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

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

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## 23 **Summary**

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

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

54

## 55 **Second abstract (Catalan - Català)**

56 • Les moltes són les plantes més simples i antigues. Gairebé arreu del món  
57 condicionen l'estructura i el funcionament dels ecosistemes. L'ur sensibilitat als  
58 canvis ambientals fa que el seu estudi sigui d'especial rellevància en el camp de  
59 l'ecologia, aportant coneixements molt valuosos sobre la història evolutiva de les  
60 plantes. Tanmateix, l'estudi de les moltes i les relacions d'aquestes amb l'ambient  
61 resta encara a les beceroles en comparació amb les plantes vasculars.

62 • Es van mostrejar 303 comunitats de moltes aquàtiques i semi-aquàtiques  
63 (higrofítiques), que habitaven fonts semi-naturals de Catalunya, per estudiar com  
64 els trets de les moltes variaven segons la seva història evolutiva, el clima i la  
65 química de l'aigua de les fonts on es trobaven. Es van analitzar 30 espècies de  
66 moltes i 17 trets fent servir mètodes filogenètics i un anàlisi RLQ, incorporant  
67 informació espacial i filogenètica. La nostra hipòtesi era que, en moltes  
68 higrofítiques, existeix un gradient d'esclerofília que opera a través d'un gradient de  
69 conductivitat de l'aigua de les fonts, de forma similar al que trobem en les plantes  
70 vasculars que viuen en ambients estressants.

71 • Els resultats indiquen que les formes de vida i els trets morfològics de les moltes  
72 estan ben preservats filogenèticament i que varien seguint els gradients de  
73 conductivitat de l'aigua i del clima. Aquest fet combinat amb l'autocorrelació  
74 espacial en les variables ambientals, resulta en una distribució agregada en l'espai  
75 de les espècies més properes filogenèticament. Les moltes que viuen en fonts de  
76 clima càlid i sec i de les quals brolla aigua d'alta conductivitat tendeixen a ser més

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

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

85

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

88

## 89 **1. Introduction**

90 Mosses are amongst the simplest and oldest plants on Earth and, despite their small  
91 size, they played a remarkable role shaping our planet in ancient times (McMahon &  
92 Davies, 2018). Still in our era, they continue to condition the structure and function of  
93 ecosystems, representing one of the largest groups of land plants, found almost  
94 everywhere in the world (Medina, Draper, & Lara, 2011). Their simplicity and particular  
95 physiology make bryophytes very interesting subjects of study in ecology, especially  
96 because the lack of thick cuticles and roots makes them extremely sensitive to  
97 environmental changes (Porley & Hodgetts, 2005) and pollution (Sayol et al., 2017).  
98 Nonetheless, the proportion of studies focusing on the response of bryophytes to  
99 environmental factors, compared to vascular plants, is dramatically low. However,  
100 understanding bryophytes better could provide important insights about unresolved  
101 questions of evolutionary ecology and physiology of plants (Fernández-Martínez et al.,  
102 2018; Proctor & Tuba, 2002; Susmilch, Roelfsema, & Hedrich, 2018) due to them  
103 being ubiquitous and simple organisms: characteristics of a potentially good model  
104 study system. The study of functional traits is definitely one of the fields that could  
105 benefit most from the study of bryophytes (Susmilch et al., 2018).

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

115 have been focused on vascular plants, several studies focused on bryophyte traits  
116 have provided the basis for understanding their relationship with the environment.

117 In 2007, Hill et al. published an extraordinarily large dataset of bryophyte traits,  
118 including morphological, reproductive and life-history traits. Several researchers have  
119 studied moss traits in boreal and arctic ecosystems (Elumeeva, Soudzilovskaia,  
120 During, & Cornelissen, 2011; Jonsson et al., 2014; Kangas et al., 2014; Mazziotta,  
121 Granath, Rydin, Bengtsson, & Norberg, 2019; Sokołowska, Turzańska, & Nilsson,  
122 2017; Turetsky et al., 2012), alpine habitats (Ah-Peng et al., 2014; Wang, Liu, Bader,  
123 Feng, & Bao, 2017), tropical forests (Waite & Sack, 2010) and even in vitro  
124 experiments (Löbel & Rydin, 2010). Despite intensive local research on moss traits and  
125 the extremely useful dataset published by Hill et al. (2007), however, it has not been  
126 until 2018 that, to the best of our knowledge, the first paper focused on the relationship  
127 between bryophyte traits, species distributions and environmental conditions was  
128 published. Löbel et al. (2018) published a study focused on traits of epiphytic mosses,  
129 elucidating interesting relationships between moss traits and environmental variables of  
130 the studied forests (e.g., fragmentation and climate), shaping moss assemblages  
131 across sites. However, they did not take into account the phylogenetic relatedness of  
132 the studied species. This could be important because the addition of phylogeny to  
133 information about traits could help to clarify the interconnections between local  
134 coexistence and macroevolution (de Bello et al., 2015; Gerhold, Cahill, Winter, Bartish,  
135 & Prinzing, 2015). In mosses in particular, it has been recently suggested that some  
136 traits and adaptations may appear as a response to environmental conditions while  
137 other traits remain preserved throughout the evolutionary history of the species  
138 (Huttunen, Bell, & Hedenäs, 2018), making phylogenetic comparative methods a  
139 necessary tool to understand the evolution of moss traits. Hence, there is still a large  
140 gap of knowledge on how environmental conditions and phylogenetic relatedness can  
141 shape moss assemblages by means of their relationship with moss traits.

142 To fill in this gap, our main aim was to explore whether traits of aquatic and semi-  
143 aquatic (hereafter, hygrophytic [Dierssen, 2001]) mosses in semi-natural springs are  
144 related to their evolutionary history or to environmental conditions such as climate and  
145 water chemical composition of the springs. To do so, we performed an extensive field  
146 sampling of 303 semi-natural Mediterranean springs, distributed across mountainous  
147 regions of the north-eastern Iberian Peninsula (**Figure 1**), from which we analysed their  
148 water chemistry and the moss assemblages in contact with spring water (Bes et al.,  
149 2018; Corbera et al., 2015; Fernández-Martínez et al., 2019; Sayol et al., 2017). We  
150 then inferred the phylogenetic relationships of the sampled species using genetic data  
151 and measured and gathered information on 17 moss traits (eight morphological traits,  
152 three reproductive traits and six life forms) for 30 moss species. Surveyed springs  
153 discharged water continuously throughout the year, which, in Mediterranean regions,  
154 means that they behave like small islands, or refugia, where water is available,  
155 surrounded by completely different habitats where water is scarce. They are, therefore,  
156 ideal habitats for hygrophytic mosses (Bes et al., 2017; Corbera et al., 2015). Also, the  
157 distribution of springs in the Mediterranean region is relatively homogeneous  
158 throughout the territory, comprising large differences in lithology, water chemical  
159 composition, climate and topology (Fernández-Martínez et al., 2019). These large  
160 gradients allowed us to investigate how moss traits vary across a very wide range of  
161 environmental conditions.

162 In order to achieve our main objective, we first explored similarities amongst moss  
163 species with regard to traits to understand which traits have been environmentally  
164 selected and which ones have been preserved through evolutionary history. Secondly,  
165 we explored the patterns of species distributions and their traits linked to those of  
166 environmental conditions using an extended version of the RLQ analysis (Pavoine,  
167 Vela, Gachet, De Bélair, & Bonsall, 2011) meant to account for species phylogenetic  
168 relatedness and environmental spatial autocorrelation. Water chemistry has been

169 suggested to influence moss species distributions because of physical and  
170 physiological constraints, especially at the high range of water conductivity and pH.  
171 Examples of these constraints are the formation of calcium carbonate crusts, lack of  
172 CO<sub>2</sub> for photosynthesis and osmotic stress (Bain & Proctor, 1980; Bernstein, 1975; Bes  
173 et al., 2018; Grime, Rincon, & Wickerson, 1990; Josep Peñuelas, 1985). Adaptations to  
174 these conditions may require similar solutions to those achieved by vascular plants  
175 growing under stressful environments. We, therefore, hypothesised that a sclerophylly  
176 continuum in hygrophytic mosses living under high and low water conductivity exists  
177 that mimics that of sclerophylly in vascular plants. We here expected to find denser  
178 (i.e., higher mass per volume and area) mosses with narrower leaves living under high  
179 conductivity water rich in calcium (Ca<sup>2+</sup>) compared to those living under low  
180 conductivity water because of the drawbacks that an excess of calcium carbonate can  
181 imply for hygrophytic mosses (i.e., less absorbable CO<sub>2</sub>, higher osmotic pressure and  
182 eventually carbonate crusts) (Bain & Proctor, 1980; Bernstein, 1975; Bes et al., 2018).  
183 We additionally investigated whether these sclerophyllic adaptations have been  
184 preserved throughout the evolutionary history of the moss species.

## 185 **2. Methods**

### 186 *2.1 Study area*

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

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

## 207 *2.2 Field sampling and laboratory analyses*

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

220 Water pH and electric conductivity were measured in the field with a combined pH and  
221 conductivity meter. Main cations ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$ ,  $\text{K}^+$ ) were analysed by ion exchange

222 chromatography and anions ( $\text{SO}_4^{2-}$ ,  $\text{Cl}^-$  and  $\text{NO}_3^-$ ) were analysed by ionic  
223 chromatography.  $\text{HPO}_4^{2-}$  was measured by the colorimetric method established by  
224 (Murphy & Riley, 1962). Water concentration of Al, As, Cd, Co, Cr, Cu, Fe, Mn, Pb, Hg,  
225 Ni, Zn was analysed by ICP-MS (Inductively Coupled Plasma-Mass Spectrometry).  
226 See Fernández-Martínez et al. (2019) for further details on the methodology used to  
227 analyse water chemical composition.

228 Each spring was geolocated using a GPS device. With these coordinates, we extracted  
229 monthly climatic data for temperature and precipitation of the springs from the digital  
230 Climatic Atlas of Catalonia (Pons [1996], Ninyerola et al., [2000], available at  
231 <http://www.opengis.uab.cat/acdc/index.htm>). The seasonal values for temperature and  
232 precipitation were calculated as the average of December-February (winter), March-  
233 May (spring), June-August (summer) and September-November (autumn). Given the  
234 high collinearity between climate variables, we only used spring and summer values  
235 because those seasons are likely to be the most influential determining spring water  
236 runoff (abundant rain during spring season make springs have water during summer).  
237 We also calculated temperature and precipitation seasonality as the coefficient of  
238 variation of monthly values to assess how different were temperature and precipitation  
239 throughout the year. Water availability was calculated as monthly precipitation minus  
240 reference evapotranspiration calculated following the Hargreaves method (Hargreaves,  
241 1994). Altitude was extracted with an elevation digital model with 30 metres resolution.  
242 We also recorded whether springs were under shade or not as a proxy of insolation. A  
243 correlation matrix of the environmental variables can be found in **Figure S2**.

244 Bryophyte sampling was carried out by collecting a sample of all moss and liverwort  
245 species present in the springs that were either in direct contact with the water of the  
246 spring or receiving drops over the splash zone (**Figure S1**). For the purpose of this  
247 study, only moss species were used. We did not standardise our sampling by area  
248 because of the small area of most of the springs (less than  $0.9 \text{ m}^2$ ) and the lack of a

249 species richness – area relationship in these habitats (Bes et al., 2018). Species were  
250 identified using Smith (1990) and Casas *et al.*, (2001, 2004) identification keys, using  
251 the nomenclature established by Hill et al., 2006. Once in the laboratory, moss samples  
252 were cleaned in order to remove the soil stuck on them and stored dried until laboratory  
253 measurements took place. The species accumulation curve confirmed that our  
254 sampling gathered most of the biodiversity present in these habitats (**Figure S3**). A  
255 total of 46 moss species were found in the sampled springs (**Figure S4**).

### 256 *2.3 Moss traits*

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

274 Moss mass per area was calculated as the ratio of moss dry mass to projected area of  
275 two to seven individual shoots (depending on the size of the species to ensure

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

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

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

#### 312 *2.4 Phylogenetic analyses*

313 We built a phylogeny covering the 44 species of mosses found in this study plus 15  
314 species of liverworts, also found at the springs, used as outgroups. The phylogeny was  
315 based on five genes obtained from GenBank (Benson et al., 2018): two nuclear genes  
316 (18S and 5.8S) and three plastid genes (rbcL, rps4, TrnL) (Stech & Quandt, 2014) (see  
317 GenBank accession numbers in **Table S3**). Genes were aligned using the program  
318 MAFFT v7 (Kato, Misawa, Kuma, & Miyata, 2002) and poorly aligned regions were  
319 removed by means of G-Blocks using low stringency options (Castresana, 2000).  
320 Phylogenetic analyses were conducted with the package BEAST v1.8.4 (Drummond &  
321 Rambaut, 2007) based on an uncorrelated log-normal relaxed clock and a “birth-death  
322 incomplete sampling” tree prior. Partitions and nucleotide substitution models were  
323 estimated by means of PartitionFinder v2 (Lanfear, Frandsen, Wright, Senfeld, &  
324 Calcott, 2017). The BEAST analysis relied on two independent MCMC chains that ran  
325 for 100,000,000 generations and were sampled each 20,000. Mixing and convergence  
326 of both runs were assessed by means of Tracer v.1.7.1 (Rambaut, Drummond, Xie,  
327 Baele, & Suchard, 2018). No calibrations were set in the analysis. A summary tree was  
328 estimated as the maximum clade credibility tree with median node heights using

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

#### 341 2.5 Statistical analyses

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

353 After, we explored whether moss traits and the two PCA axes extracted in the previous  
354 analysis presented a phylogenetic signal ( $\lambda$ ). To do so, we used the function *phylosig* in  
355 *phytools* R package (Revell, 2012) and tested each variable for 1000 trees to account

356 for phylogenetic uncertainty (we considered that there was a statistically significant  
357 phylogenetic signal if percentile 2.5% was higher than 0). We then performed a  
358 continuous character mapping of PC1 and PC2 using *contMap* function in *phytools* to  
359 further explore the evolution of traits in our phylogeny.

360 Then, we tested for spatial autocorrelation in environmental variables performing a  
361 Moran's I test using function *gearymoran* in *ade4* R package (Dray & Dufour, 2007).  
362 We tested for phylogenetic and trait clustering in our dataset using the phylogenetic  
363 and trait quadratic entropy tests (PQE, TQE) described in (Pavoine, Baguette, &  
364 Bonsall, 2010) using function *TPQE* provided in (Pavoine et al., 2011). Trait or  
365 phylogenetic clustering would occur if species assemblages in single springs present  
366 lower phylogenetic and trait diversity than expected from the pool of species found over  
367 the entire set of sampled springs (i.e., significantly higher values than random  
368 simulations in PQE and TQE tests). We repeated these tests using springs presenting  
369 one to four moss species per spring to test the potential effect of species richness per  
370 site on these analyses (**Figure S5**). For phylogenetic clustering analysis we used the  
371 44 species for which we had phylogenetic information, while for trait clustering we used  
372 the 30 species with trait data.

373 Then, to finally test the relationship between moss traits and climate and water  
374 chemical composition, we performed an extended version of the RLQ analysis  
375 developed by (Pavoine et al., 2011) using R packages *adiv* (Pavoine, 2018) and *ade4*  
376 (Dray & Dufour, 2007). RLQ analysis, as well as the corner analysis, is a multivariate  
377 method aimed at analysing information on species distribution, environmental  
378 conditions and species traits to finally assess the relationship between traits and the  
379 environment (Brown et al., 2014; Dolédec, Chessel, Ter Braak, & Champely, 1996;  
380 Dray et al., 2014; Dray & Legendre, 2008; Pease, González-Díaz, Rodiles-Hernández,  
381 & Winemiller, 2012). The extended version additionally incorporates one matrix to  
382 account for spatial autocorrelation and another one to account for phylogenetic non-

383 independence (see Pavoine et al. [2011] for further details on this analysis). To help  
384 visualising the correlation between traits and the environment, we calculated trait vs.  
385 environment correlations. To do so, for each trait, we multiplied the value of its  
386 correlation between with axis 1 (2 and 3) by the correlation of a given environmental  
387 variable with axis 1 (2 and 3), and weighted the result for the percentage of  
388 environmental variance explained of the given axis. We repeated that same process for  
389 each pair of trait-environmental variables for axes 2 and 3 and summed the three  
390 coefficients as a measure of pseudo correlation between the traits and the  
391 environment. Finally, the matrix was plotted using a clustered image map using the  
392 function *cim* in *mixOmics* R package (Le Cao et al., 2017). We first performed the RLQ  
393 analysis using all springs where at least one of the species with traits was present  
394 (N=295 springs). We then repeated the extended RLQ analysis using only springs with  
395 at least 2 species present (N=195) to test the consistency of the results (**Figure S5**).  
396 We also performed a fourth-corner analysis (model type 6), in order to test whether  
397 controlling for spatial and phylogenetic autocorrelation or not doing it would lead to  
398 different results.

### 399 **3. Results**

#### 400 *3.1 Phylogenetic analyses*

401 The final concatenated alignment, after applying G-blocks, consisted of a maximum of  
402 2660 bps. The best partition strategy estimated by PartitionFinder arranged the five  
403 genes in three partitions: partition 1 (5.8S + 18S), partition 2 (rbcl) and partition 3  
404 (TrnL + rps4) with the following substitution models: partition 1 (TRNEF+G), partition 2  
405 (GTR + I + G) and partition 3 (GTR + I + G), the last two partitions with estimated base  
406 frequencies. MCMC runs converged to similar posterior estimates and sampled trees  
407 were pooled together discarding the initial 10% of each run as 'burn in'. The summary  
408 tree produced phylogenetic relationships generally consistent with previous evidence  
409 (**Figure S6**) (Casas et al., 2001; Erzberger, 2016; M. O. Hill et al., 2006).

### 410 3.2 Moss traits and their phylogenetic signal

411 Our results indicated that there are three main distinguishable groups of mosses with  
412 regard to their traits (**Figure 2**). The first group of mosses were more likely to be  
413 monoecious and pleurocarpous mosses forming mats, with high water absorption  
414 capacity (WAC) and mainly sexual reproduction. The second group was characterised  
415 by having needle-like leaves (long and narrow), high moss mass per area (MMA) and  
416 moss density, low sporophyte frequency and more likely reproducing asexually, being  
417 dioecious and forming turfs or cushions. The third group was defined by mosses that  
418 were more likely to be acrocarpous, forming tall turfs with big leaves and spores.  
419 Overall, the two axes extracted from the PCA explained, respectively, 25.1% and  
420 20.6% of the variance in moss traits (**Figure 2b**).

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

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

### 435 3.3 Trait and phylogenetic clustering

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

#### 442 *3.4 Relationship between traits, climate and water chemistry*

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

462 in the data) almost all traits presented higher correlations with the environment and,  
463 although the general trend was very similar, a few results differed (**Figure S8**).

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

#### 474 **4. Discussion**

##### 475 *4.1 Water chemistry and climate as environmental filters of moss assemblages*

476 Our analyses clearly demonstrated the relationship between moss traits and  
477 environmental variables, especially water chemistry and climate (**Figure 5**). These  
478 findings support the fact that both water chemistry and climate act as strong  
479 environmental filters, conditioning species distribution to specific traits. These findings,  
480 however, were in disagreement with trait and phylogenetic clustering tests, reporting no  
481 significant clustering or overdispersion for any of them (equal trait or phylogenetic  
482 diversity within each spring to that expected by the pool of species found) meaning that  
483 species seem to appear in these springs just at random. The most likely explanation of  
484 these two divergent results is that moss assemblages in springs are very often  
485 characterised for having very few species present (**Figure S5**) compared to other  
486 datasets for which these tests have been performed (e.g., La Mafragh, with more than  
487 80% of the sites having 8 or more species present [Pavoine *et al.*, 2011]), which

488 obviously hinders the performance of these permutational tests. However, the lack of a  
489 clear phylogenetic or trait clustering signal could also emerge because of a potentially  
490 strong dominance of the first species to settle in the springs (priority effect). Another  
491 limitation of the methods is that, because of the spatial correlation between  
492 temperature and water availability (e.g., rainfall) our analyses do not allow us to tell  
493 between the effects of them all. Nonetheless, we suggest that water conductivity is the  
494 main driver of the observed changes in traits of mosses living in springs because: *i*) the  
495 large majority of our studied springs have water flowing almost continuously throughout  
496 the year, making climate water availability relatively unlikely to directly affect moss  
497 assemblages, *ii*) water conductivity presents the highest correlations of all  
498 environmental variables, *iii*) mean annual precipitation (similar to our climate water  
499 availability – the difference between precipitation and evapotranspiration, see methods)  
500 has been shown to reduce the concentration of most ions dissolved in spring water  
501 (Fernández-Martínez et al., 2019), therefore reducing spring water conductivity, and *iv*)  
502 water conductivity has been previously described to play an important role shaping  
503 hygrophytic moss assemblages due to the physiological constraints that water  
504 conductivity imposes on these organisms (Bain & Proctor, 1980; Bernstein, 1975; Bes  
505 et al., 2018; Brown, 1982; Sayol et al., 2017).

506 As a result of a combined effect of spatially autocorrelated environmental filters (**Table**  
507 **S2**) and the fact that traits are phylogenetically preserved (**Figure 3**) a clear spatial and  
508 phylogenetic pattern emerged in these moss assemblages (**Figure 6**). It is very  
509 interesting to note the potential role that sea spray may play on the spatial distribution  
510 of moss species. Sea spray has been demonstrated to affect atmospheric deposition of  
511 salts and even groundwater chemistry, enriching water of these springs with chloride,  
512 sulphate, sodium, potassium, magnesium and calcium (Fernández-Martínez et al.,  
513 2019). All these elements were positively aligned with axis 1 of the RLQ analysis and  
514 presented high scores in almost all springs near the coast despite belonging to a

515 granite lithology (**Figure 6a**, southernmost sites). Hence, according to our results,  
516 proximity to the coast may also condition moss establishment because of its effect on  
517 water chemistry. It is also interesting that our analyses indicate that there were more  
518 species that tend to live in springs with low rather than high conductivity water (**Figure**  
519 **6b**). This finding may indicate that high conductivity water may be more physiologically  
520 demanding than low conductivity water for mosses, potentially for the particular  
521 adaptations that they must present to be able to live under these environmental  
522 conditions. Our results also indicate that this differentiation between high conductivity-  
523 water tolerant and intolerant species may have developed long ago during their  
524 evolutionary history, given the fact that all high conductivity-water tolerant species  
525 belong to the same clade (**Figure 6b**).

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

535 The strong effect of water conductivity on moss traits may appear because of different  
536 physiological constraints. One mechanism that has been suggested in vascular plants  
537 is osmotic stress (Bernstein, 1975), reducing growth rates and overall plant vigour  
538 (Xiong & Zhu, 2002). Mosses might also potentially suffer osmotic stress and respond  
539 in the same way vascular plants do, as suggested by our results. These mosses living  
540 under osmotic stress may therefore present higher concentrations of dehydrin proteins  
541 and osmotically active sugars, increasing their density and moss mass per area, as do

542 desiccation-tolerant moss species (Proctor et al., 2007). Another potential mechanism  
543 explaining the role of water conductivity could be related to key nutrient imbalances or  
544 deficiencies. In hard waters phosphate binds with calcium, drastically reducing  
545 available phosphate for plants (Doods, 2003). The lack of available phosphate may  
546 impose a limitation on larger moss species to establish in springs with hard water,  
547 given the paramount role of phosphorus on plant metabolism (Fernández-Martínez et  
548 al., 2018; Fernández-Martínez, Vicca, Janssens, Espelta, & Peñuelas, 2016; J.  
549 Peñuelas et al., 2019). On the other hand, mosses are supposed to require very little  
550 amounts of nutrients to sustain their metabolism (Porley & Hodgetts, 2005). However,  
551 this fact should not preclude larger and, therefore, more competitive mosses from  
552 establishing preferentially in springs with higher phosphate availability, as our results  
553 also suggest – albeit presenting very low correlations (**Figure 5**). Research on moss  
554 stoichiometry is therefore warranted to answer these questions.

555 Another mechanism by which water conductivity may affect moss traits is by modifying  
556 available CO<sub>2</sub> in water. In hard water, CO<sub>2</sub> cannot be used for photosynthesis by  
557 bryophytes because it is mainly found in the form of bicarbonate (Bowden, 1999;  
558 Glime, 2014). In those cases, it has been suggested that only a small subset of  
559 species, like *F. antipyretica*, seem to be able to use HCO<sub>3</sub><sup>-</sup> as source of carbon for  
560 photosynthesis (Bain & Proctor, 1980; Josep Peñuelas, 1985), while most of them  
561 cannot (e.g., *C. filicinum*, *E. verticillatum*, *F. grandifrons*). The low concentration of free  
562 CO<sub>2</sub> may hamper the capacity of aquatic mosses to photosynthesise, and allow only  
563 stress-tolerant species to establish. In our study, though, not all moss species that can  
564 live completely submerged under water were always found living under water, and  
565 those species that cannot, do not usually suffer flooding events. Therefore, most of the  
566 mosses sampled should be able to obtain CO<sub>2</sub> directly from the atmosphere, despite  
567 the fact that being continuously surrounded by water may potentially hinder the  
568 diffusion of CO<sub>2</sub>. Nonetheless, the most potentially limiting factor that water conductivity

569 may impose on moss growth is calcium toxicity (Vicherová, Hájek, & Hájek, 2015) and  
570 the formation of calcium carbonate crusts all around them (tufa formations). These  
571 particular formations only occur because bryophytes act as a surface from which  $\text{Ca}^{2+}$ -  
572 enriched water evaporates, leaving a crust of  $\text{CaCO}_3$  (Brown, 1982; Glime, 2014). In  
573 these habitats, mosses engage in a particular dynamic of growing, dying and  
574 overgrowing on  $\text{CaCO}_3$  crusts to avoid complete coverage. This dynamic may only be  
575 achieved by a few species presenting very specialised traits (**Figure 6b**). Overall, our  
576 findings suggest the existence of some sort of *sclerophylly* gradient in hygrophytic  
577 moss traits in response to water conductivity (**Figure 7**). Sclerophyllous mosses would  
578 be characterised by being denser, having high moss mass per area, low water  
579 absorption capacity and needle-like leaves. These traits are similar to those found in  
580 vascular plants (e.g., leaf mass area) in a gradient of water availability and temperature  
581 (Niinemets & Niinemets, 2013; Wright et al., 2004). Considering that adaptations of  
582 both types of organisms (mosses and vascular plants) are very similar (e.g., small size,  
583 high density and mass per area, needle-like leaves) it seems likely that sclerophylly  
584 would have evolved in both groups following convergent evolution.

#### 585 *4.2 Reproductive traits and phylogenetic conservatism*

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

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

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

## 607 **5. Conclusions**

608 Our findings provided novel insights about the phylogenetic relatedness of moss traits  
609 and their relationship with the environment, increasing our knowledge in an  
610 understudied group of organisms. We found that climate and water chemistry act as  
611 important environmental filters of traits of hygrophytic mosses and, therefore, condition  
612 species distributions. Our results suggest the existence of a sclerophylly continuum in  
613 hygrophytic mosses, especially shown in the morphological traits, that may be  
614 particularly related to the role of water conductivity and, hence, low free CO<sub>2</sub> and high  
615 bicarbonate (CaCO<sub>3</sub>) concentration. In hard waters, Ca<sup>2+</sup> binds with CO<sub>2</sub> forming  
616 bicarbonate, reducing free CO<sub>2</sub> and potentially reducing photosynthesis and moss  
617 growth. In cases of springs with very high water conductivity (and usually Ca<sup>2+</sup>  
618 concentration), a crust of calcium carbonate grows in the springs, allowing only very  
619 specialised mosses to overgrow it and survive (Bes et al., 2018; Brown, 1982). These  
620 findings support a kind of sclerophylly gradient in hygrophytic mosses relating to water  
621 conductivity (**Figure 7**), similar to traits in vascular plants (e.g., leaf mass per area)  
622 relating to water availability and temperature (Niinemets & Niinemets, 2013; Wright et

623 al., 2004). We believe that this study highlights the possibilities and mutual benefits for  
624 joining the study of traits to the investigation of bryophytes. We show that traits can be  
625 used to further our knowledge of an understudied group of species (mosses), and we  
626 also propose to use mosses as a model study group in which to test ecological theory.

### 627 **Author contributions**

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

631

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### 640 **Data Accessibility**

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

643

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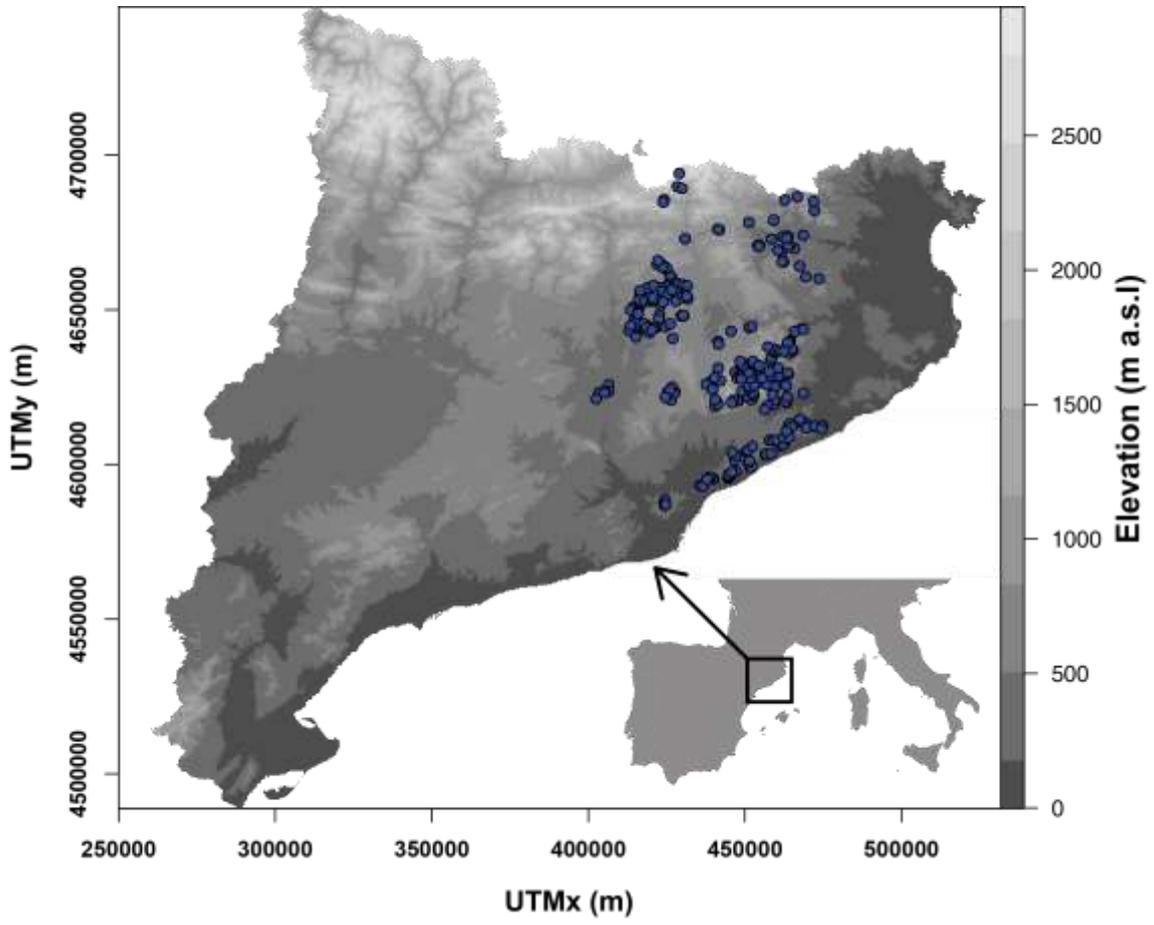
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- 903

904 **Figure captions**

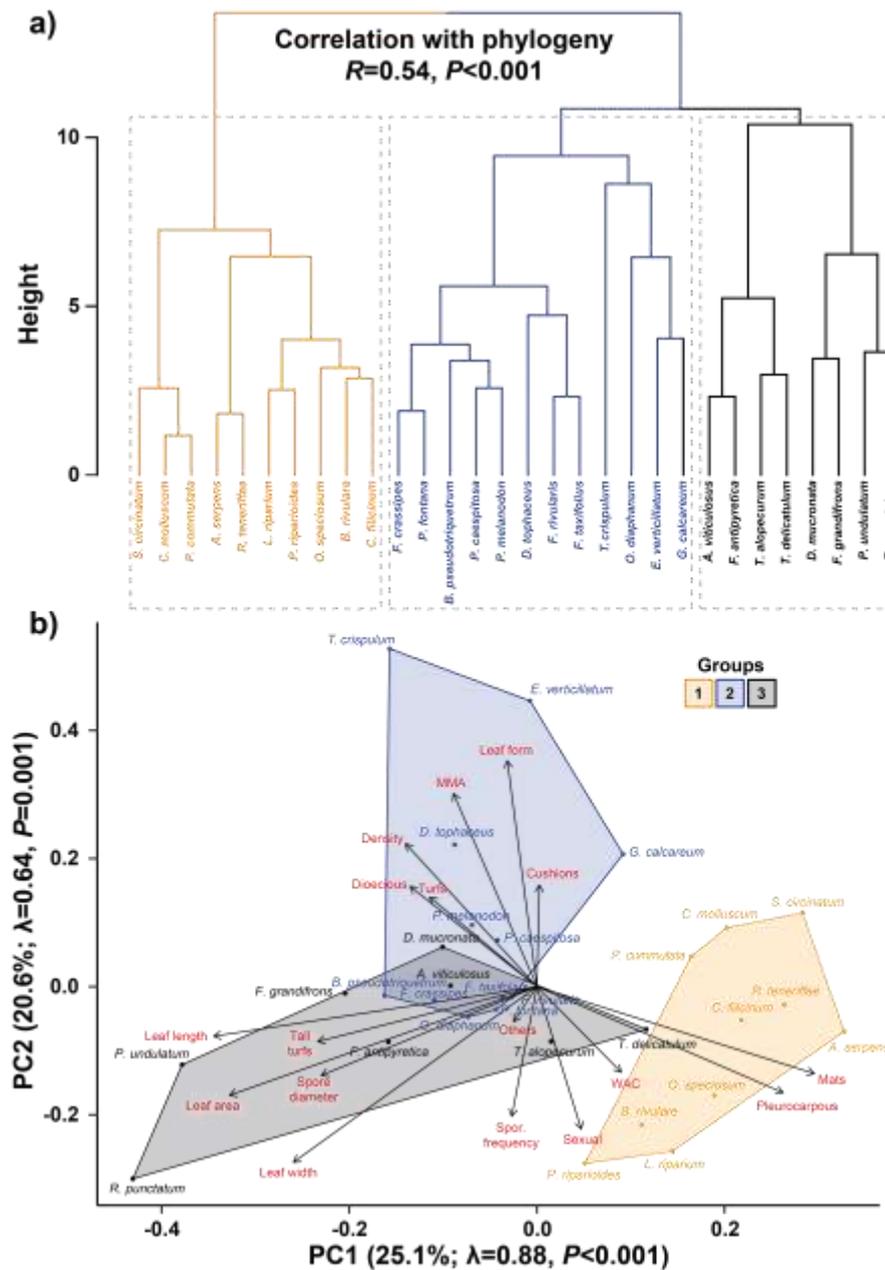
905 **Figure 1:** Map showing the springs sampled.



906

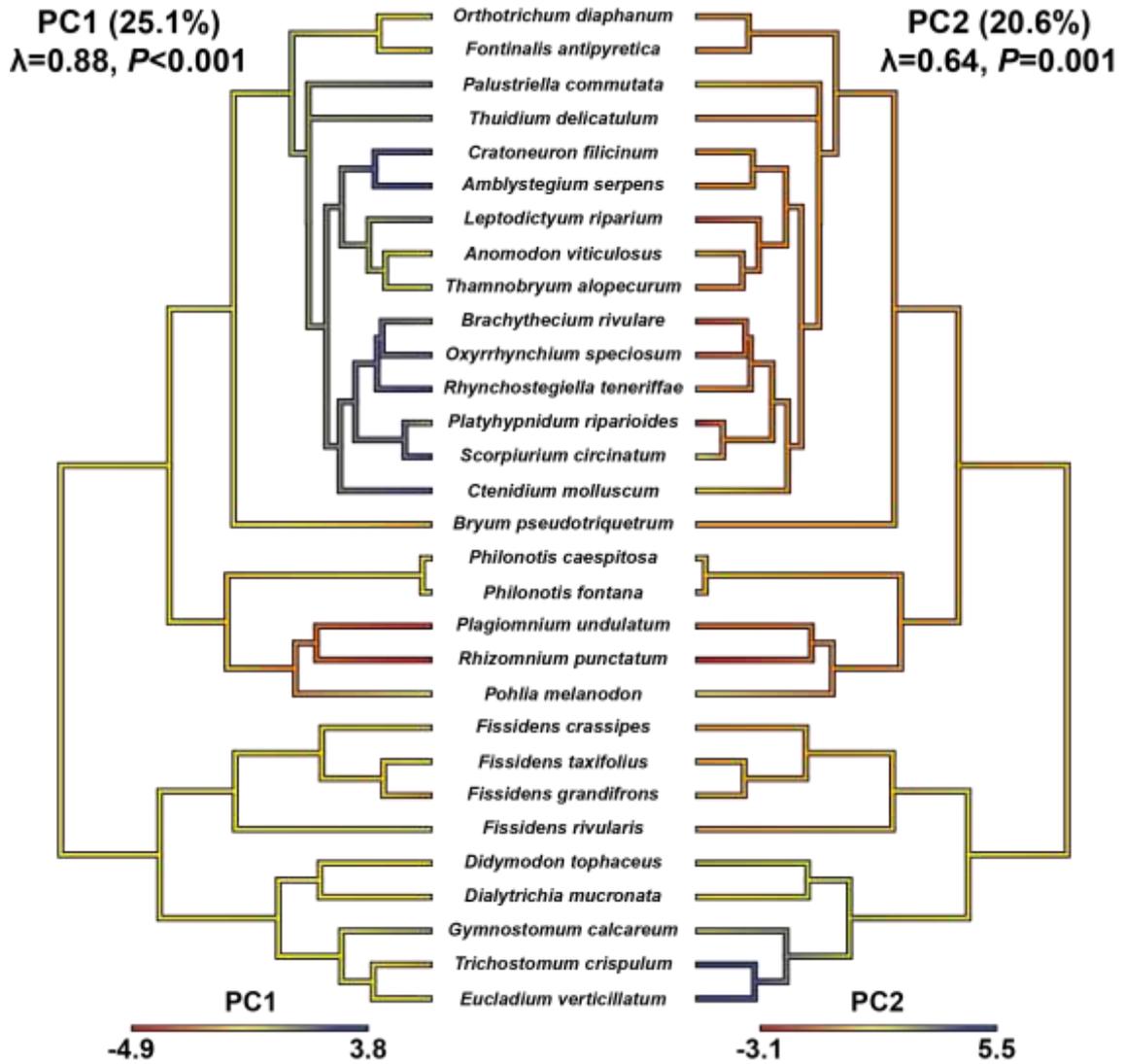
907

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



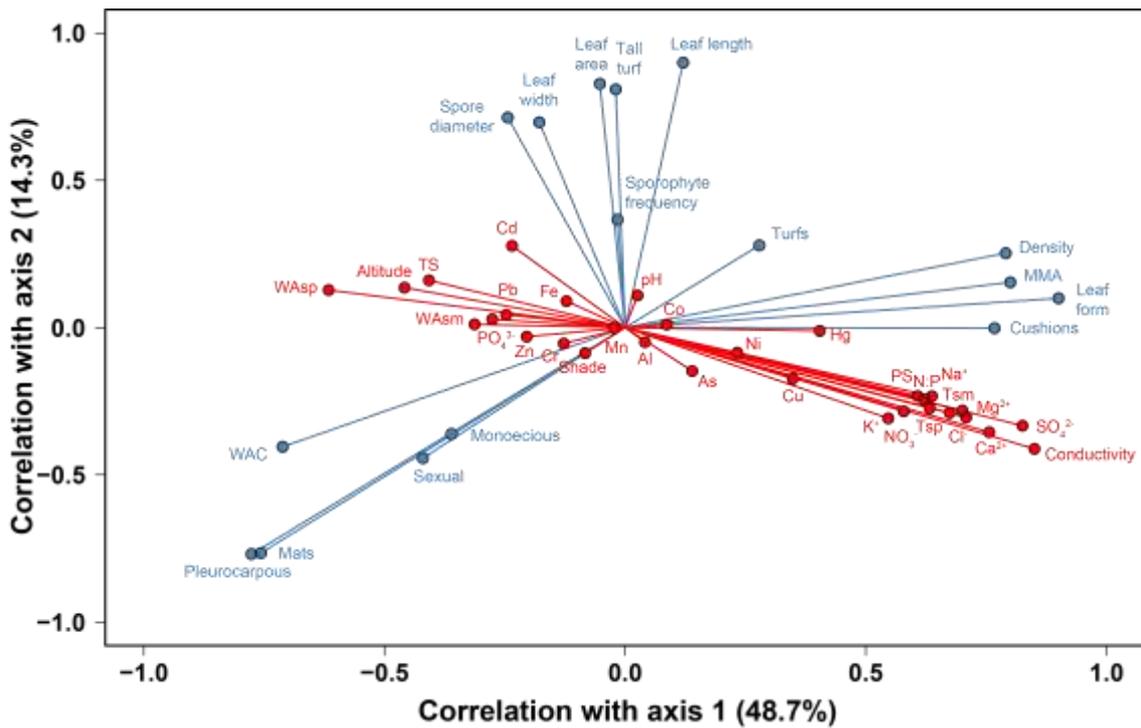
914

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



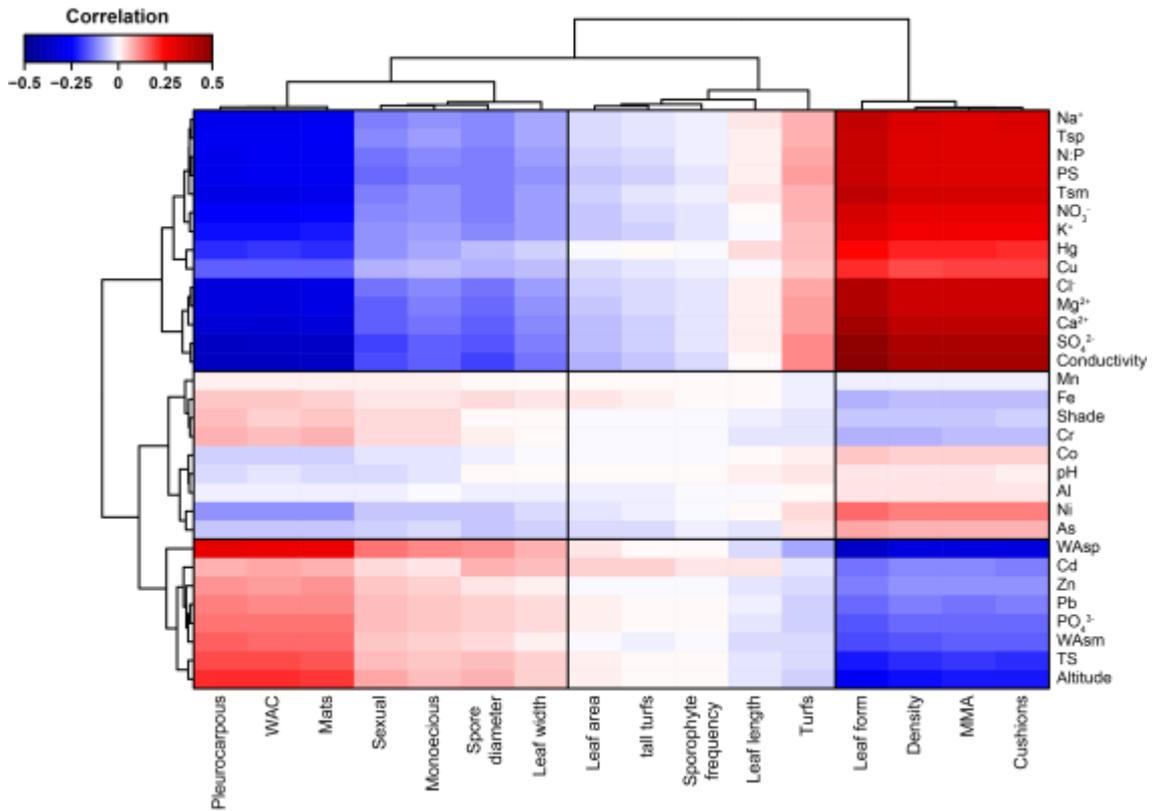
918

919 **Figure 4:** Results of the extended RLQ analysis showing correlation of traits (blue) and  
 920 the environment (red) with axes 1 and 2. The environmental variance explained by the  
 921 axes is shown between brackets. *Acronyms:* NO<sub>3</sub>:PO<sub>4</sub><sup>3-</sup> ratio (N:P), temperature (T),  
 922 precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm),  
 923 moss mass per area (MMA), water absorption capacity (WAC).



924

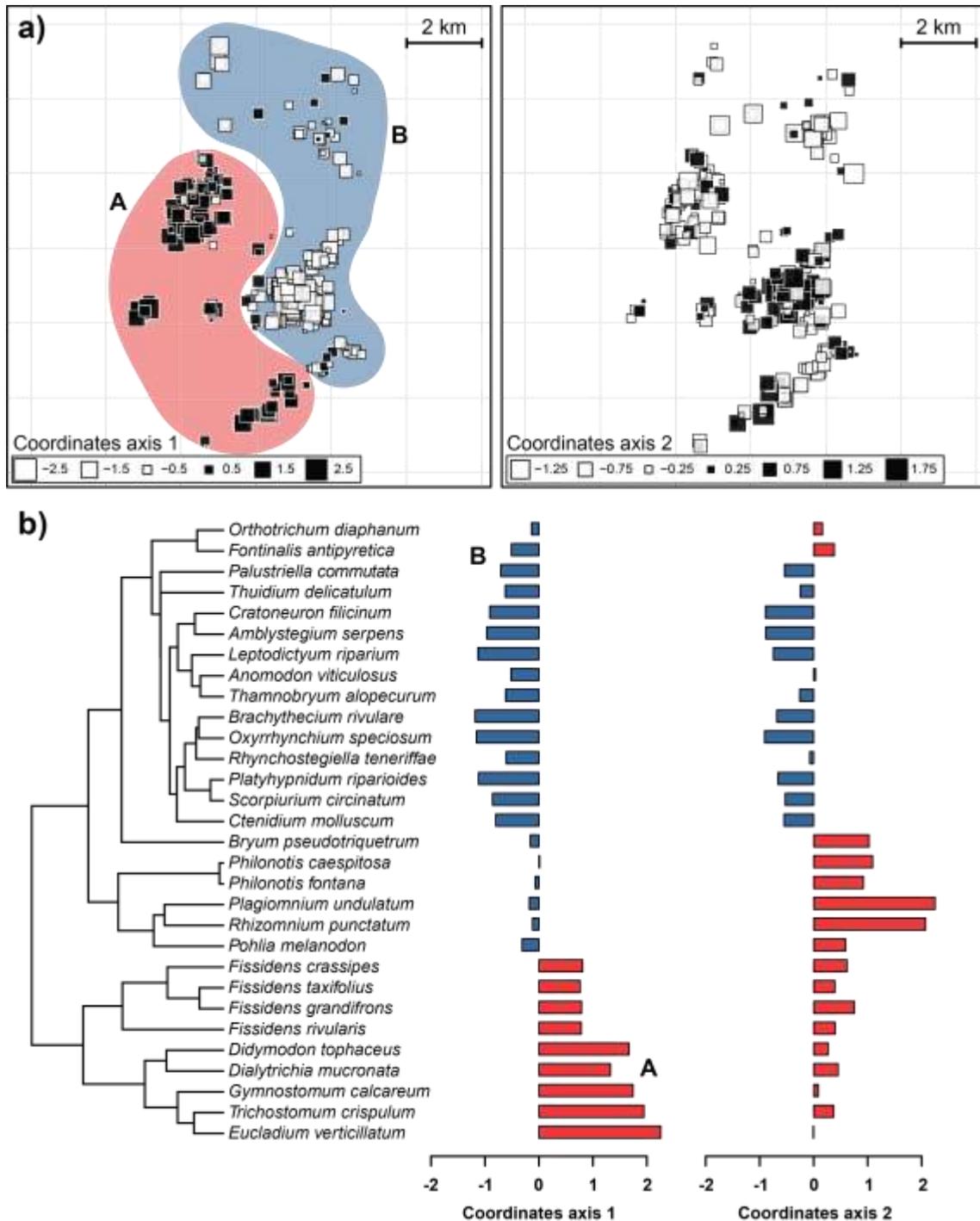
925 **Figure 5.** Clustered image map summarising the results of the extended RLQ analysis  
 926 (N=295 springs). Environmental variables are on the right side of the plot and moss  
 927 traits at the bottom. *Acronyms:* nitrate-to-phosphate ratio (N:P), temperature (T),  
 928 precipitation (P), seasonality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



930

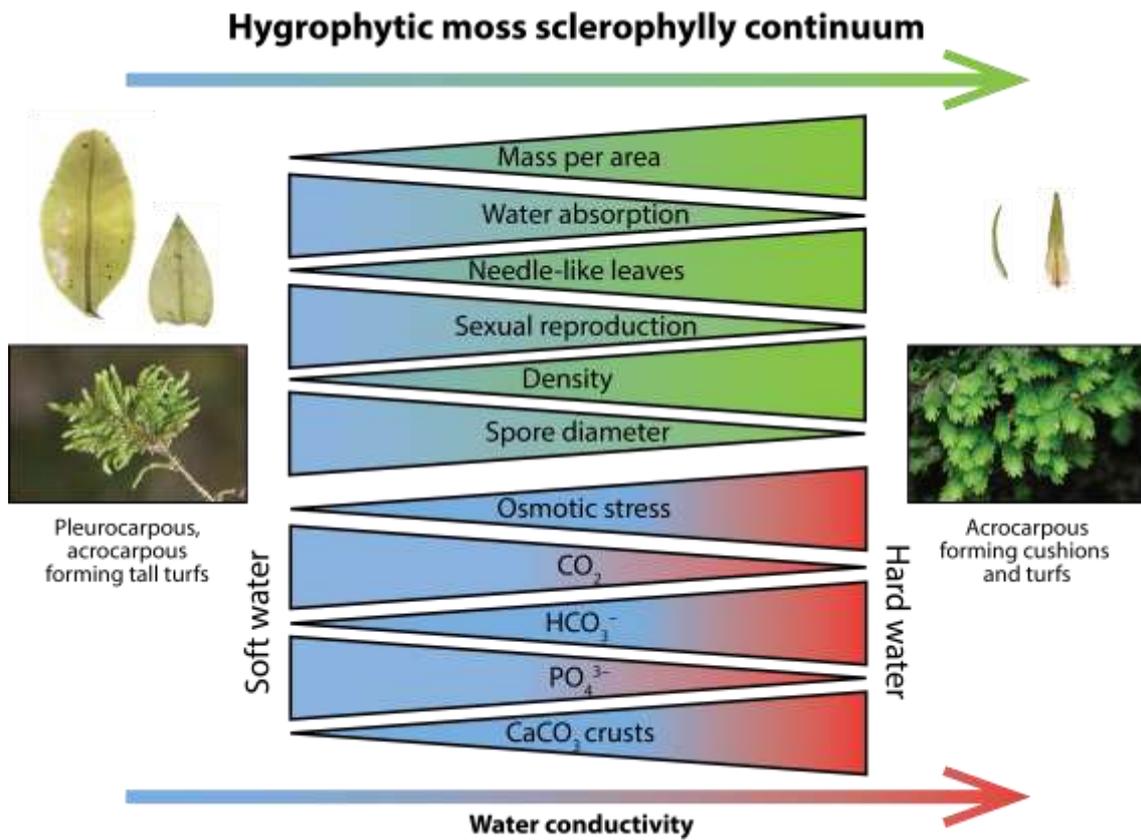
931

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



935

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



940

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

<b>Name</b>	<b>Type</b>	<b>Estimation</b>	<b>Units</b>
<b><i>Morphological</i></b>			
Leaf length	Continuous		µm
Leaf width	Continuous		µm
Leaf area	Continuous		mm <sup>2</sup>
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 <sub>2</sub> O mg <sup>-1</sup> Dry weight
Moss mass per area	Continuous	Dry weight/Area	mg mm <sup>-2</sup>
Density	Continuous	Dry weight/Volume	mg ml <sup>-1</sup>
<b><i>Reproductive</i></b>			
Sporophyte frequency	Discrete	1: Rare; 2: Occasional; 3: Frequent; 4: Abundant	
Monoecious - Dioecious	Binary	0: Dioecious; 1: Monoecious	
Sexuality	Binary	0: Asexual; 1: Sexual	
<b><i>Life forms</i></b>			
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	

943

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

950

951

<b>Trait</b>	<b><math>\lambda_{2.5\%}</math></b>	<b><math>\lambda_{50.0\%}</math></b>	<b><math>\lambda_{97.5\%}</math></b>
<b><i>Morphological</i></b>			
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
<b><i>Reproductive</i></b>			
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
<b><i>Life forms</i></b>			
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
<b><i>Principal components analysis</i></b>			
PC1 ( <b>Figures 2 and 3</b> )	0.74	0.87	1.02
PC2 ( <b>Figures 2 and 3</b> )	0.58	0.64	0.75

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

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

960 **Supplementary material**

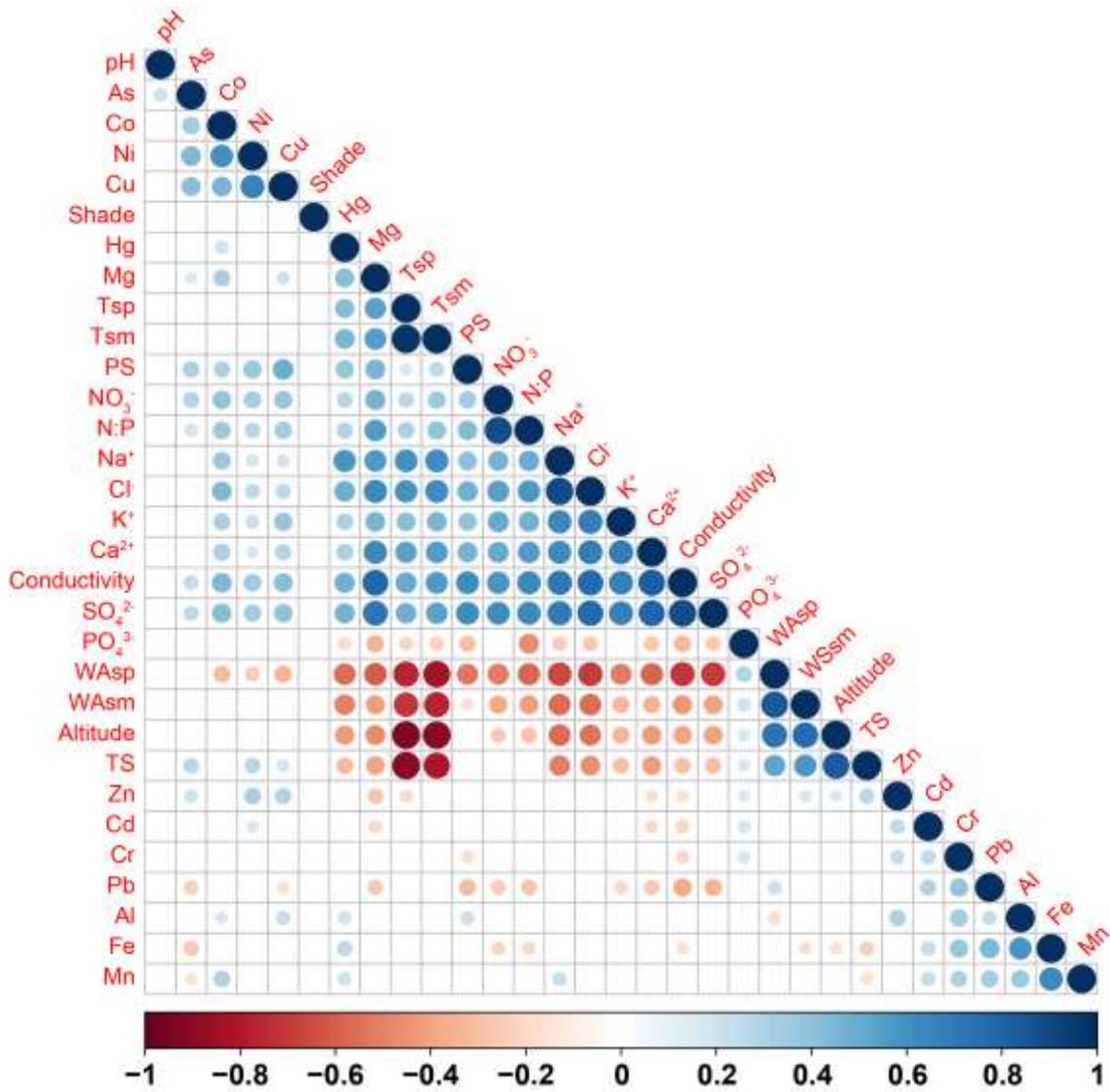
961 **Figure S1:** Example of a typical semi-natural spring. The red line delimits the area of  
962 influence of the water, from where we collected moss samples.



963

964

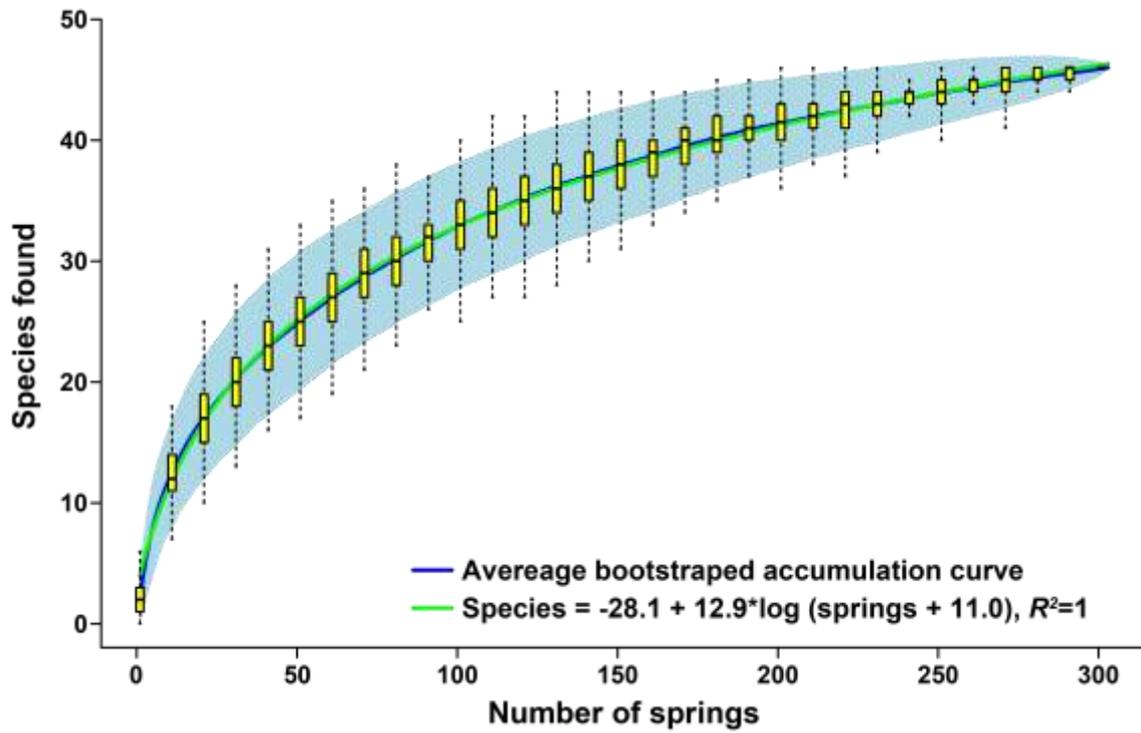
965 **Figure S2:** Plot showing Spearman's correlations between environmental variables.  
 966 The size of the circles is proportional to the correlation values. *Acronyms:* nitrate-to-  
 967 phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water  
 968 availability (WA),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



969

970

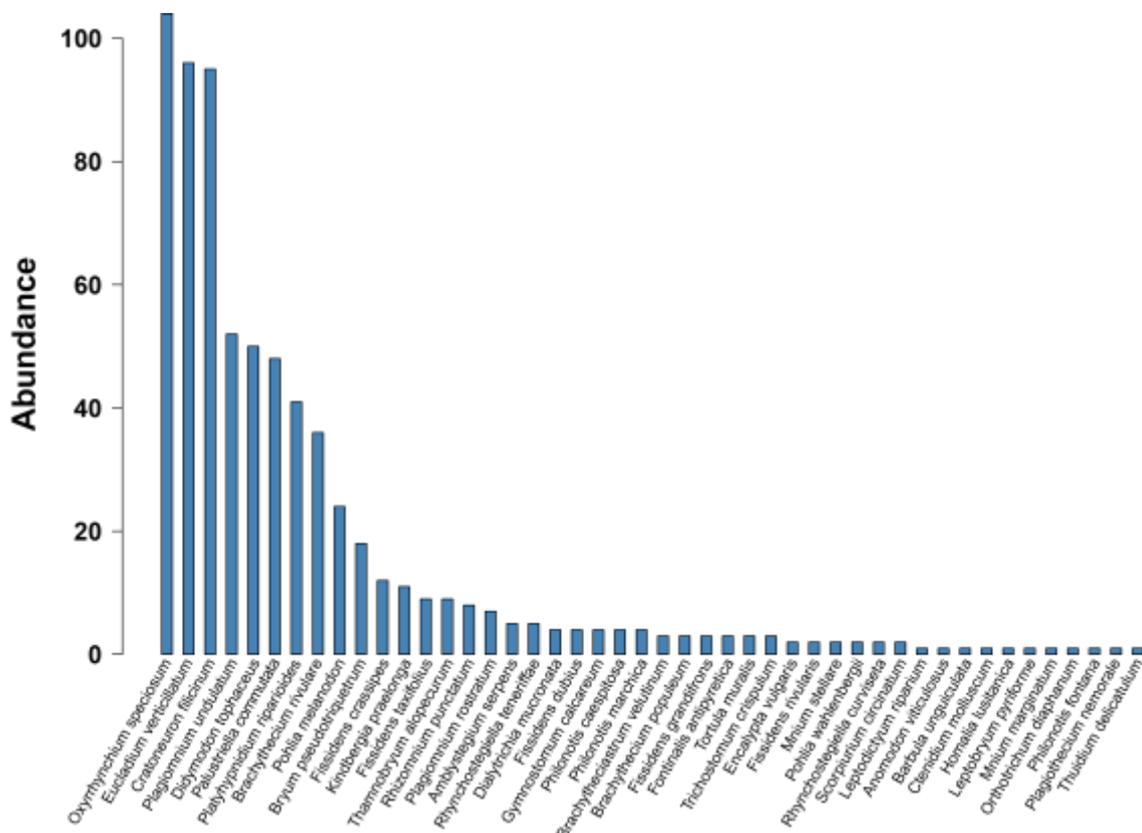
971 **Figure S3.** Species accumulation curve for the sampled springs, obtained by the  
972 bootstrap method (1000 permutations) using *vegan* (Oksanen et al., 2018) R package.  
973 Boxplots indicate bootstrap simulations and the shaded area shows the confidence  
974 intervals from standard deviation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



975

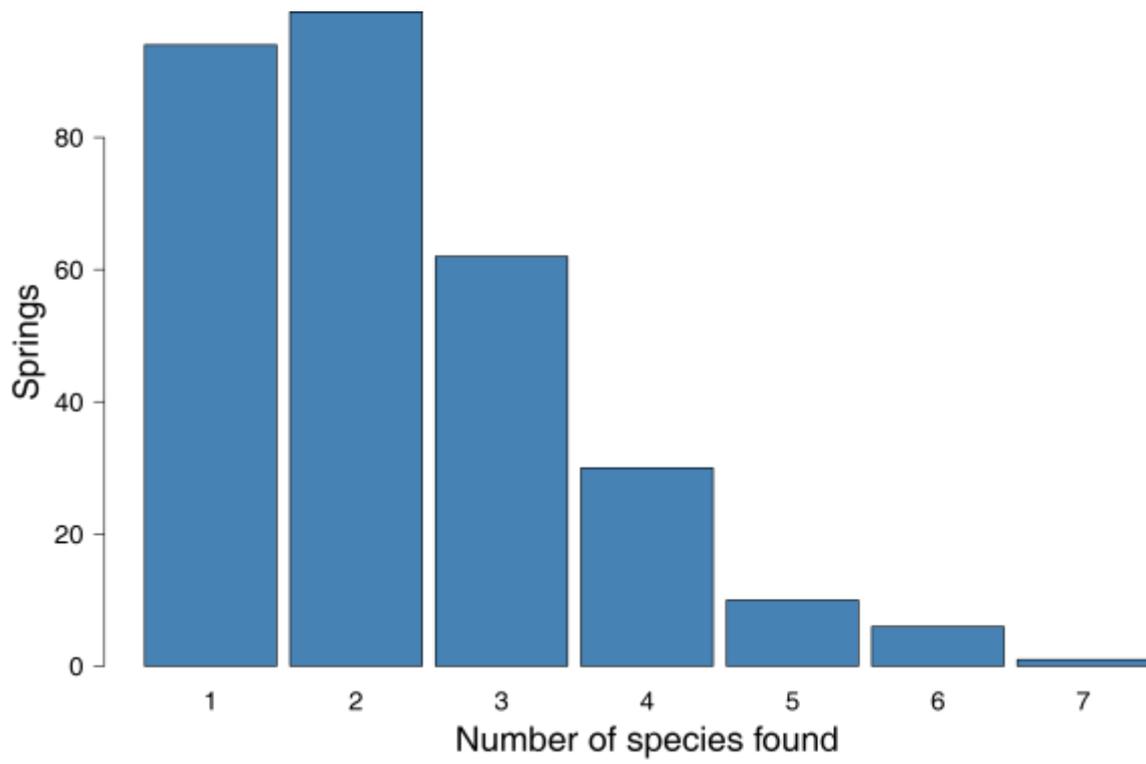
976

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



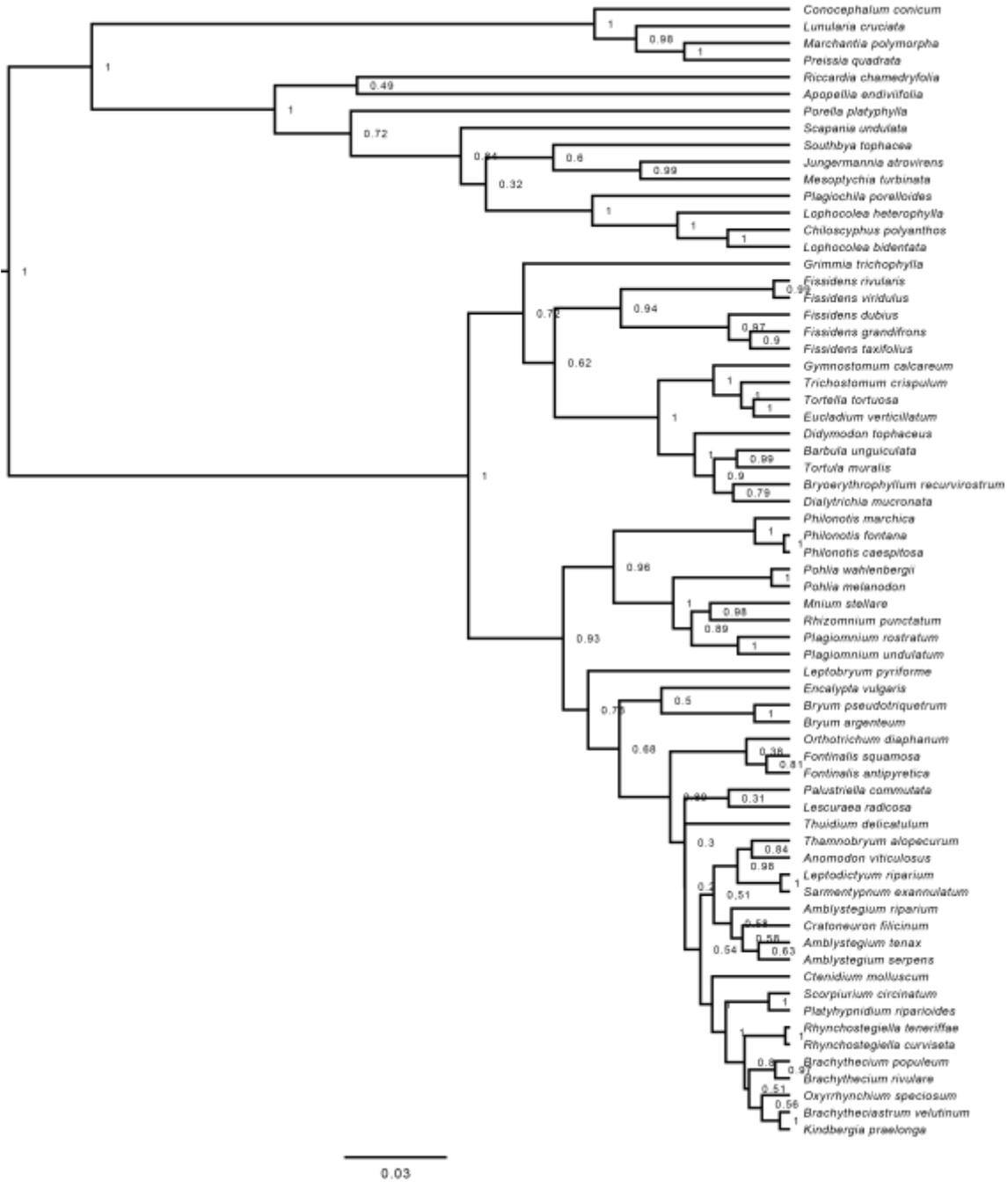
979

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



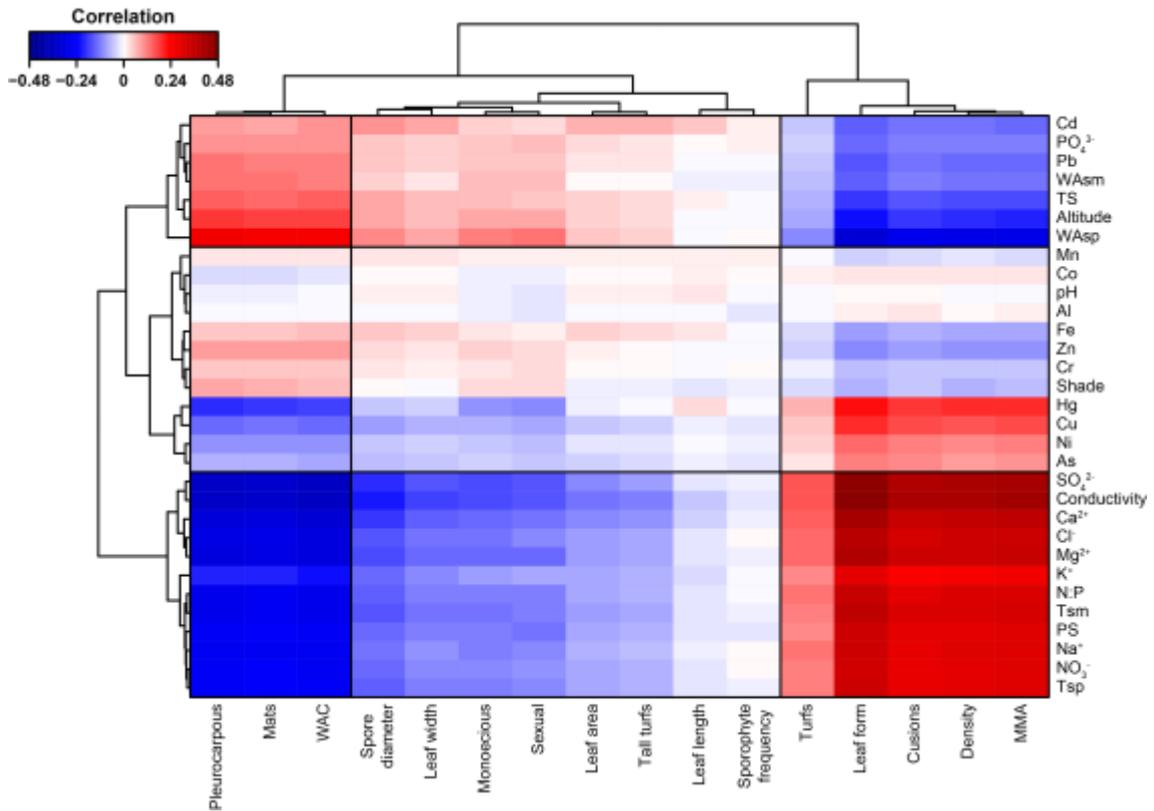
981

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



984

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

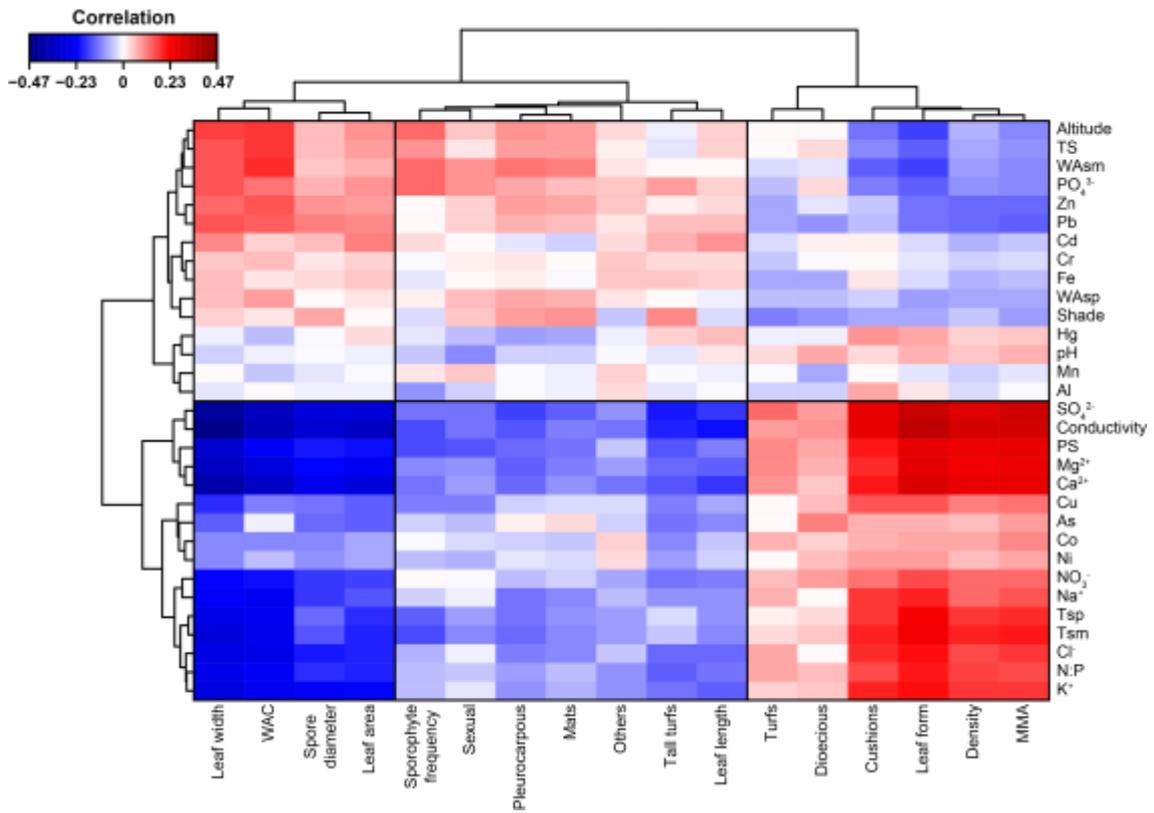


990

991

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

996



997

998 **Table S1.** Table showing the measured traits per species (mean  $\pm$  standard error), part 1. See Units in **Table 1**. The remaining moss traits can  
 999 be found in the BRYOATT database (Mark O Hill et al., 2007). *Acronyms:* moss mass per area (MMA), water absorption capacity (WAC),  
 1000 number of replicates (N), sporophyte frequency (Spo. Freq).

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

1001

1002 **Table S1.** Table showing the measured traits per species (mean  $\pm$  standard error), part 2. See Units in **Table 1**. The remaining moss traits can  
 1003 be found in the BRYOATT database (Mark O Hill et al., 2007). *Acronyms:* moss mass per area (MMA), water absorption capacity (WAC),  
 1004 number of replicates (N), sporophyte frequency (Spo. Freq).

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

<b>Test</b>	<b>Obs</b>	<b>Std.Obs</b>	<b>P</b>
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 <sup>+</sup>	0.195	6.172	0.023
K <sup>+</sup>	0.163	5.748	0.032
Mg <sup>2+</sup>	0.502	16.322	0.001
Ca <sup>2+</sup>	0.454	14.113	0.001
Cl <sup>-</sup>	0.304	9.638	0.001
NO <sub>3</sub> <sup>-</sup>	0.272	8.450	0.001
SO <sub>4</sub> <sup>2-</sup>	0.445	13.728	0.001
PO <sub>4</sub> <sup>3-</sup>	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
N:P	0.256	8.071	0.001

**Table S3.** Species list and GenBank accession numbers for the five genes used in the phylogenetic analyses. We used *Palustriella falcata*, *Rhynchostegium riparioides* and *Fissidens bryoides* species as synonyms of *Palustriella commutata*, *Platyhypnidium riparioides* and *Fissidens rivularis*, respectively (see **Methods**).

Species	5.8S	18S	rbcL	rps4	TrnL
<i>Amblystegium riparium</i>	AF168163	AF168163			AY009830
<i>Amblystegium serpens</i>	FJ535778	AF168152	FJ572313	AY908237	AY009827
<i>Amblystegium tenax</i>	AF168164	AF464988			AY009871
<i>Anomodon viticulosus</i>		FM161076		AY908201	AM990343
<i>Apopellia endiviifolia</i>			AY688786	AY688800	GQ428075
<i>Barbula unguiculata</i>	KU058176	AY437129	AB670696	EU274612	GU953733
<i>Brachytheciastrum velutinum</i>	KC299991			GQ428112	GQ428067
<i>Brachythecium populeum</i>	HM046668	HM046668			HM046633
<i>Brachythecium rivulare</i>	HM046693	FJ476032	AB024674		AM990348
<i>Bryoerythrophyllum recurvirostrum</i>	KY406828	KY406828		KY406865	GU953731
<i>Bryum argenteum</i>	KT343959	KX655725	LC270450	AY078318	LC270624
<i>Bryum pseudotriquetrum</i>	KX981161		AY163040	JF277327	AY150357
<i>Chiloscyphus polyanthos</i>			DQ268969		AY149873
<i>Conocephalum conicum</i>			KT356971	KT356981	AY688806
<i>Cratoneuron filicinum</i>	JQ281669	AY009812	AB095270	AY908250	AY009826
<i>Ctenidium molluscum</i>	AF403632		AB334103	AY907954	FM211895
<i>Dialytrichia mucronata</i>				AY908030	GU953735
<i>Didymodon tophaceus</i>	MF536585	MF536585		MF536622	JN968449
<i>Encalypta vulgaris</i>					EU128000
<i>Eucladium verticillatum</i>	JX679955	AY854392	LC176247	AF481044	AY950402
<i>Fissidens bryoides</i>			LC271962		
<i>Fissidens dubius</i>	JX679949		LC271968	JX679972	
<i>Fissidens grandifrons</i>			LC271979	LC272033	
<i>Fissidens taxifolius</i>	KC333220		LC272008	DQ463123	
<i>Fissidens viridulus</i>	KC333221		KC250514		
<i>Fontinalis antipyretica</i>			AB050949	AF023817	AF191531
<i>Fontinalis squamosa</i>					AF191520
<i>Grimmia trichophylla</i>	KX443521			AJ845240	AJ879775
<i>Gymnostomum calcareum</i>	KX588246			HM147786	KX176744
<i>Jungermannia atrovirens</i>			KF852398	KF943497	GQ220765
<i>Kindbergia praelonga</i>	HM046697	FJ476025		AY663328	AF397804
<i>Leptobryum pyriforme</i>	AB795594	AB842382	LC270367	LC270454	AF023736
<i>Leptodictyum riparium</i>	KM392101			AY907967	
<i>Lescuraea radicata</i>					AY683570
<i>Lophocolea bidentata</i>			AY149842	JX308593	AY149862
<i>Lophocolea heterophylla</i>		AJ422240	DQ268973	DQ268987	AF231899

<i>Lunularia cruciata</i>			DQ645962	AY688795	AY688810
<i>Marchantia polymorpha</i>			MF325087	KT793722	KX792409
<i>Mesoptychia turbinata</i>			JX305570	JX308591	KM501498
<i>Mnium stellare</i>			LC270374	JF277321	LC270548
<i>Orthotrichum diaphanum</i>	EU484076				
<i>Oxyrrhynchium speciosum</i>	KC788213	KC788213			DQ208201
<i>Palustriella falcata</i>					AY626006
<i>Philonotis caespitosa</i>	KC111030				KC111119
<i>Philonotis fontana</i>	LN714246		AY631192		EF107538
<i>Philonotis marchica</i>	KC111078				HF536658
<i>Plagiochila porelloides</i>		KT992543	KF943595	KX896609	KF943056
<i>Plagiomnium rostratum</i>				EF189394	DQ108962
<i>Plagiomnium undulatum</i>			GU373424	EF189416	GQ428078
<i>Pohlia melanodon</i>				JF277308	JF277342
<i>Pohlia wahlenbergii</i>	EU878222	LC270439	JF277307		LC270613
<i>Porella platyphylla</i>		JF734607	EF547189	AY462387	
<i>Preissia quadrata</i>			KT793579	KJ590959	GQ428077
<i>Rhizomnium punctatum</i>			AF478237	JF277323	JF277357
<i>Rhynchostegiella curviseta</i>					FJ262427
<i>Rhynchostegiella teneriffae</i>					FJ262437
<i>Rhynchostegium riparioides</i>	AY857616	FJ476002	AB029385	AY908298	GU552294
<i>Riccardia chamedryfolia</i>				FM210656	KX512021
<i>Sarmentypnum exannulatum</i>	AY857612	AY857612		AY907968	DQ404982
<i>Scapania undulata</i>		JN631484	AY149840	AM398286	EU791642
<i>Scorpiurium circinatum</i>	AF403598			AY663324	AF397834
<i>Southbya tophacea</i>					KF942954
<i>Thamnobryum alopecurum</i>	KC249955	FM161218	AY532392	AF023834	FM201513
<i>Thuidium delicatulum</i>	KF770640	KF770640	AF158177	KF770532	AF161132
<i>Tortella tortuosa</i>	KM020633	KM020630	AB853080	AY950387	GQ428081
<i>Tortula muralis</i>	JN544870	JN544869		AY161090	GU953736
<i>Trichostomum crispulum</i>	KM020643	KM020643	LC176257	AF480977	AY950436

## **Supplementary material**

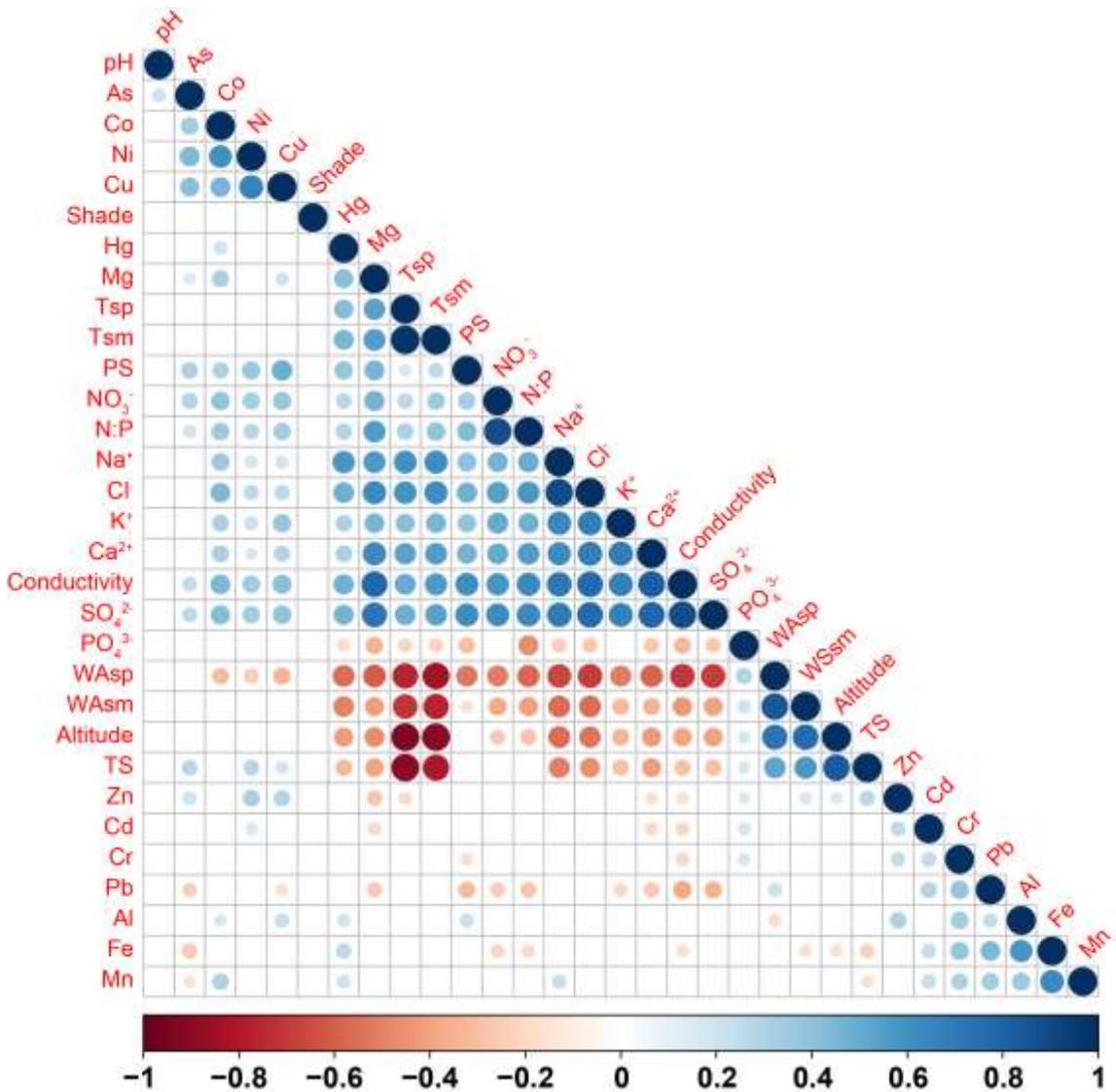
***Towards a moss sclerophylly continuum: evolutionary history, water chemistry and climate control traits of hygrophytic mosses***

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

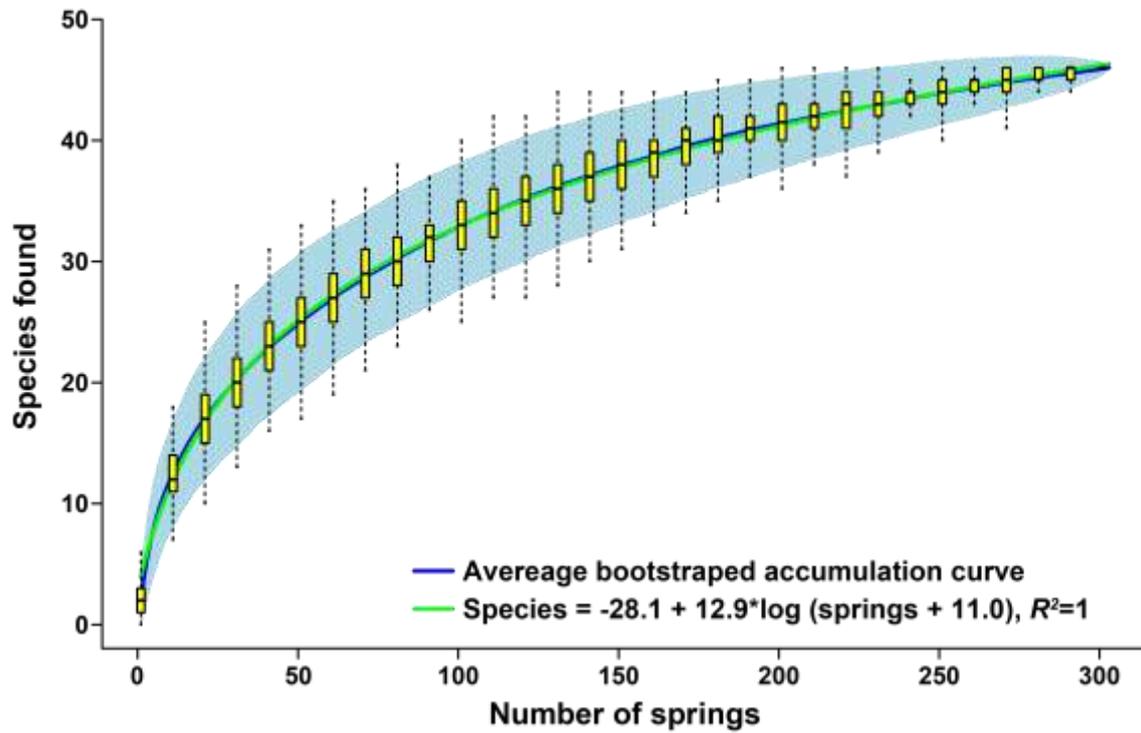
**Figure S1:** Example of a typical semi-natural spring. The red line delimits the area of influence of the water, from where we collected moss samples.



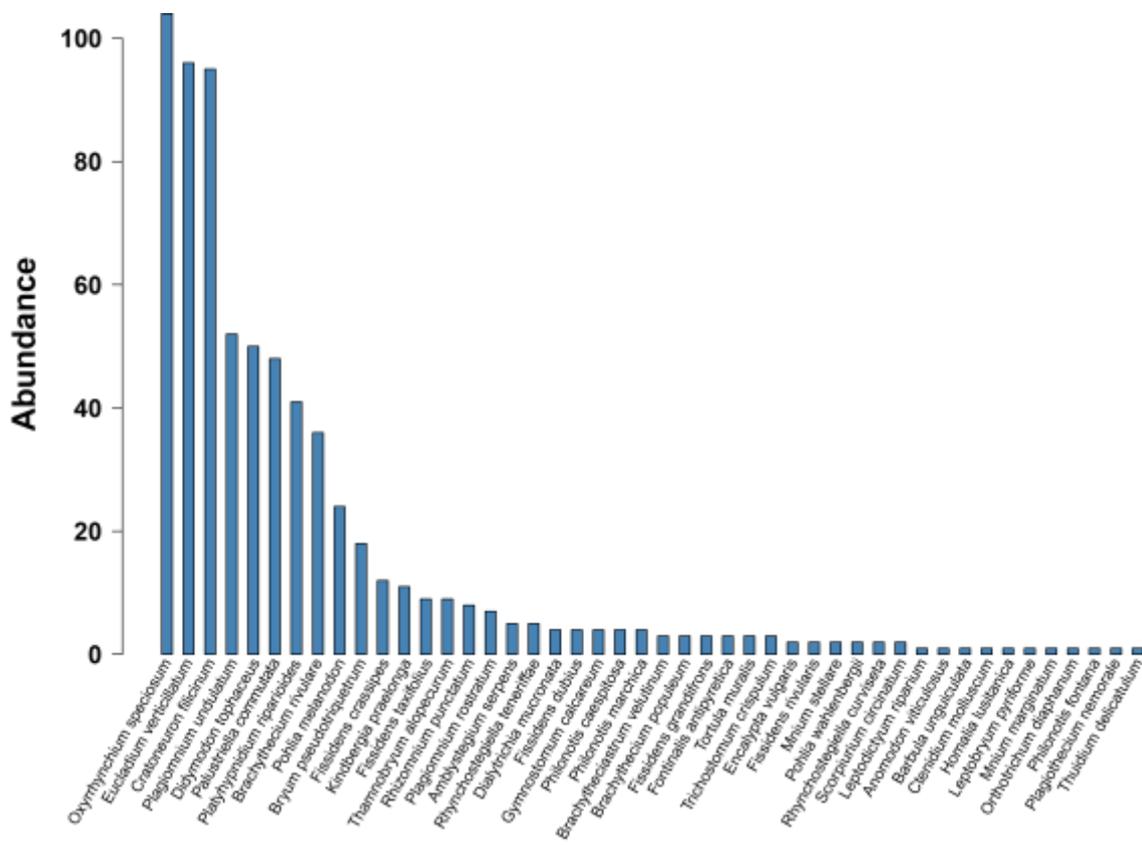
**Figure S2:** Plot showing Spearman's correlations between environmental variables. The size of the circles is proportional to the correlation values. *Acronyms:* nitrate-to-phosphate ratio (N:P), temperature (T), precipitation (P), seasonality (S), water availability (WA), spring (sp), summer (sm).



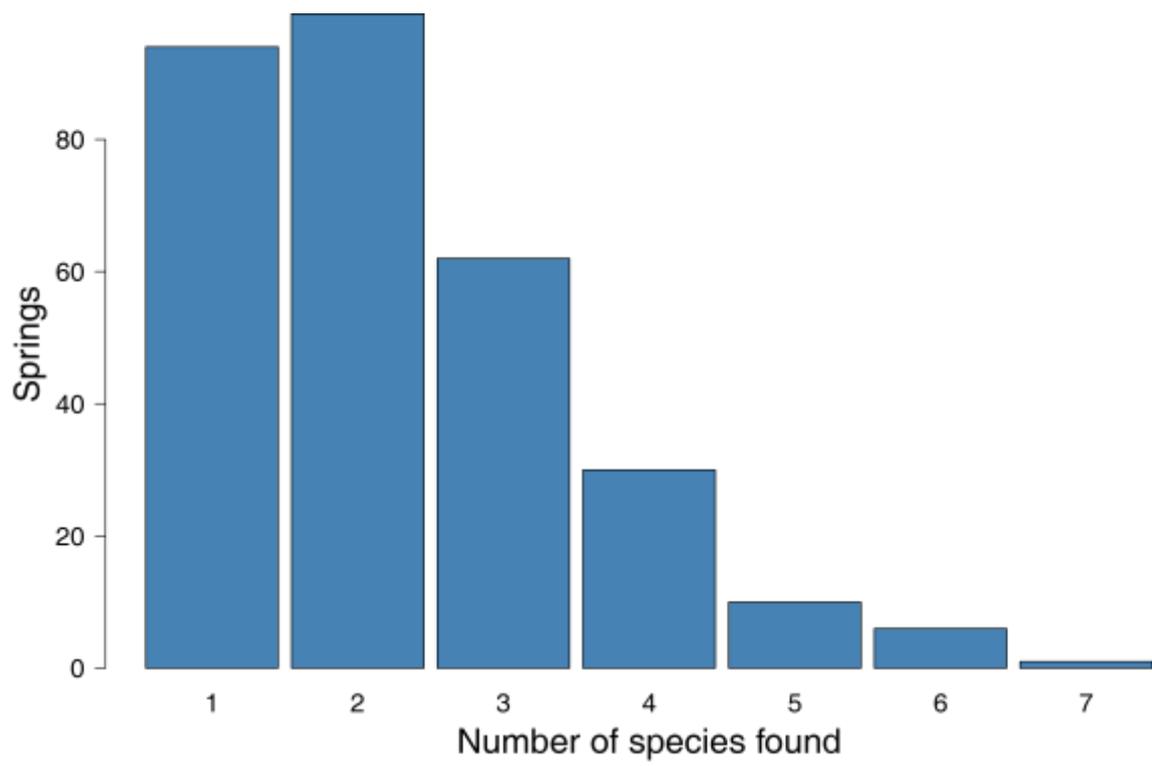
**Figure S3.** Species accumulation curve for the sampled springs, obtained by the bootstrap method (1000 permutations) using *vegan* (Oksanen et al., 2018) R package. Boxplots indicate bootstrap simulations and the shaded area shows the confidence intervals from standard deviation (standard error of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



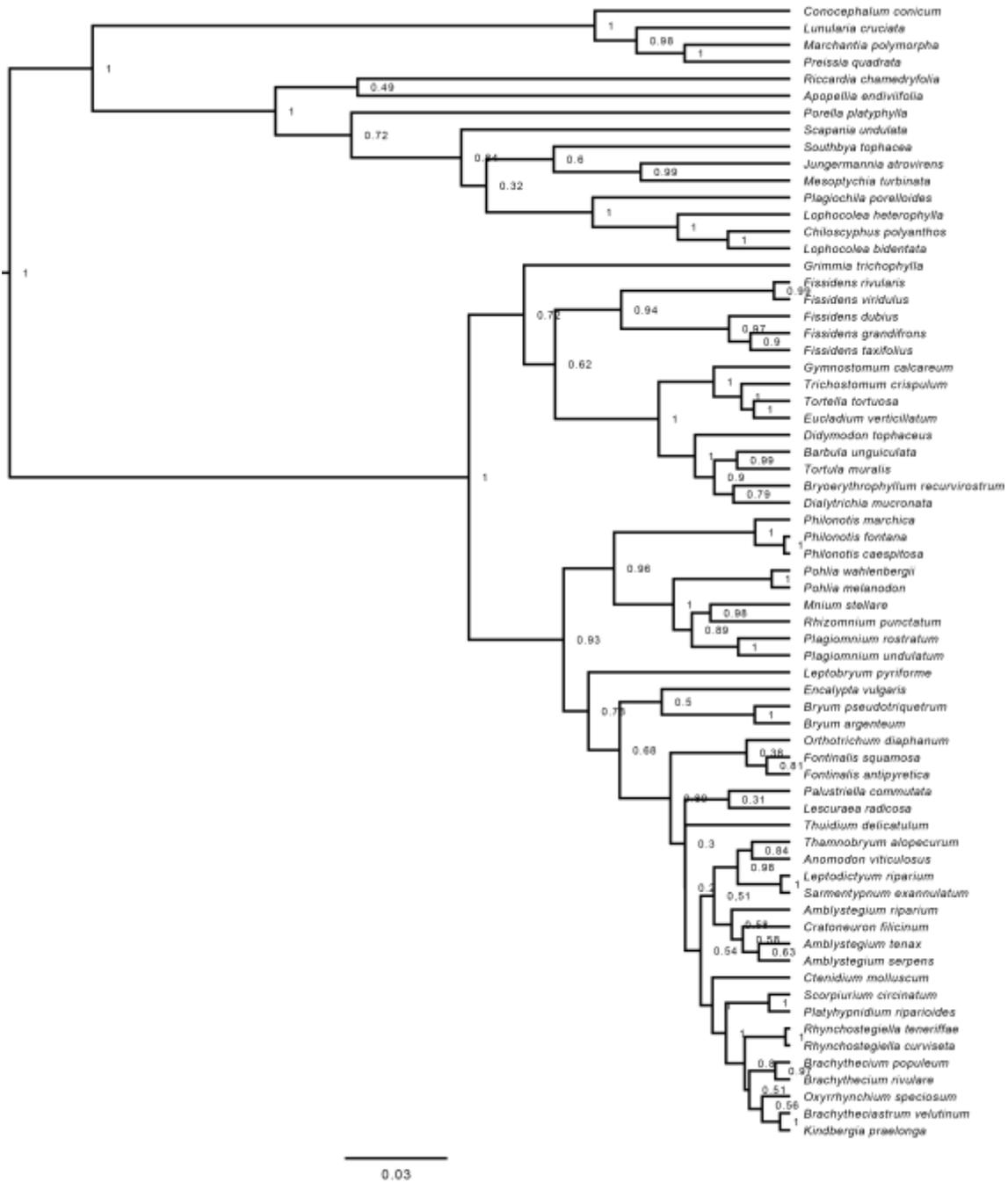
**Figure S4.** Bar plot showing the number of springs in which each moss species was found.



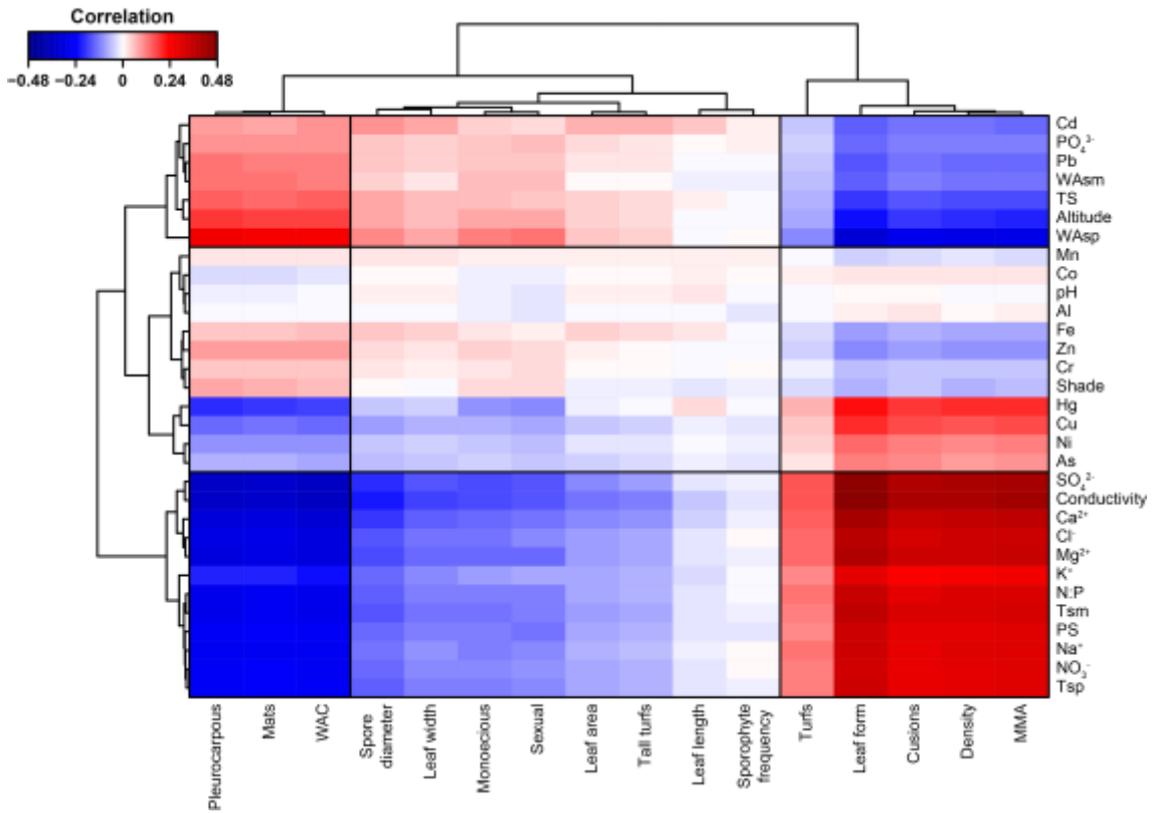
**Figure S5.** Histogram showing the frequency of species richness per spring



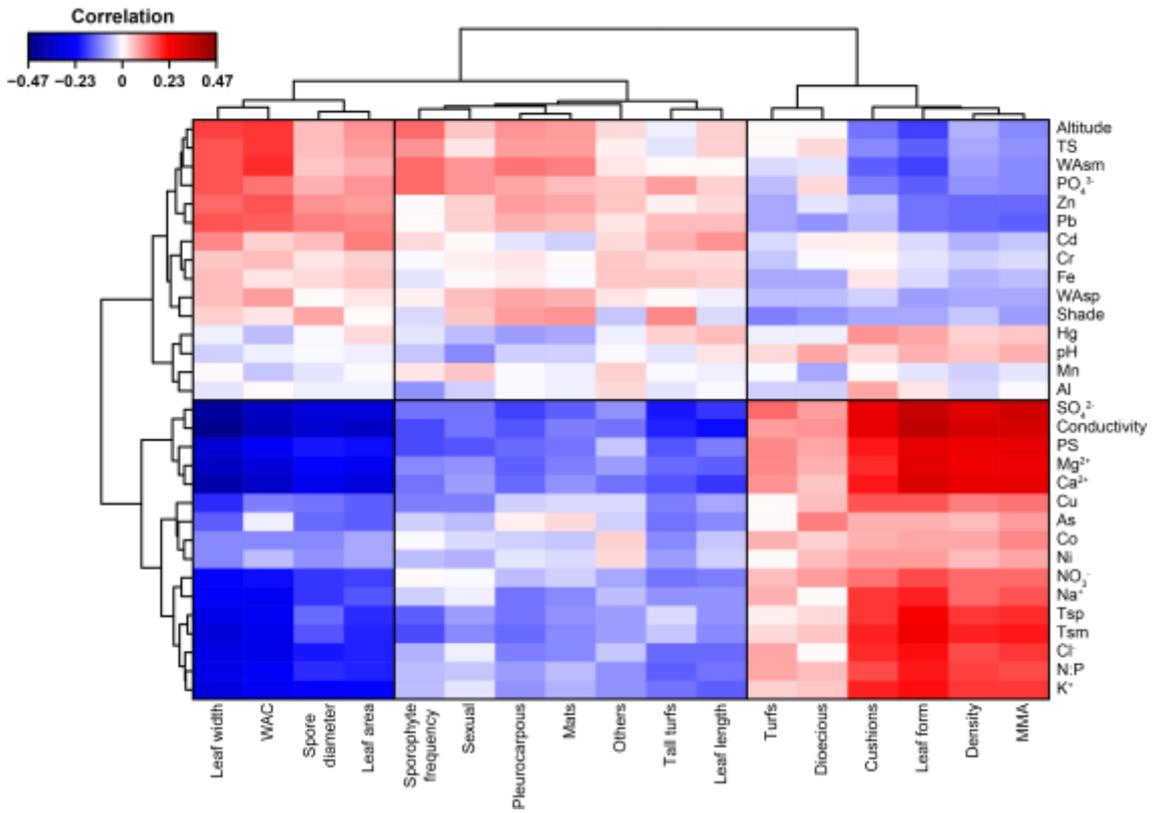
**Figure S6.** Summary tree obtained from the BEAST analysis. Node supports (in posterior probabilities) are indicated in each node, ranging from 0 to 1.



**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  $\pm$  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).

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

**Table S1.** Table showing the measured traits per species (mean  $\pm$  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).

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

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

<b>Test</b>	<b>Obs</b>	<b>Std.Obs</b>	<b><i>P</i></b>
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 <sup>+</sup>	0.195	6.172	0.023
K <sup>+</sup>	0.163	5.748	0.032
Mg <sup>2+</sup>	0.502	16.322	0.001
Ca <sup>2+</sup>	0.454	14.113	0.001
Cl <sup>-</sup>	0.304	9.638	0.001
NO <sub>3</sub> <sup>-</sup>	0.272	8.450	0.001
SO <sub>4</sub> <sup>2-</sup>	0.445	13.728	0.001
PO <sub>4</sub> <sup>3-</sup>	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
N:P	0.256	8.071	0.001

6

7 **Table S3.** Species list and GenBank accession numbers for the five genes used in the  
8 phylogenetic analyses. We used *Palustriella falcata*, *Rhynchostegium riparioides* and  
9 *Fissidens bryoides* species as synonyms of *Palustriella commutata*, *Platyhypnidium*  
10 *riparioides* and *Fissidens rivularis*, respectively (see **Methods**).

Species	5.8S	18S	rbcL	rps4	TrnL
<i>Amblystegium riparium</i>	AF168163	AF168163			AY009830
<i>Amblystegium serpens</i>	FJ535778	AF168152	FJ572313	AY908237	AY009827
<i>Amblystegium tenax</i>	AF168164	AF464988			AY009871
<i>Anomodon viticulosus</i>		FM161076		AY908201	AM990343
<i>Apopellia endiviifolia</i>			AY688786	AY688800	GQ428075
<i>Barbula unguiculata</i>	KU058176	AY437129	AB670696	EU274612	GU953733
<i>Brachytheciastrum velutinum</i>	KC299991			GQ428112	GQ428067
<i>Brachythecium populeum</i>	HM046668	HM046668			HM046633
<i>Brachythecium rivulare</i>	HM046693	FJ476032	AB024674		AM990348
<i>Bryoerythrophyllum recurvirostrum</i>	KY406828	KY406828		KY406865	GU953731
<i>Bryum argenteum</i>	KT343959	KX655725	LC270450	AY078318	LC270624
<i>Bryum pseudotriquetrum</i>	KX981161		AY163040	JF277327	AY150357
<i>Chiloscyphus polyanthos</i>			DQ268969		AY149873
<i>Conocephalum conicum</i>			KT356971	KT356981	AY688806
<i>Cratoneuron filicinum</i>	JQ281669	AY009812	AB095270	AY908250	AY009826
<i>Ctenidium molluscum</i>	AF403632		AB334103	AY907954	FM211895
<i>Dialytrichia mucronata</i>				AY908030	GU953735
<i>Didymodon tophaceus</i>	MF536585	MF536585		MF536622	JN968449
<i>Encalypta vulgaris</i>					EU128000
<i>Eucladium verticillatum</i>	JX679955	AY854392	LC176247	AF481044	AY950402
<i>Fissidens bryoides</i>			LC271962		
<i>Fissidens dubius</i>	JX679949		LC271968	JX679972	
<i>Fissidens grandifrons</i>			LC271979	LC272033	
<i>Fissidens taxifolius</i>	KC333220		LC272008	DQ463123	
<i>Fissidens viridulus</i>	KC333221		KC250514		
<i>Fontinalis antipyretica</i>			AB050949	AF023817	AF191531
<i>Fontinalis squamosa</i>					AF191520
<i>Grimmia trichophylla</i>	KX443521			AJ845240	AJ879775
<i>Gymnostomum calcareum</i>	KX588246			HM147786	KX176744
<i>Jungermannia atrovirens</i>			KF852398	KF943497	GQ220765
<i>Kindbergia praelonga</i>	HM046697	FJ476025		AY663328	AF397804
<i>Leptobryum pyriforme</i>	AB795594	AB842382	LC270367	LC270454	AF023736
<i>Leptodictyum riparium</i>	KM392101			AY907967	
<i>Lescuraea radicata</i>					AY683570
<i>Lophocolea bidentata</i>			AY149842	JX308593	AY149862
<i>Lophocolea heterophylla</i>		AJ422240	DQ268973	DQ268987	AF231899

<i>Lunularia cruciata</i>			DQ645962	AY688795	AY688810
<i>Marchantia polymorpha</i>			MF325087	KT793722	KX792409
<i>Mesoptychia turbinata</i>			JX305570	JX308591	KM501498
<i>Mnium stellare</i>			LC270374	JF277321	LC270548
<i>Orthotrichum diaphanum</i>	EU484076				
<i>Oxyrrhynchium speciosum</i>	KC788213	KC788213			DQ208201
<i>Palustriella falcata</i>					AY626006
<i>Philonotis caespitosa</i>	KC111030				KC111119
<i>Philonotis fontana</i>	LN714246		AY631192		EF107538
<i>Philonotis marchica</i>	KC111078				HF536658
<i>Plagiochila porelloides</i>		KT992543	KF943595	KX896609	KF943056
<i>Plagiomnium rostratum</i>				EF189394	DQ108962
<i>Plagiomnium undulatum</i>			GU373424	EF189416	GQ428078
<i>Pohlia melanodon</i>				JF277308	JF277342
<i>Pohlia wahlenbergii</i>	EU878222	LC270439	JF277307		LC270613
<i>Porella platyphylla</i>		JF734607	EF547189	AY462387	
<i>Preissia quadrata</i>			KT793579	KJ590959	GQ428077
<i>Rhizomnium punctatum</i>			AF478237	JF277323	JF277357
<i>Rhynchostegiella curviseta</i>					FJ262427
<i>Rhynchostegiella teneriffae</i>					FJ262437
<i>Rhynchostegium riparioides</i>	AY857616	FJ476002	AB029385	AY908298	GU552294
<i>Riccardia chamedryfolia</i>				FM210656	KX512021
<i>Sarmentypnum exannulatum</i>	AY857612	AY857612		AY907968	DQ404982
<i>Scapania undulata</i>		JN631484	AY149840	AM398286	EU791642
<i>Scorpiurium circinatum</i>	AF403598			AY663324	AF397834
<i>Southbya tophacea</i>					KF942954
<i>Thamnobryum alopecurum</i>	KC249955	FM161218	AY532392	AF023834	FM201513
<i>Thuidium delicatulum</i>	KF770640	KF770640	AF158177	KF770532	AF161132
<i>Tortella tortuosa</i>	KM020633	KM020630	AB853080	AY950387	GQ428081
<i>Tortula muralis</i>	JN544870	JN544869		AY161090	GU953736
<i>Trichostomum crispulum</i>	KM020643	KM020643	LC176257	AF480977	AY950436

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