Descriptions of *Lyellia*, a new genus of Mosses, with Observations on the Section of the Order to which it belongs; and some Remarks on *Leptostomum* and *Buxbaumia*. – *Trans. Linn. Soc. Lond.* **12**: 560-583.
- Bruch P. & Schimper P. 1837: *Bryologia Europaea*. – Stuttgart.
- Buxbaum, J. C. 1728: *Plantarum Minus Cognitarum Centuriam II*. – Petropolis.
- Callaghan D. & Taylor S. 2017: Classification of sporophyte stages in *Buxbaumia viridis*. – *Field Bryol.* **117**: 1-7.

- Castaldo, R., 1968: Una nuova stazione di “*Buxbaumia indusiata*” Brid., muschio raro per l’Italia meridionale. – *Giorn. Bot. Ital.* **102**: 549-550.
- Castaldo, R. 1972-1973: Contributo alla conoscenza dei muschi saprofiti: le *Buxbaumiaceae* (*Bryales*), con particolare riguardo a *Buxbaumia indusiata* Brid. – *Delpinoa* **14-15**: 35-48.
- Chmielewski M. W. & Eppley S. M. 2019: Forest passerines as a novel dispersal vector of viable bryophyte propagules. – *Proc. R. Soc. B* **286**: 1-8. <https://doi.org/10.1098/rspb.2018.2253>.
- Chmura, D., Żarnowiec, J. & Staniaszek-Kik, M. 2002: Altitude is a better predictor of the habitat requirements of epixylic bryophytes and lichens than the presence of coarse woody debris in mountain forests: a study in Poland. – *Ann. For. Sci.* **79(1)**: 1-15. <https://doi.org/10.1186/s13595-022-01125-z>.
- Číhal, L., Lucie Fialová, L. & Plášek W. 2020: Species distribution model for *Buxbaumia viridis*, identifying new areas of presumed distribution in the Czech Republic. – *Acta Mus. Siles. Sci. Natur.* **69**: 21-28. <https://doi.org/10.2478/cszma-2020-0002>.
- Correns, C. 1899: Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. – Jena.
- Cortini Pedrotti, C. & Aleffi, M. 1992: Lista rossa delle briofite d’Italia. – Pp. 557-637 in: Conti, F., Manzi, A. & Pedrotti, F. (eds), *Libro rosso delle piante d’Italia*. – Roma.
- Crosby, M. R., Magill, R. E., Allen, B. H. & He S. 2000: A Checklist of the Mosses. – Saint Louis.
- De Candolle, M. 1815: *Flore Francaise*, **6**. – Paris.
- Deme, J. & Csiky, J. 2021: Development and survival of *Buxbaumia viridis* (Moug. ex DC.) Brid. ex Moug. & Nestl. sporophytes in Hungary. – *J. Bryol.* **43(3)**: 213-223. <https://doi.org/10.1080/03736687.2021.1916169>.
- Deme, J., Erzberger, P., Kovács, D., Tóth, I. Z. & Csiky J. 2020: *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. in Hungary Predominantly Terricolous and Found in Managed Forests. – *Cryptogam. Bryol.* **41(8)**: 89-103. <https://doi.org/10.5252/cryptogamie-bryologie2020v41a8>
- Dening, K. 1928: Entwicklungsgeschichtliche Untersuchungen am Gametophyten von *Buxbaumia aphylla* (L.). – *Verh. Natur. Ver. Preuss. Rheinl. Westfalen* **85**: 306-344.
- De Notaris, G. 1869: *Epilogo della Briologia Italiana*. – Genova.
- Dierssen, K. 2001: Distribution, Ecological Amplitude and Phytosociological Characterization of European Bryophytes. – *Bryophyt. Bibl.* **56**: 289.
- Dillenius, J. J. 1741: *Historia Muscorum* – Oxford.
- Dixon, H. N. 1932: Classification of Mosses. – Pp. 396-412 in: Verdoorn, F. (ed.), *Manual of Bryology*. – The Hague.
- Duckett, J. G., Burch, J., Fletcher, P. W., Matcham, H. W., Read, D. J., Russel, A. J. & Pressel S. 2004: In vitro cultivation of Bryophytes: a review of practicalities, problems, progress and promise. – *J. Bryol.* **26(1)**: 3-20. <https://doi.org/10.1179/037366803235001742>.
- Eastwood, S. K. 1939: On the moss genus *Buxbaumia*. – *Trillia* **10**: 28-35.
- Edwards, S. R. 1984: Homologies and inter-relations of moss peristomes. – Pp. 658-695 in: Schuster, R. M. (ed.), *New Manual of Bryology*. – Nichinan.
- Erzberger, P., Németh, C., Deme, J. & Csiky, J. 2018: Stomatal anatomy allows clarification of historical collections of *Buxbaumia* species in Hungary. – *Studia. Bot. Hung.* **49(1)**: 71-82. <https://doi.org/10.17110/StudBot.2018.49.1.71>
- Fabricius, P. C. 1743: *Primitiae Flora Butisbacensis, sive sex decas plantarum rariorum inter alias circa Butisbacum sponte nascentium*. – Wetzlar.
- Fiori, A., 1886: Muschi del Modenese e del Reggiano. Iª contribuzione – *Atti Soc. Nat. Modena Mem.* **5**: 127-179.
- Frahm, J. P. 2001: *Biologie der Moose*. – Berlin.

- Fukasawa, Y., Osono, T. & Takeda, H. 2009: Dynamics of physicochemical properties and occurrence of fungal fruit bodies during decomposition of coarse woody debris of *Fagus crenata*. – J. For. Res. **14(1)**: 20-29. <https://doi.org/10.1007/s10310-008-0098-0>.
- Giordano I. C. 1879: *Pugillus Muscorum in Agro Neapolitano Lectorum*. – Atti Soc. Crittog. Ital. **2**: 71.
- Gleditsch, D. I. G. 1753: *Methodus Fungorum*. – Berlin.
- Goebel, K. 1892a: Archegonienstudien. – Flora **76**: 92-116.
- Goebel, K. 1892b: On the Simplest Form of Moss. – Ann. Bot. **6(24)**: 355-360.
- Goebel, K. 1905: Organography of Plants, Especially of the Archegoniatae and Spermaphyta: Special organography, **2**. – Oxford.
- Goffinet, B., Buck, W. R. & Shaw A. J. 2008: Morphology, anatomy, and classification of the Bryophyta. – Pp. 55-138 in: Goffinet, B. & Shaw, A. J. (eds.), Bryophyte biology, **2**. – Cambridge.
- Goode, J. A., Stead, D. & Duckett J. G. 1993: Redifferentiation of moss protonemata: An experimental and immunofluorescence study of brood cell formation. – Canad. J. Bot. **71**: 1510-1519. <https://doi.org/10.1139/b93-183>
- Gould, S. J. 1977: Ontogeny and Phylogeny. – Cambridge. <https://doi.org/10.1017/s0016756800041868>
- Grandstein, S. R. & Wilson, R. 2008: Protonemal Neoteny in Bryophytes. – Pp. 1-11 in: Mohamed, H., Baki, B. B., Nasrullaq-Boyce, A. & Lee, P. K. Y. (eds.), Bryology in the New Millennium. – Kuala Lumpur.
- Gruba, P. & Zwydak, M. 2010: Chemistry of Aluminium and Base Cations in Coarse Woody Debris. – Pol. J. Environ. Stud. **19(4)**: 707-713.
- Guillet, A., Hugonnot, V. & Pépin, F. 2021: The Habitat of the Neglected Independent Protonemal Stage of *Buxbaumia viridis*. – Plants **10(83)**: 1-14. <https://doi.org/10.3390/plants10010083>.
- Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N. G., Lehmann, A. & Zimmermann, N. E. 2006: Using Niche-Based Models to Improve the Sampling of Rare Species. – Cons. Biol. **20(2)**: 501-511. <https://doi.org/10.1111/J.1523-1739.2006.00354.x>.
- Gyosheva M. M., Natcheva R. 2022: First report of *Cladosporium herbarum* (Caponodiales, Dothideomycetes) on the rare moss *Buxbaumia viridis* in Bulgaria. – Phytol. Balcan. **28(2)**: 157-160. <https://doi.org/10.7546/PhB.28.2.2022.2>.
- Haberlandt, G., 1886: Beitrage zur Anatomie und Physiologie der Laubmoose – Berlin.
- Haller, A. 1742: *Enumeratio Methodica Stirpium Helvetiae Indigenarum*, **1**. – Göttingen.
- Hallingbäck, T. 1992: The effect of air pollution on mosses in Southern Sweden – Biol. Conserv. **59(2-3)**: 163-170. [https://doi.org/10.1016/0006-3207\(92\)90577-A](https://doi.org/10.1016/0006-3207(92)90577-A)
- Hancock, J. A. & Brassard, G. R. 1974: Phenology, sporophyte production, and life history of *Buxbaumia aphylla* in Newfoundland, Canada. – Briologist. **77(4)**: 501-513. <https://doi.org/10.2307/3241798>.
- Hansruedi, F. 1988: Fungi on bryophytes. – Bot. Hel. **98(2)**: 239-269. <https://doi.org/10.5169/seals-68587>.
- Hassel, K. & Gaarder, G. 1999: Grønnsko *Buxbaumia viridis*: Nyfunn, utbredelse og status i Norge. – Blyttia **57**: 173-180.
- Hedwig, J. 1801: *Species Muscorum Frondosorum*. – Leipzig.
- Hill, M. O., Bell, N., Bruggeman-Nannenga, M. A., Brugés, 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. – J. Bryol. **28**: 198-267. <https://doi.org/10.1179/174328206X119998>.
- Hodgetts, N., Cáliz, M., Englefield, E., Fettes, N., Criado, M. G., 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., ... Żarnowiec, J. 2019: A miniature world in decline: European Red List of Mosses, Liverworts and Hornworts. – Brussels.

- Hoelzel, I. G. 1758: *Dissertatio Inauguralis Botanica de Buxbaumia*. – Erlangen.
- Hoff, M., Dreger, F. & Miesch, R. 1995: L'herbier "Stirpes Cryptogamae Vogeso-Rhenanae" de J. B. Mougeot, C. G. Nestler et W. P. Schimper. – Bull. Assoc. Philom. Alsace Lorraine **31**: 77-91.
- 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 Soc. Bot. Pol. **83(2)**: 137-145. <https://doi.org/10.5586/asbp.2014.015>.
- Hugonnot V., Pépin F., Bichon V. 2023: Révision chorologique et écologique de *Buxbaumia viridis*, espèce protégée en France. – Carnets Bot. **128**: 1-9. <https://doi.org/10.34971/aqef-9m56>.
- Hytteborn, H., Liu Q-H. & Verwijst, T. 1991: Natural disturbance and gap dynamics in a Swedish boreal spruce forest. – Pp. 93-108 in: In: Nakagoshi N. & Golley F. B. (eds.) Coniferous Forest Ecology from an international perspective. – The Hague.
- Hytteborn, H. & Packham, J. R. 1987: Decay rate of *Picea abies* logs and the storm gap theory: a re-examination of Sernander plot III, Fiby urskog, Central Sweden. – Arboric. J. **11(4)**: 299-311. <https://doi.org/10.1080/03071375.1987.9756362>.
- Ignatov, M., Spirina, U. N., Kolesnikova, M. A., Volosnova, L., F., Polevova, S. V. & Ignatova, E. A. 2018: *Buxbaumia*: a moss peristome without a peristomal formula. – Arctoa **27**: 172-202. <https://doi.org/10.15298/arctoa.27.17>.
- Imhof, S., Massicotte, H. B., Melville, L. H. & Peterson, L. 2013: Subterranean Morphology and Mycorrhizal Structures. – Pp. 157-214 in: Merckx, V. (ed.), Mycoheterotrophy. The Biology of Plants Living on Fungi. – Leiden.
- Infante, M. & Heras, P. 2018: Note on the Herbivory on *Buxbaumia viridis* Sporophytes in the Pyrenees. – Cryptogam. Bryol. **39(2)**: 185-194. <https://doi.org/10.7872/cryb/v39.iss2.2018.185>.
- Karppanen, O., Venäläinen, M., Harju, A. M. & Laakso, T. 2008: The effect of brown-rot decay on water adsorption and chemical composition of Scots pine heartwood. – Ann. For. Sci. **65(6)**: 610 (1-8). <https://doi.org/10.1051/forest:2008035>.
- Koch, K., Frahm, J-P. & Pollawath, R. 2009: The cuticle of the *Buxbaumia viridis* sporophyte. – Flora **204(1)**: 34-39. <https://doi.org/10.13140/2.1.4164.7366>.
- Korhonen, L., Korhonen, K. T., Rautiainen, M. & Stenberg, P., 2006: Estimation of Forest Canopy Cover: a Comparison of Field Measurement Techniques. – Silv. Fenn. **40(4)**: 577-588.
- Kropik, M., Zechmeister, H. G. & Fuxjager, C. 2020: The Fate of Bryophyte Sporophytes-Phenology and Vectors of *Buxbaumia viridis* in the Kalkalpen National Park, Austria. – Plants **9(10)**: 1-10. <https://doi.org/10.3390/plants9101320>.
- Kuijt, J. 1969: The Biology of Parasitic Flowering Plants. – Berkeley.
- Lachat, T., Bouget, C., Büttler, R. & Müller, J. 2013: Deadwood: quantitative and qualitative requirements for the conservations of saproxylic biodiversity. – Pp. 92-102 in: Kraus D. & Krumm F. (eds), Integrative approaches as an opportunity for the conservation of forest biodiversity. – Joensuu.
- Leake, J. R. 1994: The biology of myco-heterotrophic ("saprophytic") plants. – New Phytol. **127(2)**: 171-216. <https://doi.org/10.1111/j.1469-8137.1994.tb04272.x>.
- Leake, J. R. 2005: Plants parasitic on fungi: unearthing the fungi in myco-heterotrophs and debunking the "saprophytic" plant myth – Mycologist **19(3)**: 113-122. [https://doi.org/10.1017/S0269-915X\(05\)00304-6](https://doi.org/10.1017/S0269-915X(05)00304-6).
- Limpricht, K. G. 1895: Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. Dr. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz – Leipzig.
- Linnaeus, C. 1760: *Amoenitates Academicae*, **5**. – Stockholm.
- Löbel, S. & Rydin, H. 2009: Dispersal and life history strategies in epiphyte metacommunities: alternative solutions to survival in patchy, dynamic landscapes. – Oecologia **161(3)**: 569-579. <https://doi.org/10.1007/s00442-009-1402-1>.
- Martin, A. R. 1757: *Buxbaumia* – Uppsala.

- Massalongo, C. 1896: Novità della flora briologica del Veronese. – Boll. Soc. Bot. Ital. **8**: 209-211.
- Mastracci, R., Düll, R. 1991: Le raccolte delle escursioni del Congresso Internazionale di Briologia. – Pp. 93-124 in: Mastracci, M. (ed.), Atti Congresso Internazionale Briologia – L'Aquila.
- Micheli, P. A. 1729: *Nova Plantarum Genera*. – Florence.
- Möller, H. 1923: Lövmossornas utbredning i Sverige. VIII. *Timmiaceae*, *Weberaceae*, *Buxbaumiaceae* och *Georgiaceae*. – Ark. Bot. **18**: 1-76.
- Mougeot, J. B. & Nestler, C. 1823: Stirpes Vogeso-Rhenanae quae Rheni superioris inferiorisque, nec non Vogesorum praefecturis, **1**. – Bruyerii Vogesorum.
- Mueller, M. J. 1972: Observations on the Ultrastructure of *Buxbaumia* Protonema. Plasmodesmata in the Cross Walls. – Bryologist. **75(1)**: 63-68. <https://doi.org/10.2307/3241523>
- Müller, J. 2012: Beobachtung von Herbivorie an *Buxbaumia aphylla* Hedw. – Arch. Bryol. **135**: 1-5.
- Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T. K., Virtanen, R. 2010: Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. – Conserv. Biol. **24(1)**: 101-112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>.
- Nimis, P.L. & Martello, S. 2020: Italic 7.0. The information system on Italian lichens. – <https://italic.units.it/index.php>.
- Papp B., Ódor P., Szurdoki E. 2014: Greenshield moss. – Pp. 25-27 in: Haraszty, L. (ed.), Natura 2000 species and habitats in Hungary – Csákvár.
- Pedrotti, F. 1996: Suddivisione botaniche dell'Italia. – Plant Biosyst. **130(1)**: 214-225. <https://doi.org/10.1080/11263509609439528>
- Pfeffer, W., 1871: Bryogeographische Studien aus den rhätischen Alpen – Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. **24**: 1-142.
- Plášek, V., 2001: Epixylic moss *Buxbaumia viridis* jako bioindikátor? – Acta Fac. Rer. Natur. Univ. Ostraviensis, Biologia & Ekológia **8**: 62-63.
- Plášek, V. 2004: The moss *Buxbaumia viridis* (*Bryopsida*, *Buxbaumiaceae*) in the Czech part of the Western Carpathians. Distribution and ecology. – Pp. 37-44 in: Stebel, A. & Ochyra, R. (eds), Bryological Studies in the Western Carpathians. – Pozan.
- Price, M. J. & Ellis, L. T. 2015: Lectotypification of *Buxbaumia aphylla* Hedw. and *B. aphylla* var. *viridis* DC. (*Buxbaumiaceae*). – J. Bryol. **37(3)**: 209. <https://doi.org/10.1179/1743282015Y.0000000010>.
- Proctor, M. C. F. & Tuba, Z. 2002: Poikilohydry and homoihydry: antithesis or spectrum of possibilities? – New Phytol. **156(3)**: 327-349. <https://doi.org/10.1046/j.1469-8137.2002.00526.x>.
- Rivas-Martínez S. & Loidi, A. 1999: Bioclimatology of the Iberian Peninsula. – Itinera Geobot. **13**: 41-47.
- Rossi, G., Montagnani, C., Gargano, D., Peruzzi, L., Abeli, T., Ravera, S., Cogoni, A., Fenu, G., Magrini, S., Gennai, M., Foggi, B., Wagensommer, R. P., Venturella, G., Blasi, C., Raimondo, F. M. & Orsenigo, S. 2013: Lista Rossa della Flora Italiana. 1. Policy Species e altre specie minacciate Comitato Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare. – Roma.
- Róthero, G., 2008: Ecology and management of deadwood for *Buxbaumia viridis* and other bryophytes. Course notes. – Salisbury.
- Ruete, A., Wiklund, K. & Snäll T. 2012a: Hierarchical Bayesian estimation of the population viability of an epixylic moss. – J. Ecol. **100(2)**: 499-507. <https://doi.org/10.1111/j.1365-2745.2011.01887.x>.
- Ruete, A., Yang, W., Barring, L., Stenseth, N. C. & Snäll, T. 2012b: Disentangling effects of uncertainties on population projections: climate change impact on an epixylic bryophyte. – Proc. R. Soc. B. **279**: 3098-3105. <https://doi.org/10.1098/rspb.2012.0428>.

- Saccardo, P. A., 1872: *Musci tarvisini enumerati, tabulisque dichotomicis strictim et comparate descripti*. – Atti Soc. Veneto-Trentina Sci. Nat. **1**: 21-63.
- Schall, P., Gossner M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S. C., ... Ammer, C. 2018: The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. – J. Appl. Ecol. **55**(1): 267-278. <https://doi.org/10.1111/1365-2664.12950>.
- Schmidel, D.C.C. 1783: *Dissertationes Botanici Argumenti Revisae et Recusae*. – Erlangen
- Schumacker, R. & Martiny, P. 1995: Red Data Book of European bryophytes. Part. 2: Threatened bryophytes in Europe including Macaronesia. – Trondheim.
- Schumacker, R., Soldán, Z., Aleffi, M. & Miserere, L., 1999: The bryophyte flora of the Gran Paradiso National Park (Aosta Valley and Piedmont, Italy) and its immediate surroundings: a synthesis. – *Lejeunia* **160**: 1-107.
- Sguazzin F., 2004: Contributo alla conoscenza della flora briologica delle Alpi Giulie (Friuli Venezia Giulia). Briofite raccolte nella conca dei Laghi di Fusine (Tarvisio). – *Gortania* **26**: 137-147.
- Sguazzin, F., 2005: Contributo alla conoscenza della flora briologica del Friuli-Venezia Giulia. – *Inform. Bot. Ital.* **37**(1): 92-93.
- Snäll, T., Ribeiro, P. J. Jr. & Rydin, H. 2003: Spatial occurrence and colonisations in patch-tracking metapopulations: Local conditions versus dispersal. – *Oikos* **103**(3): 566-578. <https://doi.org/10.1034/j.1600-0706.2003.12551.x>.
- Söderström, L., 1988a: The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in Northeast Sweden. – *Biol. Conserv.* **45**(3): 169-178. [https://doi.org/10.1016/0006-3207\(88\)90137-1](https://doi.org/10.1016/0006-3207(88)90137-1).
- Söderström, L., 1988b: Sequence of bryophyte and lichens in relation to substratum variables of decaying coniferous wood in northern Sweden. – *Nord. J. Bot.* **8**(1): 89-97. <https://doi.org/10.1111/j.1756-1051.1988.tb01709.x>.
- Spitale, D. & Mair, P. 2015: Predicting the distribution of a rare species of moss: The case of *Buxbaumia viridis* (Bryopsida, *Buxbaumiaceae*). – *Pl. Biosyst.* **151**(1): 9-19 <https://doi.org/10.1080/11263504.2015.1056858>.
- Spitale, D., Mair, P. & Tratter, W. 2015: Nuove segnalazioni di *Buxbaumia viridis* (Bryopsida, *Buxbaumiaceae*) in Alto Adige e relazione tra presenza e quantità di necromassa. – *Gredleriana* **15**: 17-23.
- Strazzaboschi, L. 2017: *Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl: presenza in Friuli Venezia Giulia e predisposizione di un modello distributivo finalizzato al suo monitoraggio. – *Gortania* **38**: 9-20.
- Taylor, E. C. 1962: The Philibert Peristome Articles. An abridged translation. – *Bryologist.* **65**(3): 175-212.
- Taylor, S. 2010: *Buxbaumia viridis* in Abernethy Forest and other sites in northern Scotland. – *Field Bryol.* **100**: 9-14.
- Taylor, S. 2012: Records of *Buxbaumia viridis* growing on new substrates. – *Field Bryol.* **107**: 21-22.
- Thomas, C. D. 1994: Extinction, Colonization, and Metapopulations: Environmental Tracking by Rare Species. – *Conserv. Biol.* **8**: 373-378.
- Walter, H. & Straka, H. 1970: *Arealkunde*. – *Floristisch historische Geobotanik*, **2**. – Stuttgart.
- Weber, H. C. 1993: *Parasitismus von Blütenpflanzen*. – Darmstadt.
- Wiklund, K. 2002: Substratum preference, spore output and temporal variation in sporophyte production of the epixylic moss *Buxbaumia viridis*. – *J. Bryol.* **24**: 187-195. [doi:10.1179/037366802125001358](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*. – *Canad. J. Bot.* **81**(6): 541-549. <https://doi.org/10.1139/b03-048>.

- Wiklund, K., Rydin, H. 2004: Ecophysiological constraints on spore establishment in bryophytes. – *Funct. Ecol.* **18(6)**: 907-913. <https://doi.org/10.1111/j.0269-8463.2004.00906.x>
- Wolf, T. 2015: Untersuchungen zu den Entwicklungsstadien von *Buxbaumia viridis* Lam. & DC.) Moug. & Nestl. (Grünes Koboldmoos). – *Carolinea* **73**: 5-15.

Addresses of authors:

Domenico Puntillo* & Michele Puntillo,
Museo di Storia Naturale della Calabria ed Orto Botanico. Università della Calabria,
87036 Arcavacata di Rende (Cosenza), Italy.

* Corresponding author: domenicopuntillo@virgilio.it - <https://orcid.org/0000-0003-2156-3542>.

