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Unravelling the ecological drivers of *Schistostega pennata* (Hedw.) F.Weber & D.Mohr on the Iberian Peninsula: distribution and conservation

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ABSTRACT

Introduction. In the Iberian Peninsula, *Schistostega pennata* is a rare, acidophilic, Holarctic moss with a characteristic glowing protonema when illuminated by sunlight. It is typically found in dark and humid habitats and is categorised as Threatened or Near Threatened on the Iberian Red Lists. The main aim of this study was to improve knowledge of the distribution, ecology and conservation of *S. pennata* on the Iberian Peninsula.

Methods. All data that were available to us for *Schistostega pennata* on the Iberian Peninsula (relating to distribution, ecology, phenology) were compiled from the literature, citizen science platforms, and our own observations. Species distribution models were created in Maxent to provide the first approximation to its potential Iberian distribution.

Key results. Twenty-six new populations of *Schistostega pennata* were located, making a total of 73 records for the Iberian Peninsula, mostly from natural and artificial caves, cavities, mines and crevices, and essentially on siliceous substrates. All observations corresponded to areas with abundant rainfall, mild temperatures, and at least some oceanic influence. Species distribution models predicted an expanded potential climatic range in the Iberian temperate region and several montane Mediterranean areas.

Conclusions. There remains very little information on *Schistostega pennata* on the Iberian Peninsula. Existing data coincide with the ecology of the species, although other niches are exploited in other parts of the world that do not seem to occur in this area. It is important to promote its conservation, given the fragmentation of its populations and habitat requirements. Monitoring and initiation of exhaustive sampling campaigns involving citizen science could be a good way to approach this.

KEYWORDS
Conservation biology; glowing protonema; Goblin's gold; Schistotegaceae; species distribution models; vulnerable moss

Introduction

Schistostega pennata (Hedw.) F.Weber & D.Mohr is the only member of the family Schistostegaceae and one of the most intriguing of all mosses. 'Luminous moss', 'Goblin's gold' and 'Dragon's gold' are some of its common names, referring to its most interesting feature: its ability to appear to glow in the dark. This property is due to its persistent, emerald-green, shining protonema (Glime and Turzańska 2017; Casas et al. 2020). Specialised cells in the protomena have a single, large, lens-shaped vacuole, whose curved surface is capable of redirecting and focusing light towards chloroplasts. When light comes from a single direction, chloroplasts move to the most intensely lit spot on the inner cell side, generating the characteristic luminosity of the protonema (Glime and Turzańska 2017). This characteristic has promoted many 'fantastic' stories about the taxon (Crum 1973; Berqvist 1991; Glime and Turzańska 2017), and it is one of the few mosses declared as a 'Natural Monument' in Hokkaido, Japan (Kanda 1971; Iwatsuki 1977; Kanda 1988). Beyond this feature, its tiny distichous feather-like green leaves, which go quite unnoticed, are the other diagnostic character that makes *S. pennata* practically unmistakable.

Ecologically, *Schistostega pennata* is an unsuccessful competitor, easily displaced by other moss species (Lye 1972; Opmanis 1996). It has been found in dark environments both natural and manmade, such as animal burrows, the root plates of fallen trees, slopes and spaces under boulders, but mostly in caves, shafts, mines, cavities, cracks and tunnels, generally occupying areas near the entrance characterised by low-light conditions (Lye 1972; Reinoso Franco et al. 1994; Reinoso Franco 1998; Ignatov and Ignatova 2001; Smith 2004; Harpel and Helliwell 2005; Mežaka et al. 2011; Glime and Turzańska 2017; Ignatov et al. 2017). It is an acidophilic, calcifuge species usually found on granite, gneiss, or sandstone substrates (Casas de Puig 1978; Casas et al. 1989; Reinoso Franco 1998).

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Schistostega pennata requires slightly humid conditions, and some studies indicate that it usually occurs in areas with a clear oceanic influence (Reinoso Franco 1998; Garcia et al. 2008). Its level of specialisation leads to a certain sensitivity to threats such as soil destabilisation and log removal (Mežaka et al. 2011) and others that affect natural and artificial cavities, such as vandalism, mining and water extraction (Sérgio et al. 2012). Populations of *S. pennata* are often isolated and highly fragmented (Reinoso Franco et al. 1994; Reinoso Franco 1998; Harpel and Helliwell 2005; Mežaka et al. 2011) or have disappeared from their original natural or artificial habitats due to human pressure (Reinoso Franco 1998; Mežaka et al. 2011). This highlights the need for effective conservation measures to protect the species and its habitats.

The luminous moss is defined as a Holarctic species and is limited to the northern hemisphere. It has been recorded in the USA (Harpel and Helliwell 2005; Martin Hutten, Glacier Bay National Park and Preserve, US National Park Service, personal communication) and Canada (Harpel and Helliwell 2005) in North America, and in China (Li et al. 2001), Japan (Suzuki 2016), Russia (Ignatov and Ignatova 2001; Ignatov et al. 2006) and Iraq (Aziz 2011) on the Asian continent. However, it is especially common in Europe, occurring in many countries: Austria (Köckinger et al. 2008), Belarus (Rykovsky and Maslovsky 2004), Belgium (Charissou 2014), Bulgaria (R. Natcheva and A. Ganeva in Ellis et al. 2012), the Czech Republic (Plášek 2014), Denmark (Nyholm 1960), Estonia (Kalda et al. 1992), Finland (Hallingback et al. 2006; Juutinen et al. 2016), France (Charissou 2014), Germany (Grünberg et al. 2014), Italy (Aleffi et al. 2020), Latvia (Mežaka et al. 2011), Lithuania (Jukoniene 2021), Luxembourg (Werner 2011), the Netherlands (Rozemeijer 2005), Norway (Lye 1972), Poland (Cykowska 2006; Świerkosz and Reczyńska 2013), Portugal (Hespanhol et al. 2005; Garcia et al. 2008), Romania (Mohan 1998; Erzberger et al. 2012), Slovakia (Mišíková et al. 2020), Slovenia (Martinčič 2012), Spain (Casas de Puig 1978; Reinoso Franco 1998), Switzerland (Roloff and Bertram 2020), Sweden (Hallingback et al. 2006; Perhans et al. 2007), Ukraine (Cheliag-Sosonka 1996) and the UK, but not in Ireland (Edwards 1978; Atherton et al. 2010). However, in many of these countries there are very few records, pointing to the need for more research on its distribution. In such contexts, species distribution models (SDMs) are powerful tools for predicting the potential climatic range of a species (Guisan and Zimmermann 2000; Austin 2002; Guisan and Thuiller 2005; Elith and Leathwick 2009; Mateo et al. 2011). Furthermore, SDMs can identify suitable climatic areas at which to address a variety of ecological and conservation questions (Sérgio et al. 2007; Kruijer et al. 2010; Spitale and Mair 2017).

The Iberian Peninsula represents the southwestern limit of the distribution of *Schistostega pennata* in the Eurasian region. Information on Iberian populations of the species has always been fragmentary and irregular. There are some historical records from the French Pyrenean Departments (Boulay 1884; Allorge 1955), Portugal (Machado 1918; Ervideira 1922; Machado 1930; Allorge 1931; Luisier 1950; Tavares 1955, 1956; Casas et al. 1989; Sérgio and Schumacker 1992; Sérgio 1996) and Spain (Casares 1921; Allorge 1927, 1929, 1935; Bescansa 1948; Allorge 1955; Simó et al. 1978; Fernández-Ordóñez 1985; Casas et al. 1989; Casas 1993a, 1993b; Reinoso Franco et al. 1994; Casas et al. 1997; Reinoso Franco 1998) before the twenty-first century. Since then, no studies have been carried out to review the distribution of *S. pennata* on the Iberian Peninsula. In fact, the most recent data are indirectly provided by floristic or ecological studies not necessarily focusing on the species (Sérgio et al. 2001; Hespanhol et al. 2005; Garcia et al. 2008; Sérgio et al. 2009; Sérgio and Garcia 2010; Rosa and Penado 2013; Penado et al. 2013; Luceño et al. 2016; Sérgio et al. 2021).

Schistostega pennata is categorised as Vulnerable (VU) in the Spanish Red List (Garilleti and Albertos 2012) as well as in the Galicia and Euskadi regional lists (Reinoso Franco et al. 2002; Consejería de Medio Ambiente y Política Territorial (España) 2013), and as Near Threatened (NT) in Portugal (Sérgio et al. 2012). These categories indicate the importance of efforts to conserve the species.

The main goals of the present study were: (i) to update the knowledge of the ecology and distribution of *Schistostega pennata* on the Iberian Peninsula, and (ii) to elucidate the potential distribution range of *S. pennata* on the Iberian Peninsula. We further provide several remarks on the conservation of this species.

Materials and methods

Study area

The study was carried out on the Iberian Peninsula (southwestern Europe) (Figure 1), a region mainly occupied by Spain and Portugal but also by Andorra, the British territory of Gibraltar, and the southernmost parts of the French Pyrenean Departments. The Iberian Peninsula includes two macroclimates: temperate (20.35% of total area of the Iberian Peninsula and Balearic Islands), defined by a lack of dry summer months, and Mediterranean (79.65%), with at least two dry months in the summer (Rivas-Martínez et al. 2011). A transitional area (known as submediterranean), which has a semiarid summer period, is located between these two bioclimatic regions (Sánchez de Dios et al. 2009, Rivas-Martínez et al. 2017).

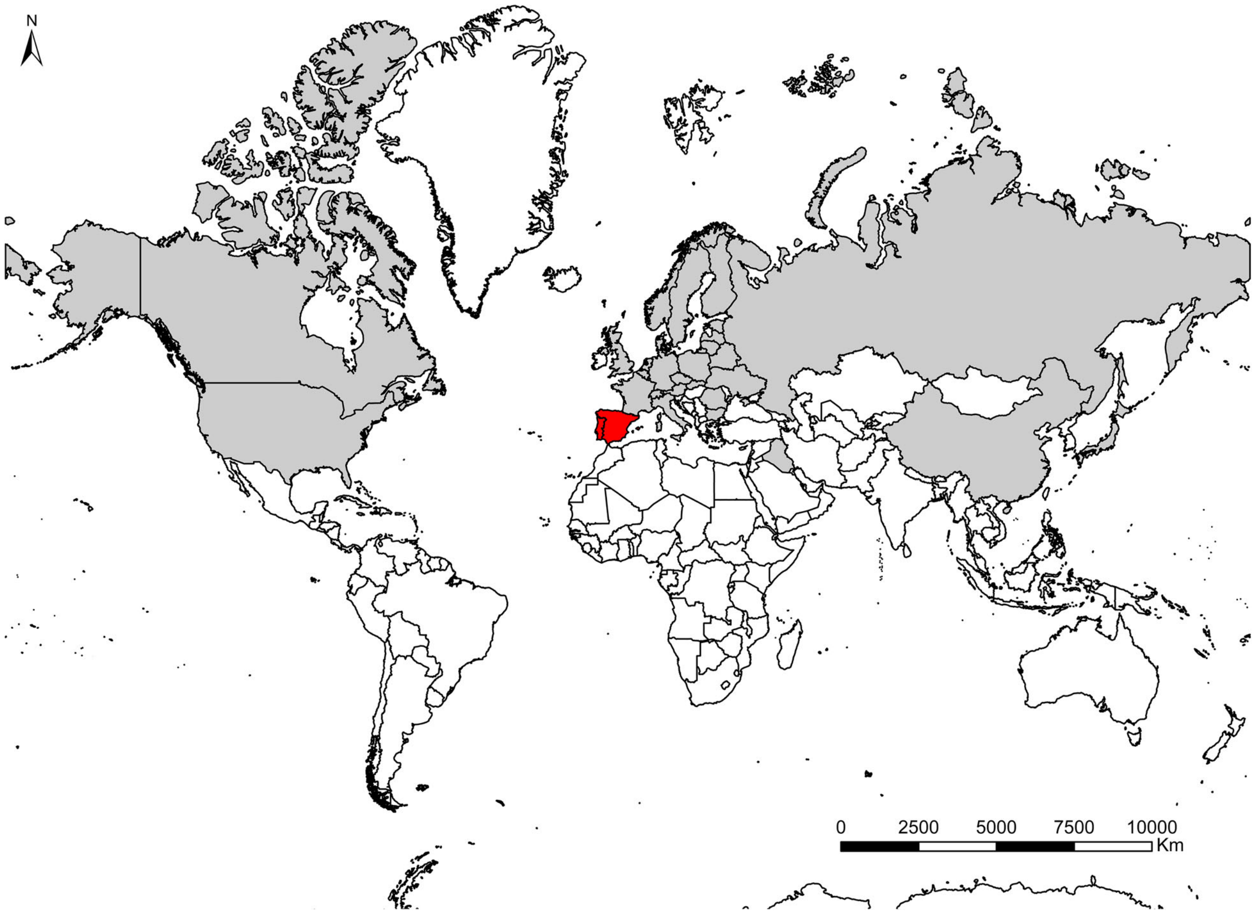

Figure 1. Distribution of *Schistostega pennata* around the world. Countries with confirmed presence of the luminous moss (solid grey), countries with no records (white), and the study area, the Iberian Peninsula (red).

Data collection

A compilation of records of *Schistostega pennata* on biodiversity data platforms (iNaturalist, http://www.inaturalist.org; Global Biodiversity Information Facility, http://www.gbif.org; Biodiversidade, http://www.biodiversidade.eu; and Observation.org, http://www.observation.org) was created, and only undoubtful records were retained in a database. Furthermore, an additional bibliographic search was carried out across scientific and grey literature. Finally, several herbaria (University of Oviedo, FCO; Atlantic Botanic Gardens of Gijon, JBAG; University of León, LEB; University Pablo de Olavide, UPOS; University of Sevilla, SEV; and University of Córdoba, COFC) were consulted to find additional occurrences. Only records collected up to 31 December 2022 were included. Additional field sampling was carried out in Galicia, Asturias, Navarra and Euskadi (northern autonomous regions in Spain) between 2019 and 2022 in search of new populations of *S. pennata*.

For all confirmed populations of *Schistostega pennata*, the following data were obtained where they were available from the information sources: observation month, substrate, elevation, habitat, and climatic conditions (mean annual temperature and annual precipitation from the nearest area weather station). Otherwise, climate data were extracted from https://es.climate-data.org/, and soil substrate from the lithological Iberian maps (Terán and Solé-Sabarís 1978). Distribution maps were generated with ArcMap 10.8 from ArcGis Desktop (ESRI, https://www.esri.com/en-us/arcgis).

Species distribution models

Modelling area. We calibrated the SDMs covering the full global geographical range of *Schistostega pennata*. The Holarctic biogeographical region was used to define the spatial extent (Barve et al. 2011; Acevedo et al. 2012; Mateo et al. 2015). The boundary of the Holarctic area was delimited using the definitions of Nearctic and Palearctic ecoregions provided by Olson et al. (2001).

Predictor variables. Annual potential evapotranspiration from the CGIAR Consortium for Spatial Information (Trabucco and Zomer 2018, https://cgiarcsi.community), at 30-second resolution (~1 × 1 km at the equator) for the 1970–2000 period, was considered a candidate variable because it had been observed to play an important role in bryophyte distributions (Mateo et al. 2015; Campbell et al. 2021; Wen et al. 2021; Hespanhol et al. 2022). Soil pH, obtained from ISRIC World Soil Information (Hengl et al. 2014; http://soilgrids.org), at 250 m resolution, was also selected as an apparently important variable for the species (Lye 1972; Casas et al. 1989; Reinoso Franco 1998). Data on bioclimatic variables were obtained from WorldClim 2.1 (Fick and Hijmans 2017; available at http://www.worldclim.org).

Variables were built at a 30 second resolution using functions from the R package raster (Hijmans and Joe 2017). Predictor variables were selected using the function 'corSelect' in the R package fuzzySim (Barbosa 2015). Among each pair of variables correlated at a higher than 0.7 Pearson correlation coefficient (Guisan et al. 2017), the one with the best fit, according to the individual *p* value, AIC (Akaike's information criterion; Akaike 1973) and BIC (Bayesian information criterion: Schwarz 1978), was selected. A VIF (variance inflation factor: Marquardt 1970; Mansfield and Helms 1982) from R package HH (Heiberger 2018) was then calculated for each selected variable to ensure that multicollinearity was not present in further analyses (VIF score retained < 13.5). A total of seven predictor variables were retained after selection analyses for SDMs construction (Table 1). All analyses were performed in R version 4.2.2 (R Core Team 2022).

Occurrence data. Species distribution models were calibrated using data from different sources. For the distribution outside the Iberian Peninsula, we used a dataset of occurrences obtained at http://www.gbif.org. In addition, the data from http://arctoa.ru/ and Charissou (2014) were also considered as a complement. A list of all these records is included in the Supplemental Material 1. For the Iberian Peninsula, we considered all known and new information compiled in the present study (Appendix 1). For the model calibration, we used only those records with uncertainty in their coordinates less than the resolution of our predictor variables (i.e. 1 km).

Table 1. Predictor variables used in the Maxent modelling of the distribution of *Schistostega pennata*.

Predictor variable	Brief description	Unit
Bio 2	Mean diurnal range (mean of monthly [maximum temperature − minimum temperature)	°C
Bio 7	Temperature annual range (Bio 5–Bio 6)[a]	Dimensionless
Bio 8	Mean temperature of wettest quarter	°C
Bio 12	Annual precipitation	mm
Bio 15	Precipitation seasonality (coefficient of variation)	Dimensionless
Bio 17	Precipitation of driest quarter	mm
Soil pH	pH–H_20 in the topsoil	–

[a]Bio 5 corresponds to the maximum temperature of the warmest month and Bio 6 to the minimum temperature of the coldest month.

Modelling settings. Maximum entropy niche–based modelling (Maxent) was used to predict the potential geographical distribution of *Schistostega pennata* (Phillips et al. 2004, 2006; Phillips and Dudík 2008). Maxent software 3.4.0 (Phillips et al. 2017) was run using the bootstrap strategy (Efron and Tibshirani 1997). Ten bootstrap replicates were chosen in which observations were resampled with replacement. In each repetition, Maxent randomly selected 70% of the occurrence points for training and 30% for validation (552 and 236 points, respectively). All other Maxent default settings for the calibration of the algorithm were maintained. The layer representing the mean probability of the 10 Maxent bootstrap logistic outputs was recreated with Quantum GIS 3.6.3-Noosa (QGIS Geographical Information System, https://www.qgis.org).

Evaluation. The area under receiver operating characteristic curve (hereafter AUC) was used as a threshold-independent measure of discrimination (Fielding and Bell 1997). The closer the AUC is to 1, the better the model's predictive ability. Models reaching AUC ≥ 0.9 are classified as having an excellent performance (Swets 1988; Araújo et al. 2005). Percentage contribution and permutation importance of each variable to the SDM, and jackknife test results were observed to interpret the importance of the variables for predictive modelling.

Results

Morphological description

Schistostega pennata is a short, dioicous moss with tiny, distichous green leaves that are decurrent and lack a nerve (Figure 2A, B, Figure 3A, B). The fertile stems support sporophytes with erect setae and capsules lacking peristomes (Figure 2D). It has a characteristic emerald-green glowing protonema, caused by reflecting light (Figure 3C, D) due to the large vacuoles, inside specialised cells, that act like lenses (Figure 2G). Protonemal cells develop different forms depending on environmental conditions, acquiring a rounded shape in low-light conditions and an elongated shape in better illuminated situations (Figure 2H, I) (Edwards 1978).

Distribution of *Schistostega pennata*

A total of 73 records of *Schistostega pennata* on the Iberian Peninsula were found (Figure 4; Appendix 1). Of these, 47 (64.4%) were previously published records, 11 (15.1%) were from biodiversity data platforms, and 15 (20.5%) corresponded to new occurrences found during our field trips. Regarding geographical distribution, 34 (46.6%) were from Portugal, 33 (45.2%) from Spain and 6 (8.2%) from the

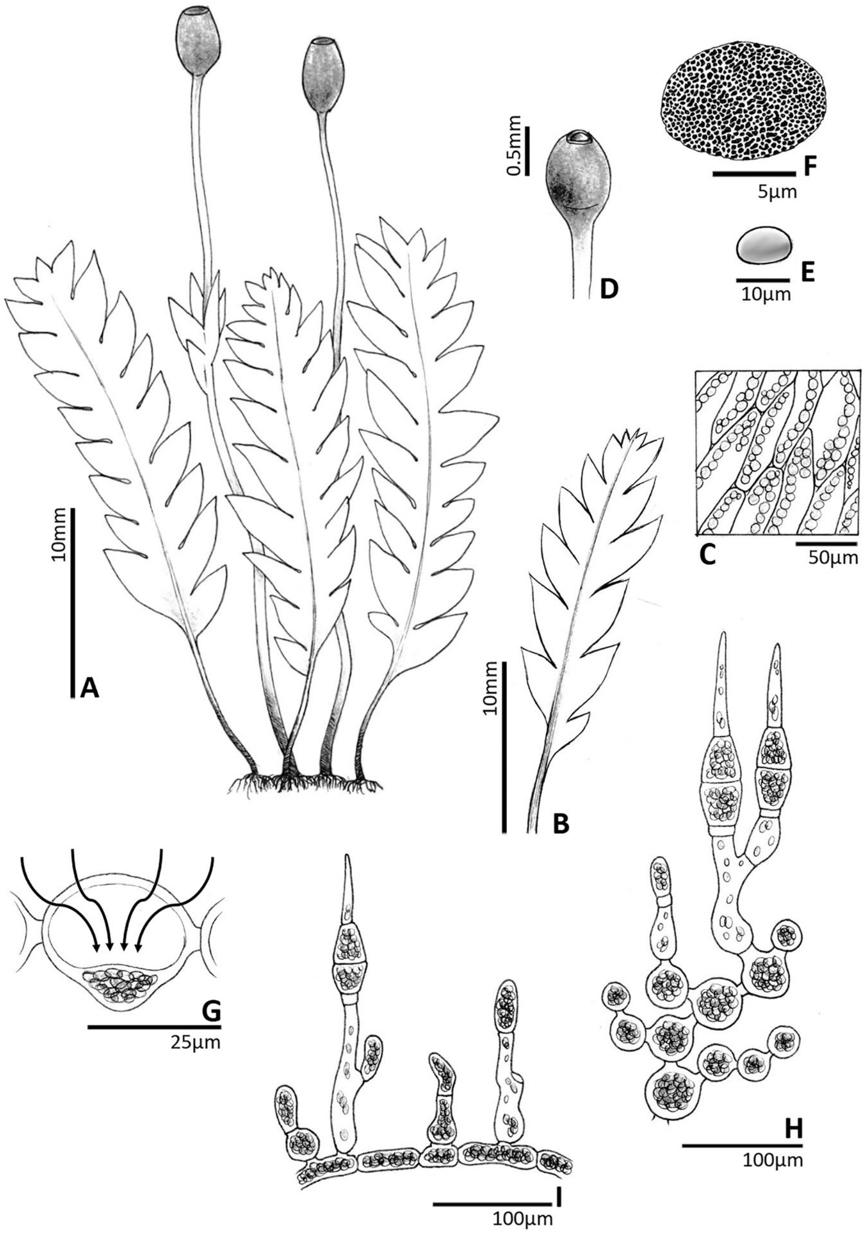

Figure 2. Morphology of *Schistostega pennata*. (A) General aspect (fertile and sterile stems). (B) Leaves from a sterile stem. (C) Laminal leaf cells. (D) Sporophyte capsule. (E) Spore. (F) Detail of spore ornamentation. (G) Protonema specialised cells with lens-like vacuole; arrows indicate light passing through the vacuole and being redirected to chloroplasts. (H) Protonemal cells under low-light conditions. (I) Protonemal cells in more strongly illuminated conditions. H and I are modified from Edwards (1978). Drawn by Víctor González-García.

French Pyrenees (see Figure 4). In addition, *S. pennata* is here reported for the first time from Ourense (Galicia, Spain) and Zamora (Castile and León, Spain). Additional data for several new locations are provided in Supplemental Material 2.

Ecology

A total of 68 (93.1%) records were from inside natural or artificial cavities, caves, mines, cracks or hollows. Only two (2.7%) were from outside such enclosed environments: on a shaded slope (Langreo, Asturias, Spain) and on the root system of a chestnut tree (Muñís, Navia de Suarna, Galicia, Spain). The remaining three records (4.1%) were from unspecified habitats. All observations were of plants on siliceous substrates.

Records of *Schistostega pennata* were made all year round. The mean (± standard deviation) annual temperature of all observation localities was 12.6 ± 1.5°C; the annual precipitation, 1240 ± 264 mm; and the elevation, 607 ± 370 m a.s.l. Data for all Iberian populations are provided in Appendix 1.

Distribution models

The model adequately discriminated between suitable and unsuitable areas for *Schistostega pennata* (average training AUC = 0.955; average AUC standard deviation

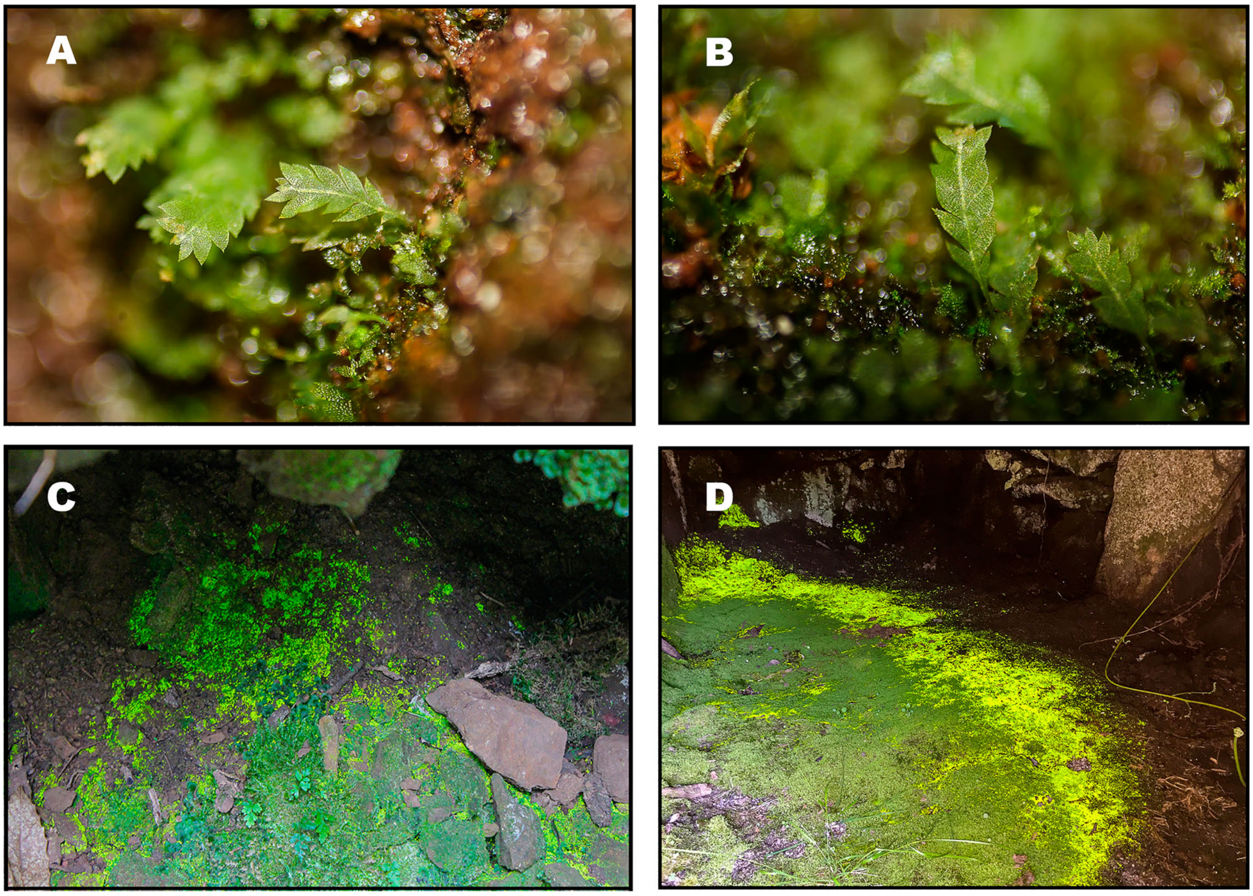

Figure 3. (A, B) Sterile stems with the characteristic distichous fern-like green leaves of *Schistostega pennata*, Pista Finlandesa in Oviedo (Asturias, Spain), UTM 30T 270493 4808966. (C) Glowing protonema of *S. pennata* in a cavity in Pista Finlandesa in Oviedo (Asturias), UTM 30T 270493 4808966. (D) Glowing protonema in a cave in Fornelos de Montes in Pontevedra (Galicia, Spain), UTM 29T 554527 4688643. Photographs: Omar Sánchez (A–C) and J. Eiroa (D).

= 0.002). According to variable percentage contributions and permutation importance together with Jackknife test results (Supplemental material 3 and 4), precipitation in the driest quarter (Bio17) was the most important variable for explaining the distribution of *S. pennata*. Soil pH and annual temperature range (Bio 7) also influenced the species range (Supplemental Material 3–5).

Generally, SDM displayed suitability values within the temperate-oceanic bioclimate area of the Iberian Peninsula, specifically in the northern half of Portugal, in the northern coastal areas of Spain, and in the Pyrenees Departments (Figure 5). Large continuous areas with conditions strongly suited for *Schistostega pennata* were mostly predicted in the Peneda-Gerês Natural Park and in the Serra da Estrela. Similar conditions occur close to the Serra de Xistral in Galicia and in the Peñas de Aya Natural Park between Euskadi and Navarra. Areas with high suitability values were also found far from currently known populations, such as in the Serra of Barbanza or close to the Serra de Outes (both in Galicia), and in the Sierra de Peña de Francia in Castille and Leon (see Figure 5). The SDM showed that the conditions in the central, southern and eastern Iberian Peninsula (mostly Mediterranean areas) seemed unsuitable for this species to thrive.

Discussion

The findings of the present study represent a significant advance in our knowledge of *Schistostega pennata*. The study is, to our knowledge, the first to investigate the potential worldwide distribution of the species in detail, and it also represents the most exhaustive floristic study of *S. pennata* on the Iberian Peninsula. In fact, the number of detected Iberian populations has increased by almost 55%, a considerable value for an apparently patchily distributed moss species.

Distribution and ecology

Patiño et al. (2022) identified a number of important issues as directions for the future of bryological research, one of these being the need to improve our knowledge of biogeographical patterns and processes. Traditionally, *Schistostega pennata* has been represented as a boreal and temperate moss (Reinoso Franco 1998) with a Holarctic distribution

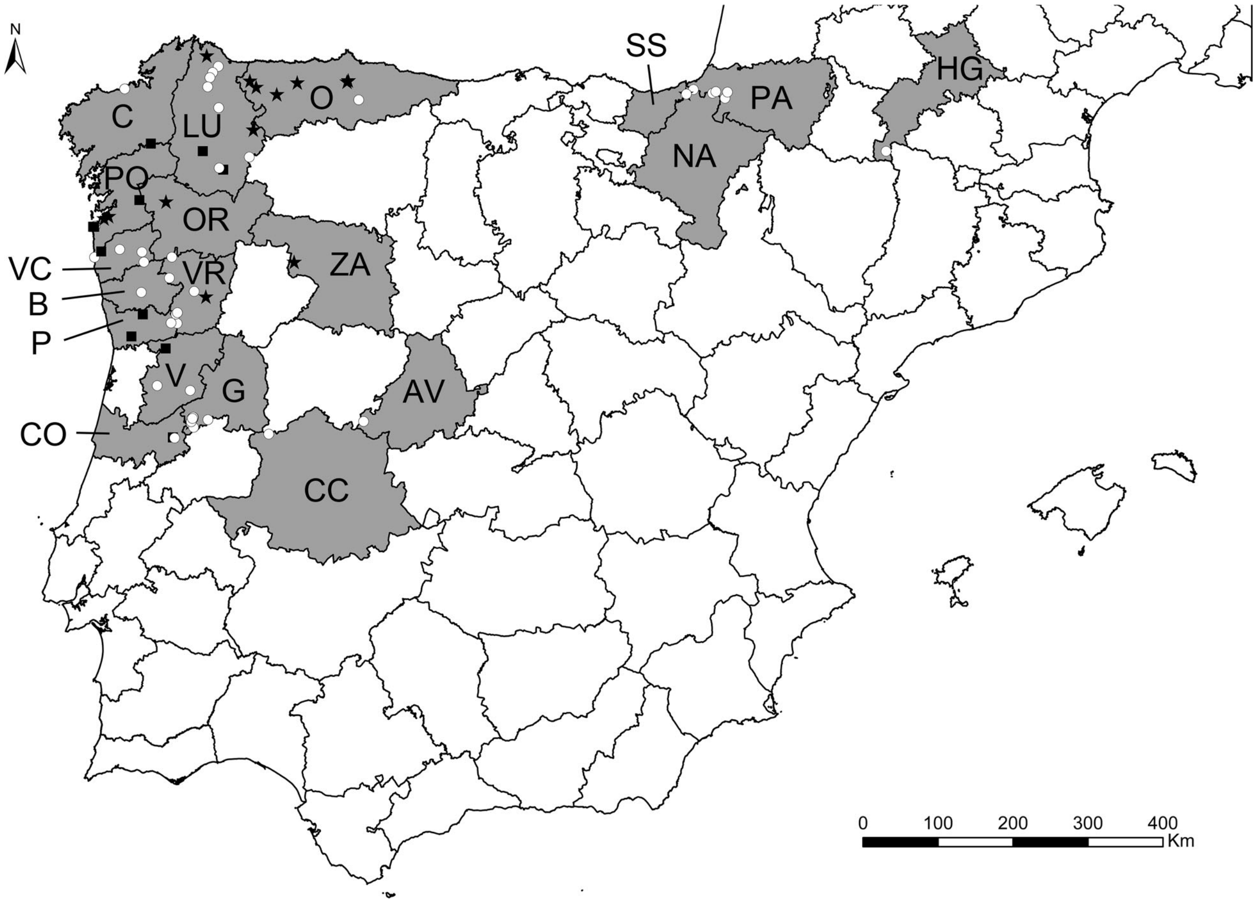

Figure 4. *Schistostega pennata* localities on the Iberian Peninsula (see also Appendix 1). White circles = bibliographic records. Black squares = unpublished new records from citizen science platforms. Black stars = unpublished new records from direct observations. Provinces are classified as confirmed presence (solid grey) and no presence (white) of *Schistostega pennata*. French departments: HG, Haute-Garonne; PA, Pyrénées-Atlantiques. Portuguese districts: B, Braga; CO, Coimbra; G, Guarda; P, Porto; V, Viseu; VC, Viana do Castelo; VR, Vila Real. Spanish provinces (abbreviations based on International Organization for Standardization codes): AV, Ávila; C, A Coruña; CC, Cáceres; LU, Lugo; NA, Navarra; O, Asturias; OR, Ourense; PO, Pontevedra; SS, Gipuzkoa; ZA, Zamora.

(Ignatov and Ignatova 2001; Ignatov et al. 2017). However, certain localities, both new and already known, belong to regions with a slight Mediterranean influence (Casas de Puig 1978; Reinoso Franco 1998). This distribution, coupled with its occurrence in Iraq (Aziz 2011), suggests that *S. pennata* is able survive in a Mediterranean-type climate. In fact, our SDM predicted potential new range within this macroclimatic zone, suggesting that its distribution across the Mediterranean basin could have been underestimated.

A possible explanation for the presence of *Schistostega pennata* in regions characterised by a Mediterranean climate may be its presence in microhabitats that provide the appropriate microecological conditions for persistence, as suggested for other moss species (Fritz and Heilmann-Clausen 2010; Hespanhol et al. 2011; Kraichak 2014; Goia and Gafta 2019; Táborská et al. 2020; Ren et al. 2021). Thus, variables operating at microscale may have more importance on the distribution of *S. pennata* than expected, although they are difficult to model.

Our findings are consistent with *Schistostega pennata* having a preference for acidic substrates, growing mainly on siliceous rocks such as granite, sandstone or gneiss (Lye 1972; Crum and Anderson 1981; Hill et al. 1994; Reinoso Franco 1998; Smith 2004). The importance of soil properties can be observed in northern and central localities where the species occurs on reduced granitic siliceous 'islands' or large terrains (Allorge 1935, 1955; Casas 1993a; Charissou 2014) between calcareous areas (Terán and Solé-Sabarís 1978). In fact, the SDMs captured the acidic soil pH preferences of *S. pennata* as an important explanatory variable, and although we cannot rule out the possibility of populations occurring in calcareous areas, they should be searched for on siliceous outcrops.

Our SDMs present an approach sometimes used to predict moss distributions (see, e.g., Sérgio et al. 2007; Kruijer et al. 2010; Patiño et al. 2016; Spitale and Mair 2017). It is important to note that the SDM must be considered only as a first step towards further elucidating the potential distribution of *Schistostega pennata* on the Iberian Peninsula, and new approximations will need to be carried out using other variables (e.g. topography, substrate, geology, humidity, insolation, orientation). Our SDM predictions can be used to

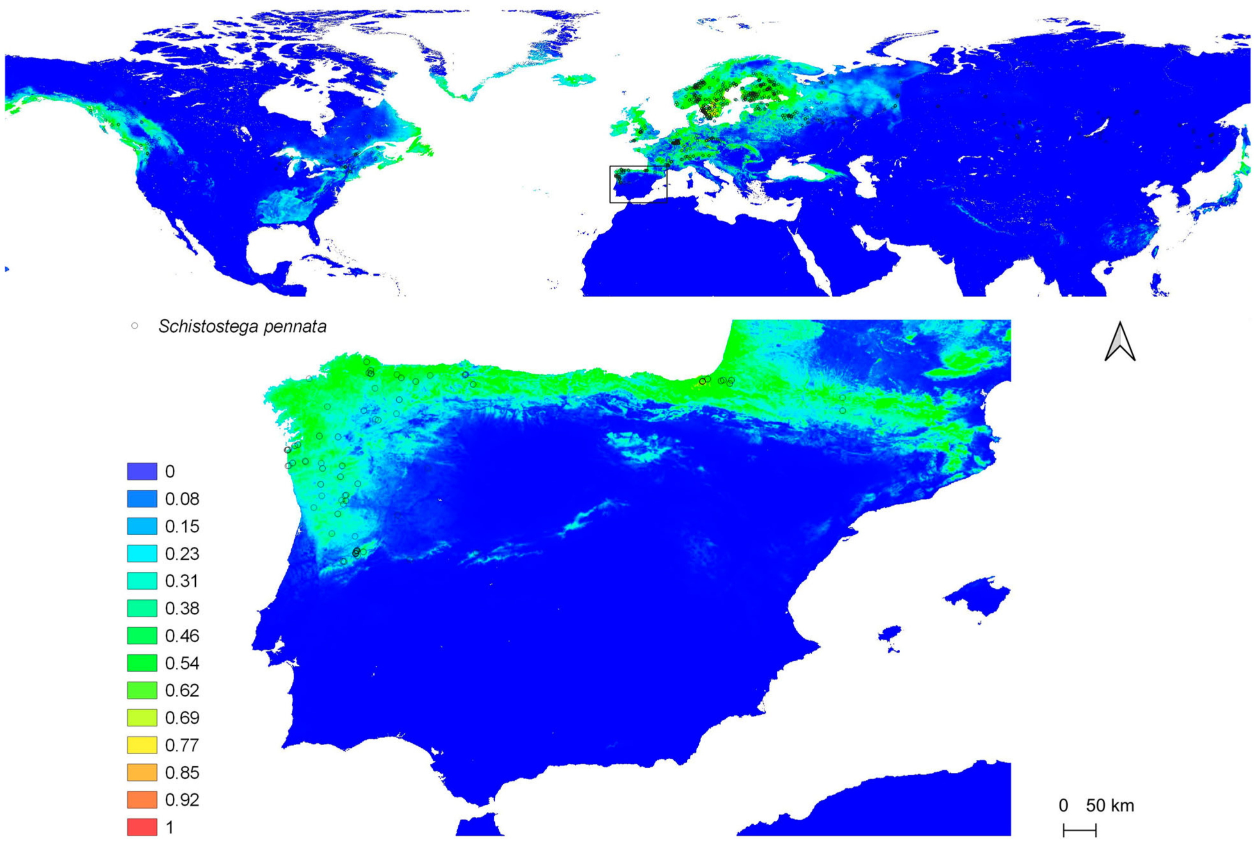

Figure 5. Map of the predictions of Maxent species distribution models (SDMs) of *Schistostega pennata* (Maxent logistic output recreation). (A) Complete worldwide range including a selection of accurate locations. (B) Iberian Peninsula study area; cold colours indicate areas with predicted low suitable conditions for *S. pennata*, and warmer colours indicate higher suitable predicted conditions.

optimise resources in the search for new populations of *S. pennata*, as has been successfully achieved for other species (Edvardsen et al. 2011; Särkinen et al. 2013; Alfaro-Saiz et al. 2015; Fois et al. 2018).

Conservation remarks

Schistostega pennata is considered a rare moss, classified as 'Vulnerable' or 'Endangered' and having some form of statutory protection in several countries (Kalda et al. 1992; Harpel and Helliwell 2005; Hespanhol et al. 2005; Maslovsky 2005; Mežaka et al. 2011; Mišíková et al. 2020). This matches the status of the species in several regions of the Iberian Peninsula (Hespanhol et al. 2005; Garilleti and Albertos 2012; Sérgio et al. 2012). It has been shown that most records occur in natural or artificial caves which are especially sensitive to the transit of people and vehicles (Sérgio et al. 2012). This can be an important threat factor increasing the risk of extinction (Mežaka et al. 2011) and should be taken into account for the Iberian Peninsula. Closing or limiting access to these caves, and thereby minimizing threats such as vandalism, fires, mine exploitation, pollution from vehicles, trampling and water extraction, could be a first step towards preventing further decline of *S. pennata* (Sérgio et al. 2012). Furthermore, this species, given its apparent ecological requirements, might be affected by the higher temperatures and lower precipitation (He et al. 2016) recorded in northern Iberian regions due to climatic change (Esteban-Parra et al. 2003; India et al. 2007; Lorenzo and Alvarez 2020).

Finally, little information is available about demographic trends for *Schistostega pennata* on the Iberian Peninsula, despite its threat status (Garilleti and Albertos 2012). The situation of the species before the 1900s is unknown, and information from the twentieth century is scarce. Therefore, it is necessary to start monitoring the known populations and studying their demographic features, including dispersal, genetic diversity, and recent changes in effective population size. Complementing that is an urgent need to exhaustively search for new populations, a task for which citizen science platforms could be very useful. In this study, half of the new populations were discovered by contributors to citizen science platforms, which reflects the importance of these new resources. Several fundamental questions are key to the advancement of bryology in the coming decades (Patiño et al. 2022) and identifying the best avenues for studying them is the basis for continuing progress in an increasingly changing world. In fact, although all species are potentially impacted by anthropogenic disturbances, rare and threated species may be the first to disappear locally or to become globally extinct.

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Supplemental material

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Supplemental Material 1. Dataset used in the present study for modelling distribution from outside the Iberian Peninsula. GBIF = Global Biodiversity Information Facility (http://www.gbif.org), pers. comm. = personal communication.

Supplemental Material 2. Complete data for the populations examined by the authors.

Supplemental Material 3. Results of the estimates of relative contributions of predictor variables used to estimate their importance to model the distribution of *Schistostega pennata*.

Supplemental Material 4. Results of the jackknife test of variable importance used to estimate the importance of predictor variables to model the distribution of *Schistostega pennata*.

Supplemental Material 5. *Schistostega pennata* occurrences on predictor variables used in this work to model its Iberian distribution.

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Appendix 1. All known Iberian populations of *Schistostega pennata*

Columns are as follows: UTM (population coordinates in UTM system), Locality (with a toponymy, if available), Province (or district), Soil (data extracted from references and Iberian lithological maps), Habitat (extracted from references or obtained from the authors), Elevation (m a.s.l.), T (mean annual temperature in °C), ppt (annual precipitation in mm), Month (month or months of observation) and Source (data origin). For those populations where UTM and Elevation were not clearly known or indicated (or were converted from inaccurate MGRS coordinates), estimated data are provided (*). Where there is more than one record or observation from a given locality, the number of each record is indicated in parentheses.

UTM	Locality	Province	Soil	Habitat	Elevation (m)	T (°C)	ppt (mm)	Month	Source(s)
France									
31 T 304265 4739161*	Grotte de Saint-Mamet – Bagnères-de-Luchon (2)	Haute-Garonne	Siliceous	Cave	750*	6.8	1374	–	Boulay (1884), Charissou (2014)
30 T 624012 4793932	Ainhoa region	Pyrénées-Atlantiques	Siliceous	–	150	12.7	1387	–	Charissou (2014)
30 T 605372 4797153	Col d'Ibardin – Urrugne	Pyrénées-Atlantiques	Siliceous	Mine	370	13.2	1416	–	Charissou (2014)
30 T 636225 4789269*	Mine of Saint-Martin-d'Arrosa	Pyrénées-Atlantiques	Siliceous	Iron mine	310*	12.6	1345	August	Charissou (2014)
30 T 627151 4795517	Mondarrain – Itxassou	Pyrénées-Atlantiques	Siliceous	Cave	716	12.6	1387	–	Allorge (1955), Charissou (2014)
30 T 638492 4795265	Mount Baïgura – Macaye	Pyrénées-Atlantiques	Siliceous	Natural cavity	678	12.6	1345	April	Charissou (2014)
Portugal									
29 T 557128 4597463*	Citânia de Briteiros – Guimarães	Braga	Siliceous	Probably ruins	300*	13.5	1706	–	Luisier (1950)
29 T 590522 4451727	Sardal – Benfeita	Coimbra	Siliceous	Artificial cavity	527	13.1	1049	July	J. Costa (iNaturalist)
29 T 592284 4451220	Arganil – Côja – Mata da Margaraça	Coimbra	Siliceous	Slate cave	970	13.9	1049	–	Casas et al. (1989)
29 T 620000 4470000*	Poço do Inferno, near Manteigas – Serra da Estrela	Guarda	Siliceous	Mine	1000*	11.3	855	–	Allorge (1931)
29 T 620000 4470000*	Poço do Inferno – Serra da Estrela (2)	Guarda	Siliceous	Cave	1000*	11.3	855	–	Casas et al. (1989)
29 T 608358 4466734	Sazes da Beira – Serra da Estrela	Guarda	Siliceous	Cave	730	11.9	1092	May–June, November	G. M. Rosa, observation
29 T 609155 4466687	Sazes da Beira – Serra da Estrela	Guarda	Siliceous	Drainage tunnel galleries	985	11.9	1092	May	Rosa and Penado (2013)
29 T 609101 4470606	Sazes da Beira – Serra da Estrela	Guarda	Siliceous	Drainage tunnel galleries	995	11.8	1043	December–February	Penado et al. (2013)
29 T 609000 4466000*	Near Loriga (Malha Pão) – Serra da Estrela	Guarda	Siliceous	Granitic cave	900	11.9	1092	January	Sérgio (1996)
29 T 611425 4462303	Between Loriga e Alvôco da Serra – Serra da Estrela	Guarda	Siliceous	Cave	800	11.9	1092	March	Sérgio and Garcia (2010)

(*Continued*)

Continued.

UTM	Locality	Province	Soil	Habitat	Elevation (m)	T (°C)	ppt (mm)	Month	Source(s)
29 T 609000 4468000*	Valezim, Ribeira de Coruche – Serra da Estrela	Guarda	Siliceous	Granitic cave	1000	11.8	1092	January	Sérgio (1996), Sérgio and Garcia (2010)
29 T 611209 4472467	Senhora do Desterro – Serra da Estrela	Guarda	Siliceous	Granitic mine	830	11.8	1043	August	Tavares (1955, 1956)
29 T 610424 4472324	Senhora do Desterro – Serra da Estrela	Guarda	Siliceous	Granitic mine	841	11.8	1043	August	Tavares (1955, 1956)
29 T 610869 4472556	Senhora do Desterro – Serra da Estrela	Guarda	Siliceous	Granitic mine	801	11.8	1043	August	Tavares (1955, 1956)
29 T 610131 4471306	Buraco da Moura (Cabeço do Castro) – Serra da Estrela	Guarda	Siliceous	Granitic cave	600	11.8	1043	January	Sérgio et al. (2001)
29 T 593395 4566841	Serra do Marão (2)	Porto	Siliceous	Mine of water	1399*	13.1	1049	–	Ervideira (1922), Casas et al. (1989)
29 T 594091 4567303	Serra do Marão – Pousada	Porto	Siliceous	Granitic cave	1154	13.1	1049	March	Casas et al. (1989)
29 T 558869 4575417	Lousada do Porto	Porto	Siliceous	Cave	377	13.3	1256	March	L. G. Sousa (iNaturalist)
29 T 547592 4553183	Parque Natural Senhora do Salto	Porto	Siliceous	Cave	66	15.0	1186	May	J. Silva (iNaturalist)
29 T 510329 4632007*	Moledo do Minho	Viana do Castelo	Siliceous	Cave or mine	1*	14.6	1758	September	Machado (1930)
29 T 535412 4639931*	Paredes de Coura – Vascões	Viana do Castelo	Siliceous	Probably cave	400*	13.2	1680	–	Machado (1918, 1930), Casas et al. (1989)
29 T 557500 4637500	Peneda-Gêres National Park – Minho	Viana do Castelo	Siliceous	Probably cavity	651	11.5	1299	–	Hespanhol et al. (2005)
29 T 559500 4627500	Peneda-Gêres National Park – Minho	Viana do Castelo	Siliceous	Probably cavity	461	12.7	1946	–	Hespanhol et al. (2005)
29 T 517051 4637738	Vilar de Mouros – Caminha	Viana do Castelo	Siliceous	Mine	27	13.7	1678	August	V. da Silva (iNaturalist)
29 T 585068 4611946	Mina do Borralha – Borralha (2)	Vila Real	Siliceous	Tungsten mines	773	14.9	1009	–	Luisier (1950), Casas et al. (1989)
29 T 587294 4632694	Montalegre – Pitões das Júnias (2)	Vila Real	Siliceous	Font cavity	1050	10.8	1590	June–July	Casas et al. (1989), Sérgio and Schumacker (1992)
29 T 610000 4599000*	Vila Pouca – Carvalhal de Pontido – Mata do Castelo (2)	Vila Real	Siliceous	Cave	800–822	14.4	1248	April–May	Sérgio et al. (2009)
29 T 592000 4576000*	Pardelhas – near Ribeira da Ribeira	Vila Real	Siliceous	Cave	474	15.7	1064	May	Sérgio et al. (2009)
29 T 593500 4577500*	Serra do Alvão – near Pardelhas	Vila Real	Siliceous	Cave	693	15.7	1064	May	Sérgio et al. (2009)
29 T 593500 4577500*	Mondim de Bastos, near Pardelhas	Vila Real	Siliceous	Cave	502	15.7	1064	May	Sérgio and Garcia (2010)
29 T 668208 4540684	Tresminas	Vila Real	Siliceous	Several gold mines	735	11,49	849	August	L. Carlón, observation
29 T 582175 4541432	Bustelo – near Vila Boa de Baixo	Viseu	Siliceous	Artificial cavity	789	14.2	1285	June	J. Costa (iNaturalist)
29 T 574000 45040000*	Serra do Penoita, near Vouzela	Viseu	Siliceous	Probably cavity	750*	14.9	1248	–	Luisier (1950)
29 T 607484 4499541*	Penalva do Castelo (between Peges and Vila Mendo) (2)	Viseu	Siliceous	Probably cavity	615*	13.3	888	–	Luisier (1950), Casas et al. (1989)
Spain									
29 T 539426 4797126*	Sabón beach – Arteixo	A Coruña	Siliceous	Granite cliff mine	8*	13.4	1228	–	Bescansa (1948)
29 T 565286 4744092	River Ulla, close to San Xusto	A Coruña	Siliceous	Cave	192	12.8	1509	March	Iván (iNaturalist)
29 T 667164 4800726	Excomulgada mine – San Martín de Oscos	Asturias	Siliceous	Iron mine	922	10.8	1229	July–August	N. Blanco, observation
30 T 270493 4808966	Pista Finlandesa – Oviedo	Asturias	Siliceous	Granite cavity	309	12.1	1293	December–May	Authors' observation
30 T 279933 4789922*	Las Piezas road – Sama de Langreo	Asturias	Siliceous	Shadowed slope	200	11.3	1293	–	Simó et al. (1978)
30 T 269186 4807752	Mount Naranco – Oviedo	Asturias	Siliceous	Granite cavity	541	12.1	1293	July	Authors' observation
29 T 687390 4794258	Xan Rata cave – Allande	Asturias	Siliceous	Cave	890	9.6	1296	April	L. Carlón, observation
29 T 660895 4806681	Espina – Vegadeo	Asturias	Siliceous	Cave	477	12.8	1167	September	N. Blanco, D. Saldaña et al., observation

(Continued)

Continued.

UTM	Locality	Province	Soil	Habitat	Elevation (m)	T (°C)	ppt (mm)	Month	Source(s)
29 T 706936 4806211	Villatresmil – Tineo	Asturias	Siliceous	Cavity in clay slate-soil	367	10.7	1227	September	F. J. Linares Ferreiro, observation
30 T 274843 4470840	Garci Sánchez rock – Sierra de Gredos	Ávila	Siliceous	Granite cracks	1940	11.5	838	August	Luceño et al. (2016)
29 T 688157 4456969	Los Cortaderos – Sierra de Gata	Cáceres	Siliceous	Granite cavities	1040	14.2	804	May	Luceño et al. (2016)
30 T 597840 4791995*	Montes Haya – Peñas de Aya	Gipuzkoa	Siliceous	Granite caves	500	12.4	1417	–	Allorge (1935), Allorge (1955)
30 T 598502 4792736	Peñas de Aya – Oiartzun	Gipuzkoa	Siliceous	Granite cracks	759	12.4	1417	February and December	Authors' observation
29 T 636681 4719624	A Veneira de Roques – Ferreiro	Lugo	Siliceous	Iron cave or mine	922	11.0	1138	September	I. Reguero (iNaturalist)
29 T 631117 4780007*	Castro de Viladonga – Castro de Rei	Lugo	Siliceous	Mine near the ruins	535*	11.5	1167	–	Reinoso Franco (1998)
29 T 632699 4721228*	Cova das Choias – Incio	Lugo	Siliceous	Iron mine	554*	11.0	1138	August	Casares (1921)
29 T 661994 4732601*	Pedrafita do Cebreiro – Piedrafita	Lugo	Siliceous	Pyrite mine	1150	11.5	1084	–	Allorge (1927)
29 T 630000 4820000*	Valadouro	Lugo	Siliceous	–	100*	12.1	1657	–	Casas et al. (1989)
29 T 616317 4737336	Suar	Lugo	Siliceous	Font cavity	543	11.5	998	May	M. Cabana and A. Romeo (iNaturalist)
29 T 624567 4813945	Val do Inferno – Monndoñedo	Lugo	Siliceous	Excavation in a peat bog	550	11.3	1203	July	Casas (1993b)
29 T 622000 4809000	Xestido – Abadín	Lugo	Siliceous	Granite excavations	610	11.0	1167	July	Reinoso Franco et al. (1994)
29 T 620000 4800000*	Xistral mount – Xestido	Lugo	Siliceous	–	600	11.0	1167	September	Casas et al. (1997)
29 T 665303 4759211	Muñís – Navia de Suarna	Lugo	Siliceous	Root system	770	12.6	1362	June	E. Díaz, observation
29 T 618610 4830107	Jove, near Rego do Loureiro river	Lugo	Siliceous	Cave	325	11.6	1413	June	E. Sulmont, A. Labroche, P. Aguado-Ramsay et al., observation
30 T 598601 4792726*	Aiako Harriak – Lesaka	Navarra	Siliceous	Hole in granite wall	640*	12.4	1417	February	Casas (1993a)
29 T 580873 4687343	Cova da Moura – Laias	Ourense	Siliceous	Artificial cavity	143	13.0	1121	–	C. Pizcueta, observation
29 T 511000 4663000	Baiona beach – Baiona	Pontevedra	Siliceous	Granite cliff cave	10	13.7	1678	May	Reinoso Franco et al. (1994)
29 T 519835 4670318	Covas do Folón – Coruxo	Pontevedra	Siliceous	Granite cave	76	13.9	1739	–	C. Pizcueta, observation
29 T 554527 4688643	Fornelos de Montes	Pontevedra	Siliceous	Cave or mine	941	13.9	1409	June–August	J. Eiroa and G. Mucientes (iNaturalist)
29 T 509000 4662187	Cova das Lagoas	Pontevedra	Siliceous	Cave	12	14.5	1402	May	J. L. Camaño (iNaturalist)
29 T 510021 4662059	Cova de Baredo ou das Figosas	Pontevedra	Siliceous	Cave	11	14.8	1589	May	J. L. Camaño (iNaturalist)
29 T 524324 4672613	Beade – Vigo	Pontevedra	Siliceous	Mine	68	14.5	1601	All year	A. Pascual and J. H. Rodríguez, observation
29 T 709122 4630363	Mary Carmen mine – San Blas	Zamora	Siliceous	Barite mine	639	12.9	469	–	J. M. Domínguez and A. Rivas, observation