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Towards a moss sclerophylly continuum: evolutionary history, water chemistry and climate control traits of hygrophytic mosses

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Summary

- Mosses are amongst the oldest and simplest plants, they can be found almost everywhere in the world, and they condition the structure and function of many ecosystems. Their sensitivity to environmental changes makes them very interesting subjects of study in ecology and understanding them can provide insights into the evolutionary history of plants. However, the study of moss traits and their relationship with their environment is far behind that of vascular plants.
- We sampled 303 assemblages of aquatic and semi-aquatic (hygrophytic) mosses growing in semi-natural springs distributed around the north-east of the Iberian Peninsula to study how moss traits vary depending on their evolutionary history, climate and water chemistry. To do so, we analysed 30 moss species and 17 traits using phylogenetic comparative methods and an extended RLQ analysis, accounting for spatial and phylogenetic information. We hypothesised that there is a sclerophylly continuum in mosses living across a gradient of high and low water conductivity springs that may mimic sclerophylly in vascular plants that live in stressful environments.
- Results indicated that life forms and, especially, morphological traits were well preserved phylogenetically and responsive to water chemistry and climate. That combined with spatial autocorrelation in environmental variables resulted in a clustered distribution of phylogenetically closely-related mosses in space. Mosses living in springs with a warm and dry climate that discharge hard water mainly presented species with needle-like leaves, were denser and had lower water absorption capacity. The opposite was found in cold, humid and soft water springs.
- *Synthesis*: Our results suggest that climate and water chemistry are main determinants of traits of hygrophytic mosses and of species distributions. We found evidence of a potential sclerophylly continuum in moss traits, which we hypothesise may be mainly related to physical and physiological constraints produced by water

chemistry. Our findings describe moss sclerophylly in a gradient of water conductivity similar to that found in vascular plants with water availability and temperature. Further experimental studies will be required to confirm the observations found in this study.

Second abstract (Catalan - Català)

- Les molses són les plantes més simples i antigues. Gairebé arreu del món condicionen l’estructura i el funcionament dels ecosistemes. Llur sensibilitat als canvis ambientals fa que el seu estudi sigui d’especial rellevància en el camp de l’ecologia, aportant coneixements molt valuosos sobre la història evolutiva de les plantes. Tanmateix, l’estudi de les molses i les relacions d'aquestes amb l’ambient resta encara a les beceroles en comparació amb les plantes vasculars.
- Es van mostrejar 303 comunitats de molses aquàtiques i semi-aquàtiques (higrofítiques), que habitaven fonts semi-naturals de Catalunya, per estudiar com els trets de les molses variaven segons la seva història evolutiva, el clima i la química de l’aigua de les fonts on es trobaven. Es van analitzar 30 espècies de molses i 17 trets fent servir mètodes filogenètics i un anàlisi RLQ, incorporant informació espacial i filogenètica. La nostra hipòtesi era que, en molses higrofítiques, existeix un gradient d’esclerofília que opera a través d’un gradient de conductivitat de l’aigua de les fonts, de forma similar al que trobem en les plantes vasculars que viuen en ambients estressants.
- Els resultats indiquen que les formes de vida i els trets morfològics de les molses estan ben preservats filogenèticament i que varien seguint els gradients de conductivitat de l’aigua i del clima. Aquest fet combinat amb l’autocorrelació espacial en les variables ambientals, resulta en una distribució agregada en l’espai de les espècies més properes filogenèticament. Les molses que viuen en fonts de clima càlid i sec i de les quals brolla aigua d’alta conductivitat tendeixen a ser més

denses, absorbir menys aigua i a tenir fil·lidis més allargassats. La tendència oposada es troba en fonts de clima fred, humit i amb aigua de baixa conductivitat.

- *Síntesi*: Els nostres resultats suggereixen que el clima i la química de l'aigua determinen els trets de les molses higrofítiques i llurs distribucions. Hem trobat evidències d'un potencial gradient d'esclerofília en els trets de les molses que hipotetitzem que està relacionat amb els constrenyiments físics i fisiològics imposats per la química de l'aigua de les fonts. Seran necessaris treballs experimentals per a confirmar les observacions trobades en aquest estudi.

Keywords: bryophytes, morphology, life-history traits, water conductivity, calcium carbonate

1. Introduction

Mosses are amongst the simplest and oldest plants on Earth and, despite their small size, they played a remarkable role shaping our planet in ancient times (McMahon & Davies, 2018). Still in our era, they continue to condition the structure and function of ecosystems, representing one of the largest groups of land plants, found almost everywhere in the world (Medina, Draper, & Lara, 2011). Their simplicity and particular physiology make bryophytes very interesting subjects of study in ecology, especially because the lack of thick cuticles and roots makes them extremely sensitive to environmental changes (Porley & Hodgetts, 2005) and pollution (Sayol et al., 2017). Nonetheless, the proportion of studies focusing on the response of bryophytes to environmental factors, compared to vascular plants, is dramatically low. However, understanding bryophytes better could provide important insights about unresolved questions of evolutionary ecology and physiology of plants (Fernández-Martínez et al., 2018; Proctor & Tuba, 2002; Sussmilch, Roelfsema, & Hedrich, 2018) due to them being ubiquitous and simple organisms: characteristics of a potentially good model study system. The study of functional traits is definitely one of the fields that could benefit most from the study of bryophytes (Sussmilch et al., 2018).

Functional traits are often considered to be morphological, physiological, reproductive and life-history features measurable at the individual level but relatively consistent within populations and species that affect performance or fitness of the individuals (Violle et al., 2007). Plant traits define ecological strategies and determine how species respond to environmental conditions, how they interact with higher trophic levels and how they influence ecosystem function (Kattge et al., 2011). The study of plant traits and their relationship with ecological strategies and ecosystem trade-offs has been a long-standing focus in plant ecology (Poorter et al., 2009; Shipley, Lechowicz, Wright, & Reich, 2006; Wright et al., 2004). However, although the main efforts of researchers have been focused on vascular plants, several studies focused on bryophyte traits have provided the basis for understanding their relationship with the environment.

In 2007, Hill et al. published an extraordinarily large dataset of bryophyte traits, including morphological, reproductive and life-history traits. Several researchers have studied moss traits in boreal and arctic ecosystems (Elumeeva, Soudzilovskaia, During, & Cornelissen, 2011; Jonsson et al., 2014; Kangas et al., 2014; Mazziotta, Granath, Rydin, Bengtsson, & Norberg, 2019; Sokołowska, Turzańska, & Nilsson, 2017; Turetsky et al., 2012), alpine habitats (Ah-Peng et al., 2014; Wang, Liu, Bader, Feng, & Bao, 2017), tropical forests (Waite & Sack, 2010) and even in vitro experiments (Löbel & Rydin, 2010). Despite intensive local research on moss traits and the extremely useful dataset published by Hill et al. (2007), however, it has not been until 2018 that, to the best of our knowledge, the first paper focused on the relationship between bryophyte traits, species distributions and environmental conditions was published. Löbel et al. (2018) published a study focused on traits of epiphytic mosses, elucidating interesting relationships between moss traits and environmental variables of the studied forests (e.g., fragmentation and climate), shaping moss assemblages across sites. However, they did not take into account the phylogenetic relatedness of the studied species. This could be important because the addition of phylogeny to information about traits could help to clarify the interconnections between local coexistence and macroevolution (de Bello et al., 2015; Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015). In mosses in particular, it has been recently suggested that some traits and adaptations may appear as a response to environmental conditions while other traits remain preserved throughout the evolutionary history of the species (Huttunen, Bell, & Hedenäs, 2018), making phylogenetic comparative methods a necessary tool to understand the evolution of moss traits. Hence, there is still a large gap of knowledge on how environmental conditions and phylogenetic relatedness can shape moss assemblages by means of their relationship with moss traits.

To fill in this gap, our main aim was to explore whether traits of aquatic and semi-aquatic (hereafter, hygrophytic [Dierssen, 2001]) mosses in semi-natural springs are related to their evolutionary history or to environmental conditions such as climate and water chemical composition of the springs. To do so, we performed an extensive field sampling of 303 semi-natural Mediterranean springs, distributed across mountainous regions of the north-eastern Iberian Peninsula (**Figure 1**), from which we analysed their water chemistry and the moss assemblages in contact with spring water (Bes et al., 2018; Corbera et al., 2015; Fernández-Martínez et al., 2019; Sayol et al., 2017). We then inferred the phylogenetic relationships of the sampled species using genetic data and measured and gathered information on 17 moss traits (eight morphological traits, three reproductive traits and six life forms) for 30 moss species. Surveyed springs discharged water continuously throughout the year, which, in Mediterranean regions, means that they behave like small islands, or refugia, where water is available, surrounded by completely different habitats where water is scarce. They are, therefore, ideal habitats for hygrophytic mosses (Bes et al., 2017; Corbera et al., 2015). Also, the distribution of springs in the Mediterranean region is relatively homogeneous throughout the territory, comprising large differences in lithology, water chemical composition, climate and topology (Fernández-Martínez et al., 2019). These large gradients allowed us to investigate how moss traits vary across a very wide range of environmental conditions.

In order to achieve our main objective, we first explored similarities amongst moss species with regard to traits to understand which traits have been environmentally selected and which ones have been preserved through evolutionary history. Secondly, we explored the patterns of species distributions and their traits linked to those of environmental conditions using an extended version of the RLQ analysis (Pavoine, Vela, Gachet, De Bélair, & Bonsall, 2011) meant to account for species phylogenetic relatedness and environmental spatial autocorrelation. Water chemistry has been suggested to influence moss species distributions because of physical and physiological constraints, especially at the high range of water conductivity and pH. Examples of these constraints are the formation of calcium carbonate crusts, lack of CO_2 for photosynthesis and osmotic stress (Bain & Proctor, 1980; Bernstein, 1975; Bes et al., 2018; Grime, Rincon, & Wickerson, 1990; Josep Peñuelas, 1985). Adaptations to these conditions may require similar solutions to those achieved by vascular plants growing under stressful environments. We, therefore, hypothesised that a sclerophylly continuum in hygrophytic mosses living under high and low water conductivity exists that mimics that of sclerophylly in vascular plants. We here expected to find denser (i.e., higher mass per volume and area) mosses with narrower leaves living under high conductivity water rich in calcium (Ca^{2+}) compared to those living under low conductivity water because of the drawbacks that an excess of calcium carbonate can imply for hygrophytic mosses (i.e., less absorbable CO_2, higher osmotic pressure and eventually carbonate crusts) (Bain & Proctor, 1980; Bernstein, 1975; Bes et al., 2018). We additionally investigated whether these sclerophyllic adaptations have been preserved throughout the evolutionary history of the moss species.

2. Methods

2.1 Study area

From 2013 to 2018, we surveyed 303 springs located in mountain regions of the north eastern Iberian Peninsula (**Figure 1**) comprising five different mountain ranges: the Central Littoral mountain range, Montseny-Guilleries, Lluçanès, La Garrotxa and the eastern Pyrenees. Accordingly, the spatial distribution of these springs captured a large gradient in climatic and lithological conditions (Fernández-Martínez et al., 2019). Climate was mainly Mediterranean, being humid and sub-humid in the central and north-western springs, maritime Mediterranean in the southern ones (near the coast) and Mediterranean pre-Pyreneal in the north (Martín-Vide, 1992).

The Central Littoral mountain range is mainly composed of granodiorites and granitoids, except for the eastern side which is dominated by phyllites and other metamorphic rocks (Fernández-Martínez, Bagaria, et al., 2016; Sabater et al., 2015). In Montseny-Guilleries we found springs mainly located over granite, granodiorites and metamorphic rocks, although some were also located over calcareous rocks such as sandstone, limestone, siltstones and marl, which were predominant in Lluçanès region. Further north, near to the Pyrenees, La Garrotxa's springs were located over a Quaternary volcanic field (basalts). Finally, the Pyrenees area was geologically very complex, but most springs surveyed were located over limestone, shale or calcareous rocks. This rich lithology resulted in a very large gradient in water chemical characteristics from the surveyed springs (see Fernández-Martínez et al. [2019]) for further details on lithology and water chemical composition of the springs).

2.2 Field sampling and laboratory analyses

The springs sampled are usually small human-made constructions to collect water from underground and release it through a spout (**Figure S1**). Some springs were built in naturally occurring springs while others collect water from aquifers through water mines. The morphology of the springs is relatively similar amongst them, containing the same four microhabitats: a wet rock wall, the spout from where the water emerges, a little sink where water is partially retained and a canal from where the water drains. Springs surveyed did not receive any sanitary treatment and only those pouring water at the moment of sampling were surveyed. Springs with a tap to control water flow were discarded, given that water was not flowing constantly. Therefore, mosses in our springs were in continuous contact with water during most of the year, interrupted only in some springs because of frozen water in winter or because of intense drought in summer.

Water pH and electric conductivity were measured in the field with a combined pH and conductivity meter. Main cations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) were analysed by ion exchange chromatography and anions (SO_4^{2-}, Cl^- and NO_3^-) were analysed by ionic chromatography. HPO_4^{2-} was measured by the colorimetric method established by (Murphy & Riley, 1962). Water concentration of Al, As, Cd, Co, Cr, Cu, Fe, Mn, Pb, Hg, Ni, Zn was analysed by ICP-MS (Inductively Coupled Plasma-Mass Spectrometry). See Fernández-Martínez et al. (2019) for further details on the methodology used to analyse water chemical composition.

Each spring was geolocated using a GPS device. With these coordinates, we extracted monthly climatic data for temperature and precipitation of the springs from the digital Climatic Atlas of Catalonia (Pons [1996], Ninyerola et al., [2000], available at http://www.opengis.uab.cat/acdc/index.htm). The seasonal values for temperature and precipitation were calculated as the average of December-February (winter), March-May (spring), June-August (summer) and September-November (autumn). Given the high collinearity between climate variables, we only used spring and summer values because those seasons are likely to be the most influential determining spring water runoff (abundant rain during spring season make springs have water during summer). We also calculated temperature and precipitation seasonality as the coefficient of variation of monthly values to assess how different were temperature and precipitation throughout the year. Water availability was calculated as monthly precipitation minus reference evapotranspiration calculated following the Hargreaves method (Hargreaves, 1994). Altitude was extracted with an elevation digital model with 30 metres resolution. We also recorded whether springs were under shade or not as a proxy of insolation. A correlation matrix of the environmental variables can be found in **Figure S2**.

Bryophyte sampling was carried out by collecting a sample of all moss and liverwort species present in the springs that were either in direct contact with the water of the spring or receiving drops over the splash zone **(Figure S1)**. For the purpose of this study, only moss species were used. We did not standardise our sampling by area because of the small area of most of the springs (less than 0.9 m^2) and the lack of a species richness – area relationship in these habitats (Bes et al., 2018). Species were identified using Smith (1990) and Casas *et al.*, (2001, 2004) identification keys, using the nomenclature established by Hill et al., 2006. Once in the laboratory, moss samples were cleaned in order to remove the soil stuck on them and stored dried until laboratory measurements took place. The species accumulation curve confirmed that our sampling gathered most of the biodiversity present in these habitats (**Figure S3**). A total of 46 moss species were found in the sampled springs (**Figure S4**).

2.3 Moss traits

We used three types of moss traits: eight morphological and three reproductive traits, and six life forms (**Table 1**). We measured morphological traits trying to mimic those usually measured in vascular plants (e.g., leaf mass area) to test if variation in moss morphological traits followed the same sclerophylly pattern that vascular plants show. We additionally gathered information on reproductive traits and life forms because they have been suggested to be important determinants of moss species distribution in previous studies (Huttunen et al., 2018; Löbel et al., 2018; Löbel & Rydin, 2010; Pohjamo, Laaka-Lindberg, Ovaskainen, & Korpelainen, 2006). Morphological traits were leaf length, width, form (as the leaf length-to-width ratio) and area, spore diameter, moss mass per area (MMA), water absorption capacity (WAC) and moss density (i.e., dry weight per volume). To measure moss leaves, we used lab tweezers to carefully separate three leaves from the stems and placed them in a coverslip, where they were rehydrated. Once rehydrated, we flattened the leaves as much as possible and photographed them above a piece of graph paper with a camera mounted on a microscope. Measurements of leaf length, width and area were then taken using *ImageJ* software. Spore diameter was calculated as the average between maximum and minimum spore diameter provided in BRYOATT (Hill et al., 2007).

Moss mass per area was calculated as the ratio of moss dry mass to projected area of two to seven individual shoots (depending on the size of the species to ensure measurement with minimum error), arranged lying down, similar to the sclerophylly index developed in Monforte *et al.*, (2018). Mosses were weighed with a precision balance at 0.01 mg resolution. Similar to leaf measurements, we photographed moss samples on top of a piece of graph paper and calculated their area using *ImageJ*. Water absorption capacity was calculated as the fresh-to-dry weight ratio of a few moss individual shoots (the same ones used to calculate MMA). To rehydrate our samples, we submerged them into water for three minutes in a graduated cylinder of 10 ml, recorded the volume of water displaced by the mosses, and then removed the excess of water by gently pressing the mosses against laboratory paper. We then weighed the samples again to obtain fresh weight and calculated water absorption capacity. Moss density was then calculated by dividing dry weight by the volume of water moved by the samples in the pipette. For all these morphological traits (except spore diameter) we repeated these measurements for three to five samples per species from different springs depending on the availability of samples and their state of conservation.

Out of the 46 moss species found, we could only successfully measure morphological traits for 30 of them: *Amblystegium serpens, Anomodon viticulosus, Brachythecium rivulare, Bryum pseudotriquetrum, Cratoneuron filicinum, Ctenidium molluscum, Dialytrichia mucronata, Didymodon tophaceus, Eucladium verticillatum, Fissidens crassipes, Fissidens grandifrons, Fissidens rivularis, Fissidens taxifolius, Fontinalis antipyretica, Gymnostomum calcareum, Leptodictyum riparium, Orthotrichum diaphanum, Oxyrrhynchium speciosum, Palustriella commutata, Philonotis caespitosa, Philonotis fontana, Plagiomnium undulatum, Platyhypnidum riparioides, Pohlia melanodon, Rhizomnium punctatum, Rhynchostegiella teneriffae, Scorpiurium circinatum, Thamnobryum alopecurum, Thuidium delicatulum and Trichostomum crispulum*. The rest of the species were only used in the phylogenetic clustering analyses (see Statistical analyses below).

Information about reproductive traits and life forms (**Table 1**) was extracted from BRYOATT database (Hill et al., 2007). Sporophyte frequency, however, was modified according to the percentage of our samples presenting sporophytes and following the same code proposed by BRYOATT. We used five types of life forms (organization of moss shoots into colonies) following (Mägdefrau, 1982): mats or roughs, turfs, tall turfs, cushions or other life forms. Finally, we also identified moss species as pleurocarpous (female sex organs and capsules are found on short, lateral branches, and not at the tips of branches, and they have a prostrate growth habit) or acrocarpous (with female sex organs and capsules at the tips of stems or branches, and an upright growth habit). Measured moss traits per species can be found in **Table S1**.

2.4 Phylogenetic analyses

We built a phylogeny covering the 44 species of mosses found in this study plus 15 species of liverworts, also found at the springs, used as outgroups. The phylogeny was based on five genes obtained from GenBank (Benson et al., 2018): two nuclear genes (18S and 5.8S) and three plastid genes (rbcL, rps4, TrnL) (Stech & Quandt, 2014) (see GenBank accession numbers in **Table S3**). Genes were aligned using the program MAFFT v7 (Katoh, Misawa, Kuma, & Miyata, 2002) and poorly aligned regions were removed by means of G-Blocks using low stringency options (Castresana, 2000). Phylogenetic analyses were conducted with the package BEAST v1.8.4 (Drummond & Rambaut, 2007) based on an uncorrelated log-normal relaxed clock and a “birth-death incomplete sampling” tree prior. Partitions and nucleotide substitution models were estimated by means of PartitionFinder v2 (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2017). The BEAST analysis relied on two independent MCMC chains that ran for 100,000,000 generations and were sampled each 20,000. Mixing and convergence of both runs were assessed by means of Tracer v.1.7.1 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018). No calibrations were set in the analysis. A summary tree was estimated as the maximum clade credibility tree with median node heights using

TreeAnnotator (included in the BEAST package), setting the posterior probability limit to 0.5. We also resampled 1,000 trees from the posterior distribution to integrate topological and branch length uncertainty in all subsequent analyses. Two species that were not available in GenBank were placed randomly within the clades of other species of their genera (*Fissidens crassipes* and *Mnium marginatum*). In absence of sufficient GenBank data we used data of closely related species: for *Fissidens rivularis* and *Palustriella commutata*, we used genetic information of *Fissidens bryoides* and *Palustriella falcata* respectively (both have been even used as synonyms, see TROPICOS database [http://www.tropicos.org/] and Erzberger [2016]). *Homalia lusitanica* and *Plagiothecium nemorale* were not included in the phylogenetic analysis because their small samples did not allow us to determine their species without uncertainty.

2.5 Statistical analyses

We first explored similarities amongst moss species with regard to traits and how these differences were related to their evolutionary history. To do so, we first performed a hierarchical cluster analysis using Euclidean distances and Ward D2 agglomeration method on the log-transformed (with the natural logarithm) dataset of traits with the *hclust* function in R statistical software (R Core Team, 2018). Binary variables (e.g., pleurocarpous vs. acrocarpous) were coded as 1 and 0 (e.g., pleurocarpous: 1, acrocarpous: 0). A principal components analysis (PCA) was performed with the same log-transformed dataset of traits to visualise how the species would score in two dimensions based on traits. We then tested for the correlation between distance amongst species in the cluster analysis and the phylogenetic tree using a Pearson's correlation.

After, we explored whether moss traits and the two PCA axes extracted in the previous analysis presented a phylogenetic signal (λ). To do so, we used the function *phylosig* in *phytools* R package (Revell, 2012) and tested each variable for 1000 trees to account for phylogenetic uncertainty (we considered that there was a statistically significant phylogenetic signal if percentile 2.5% was higher than 0). We then performed a continuous character mapping of PC1 and PC2 using *contMap* function in *phytools* to further explore the evolution of traits in our phylogeny.

Then, we tested for spatial autocorrelation in environmental variables performing a Moran's I test using function *gearymoran* in ade4 R package (Dray & Dufour, 2007). We tested for phylogenetic and trait clustering in our dataset using the phylogenetic and trait quadratic entropy tests (PQE, TQE) described in (Pavoine, Baguette, & Bonsall, 2010) using function *TPQE* provided in (Pavoine et al., 2011). Trait or phylogenetic clustering would occur if species assemblages in single springs present lower phylogenetic and trait diversity than expected from the pool of species found over the entire set of sampled springs (i.e., significantly higher values than random simulations in PQE and TQE tests). We repeated these tests using springs presenting one to four moss species per spring to test the potential effect of species richness per site on these analyses (**Figure S5**). For phylogenetic clustering analysis we used the 44 species for which we had phylogenetic information, while for trait clustering we used the 30 species with trait data.

Then, to finally test the relationship between moss traits and climate and water chemical composition, we performed an extended version of the RLQ analysis developed by (Pavoine et al., 2011) using R packages *adiv* (Pavoine, 2018) and *ade4* (Dray & Dufour, 2007). RLQ analysis, as well as the corner analysis, is a multivariate method aimed at analysing information on species distribution, environmental conditions and species traits to finally assess the relationship between traits and the environment (Brown et al., 2014; Dolédec, Chessel, Ter Braak, & Champely, 1996; Dray et al., 2014; Dray & Legendre, 2008; Pease, González-Díaz, Rodiles-Hernández, & Winemiller, 2012). The extended version additionally incorporates one matrix to account for spatial autocorrelation and another one to account for phylogenetic nonindependence (see Pavoine et al. [2011] for further details on this analysis). To help visualising the correlation between traits and the environment, we calculated trait vs. environment correlations. To do so, for each trait, we multiplied the value of its correlation between with axis 1 (2 and 3) by the correlation of a given environmental variable with axis 1 (2 and 3), and weighted the result for the percentage of environmental variance explained of the given axis. We repeated that same process for each pair of trait-environmental variables for axes 2 and 3 and summed the three coefficients as a measure of pseudo correlation between the traits and the environment. Finally, the matrix was plotted using a clustered image map using the function *cim* in *mixOmics* R package (Le Cao et al., 2017). We first performed the RLQ analysis using all springs where at least one of the species with traits was present (N=295 springs). We then repeated the extended RLQ analysis using only springs with at least 2 species present (N=195) to test the consistency of the results (**Figure S5**). We also performed a fourth-corner analysis (model type 6), in order to test whether controlling for spatial and phylogenetic autocorrelation or not doing it would lead to different results.

3. Results

3.1 Phylogenetic analyses

The final concatenated alignment, after applying G-blocks, consisted of a maximum of 2660 bps. The best partition strategy estimated by PartitionFinder arranged the five genes in three partitions: partition 1 (5.8S + 18S), partition 2 (rbcL) and partition 3 (TrnL + rps4) with the following substitution models: partition 1 (TRNEF+G), partition 2 (GTR + I + G) and partition 3 (GTR + I + G), the last two partitions with estimated base frequencies. MCMC runs converged to similar posterior estimates and sampled trees were pooled together discarding the initial 10% of each run as ‘burn in’. The summary tree produced phylogenetic relationships generally consistent with previous evidence (**Figure S6**) (Casas et al., 2001; Erzberger, 2016; M. O. Hill et al., 2006).

3.2 Moss traits and their phylogenetic signal

Our results indicated that there are three main distinguishable groups of mosses with regard to their traits (**Figure 2**). The first group of mosses were more likely to be monoecious and pleurocarpous mosses forming mats, with high water absorption capacity (WAC) and mainly sexual reproduction. The second group was characterised by having needle-like leaves (long and narrow), high moss mass per area (MMA) and moss density, low sporophyte frequency and more likely reproducing asexually, being dioecious and forming turfs or cushions. The third group was defined by mosses that were more likely to be acrocarpous, forming tall turfs with big leaves and spores. Overall, the two axes extracted from the PCA explained, respectively, 25.1% and 20.6% of the variance in moss traits (**Figure 2b**).

The PC1 axis, positively describing pleurocarps and mat life forms of small-size leaves, was fairly well preserved in the phylogeny (λ=0.88, **Figure 3, Table 2**). The phylogenetic clade containing from *P. commutata* to *C. molluscum* scored relatively high in PC1, with the exception of *A. viticulosus* and *T. alopecurum*. Instead, *P. undulatum* and *R. punctatum* scored very low for PC1. The PC2 axis, positively related to dense mosses with needle-like leaves and asexual reproduction was not so strongly preserved in the phylogeny (λ=0.64). *G. calcareum* and especially *T. crispulum* and *E. verticillatum* scored high for PC2, while the rest of the species mainly scored negative, especially *R. punctatum, P. riparioides*, and *L. riparium*.

Phylogenetically, morphological traits were, on average, better preserved than life forms, and reproductive traits were not preserved at all (**Table 2**). WAC, MMA and moss density were the three morphological traits with the lowest phylogenetic signal while mats, turfs and being acrocarpous or pleurocarpous were the life forms better preserved in the phylogeny.

3.3 Trait and phylogenetic clustering

We did not find significant trait and phylogenetic clustering nor overdispersion in the moss assemblages of our springs (**Table 3**). Results for traits did not substantially change when analysing all springs or selecting only those presenting two, three or four species present. Instead, for phylogenetic clustering, we detected a shift from results tending towards overdispersion, when using all springs, to clustering when using springs containing at least four species.

3.4 Relationship between traits, climate and water chemistry

The three first RLQ axis extracted explained 48.7%, 14.3% and 8.9% of the variance in environmental conditions. The first axis was clearly positively dominated by water conductivity (and its associated ions such as Ca^{2+} and Mg^{2+}), high temperatures (low altitude) and drought (**Figure 4**). The second axis was mainly the opposite of axis 1, but a few other elements such as temperature seasonality (TS) or cadmium (Cd) had a proportionally higher weight than in axis 1. Our results elucidated three main groups of traits, with regard to their relationship with climate and water chemistry (**Figure 5**). In summary, pleurocarpous mosses forming mats, with high water absorption capacity and low moss density and mass per area that tend to reproduce sexually and are monoecious with big spores and wide leaves are more likely to occur in springs located under a cold and humid climate with high temperature but low precipitation seasonality and oligotrophic water. Conversely, in springs with a warmer and dryer climate and high water conductivity they tend to be occupied by dense acrocarpous mosses forming cushions, presenting needle-like leaves with little capacity to absorb water. They mainly reproduce asexually, are dioecious and have small spores. Turfs, sporophyte frequency and leaf area and length presented very low correlations with environmental variables. Repeating these analyses using springs with at least 2 species per spring did not change the results (**Figure S7**). However, when using the fourth-corner method (which does not account for space nor phylogenetic relatedness in the data) almost all traits presented higher correlations with the environment and, although the general trend was very similar, a few results differed (**Figure S8**).

Spatially, RLQ axis 1 was clustered on the western and southernmost springs (those last ones, very close to the sea, see **Figure 1**) indicating a strong spatial autocorrelation (**Figure 6a,** group A), as also indicated by Moran's I test (**Table S2**). The rest of the springs, located over less calcareous lithology, were mainly aligned with negative values for axis 1 (group B). Our analyses indicated phylogenetic relatedness in the spatial distribution of mosses (**Figure 6b**), some of them most likely found in group A (e.g., *E. verticillatum*, *D. tophaceus*) and some others more likely to occur in group B (e.g., *L. riparium*, *R. riparioides*). Spatially, axis 2 was not so well defined as axis 1, but still, the centremost springs tended to be aligned with high values of axis 2 and the presence of *P. undulatum* or *R. punctatum*.

4. Discussion

4.1 Water chemistry and climate as environmental filters of moss assemblages

Our analyses clearly demonstrated the relationship between moss traits and environmental variables, especially water chemistry and climate (**Figure 5**). These findings support the fact that both water chemistry and climate act as strong environmental filters, conditioning species distribution to specific traits. These findings, however, were in disagreement with trait and phylogenetic clustering tests, reporting no significant clustering or overdispersion for any of them (equal trait or phylogenetic diversity within each spring to that expected by the pool of species found) meaning that species seem to appear in these springs just at random. The most likely explanation of these two divergent results is that moss assemblages in springs are very often characterised for having very few species present (**Figure S5**) compared to other datasets for which these tests have been performed (e.g., La Mafragh, with more than 80% of the sites having 8 or more species present [Pavoine *et al.*, 2011]), which obviously hinders the performance of these permutational tests. However, the lack of a clear phylogenetic or trait clustering signal could also emerge because of a potentially strong dominance of the first species to settle in the springs (priority effect). Another limitation of the methods is that, because of the spatial correlation between temperature and water availability (e.g., rainfall) our analyses do not allow us to tell between the effects of them all. Nonetheless, we suggest that water conductivity is the main driver of the observed changes in traits of mosses living in springs because: *i*) the large majority of our studied springs have water flowing almost continuously throughout the year, making climate water availability relatively unlikely to directly affect moss assemblages, *ii*) water conductivity presents the highest correlations of all environmental variables, *iii*) mean annual precipitation (similar to our climate water availability – the difference between precipitation and evapotranspiration, see methods) has been shown to reduce the concentration of most ions dissolved in spring water (Fernández-Martínez et al., 2019), therefore reducing spring water conductivity, and *iv*) water conductivity has been previously described to play an important role shaping hygrophytic moss assemblages due to the physiological constraints that water conductivity imposes on these organisms (Bain & Proctor, 1980; Bernstein, 1975; Bes et al., 2018; Brown, 1982; Sayol et al., 2017).

As a result of a combined effect of spatially autocorrelated environmental filters (**Table S2**) and the fact that traits are phylogenetically preserved (**Figure 3**) a clear spatial and phylogenetic pattern emerged in these moss assemblages (**Figure 6**). It is very interesting to note the potential role that sea spray may play on the spatial distribution of moss species. Sea spray has been demonstrated to affect atmospheric deposition of salts and even groundwater chemistry, enriching water of these springs with chloride, sulphate, sodium, potassium, magnesium and calcium (Fernández-Martínez et al., 2019). All these elements were positively aligned with axis 1 of the RLQ analysis and presented high scores in almost all springs near the coast despite belonging to a granite lithology (**Figure 6a**, southernmost sites). Hence, according to our results, proximity to the coast may also condition moss establishment because of its effect on water chemistry. It is also interesting that our analyses indicate that there were more species that tend to live in springs with low rather than high conductivity water (**Figure 6b**). This finding may indicate that high conductivity water may be more physiologically demanding than low conductivity water for mosses, potentially for the particular adaptations that they must present to be able to live under these environmental conditions. Our results also indicate that this differentiation between high conductivity-water tolerant and intolerant species may have developed long ago during their evolutionary history, given the fact that all high conductivity-water tolerant species belong to the same clade (**Figure 6b**).

According to our results, the adaptations that hygrophytic mosses require to live in springs with high conductivity water are mainly morphological: needle-like leaves, small spores, high moss density and moss mass per area, low water absorption capacity and being predominantly acrocarpous and forming cushions. These findings agree with previous research suggesting that stress-tolerant species tend to present smaller and needle-like leaves, following an r-selected strategy (During, 1979; Grime et al., 1990). Additionally, small diaspores, suitable for long distance dispersal, have been suggested to be associated with disturbed or with habitats in continuous transition (e.g., springs with growing calcium carbonate crusts) (During, 1992; Löbel et al., 2018).

The strong effect of water conductivity on moss traits may appear because of different physiological constraints. One mechanism that has been suggested in vascular plants is osmotic stress (Bernstein, 1975), reducing growth rates and overall plant vigour (Xiong & Zhu, 2002). Mosses might also potentially suffer osmotic stress and respond in the same way vascular plants do, as suggested by our results. These mosses living under osmotic stress may therefore present higher concentrations of dehydrin proteins and osmotically active sugars, increasing their density and moss mass per area, as do desiccation-tolerant moss species (Proctor et al., 2007). Another potential mechanism explaining the role of water conductivity could be related to key nutrient imbalances or deficiencies. In hard waters phosphate binds with calcium, drastically reducing available phosphate for plants (Doods, 2003). The lack of available phosphate may impose a limitation on larger moss species to establish in springs with hard water, given the paramount role of phosphorus on plant metabolism (Fernández-Martínez et al., 2018; Fernández-Martínez, Vicca, Janssens, Espelta, & Peñuelas, 2016; J. Peñuelas et al., 2019). On the other hand, mosses are supposed to require very little amounts of nutrients to sustain their metabolism (Porley & Hodgetts, 2005). However, this fact should not preclude larger and, therefore, more competitive mosses from establishing preferentially in springs with higher phosphate availability, as our results also suggest – albeit presenting very low correlations (**Figure 5**). Research on moss stoichiometry is therefore warranted to answer these questions.

Another mechanism by which water conductivity may affect moss traits is by modifying available CO_2 in water. In hard water, CO_2 cannot be used for photosynthesis by bryophytes because it is mainly found in the form of bicarbonate (Bowden, 1999; Glime, 2014). In those cases, it has been suggested that only a small subset of species, like *F. antipyretica*, seem to be able to use HCO_3^- as source of carbon for photosynthesis (Bain & Proctor, 1980; Josep Peñuelas, 1985), while most of them cannot (e.g., *C. filicinum, E. verticillatum, F. grandifrons*). The low concentration of free CO_2 may hamper the capacity of aquatic mosses to photosynthesise, and allow only stress-tolerant species to establish. In our study, though, not all moss species that can live completely submerged under water were always found living under water, and those species that cannot, do not usually suffer flooding events. Therefore, most of the mosses sampled should be able to obtain CO_2 directly from the atmosphere, despite the fact that being continuously surrounded by water may potentially hinder the diffusion of CO_2. Nonetheless, the most potentially limiting factor that water conductivity may impose on moss growth is calcium toxicity (Vicherová, Hájek, & Hájek, 2015) and the formation of calcium carbonate crusts all around them (tufa formations). These particular formations only occur because bryophytes act as a surface from which Ca^{2+}-enriched water evaporates, leaving a crust of $CaCO_3$ (Brown, 1982; Glime, 2014). In these habitats, mosses engage in a particular dynamic of growing, dying and overgrowing on $CaCO_3$ crusts to avoid complete coverage. This dynamic may only be achieved by a few species presenting very specialised traits (**Figure 6b**). Overall, our findings suggest the existence of some sort of *sclerophylly* gradient in hygrophytic moss traits in response to water conductivity (**Figure 7**). Sclerophyllous mosses would be characterised by being denser, having high moss mass per area, low water absorption capacity and needle-like leaves. These traits are similar to those found in vascular plants (e.g., leaf mass area) in a gradient of water availability and temperature (Niinemets & Niinemets, 2013; Wright et al., 2004). Considering that adaptations of both types of organisms (mosses and vascular plants) are very similar (e.g., small size, high density and mass per area, needle-like leaves) it seems likely that sclerophylly would have evolved in both groups following convergent evolution.

4.2 Reproductive traits and phylogenetic conservatism

Contrary to morphological traits and life forms, reproductive traits were not phylogenetically preserved. These results may suggest that, apart from being monoecious or dioecious, which is genetically controlled, the main type of reproduction (sexual vs. asexual) and sporophyte frequency may entirely depend on environmental conditions (Huttunen et al., 2018). Our results support this hypothesis across species (**Figure 5**), indicating that sexual reproduction was more likely to occur in cooler and more humid springs with low water conductivity. These results show the opposite to previous research using epiphytic bryophytes (Löbel et al., 2018). Asexual reproduction is thought to be beneficial under wet climates during the early stages of colonisation (priority effect) because of faster germination rates (Löbel & Rydin, 2010; Pohjamo &

Laaka-lindberg, 2004) and because rainy conditions facilitate the release of gemmae (Pohjamo et al., 2006). However, the advantage of asexual reproduction may not be such in our springs, where water is continuously available. Sporophyte frequency, instead, showed no correlation with any environmental variable.

Despite the large similarities in all springs surveyed with regards to microhabitats, we had a very large gradient in climate and water chemistry and a large variety of moss traits. As discussed above, our analyses point towards specific adaptations in moss traits to cope with environmental constraints. The fact that these adaptations have been preserved throughout the phylogeny (**Table 2**, **Figure 2 and Figure 3**) suggests that different lineages may have preferentially evolved within different ecological niches (**Figure 6**).

5. Conclusions

Our findings provided novel insights about the phylogenetic relatedness of moss traits and their relationship with the environment, increasing our knowledge in an understudied group of organisms. We found that climate and water chemistry act as important environmental filters of traits of hygrophytic mosses and, therefore, condition species distributions. Our results suggest the existence of a sclerophylly continuum in hygrophytic mosses, especially shown in the morphological traits, that may be particularly related to the role of water conductivity and, hence, low free CO_2 and high bicarbonate ($CaCO_3$) concentration. In hard waters, Ca^{2+} binds with CO_2 forming bicarbonate, reducing free CO_2 and potentially reducing photosynthesis and moss growth. In cases of springs with very high water conductivity (and usually Ca^{2+} concentration), a crust of calcium carbonate grows in the springs, allowing only very specialised mosses to overgrow it and survive (Bes et al., 2018; Brown, 1982). These findings support a kind of sclerophylly gradient in hygrophytic mosses relating to water conductivity (**Figure 7**), similar to traits in vascular plants (e.g., leaf mass per area) relating to water availability and temperature (Niinemets & Niinemets, 2013; Wright et al., 2004). We believe that this study highlights the possibilities and mutual benefits for joining the study of traits to the investigation of bryophytes. We show that traits can be used to further our knowledge of an understudied group of species (mosses), and we also propose to use mosses as a model study group in which to test ecological theory.

Author contributions

MFM and FrS planned and designed the research. MFM, FB, JC, CP, FS and FrS conducted fieldwork and laboratory analyses. MFM and JGP analysed data. All authors contributed to writing the manuscript.

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Data Accessibility

Data and R scripts to perform the RLQ analysis is available at: https://doi.org/10.6084/m9.figshare.9209351.v1

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Figure captions

Figure 1: Map showing the springs sampled.

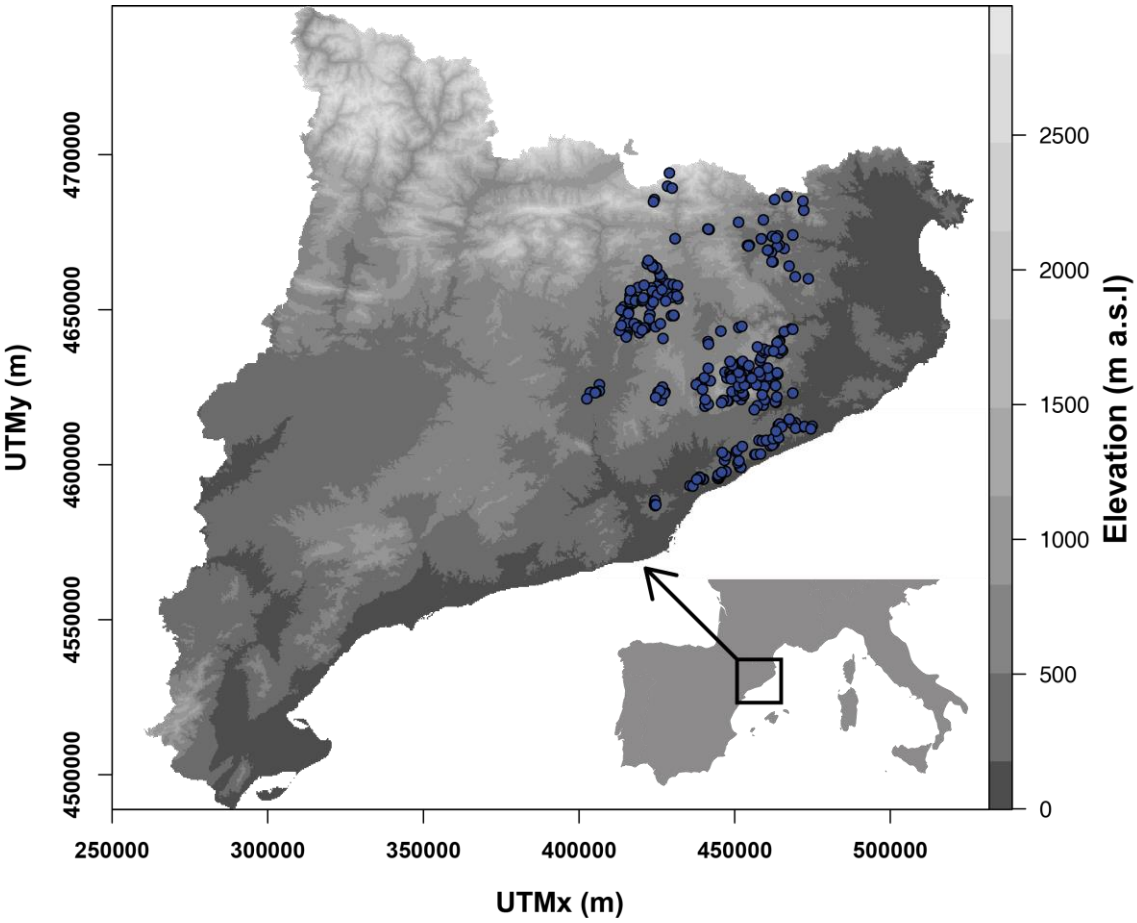

Figure 2. Hierarchical cluster analysis showing the similarity between species with regard to their traits (a) and two first axes of the principal components analysis performed with traits with the grouping established in the cluster analysis (b). Correlation between the phylogeny and the dendrogram and the phylogenetic signal (λ) of PC1 and PC2 were estimated using the summary phylogenetic tree. *Acronyms*: moss mass per area (MMA), water absorption capacity (WAC).

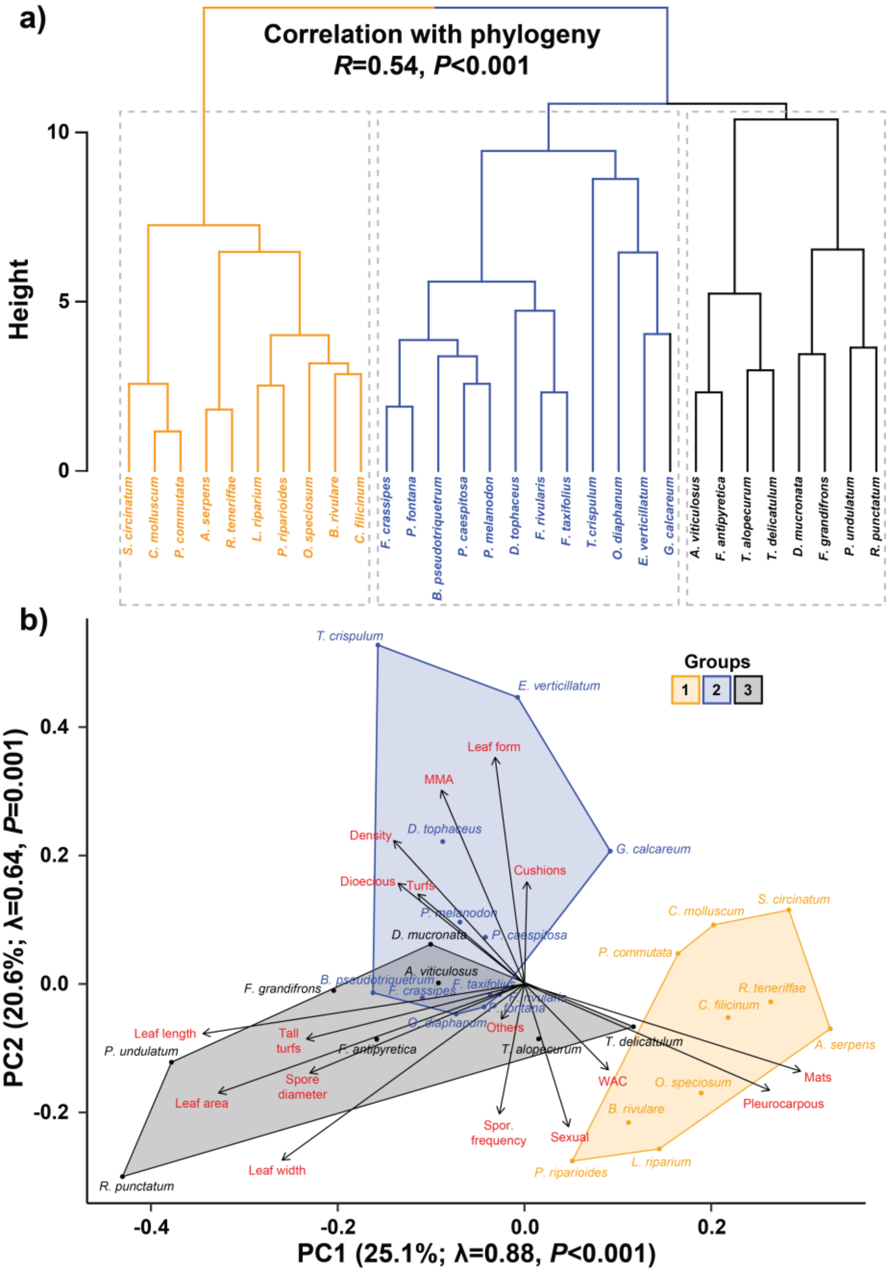

Figure 3: Continuous character mapping of PC1 and PC2. See **Figure 2** to interpret PC1 and PC2 axes. Phylogenetic signal was estimated using the average phylogenetic tree.

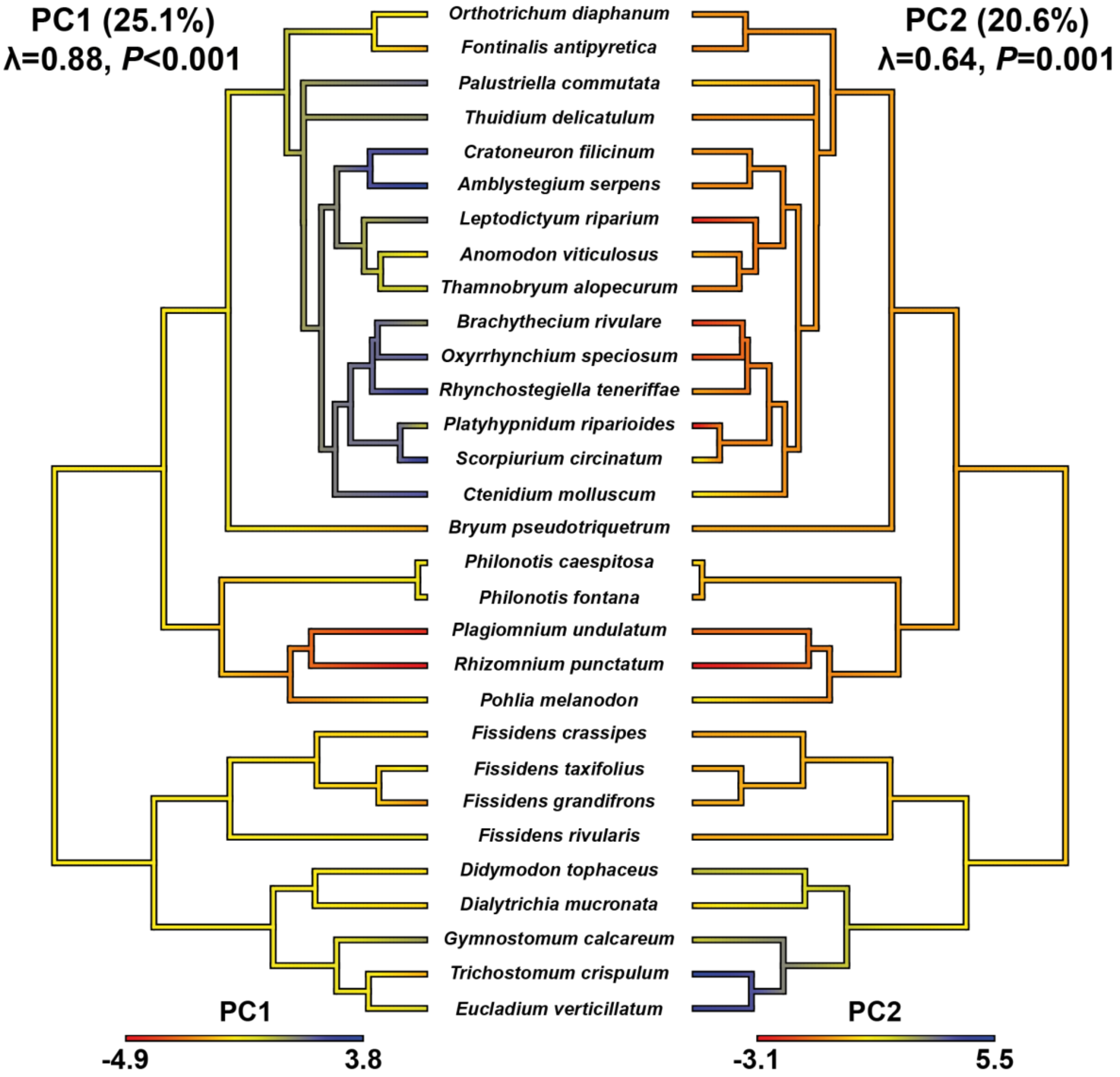

Figure 4: Results of the extended RLQ analysis showing correlation of traits (blue) and the environment (red) with axes 1 and 2. The environmental variance explained by the axes is shown between brackets. *Acronyms*: $NO_3^-:PO_4^{3-}$ ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm), moss mass per area (MMA), water absorption capacity (WAC).

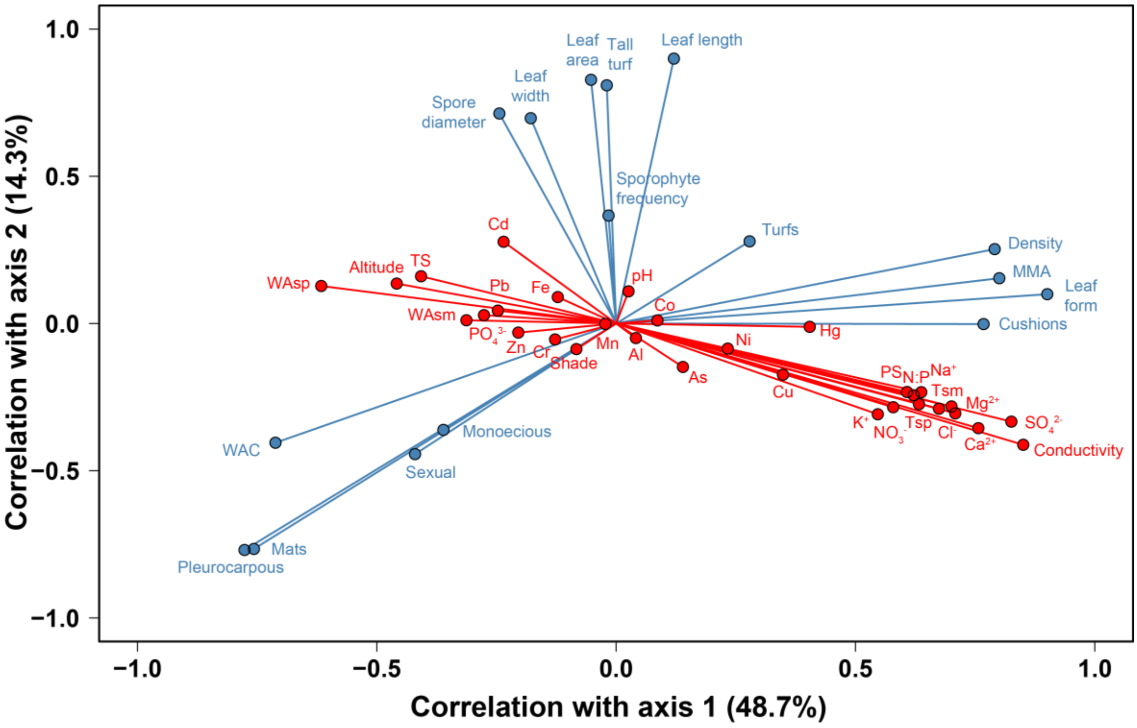

Figure 5. Clustered image map summarising the results of the extended RLQ analysis (N=295 springs). Environmental variables are on the right side of the plot and moss traits at the bottom. *Acronyms*: nitrate-to-phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm), moss mass per area (MMA), water absorption capacity (WAC).

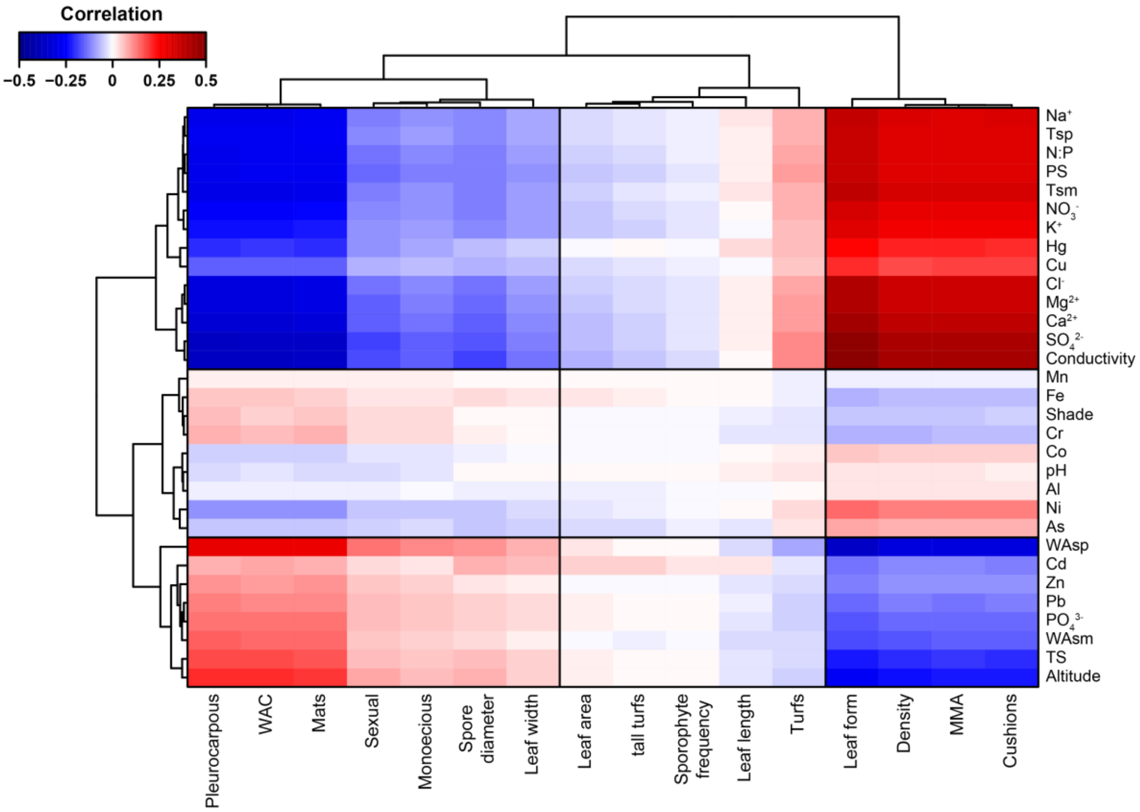

Figure 6: Results of the extended RLQ analysis showing environmental-space (a) and trait-phylogeny (b) global scores for axes 1 and 2. A and B define mainly positive and negative scoring groups of springs and species for axis 1.

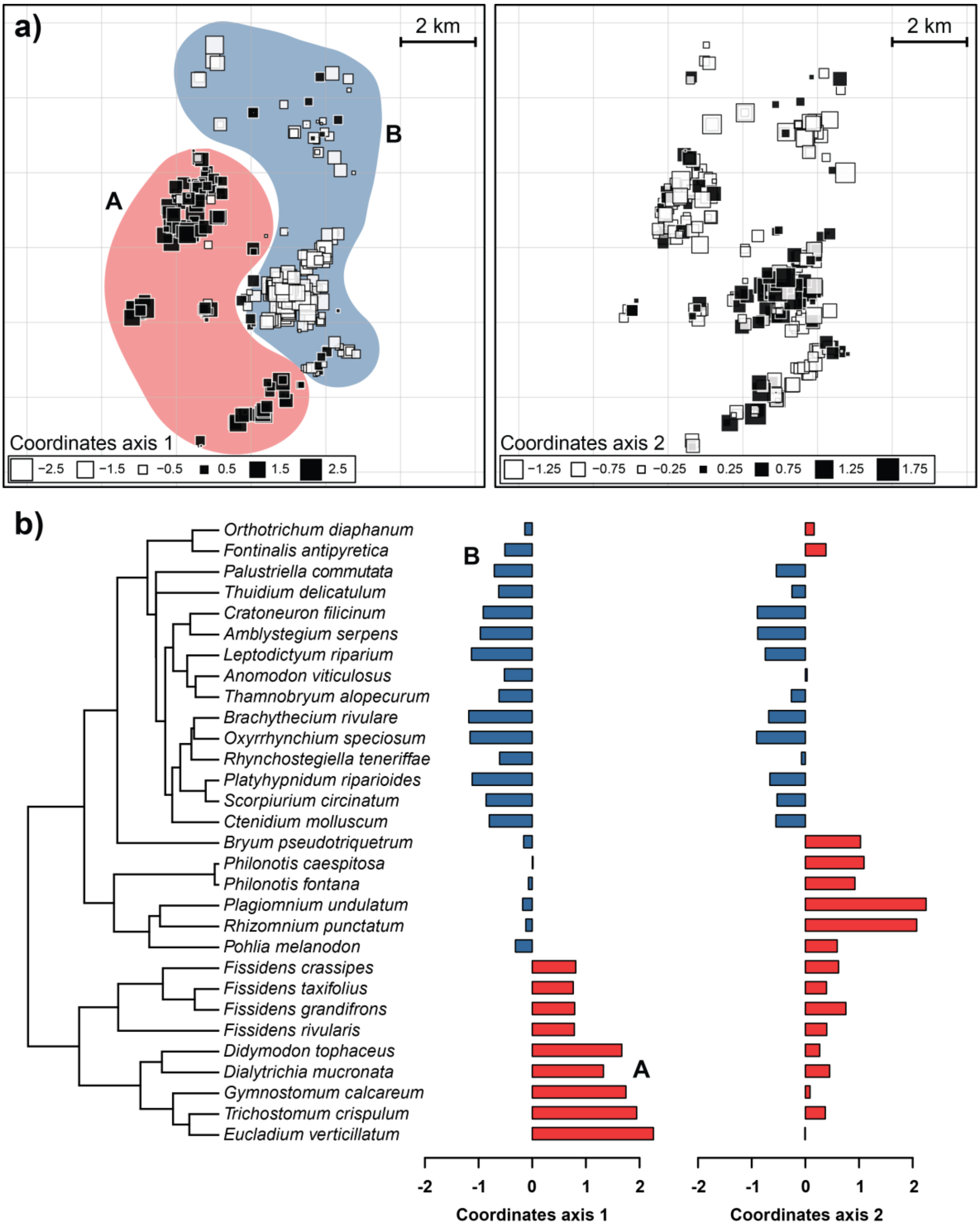

Figure 7: Scheme showing the hygrophytic moss sclerophylly continuum, including the relationship between moss traits and water features. From left to right, leaves correspond to *P. undulatum*, *P. riparioides*, *E. verticillatum* and *T. crispulum.* Below mosses are the pleurocarpous *T. alopecurum* and the acrocarpous *F. taxifolius*.

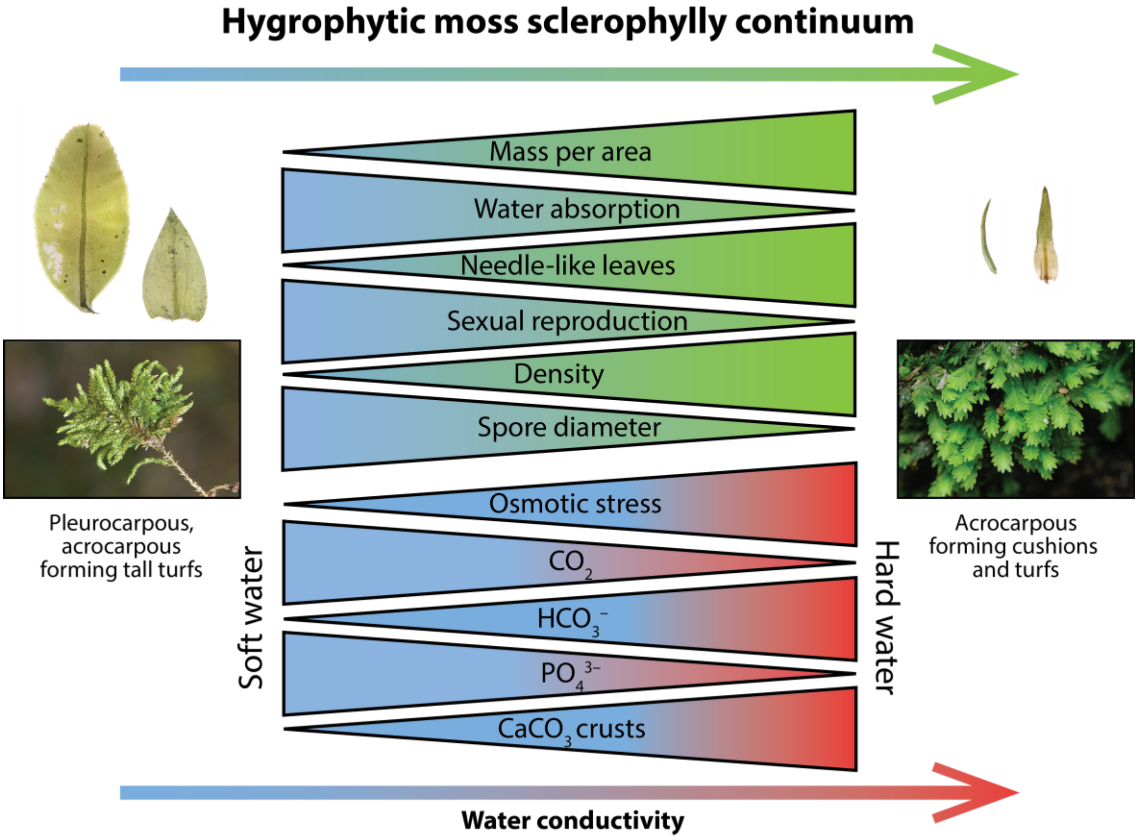

Table 1. Summary of the morphological and life history traits analysed in moss species.

Name	Type	Estimation	Units
Morphological			
Leaf length	Continuous		µm
Leaf width	Continuous		µm
Leaf area	Continuous		mm^2
Leaf form	Continuous	Leaf length/Leaf width	unitless
Spore diameter	Continuous	Mean of minimum and maximum spore diameter	µm
Water absorption capacity (WAC)	Continuous	Fresh - Dry weight/Dry weight	mg H_2O mg^{-1} Dry weight
Moss mass per area	Continuous	Dry weight/Area	mg mm^{-2}
Density	Continuous	Dry weight/Volume	mg ml^{-1}
Reproductive			
Sporophyte frequency	Discrete	1: Rare; 2: Occasional; 3: Frequent; 4: Abundant	
Monoecious - Dioecious	Binary	0: Dioecious; 1: Monoeciuous	
Sexuality	Binary	0: Asexual; 1: Sexual	
Life forms			
Mats-roughs	Binary	0: Not mats-roughs; 1: Mats-roughs	
Turf	Binary	0: Not turfs; 1: Turfs	
Tall Turf	Binary	0: Not tall turfs; 1: Tall turfs	
Cushions	Binary	0: Not cushions; 1: Cushions	
Other life forms	Binary	0: Any previous life forms; 1: Other life forms	
Pleurocarpous - Acrocarpous	Binary	0: Acrocarpous; 1: Pleurocarpous	

Table 2. Phylogenetic signal (λ) of the moss traits studied and the two axes extracted using a principal component analysis (PCA) shown in **Figure 2**. Phylogenetic signal was assessed using 1000 phylogenetic trees to account for phylogenetic uncertainty. Presented values represent the 2.5, 50 and 97.5% percentiles of the estimated distributions. Acronyms: water absorption capacity (WAC), moss mass per area (MMA).

Trait	$\lambda_{2.5\%}$	$\lambda_{50.0\%}$	$\lambda_{97.5\%}$
Morphological			
Leaf length	0.70	0.98	1.04
Leaf width	0.60	0.98	1.04
Leaf area	0.91	1.01	1.05
Leaf form	0.52	0.66	1.01
Spore diameter	0.71	0.84	0.93
WAC	0.12	0.15	0.19
MMA	0.20	0.27	0.43
Density	0.14	0.24	0.48
Reproductive			
Sporophyte frequency	0.00	0.00	0.00
Dioecious/Monoecious	0.00	0.00	0.00
Sexual/Asexual reproduction	0.00	0.00	0.00
Life forms			
Mats	0.64	1.01	1.05
Cushions	0.05	0.22	1.04
Turfs	0.53	0.70	1.04
Tall turfs	0.22	0.61	1.04
Other life forms	0.01	0.06	1.03
Acrocarpous/Pleurocarpous	0.74	1.01	1.05
Principal components analysis			
PC1 (**Figures 2 and 3**)	0.74	0.87	1.02
PC2 (**Figures 2 and 3**)	0.58	0.64	0.75

Table 3. Summary table showing trait and phylogenetic quadratic entropy (respectively, TQE and PQE) tests for clustering. Number of springs used for traits and phylogenetic tests differ because for trait tests we removed those springs in which none of the species with traits were present. Std. Obs stands for standardised value of the observation with respect to 999 random permutations in our data. If negative and statistically significant, it indicates that moss assemblages in springs present higher trait or phylogenetic diversity than expected from the pool of species). See methods (Pavoine et al., 2010) for further details.

	Traits	**Phylogeny**
One species per spring		
Std. Obs	-1.540	-0.970
***P*-value**	0.125	0.318
Springs	295	302
Two species per spring		
Std. Obs	-1.133	-0.008
***P*-value**	0.258	0.994
Springs	195	208
Three species per spring		
Std. Obs	-0.638	0.632
***P*-value**	0.525	0.513
Springs	101	109
Four species per spring		
Std. Obs	-0.503	0.525
***P*-value**	0.595	0.614
Springs	34	45

Supplementary material

Figure S1: Example of a typical semi-natural spring. The red line delimits the area of influence of the water, from where we collected moss samples.

Figure S2: Plot showing Spearman's correlations between environmental variables. The size of the circles is proportional to the correlation values. *Acronyms*: nitrate-to-phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm).

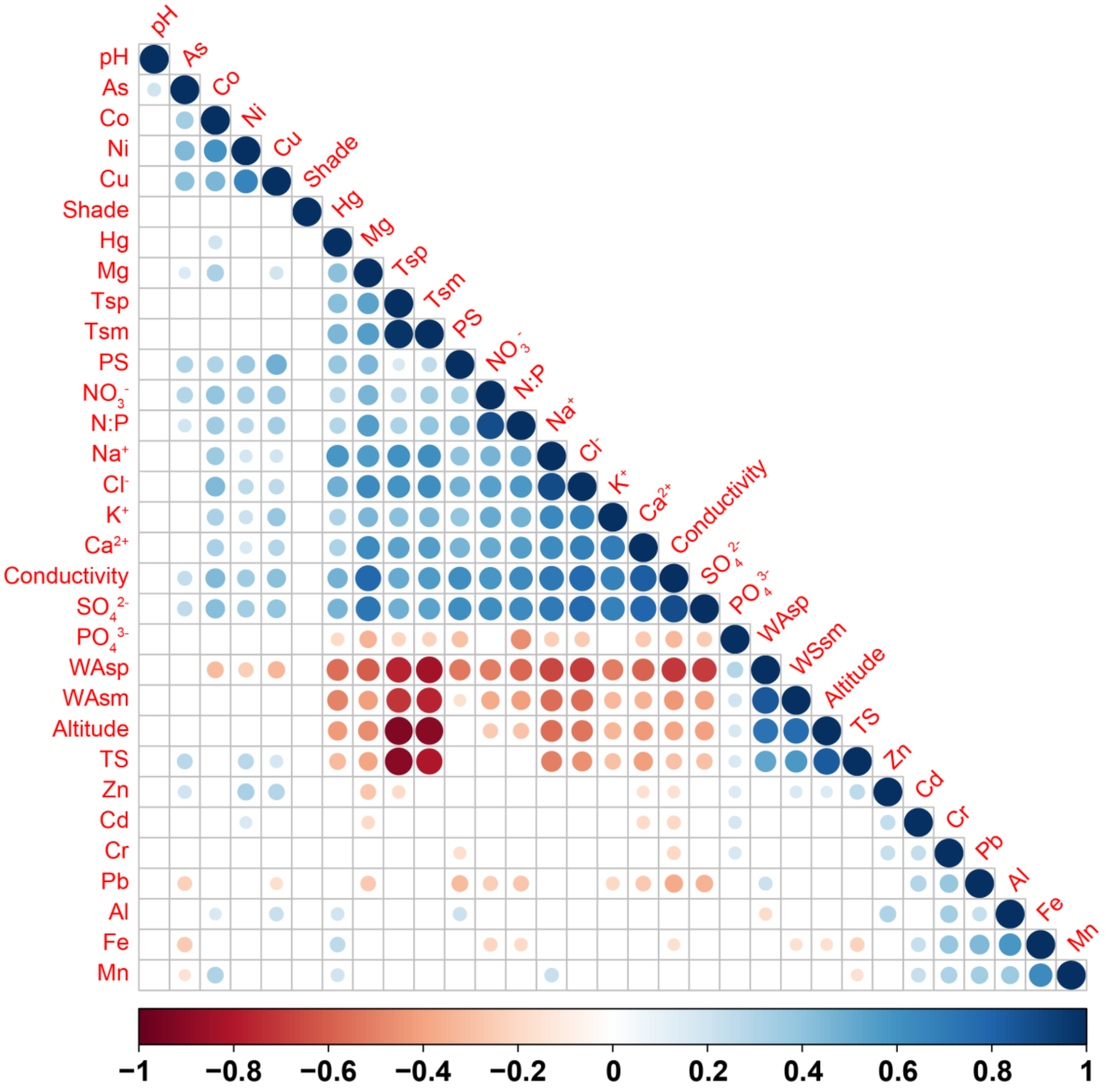

Figure S3. Species accumulation curve for the sampled springs, obtained by the bootstrap method (1000 permutations) using *vegan* (Oksanen et al., 2018) R package. Boxplots indicate bootstrap simulations and the shaded area shows the confidence intervals from standard deviation (standard error of the estimate).

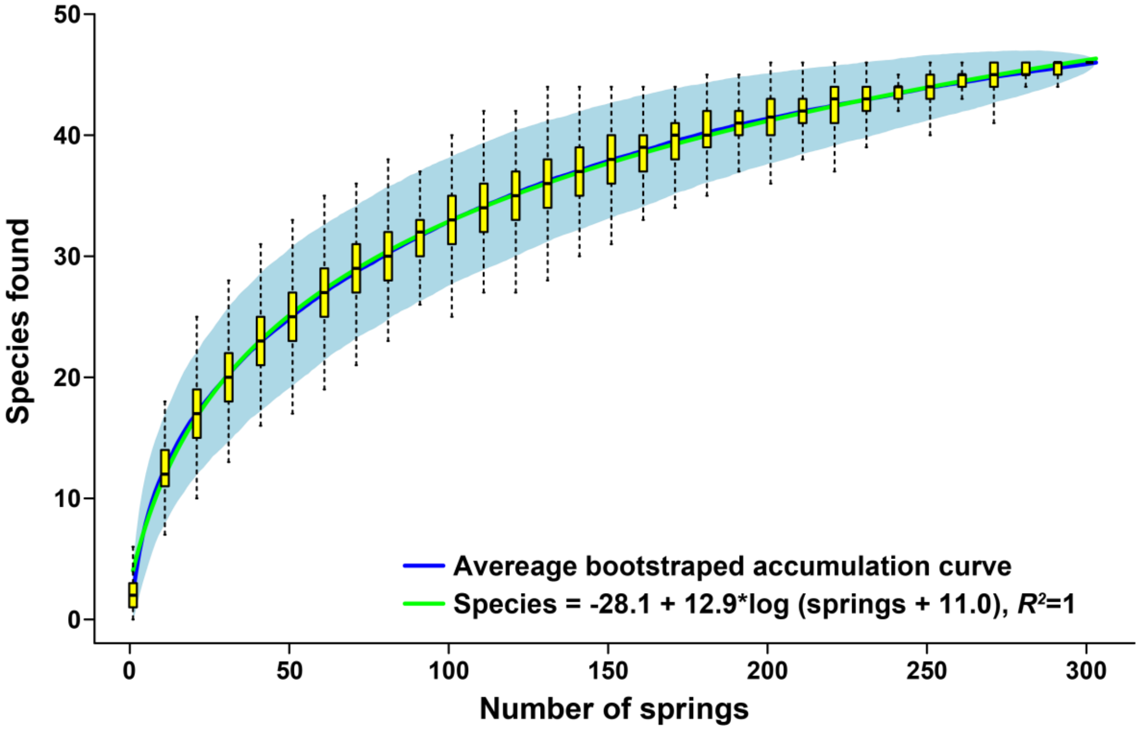

Figure S4. Bar plot showing the number of springs in which each moss species was found.

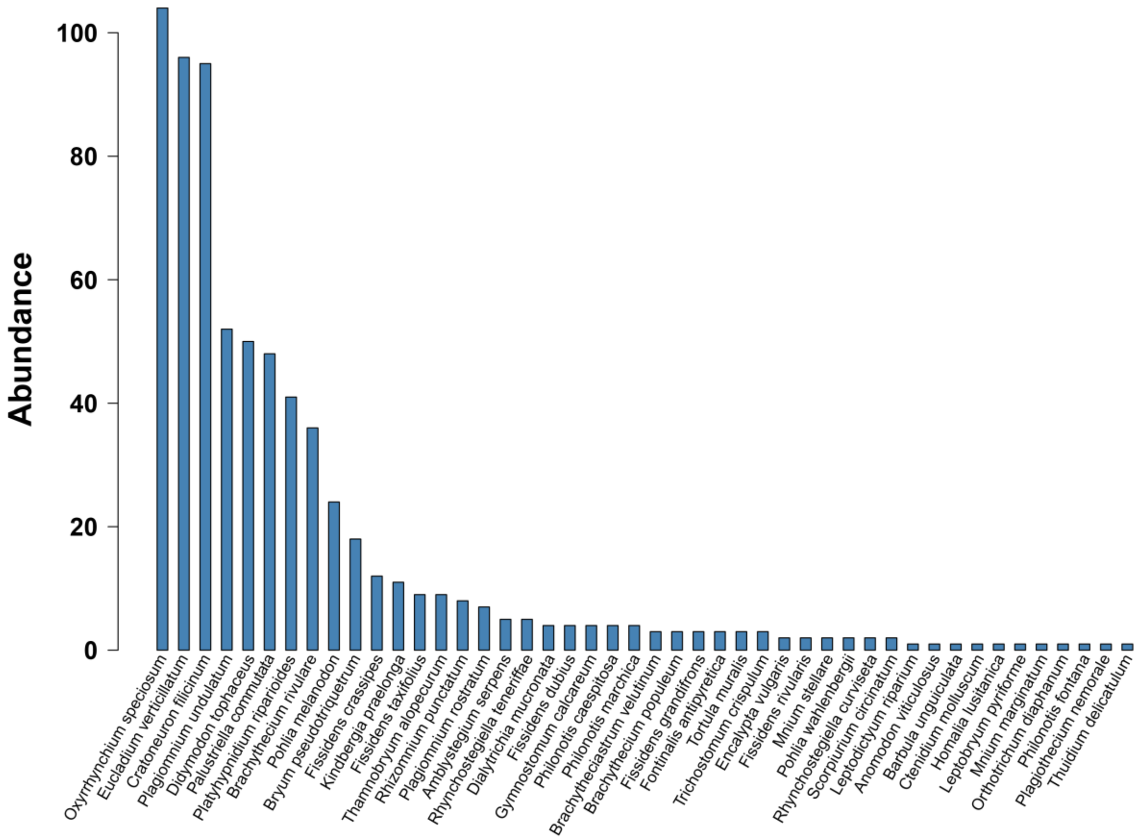

Figure S5. Histogram showing the frequency of species richness per spring

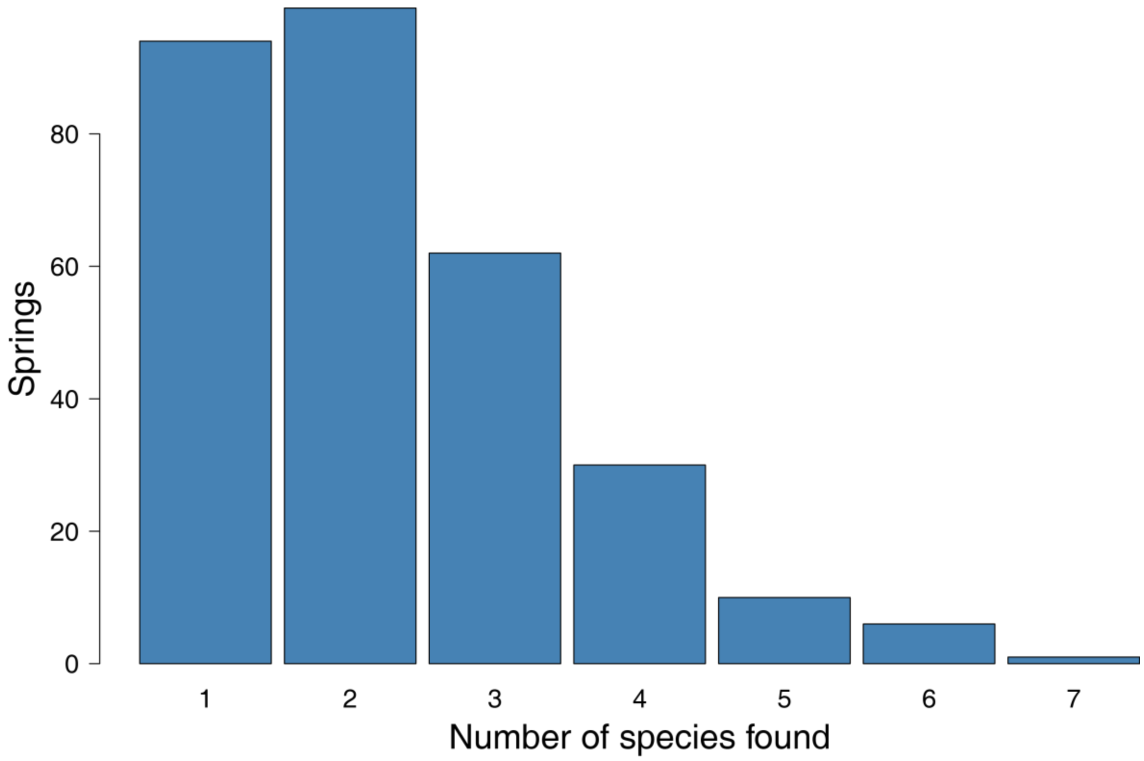

Figure S6. Summary tree obtained from the BEAST analysis. Node supports (in posterior probabilities) are indicated in each node, ranging from 0 to 1.

Figure S7. Clustered image map showing the results of the extended RLQ analysis (only springs with at least two of the species with traits, N=195). *Acronyms*: nitrate-to-phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm), moss mass per area (MMA), water absorption capacity (WAC).

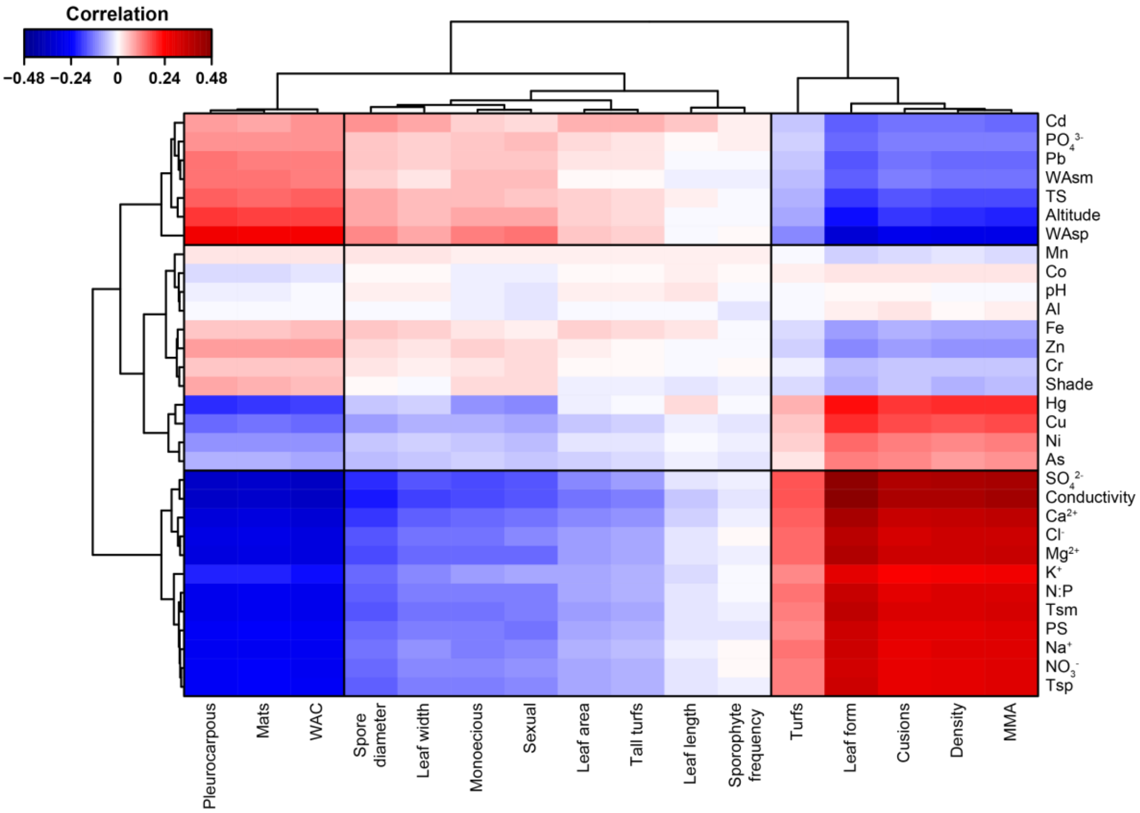

Figure S8. Clustered image map showing the results of the fourth corner analysis (all sites included, N=295). *Acronyms*: nitrate-to-phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm), moss mass per area (MMA), water absorption capacity (WAC).

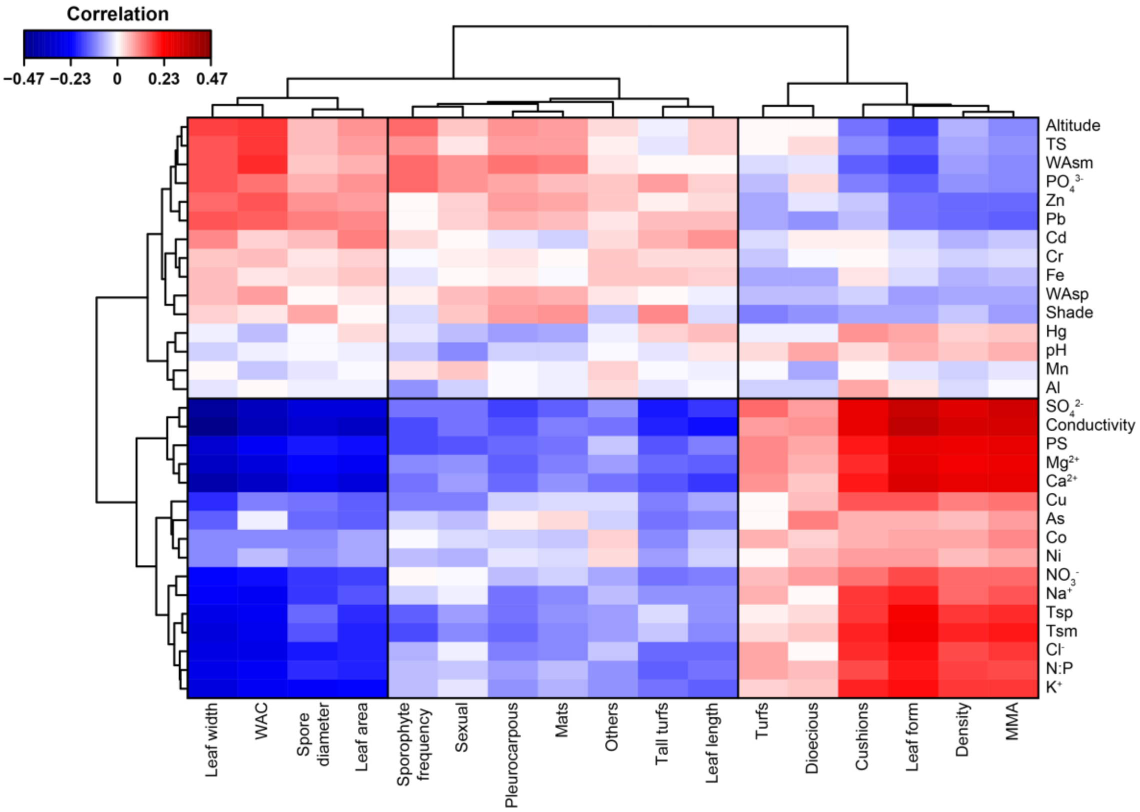

Table S1. Table showing the measured traits per species (mean ± standard error), part 1. See Units in **Table 1**. The remaining moss traits can be found in the BRYOATT database (Mark O Hill et al., 2007). *Acronyms*: moss mass per area (MMA), water absorption capacity (WAC), number of replicates (N), sporophyte frequency (Spo. Freq).

Species	**Leaf length**	**Leaf width**	**Leaf form**	**Leaf area**	**WAC**	**MMA**	**Density**	**N**	**Spo. Freq**
Amblystegium serpens	558.4 ± NA	191.6 ± NA	2.95 ± NA	0.06 ± NA	1.08 ± NA	0.085 ± NA	0.066 ± NA	1	4
Anomodon viticulosus	2712.8 ± NA	1081.5 ± NA	2.61 ± NA	1.81 ± NA	1.33 ± NA	0.147 ± NA	0.195 ± NA	1	1
Brachythecium rivulare	1608.4 ± 88.1	738.0 ± 65.7	2.22 ± 0.15	0.88 ± 0.13	2.69 ± 0.18	0.054 ± 0.011	0.047 ± 0.010	5	2
Bryum pseudotriquetrum	2749.2 ± 297.5	1113.5 ± 143.4	2.52 ± 0.18	2.35 ± 0.47	2.20 ± 0.38	0.113 ± 0.012	0.129 ± 0.025	6	2
Cratoneuron filicinum	848.0 ± 103.1	313.3 ± 36.7	2.72 ± 0.16	0.20 ± 0.04	1.66 ± 0.23	0.069 ± 0.010	0.111 ± 0.028	9	2
Ctenidium molluscum	971.0 ± NA	256.8 ± NA	3.90 ± NA	0.15 ± NA	2.06 ± NA	0.100 ± NA	0.159 ± NA	1	1
Dialytrichia mucronata	1663.9 ± NA	350.7 ± NA	5.18 ± NA	0.56 ± NA	0.53 ± NA	0.134 ± NA	0.076 ± NA	1	2
Didymodon tophaceus	1725.2 ± 149.5	285.9 ± 50.8	6.86 ± 1.03	0.63 ± 0.15	0.75 ± 0.07	0.201 ± 0.022	0.264 ± 0.043	6	3
Eucladium verticillatum	1878.0 ± 154.6	149.9 ± 15.4	12.94 ± 1.23	0.29 ± 0.03	0.91 ± 0.11	0.0002 ± 0.0000	0.215 ± 0.014	6	1
Fissidens crassipes	2274.1 ± 296.7	507.7 ± 4.6	4.47 ± 0.55	1.02 ± 0.15	1.41 ± 0.11	0.082 ± 0.019	0.056 ± 0.007	3	3
Fissidens grandifrons	3675.5 ± 67.4	523.5 ± 17.3	7.03 ± 0.36	1.59 ± 0.01	1.63 ± 0.05	0.104 ± 0.032	0.108 ± 0.001	2	2
Fissidens rivularis	2001.7 ± NA	419.8 ± NA	4.65 ± NA	0.68 ± NA	1.11 ± NA	0.051 ± NA	0.036 ± NA	1	2
Fissidens taxifolius	2105.7 ± NA	610.0 ± NA	3.45 ± NA	1.12 ± NA	1.47 ± NA	0.058 ± NA	0.144 ± NA	1	2
Fontinalis antipyretica	5375.4 ± 148.7	1724.4 ± 47.8	3.12 ± 0.00	6.52 ± 0.62	1.09 ± 0.15	0.070 ± 0.017	0.097 ± 0.027	2	1
Gymnostomum calcareum	1102.2 ± 338.9	269.5 ± 113.1	4.77 ± 0.91	0.30 ± 0.14	1.33 ± 0.47	0.068 ± 0.010	0.044 ± 0.017	3	1
Leptodictyum riparium	2080.7 ± 54.7	748.5 ± 10.5	2.78 ± 0.11	0.93 ± 0.01	3.10 ± 1.20	0.048 ± 0.011	0.047 ± 0.023	2	3
Orthotrichum diaphanum	2860.2 ± NA	817.2 ± NA	3.52 ± NA	1.83 ± NA	1.73 ± NA	0.195 ± NA	0.070 ± NA	1	4
Oxyrrhynchium speciosum	1063.2 ± 184.3	507.2 ± 75.0	2.07 ± 0.05	0.46 ± 0.17	1.79 ± 0.20	0.046 ± 0.008	0.065 ± 0.008	7	1
Palustriella commutata	987.9 ± 98.1	308.9 ± 36.4	3.37 ± 0.31	0.21 ± 0.03	1.74 ± 0.35	0.097 ± 0.015	0.135 ± 0.020	7	1
Philonotis caespitosa	1373.6 ± 153.1	433.1 ± 78.8	3.46 ± 0.61	0.38 ± 0.07	1.76 ± 0.22	0.087 ± 0.003	0.041 ± 0.009	4	1
Philonotis fontana	1299.6 ± NA	415.9 ± NA	3.13 ± NA	0.41 ± NA	1.60 ± NA	0.057 ± NA	0.035 ± NA	1	2

Table S1. Table showing the measured traits per species (mean ± standard error), part 2. See Units in **Table 1**. The remaining moss traits can be found in the BRYOATT database (Mark O Hill et al., 2007). *Acronyms*: moss mass per area (MMA), water absorption capacity (WAC), number of replicates (N), sporophyte frequency (Spo. Freq).

Species	**Leaf length**	**Leaf width**	**Leaf form**	**Leaf area**	**WAC**	**MMA**	**Density**	**N**	**Spo. Freq**
Plagiomnium undulatum	7141.6 ± 321.4	1801.3 ± 277.8	4.30 ± 0.51	11.77 ± 2.01	1.37 ± 0.21	0.072 ± 0.011	0.119 ± 0.030	6	2
Platyhypnidum riparioides	2201.6 ± 72.8	1143.8 ± 81.3	1.96 ± 0.11	1.86 ± 0.17	1.61 ± 0.21	0.062 ± 0.006	0.110 ± 0.012	6	3
Pohlia melanodon	1543.3 ± 261.4	420.4 ± 99.2	3.87 ± 0.44	0.54 ± 0.17	0.91 ± 0.16	0.086 ± 0.029	0.062 ± 0.031	3	2
Rhizomnium punctatum	5150.2 ± 889.8	3986.8 ± 133.9	1.29 ± 0.18	15.93 ± 2.83	0.94 ± 0.50	0.072 ± 0.013	0.190 ± 0.008	2	3
Rhynchostegiella teneriffae	867.3 ± 82.0	177.1 ± 15.3	4.89 ± 0.04	0.11 ± 0.03	0.88 ± 0.39	0.083 ± 0.013	0.054 ± 0.014	2	3
Scorpiurium circinatum	589.6 ± NA	137.6 ± NA	4.08 ± NA	0.06 ± NA	1.41 ± NA	0.084 ± NA	0.049 ± NA	1	1
Thamnobryum alopecurum	1731.4 ± 249.4	794.3 ± 100.6	2.17 ± 0.09	1.06 ± 0.25	1.07 ± 0.06	0.094 ± 0.012	0.126 ± 0.008	5	2
Thuidium delicatulum	872.4 ± NA	342.0 ± NA	2.87 ± NA	0.17 ± NA	1.63 ± NA	0.092 ± NA	0.073 ± NA	1	2
Trichostomum crispulum	2370.2 ± 143.8	233.1 ± 73.2	11.50 ± 4.23	0.47 ± 0.12	1.50 ± 0.30	0.593 ± 0.483	0.384 ± 0.317	2	1
Mean	2068.5 ± 160.0	681.4 ± 69.0	4.15 ± 0.32	1.76 ± 0.36	1.53 ± 0.07	0.093 ± 0.011	0.117 ± 0.010	98	

Table S2. Moran's I spatial autocorrelation tests for environmental variables (295 sites). Significant *P*-values indicate statistically significant spatial autocorrelation. *Acronyms*: mean spring temperature (Tsp), mean summer temperature (Tsm), spring water availability (WAsp), summer water availability (WAsm), nitrate-to-phosphate ratio (N:P).

Test	**Obs**	**Std.Obs**	***P***
Shade	0.048	1.493	0.058
Altitude	0.723	22.419	0.001
Tsp	0.809	25.533	0.001
Tsm	0.798	24.866	0.001
WAsp	0.808	24.904	0.001
WAsm	0.763	22.493	0.001
TS	0.776	24.196	0.001
PS	0.877	26.508	0.001
pH	0.233	6.999	0.001
Conductivity	0.659	20.065	0.001
Na^+	0.195	6.172	0.023
K^+	0.163	5.748	0.032
Mg^{2+}	0.502	16.322	0.001
Ca^{2+}	0.454	14.113	0.001
Cl^-	0.304	9.638	0.001
NO_3^-	0.272	8.450	0.001
SO_4^{2-}	0.445	13.728	0.001
PO_4^{3-}	0.112	4.209	0.221
As	0.358	14.047	0.230
Cr	0.218	6.835	0.074
Ni	0.033	1.299	0.113
Co	-0.001	0.090	0.141
Fe	0.036	1.479	0.210
Zn	0.142	5.291	0.008
Cu	0.032	1.573	0.087
Mn	0.005	0.299	0.024
Al	0.157	5.040	0.101
Cd	0.122	5.675	0.001
Hg	0.379	11.966	0.001
Pb	0.155	4.793	0.001
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Anomodon viticulosus		FM161076		AY908201	AM990343
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Bryoerythrophyllum recurvirostrum	KY406828	KY406828		KY406865	GU953731
Bryum argenteum	KT343959	KX655725	LC270450	AY078318	LC270624
Bryum pseudotriquetrum	KX981161		AY163040	JF277327	AY150357
Chiloscyphus polyanthos			DQ268969		AY149873
Conocephalum conicum			KT356971	KT356981	AY688806
Cratoneuron filicinum	JQ281669	AY009812	AB095270	AY908250	AY009826
Ctenidium molluscum	AF403632		AB334103	AY907954	FM211895
Dialytrichia mucronata				AY908030	GU953735
Didymodon tophaceus	MF536585	MF536585		MF536622	JN968449
Encalypta vulgaris					EU128000
Eucladium verticillatum	JX679955	AY854392	LC176247	AF481044	AY950402
Fissidens bryoides			LC271962		
Fissidens dubius	JX679949		LC271968	JX679972	
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Philonotis fontana	LN714246		AY631192		EF107538
Philonotis marchica	KC111078				HF536658
Plagiochila porelloides		KT992543	KF943595	KX896609	KF943056
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Sarmentypnum exannulatum	AY857612	AY857612		AY907968	DQ404982
Scapania undulata		JN631484	AY149840	AM398286	EU791642
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Tortula muralis	JN544870	JN544869		AY161090	GU953736
Trichostomum crispulum	KM020643	KM020643	LC176257	AF480977	AY950436

Supplementary material

Towards a moss sclerophylly continuum: evolutionary history, water chemistry and climate control traits of hygrophytic mosses

Authors: M. Fernández-Martínez, F. Berloso, J. Corbera, J. Garcia-Porta, F. Sayol, C. Preece, F. Sabater

Figure S1: Example of a typical semi-natural spring. The red line delimits the area of influence of the water, from where we collected moss samples.

Figure S2: Plot showing Spearman's correlations between environmental variables. The size of the circles is proportional to the correlation values. *Acronyms*: nitrate-to-phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm).

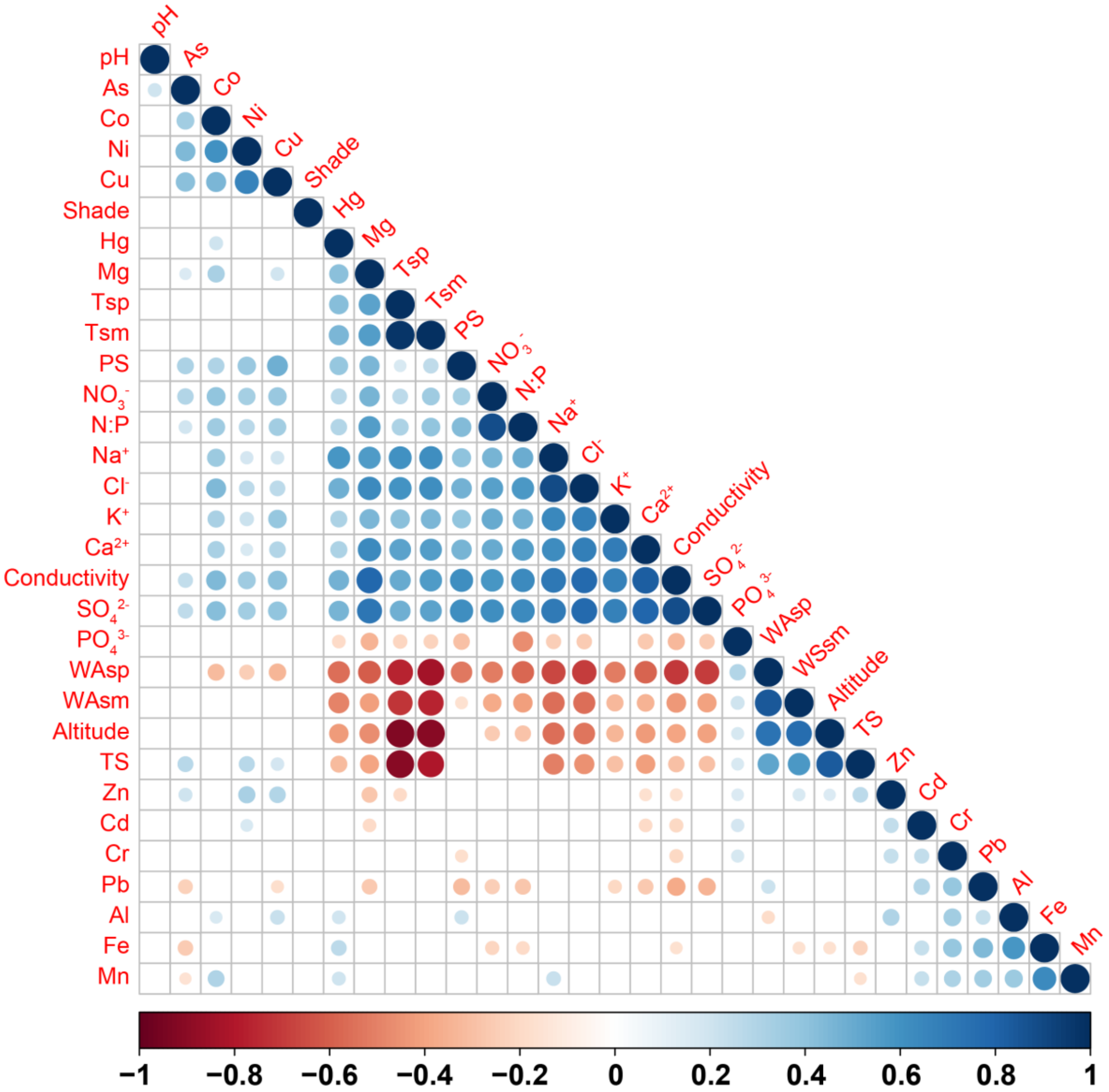

Figure S3. Species accumulation curve for the sampled springs, obtained by the bootstrap method (1000 permutations) using *vegan* (Oksanen et al., 2018) R package. Boxplots indicate bootstrap simulations and the shaded area shows the confidence intervals from standard deviation (standard error of the estimate).

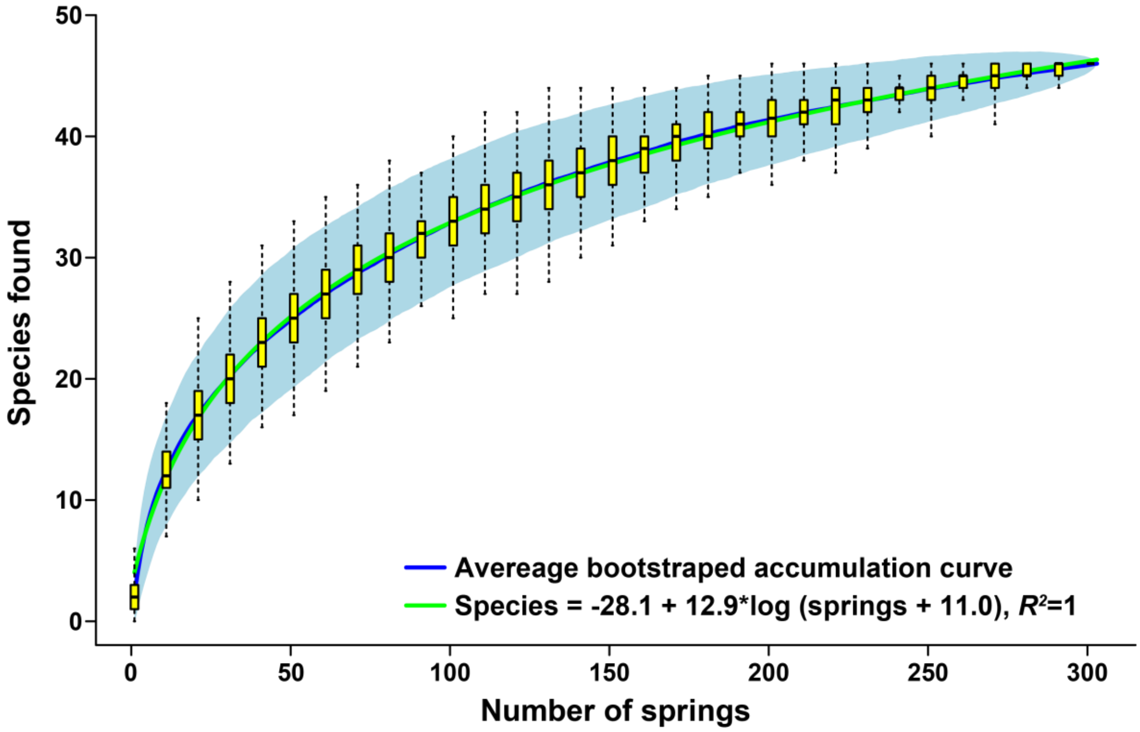

Figure S4. Bar plot showing the number of springs in which each moss species was found.

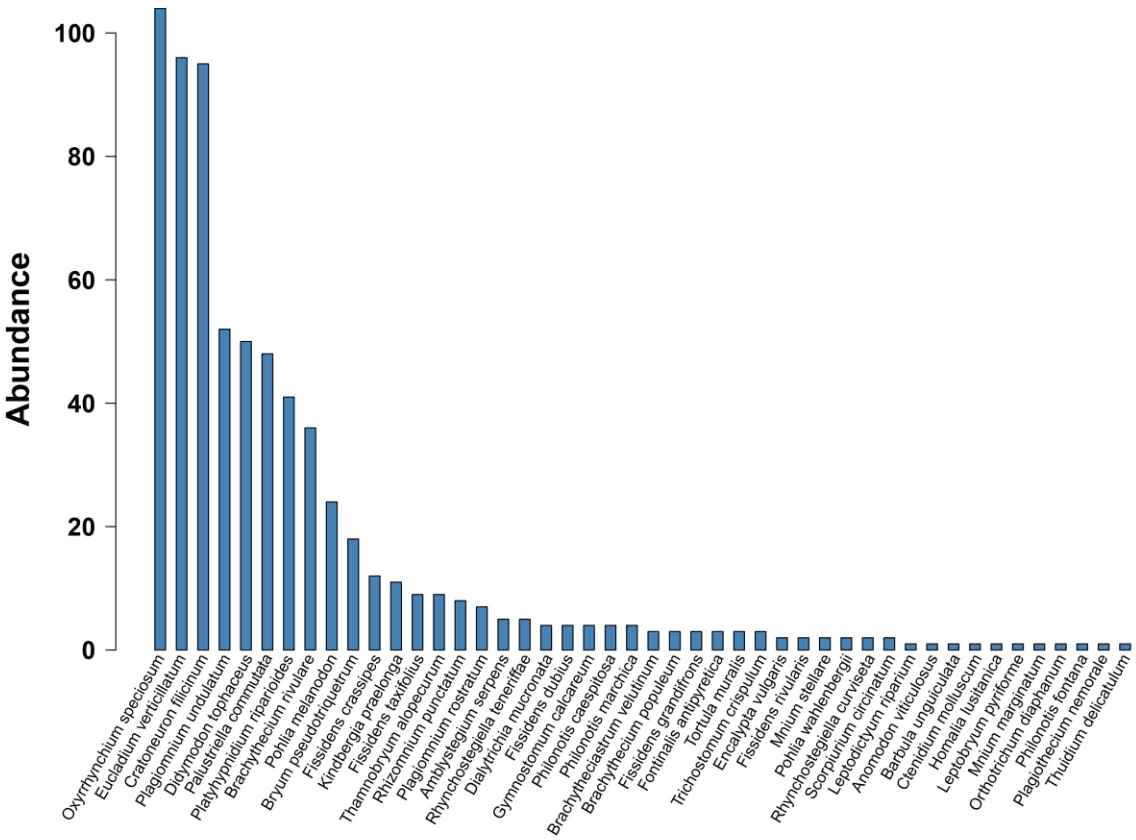

Figure S5. Histogram showing the frequency of species richness per spring

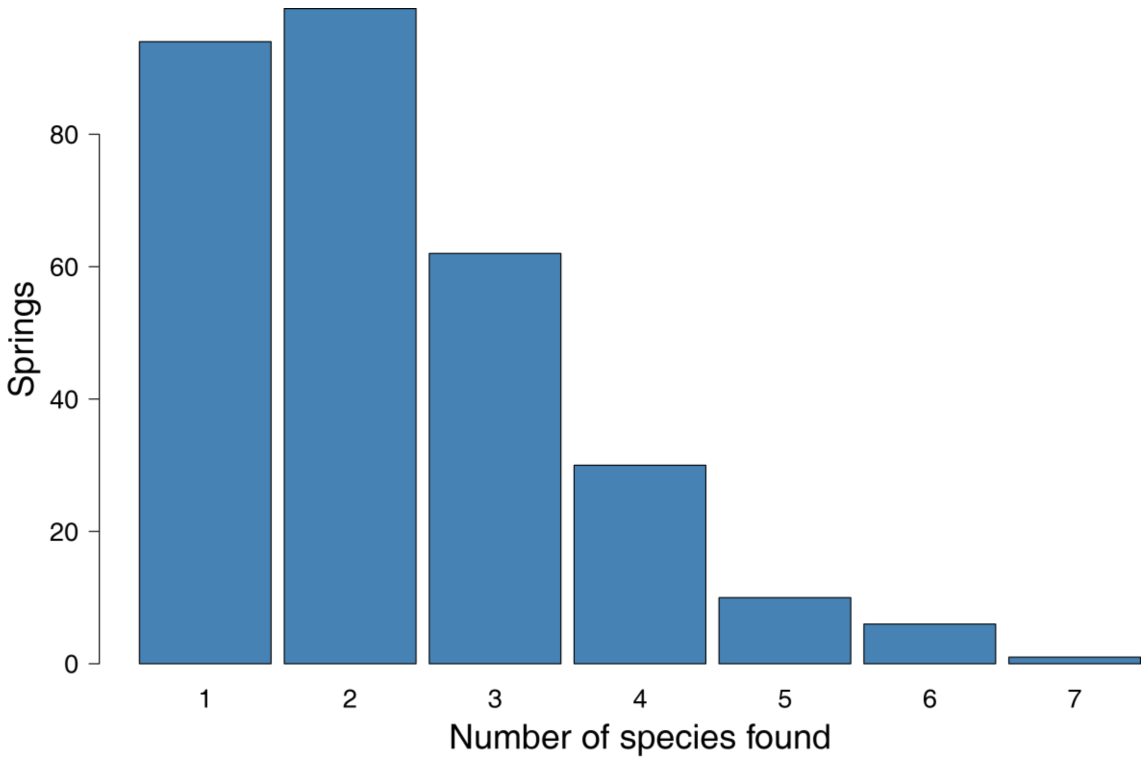

Figure S6. Summary tree obtained from the BEAST analysis. Node supports (in posterior probabilities) are indicated in each node, ranging from 0 to 1.

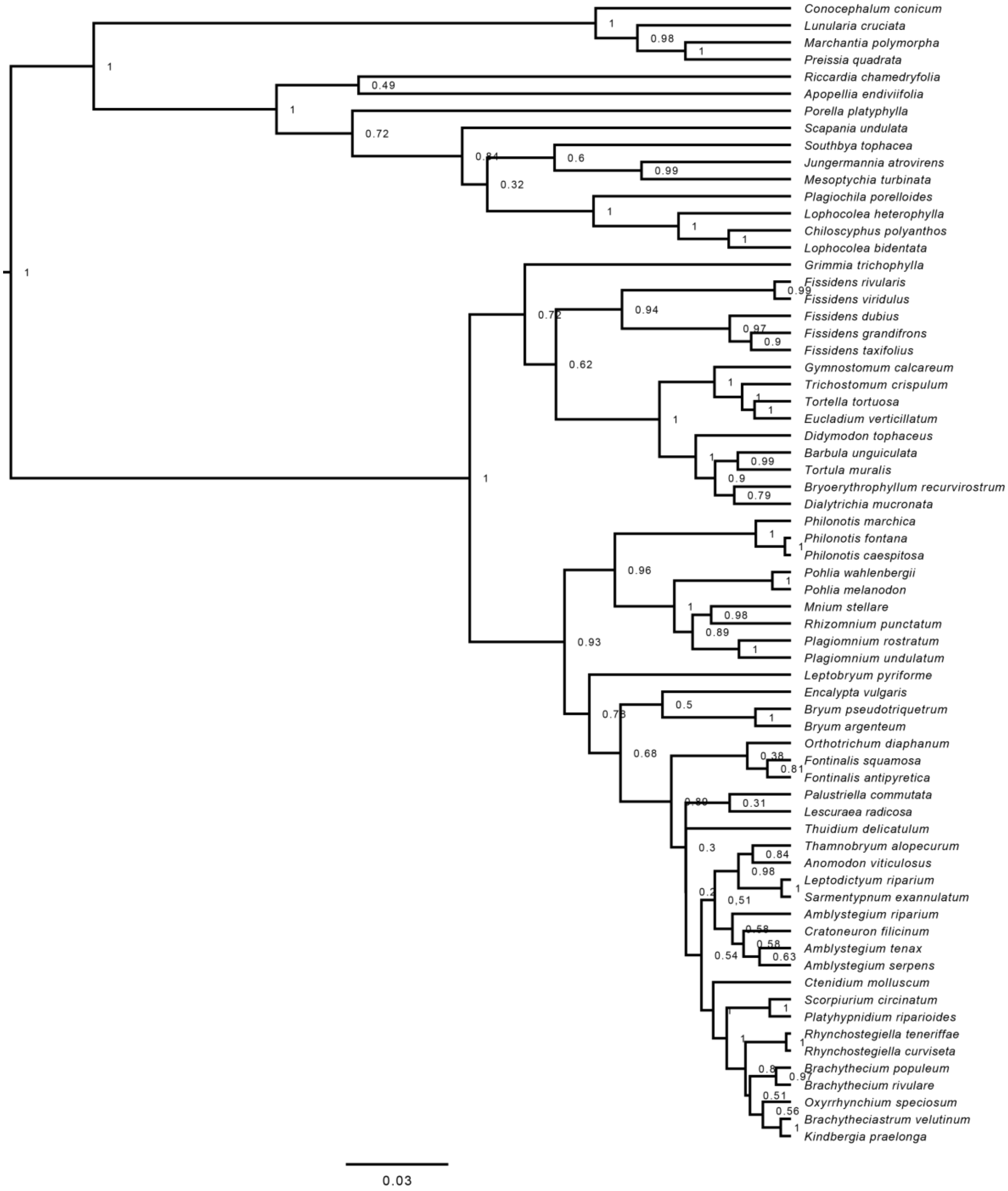

Figure S7. Clustered image map showing the results of the extended RLQ analysis (only springs with at least two of the species with traits, N=195). *Acronyms*: nitrate-to-phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm), moss mass per area (MMA), water absorption capacity (WAC).

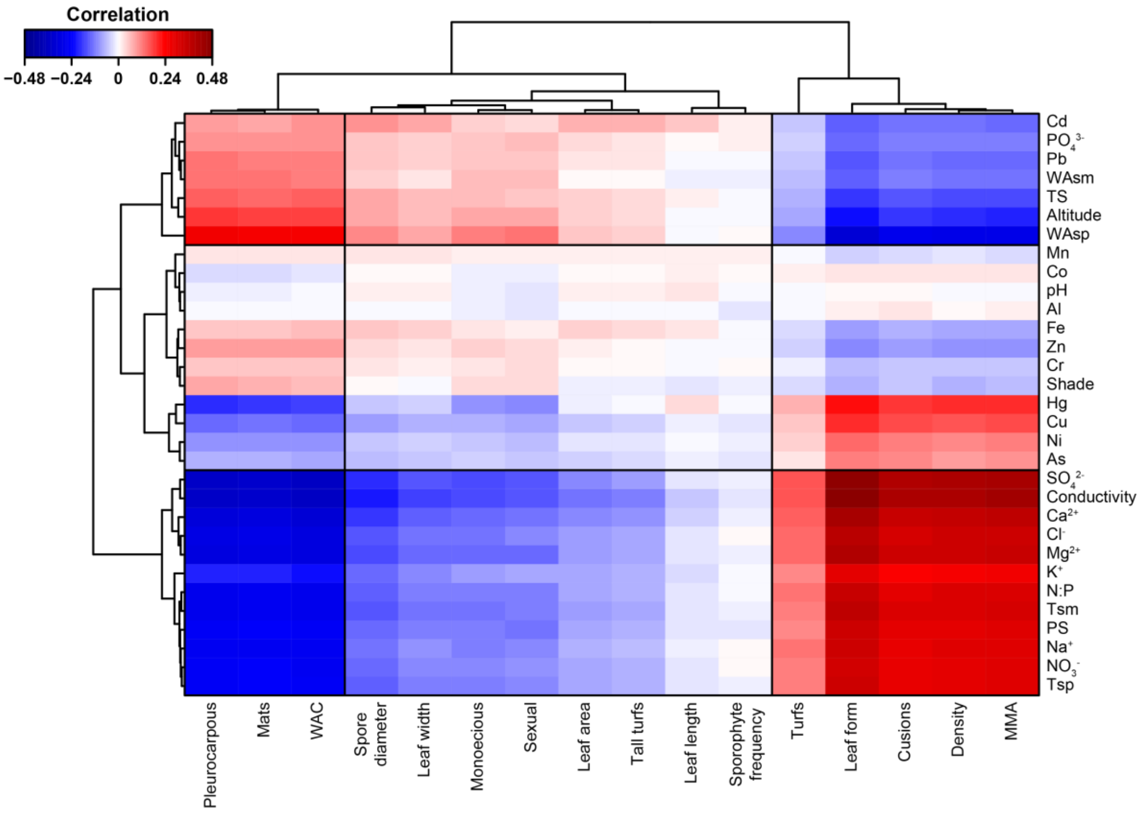

Figure S8. Clustered image map showing the results of the fourth corner analysis (all sites included, N=295). *Acronyms*: nitrate-to-phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm), moss mass per area (MMA), water absorption capacity (WAC).

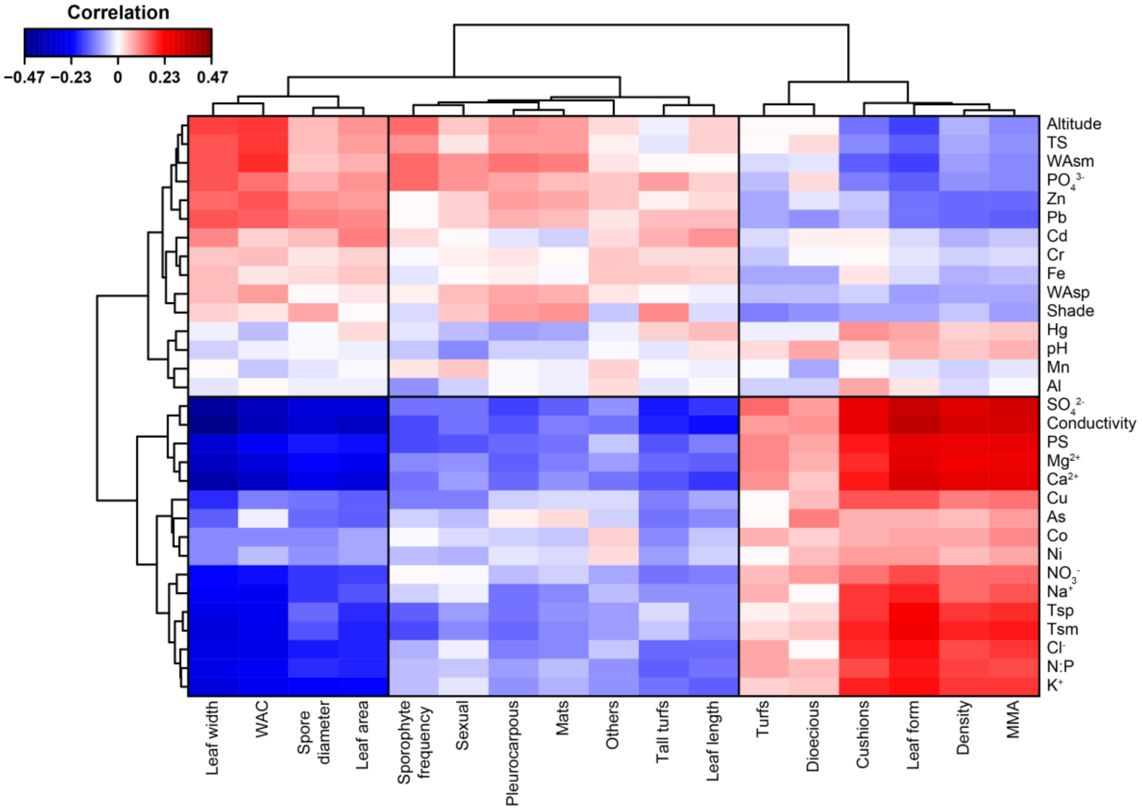

Table S1. Table showing the measured traits per species (mean ± standard error), part 1. See Units in **Table 1**. The remaining moss traits can be found in the BRYOATT database (Hill, Preston, Bosanquet, & Roy, 2007). *Acronyms*: moss mass per area (MMA), water absorption capacity (WAC), number of replicates (N), sporophyte frequency (Spo. Freq).

Species	**Leaf length**	**Leaf width**	**Leaf form**	**Leaf area**	**WAC**	**MMA**	**Density**	**N**	**Spo. Freq**
Amblystegium serpens	558.4 ± NA	191.6 ± NA	2.91 ± NA	0.06 ± NA	1.08 ± NA	0.085 ± NA	0.066 ± NA	1	4
Anomodon viticulosus	2712.8 ± NA	1081.5 ± NA	2.51 ± NA	1.81 ± NA	1.33 ± NA	0.147 ± NA	0.195 ± NA	1	1
Brachythecium rivulare	1608.4 ± 88.1	738.0 ± 65.7	2.18 ± 0.23	0.88 ± 0.13	2.69 ± 0.18	0.054 ± 0.011	0.047 ± 0.010	5	2
Bryum pseudotriquetrum	2749.2 ± 297.5	1113.5 ± 143.4	2.47 ± 0.42	2.35 ± 0.47	2.20 ± 0.38	0.112 ± 0.012	0.129 ± 0.025	6	2
Cratoneuron filicinum	848.0 ± 103.1	313.3 ± 36.7	2.72 ± 0.46	0.20 ± 0.04	1.66 ± 0.23	0.069 ± 0.010	0.111 ± 0.028	9	2
Ctenidium molluscum	971.0 ± NA	256.8 ± NA	3.78 ± NA	0.15 ± NA	2.06 ± NA	0.100 ± NA	0.159 ± NA	1	1
Dialytrichia mucronata	1663.9 ± NA	350.7 ± NA	4.74 ± NA	0.55 ± NA	0.53 ± NA	0.134 ± NA	0.076 ± NA	1	2
Didymodon tophaceus	1725.2 ± 149.5	285.9 ± 50.8	6.03 ± 1.19	0.63 ± 0.15	0.75 ± 0.07	0.201 ± 0.022	0.264 ± 0.043	6	3
Eucladium verticillatum	1878.0 ± 154.6	149.9 ± 15.4	12.53 ± 1.65	0.29 ± 0.03	0.91 ± 0.11	0.178 ± 0.022	0.215 ± 0.014	6	1
Fissidens crassipes	2274.1 ± 296.7	507.7 ± 4.6	4.48 ± 0.59	1.02 ± 0.15	1.41 ± 0.11	0.082 ± 0.019	0.056 ± 0.007	3	3
Fissidens grandifrons	3675.5 ± 67.4	523.5 ± 17.3	7.02 ± 0.27	1.59 ± 0.01	1.63 ± 0.05	0.104 ± 0.032	0.108 ± 0.001	2	2
Fissidens rivularis	2001.7 ± NA	419.8 ± NA	4.77 ± NA	0.68 ± NA	1.11 ± NA	0.051 ± NA	0.036 ± NA	1	2
Fissidens taxifolius	2105.7 ± NA	610.0 ± NA	3.45 ± NA	1.12 ± NA	1.47 ± NA	0.058 ± NA	0.144 ± NA	1	2
Fontinalis antipyretica	5375.4 ± 148.7	1724.4 ± 47.8	3.12 ± 0.12	6.52 ± 0.62	1.09 ± 0.15	0.070 ± 0.017	0.097 ± 0.027	2	1
Gymnostomum calcareum	1102.2 ± 338.9	269.5 ± 113.1	4.09 ± 2.13	0.30 ± 0.14	1.33 ± 0.47	0.068 ± 0.010	0.044 ± 0.017	3	1
Leptodictyum riparium	2166.8 ± 91.7	742.0 ± 8.9	2.92 ± 0.13	0.95 ± 0.02	2.80 ± 0.75	0.047 ± 0.006	0.043 ± 0.014	3	3
Orthotrichum diaphanum	2860.2 ± NA	817.2 ± NA	3.50 ± NA	1.83 ± NA	1.73 ± NA	0.195 ± NA	0.070 ± NA	1	4
Oxyrrhynchium speciosum	1063.2 ± 184.3	507.2 ± 75.0	2.10 ± 0.48	0.46 ± 0.17	1.79 ± 0.20	0.046 ± 0.008	0.065 ± 0.008	7	1
Palustriella commutata	987.9 ± 98.1	308.9 ± 36.4	3.20 ± 0.49	0.21 ± 0.03	1.73 ± 0.35	0.097 ± 0.015	0.135 ± 0.020	7	1
Philonotis caespitosa	1373.6 ± 153.1	433.1 ± 78.8	3.17 ± 0.68	0.38 ± 0.07	1.76 ± 0.22	0.087 ± 0.003	0.041 ± 0.009	4	1
Philonotis fontana	1299.6 ± NA	415.9 ± NA	3.12 ± NA	0.40 ± NA	1.60 ± NA	0.057 ± NA	0.035 ± NA	1	2

Table S1. Table showing the measured traits per species (mean ± standard error), part 2. See Units in **Table 1**. The remaining moss traits can be found in the BRYOATT database (Hill et al., 2007). *Acronyms*: moss mass per area (MMA), water absorption capacity (WAC), number of replicates (N), sporophyte frequency (Spo. Freq).

Species	**Leaf length**	**Leaf width**	**Leaf form**	**Leaf area**	**WAC**	**MMA**	**Density**	**N**	**Spo. Freq**
Plagiomnium undulatum	7141.6 ± 321.4	1801.3 ± 277.8	3.96 ± 0.64	11.77 ± 2.01	1.37 ± 0.21	0.072 ± 0.011	0.119 ± 0.030	6	2
Platyhypnidum riparioides	2201.6 ± 72.8	1143.8 ± 81.3	1.92 ± 0.15	1.86 ± 0.17	1.61 ± 0.21	0.062 ± 0.006	0.110 ± 0.012	6	3
Pohlia melanodon	1628.2 ± 203.4	454.1 ± 77.8	3.59 ± 0.76	0.59 ± 0.13	0.87 ± 0.12	0.092 ± 0.021	0.063 ± 0.031	4	2
Rhizomnium punctatum	5150.2 ± 889.8	3986.8 ± 133.9	1.29 ± 0.23	15.93 ± 2.83	0.94 ± 0.50	0.072 ± 0.013	0.190 ± 0.008	2	3
Rhynchostegiella teneriffae	867.3 ± 82.0	177.1 ± 15.3	4.90 ± 0.63	0.11 ± 0.03	0.88 ± 0.39	0.083 ± 0.013	0.054 ± 0.014	2	3
Scorpiurium circinatum	589.6 ± NA	137.6 ± NA	4.28 ± NA	0.06 ± NA	1.41 ± NA	0.084 ± NA	0.049 ± NA	1	1
Thamnobryum alopecurum	1731.4 ± 249.4	794.3 ± 100.6	2.18 ± 0.42	1.06 ± 0.25	1.07 ± 0.06	0.094 ± 0.012	0.126 ± 0.008	5	2
Thuidium delicatulum	872.4 ± NA	342.0 ± NA	2.55 ± NA	0.17 ± NA	1.63 ± NA	0.092 ± NA	0.073 ± NA	1	2
Trichostomum crispulum	2370.2 ± 143.8	233.1 ± 73.2	10.17 ± 3.25	0.47 ± 0.12	1.50 ± 0.30	0.593 ± 0.483	0.384 ± 0.317	2	1

Table S2. Moran's I spatial autocorrelation tests for environmental variables (295 sites). Significant *P*-values indicate statistically significant spatial autocorrelation. *Acronyms*: mean spring temperature (Tsp), mean summer temperature (Tsm), spring water availability (WAsp), summer water availability (WAsm), nitrate-to-phosphate ratio (N:P).

Test	**Obs**	**Std.Obs**	***P***
Shade	0.048	1.493	0.058
Altitude	0.723	22.419	0.001
Tsp	0.809	25.533	0.001
Tsm	0.798	24.866	0.001
WAsp	0.808	24.904	0.001
WAsm	0.763	22.493	0.001
TS	0.776	24.196	0.001
PS	0.877	26.508	0.001
pH	0.233	6.999	0.001
Conductivity	0.659	20.065	0.001
Na^+	0.195	6.172	0.023
K^+	0.163	5.748	0.032
Mg^{2+}	0.502	16.322	0.001
Ca^{2+}	0.454	14.113	0.001
Cl^-	0.304	9.638	0.001
NO_3^-	0.272	8.450	0.001
SO_4^{2-}	0.445	13.728	0.001
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Anomodon viticulosus		FM161076		AY908201	AM990343
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Brachythecium rivulare	HM046693	FJ476032	AB024674		AM990348
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Porella platyphylla		JF734607	EF547189	AY462387	
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Rhizomnium punctatum			AF478237	JF277323	JF277357
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Tortula muralis	JN544870	JN544869		AY161090	GU953736
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