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Environmental factors shaping the aquatic bryophyte community with focus on *Hygrohypnum luridum* in selected mountain streams of South Tyrol

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Content

1 Abstract

The aim of this study was to investigate which environmental factor best explains the distribution of *Hygrohypnum lurid*um (Hedw.) Jenn. and other aquatic bryophytes in water systems of the eastern Alps. In order to tackle this research question streams located in South Tyrol (a province of Northern Italy) were selected and environmental factors such as elevation, water temperature, pH, electrolytic conductivity, total nitrogen and total phosphorus were collected. Further a stratified random sampling of submersed and riparian bryophytes found within segments of 40 meters were performed at each sample site.

In total 77 species were found of which 16 are obligate aquatic bryophytes. Most frequent species detected was *Hygrohypnum luridum* (54% sites), followed by *Brachythecium rivulare* Schimp (48% sites) and *Platyhypnidium riparioides* (Hedw.) Dixon (42% sites).

The factors shaping the aquatic bryophyte community composition were assessed by performing a partial canonical correspondence analysis (pCCA). The factors elevation, electrolytic conductivity, water temperature, and pH temperature were significantly determining the species community composition, although the total variance was low (19.5%). Additionally, environmental factors determining the occurrence of the ten most dominant species were evaluated by modelling the presence of bryophytic species to the measured environmental variables and the to a data set of arithmetic means of Ellenberg indicator values computed from the presence of species at each site. Subsequently these two datasets had been added as predictor values in generalized linear mixed effect models (GLMMs). The water bodies had been included as random effect to incorporate the spatial autocorrelation into the model. According to the models the factors influencing the occurrence of *Hygrohypnum luridum* could be detected as light availability indicator value, continentality indicator value, soil reactivity indicator value and total phosphorus. Furthermore, results of the computed models showed, that the measured factors and indicator values only partly overlap for the same species. Therefore, it can be concluded that the measured factors were better applicable to explain the species community composition and the Ellenberg indicator values were more suitable to describe the occurrence of species.

2 Introduction

The Alps, a mountain range found in the center of Europe form an ecological important watershed for the adjacent lowlands (Alcamo et al., 2007; Jasper et al., 2004). The originated alpine waterbodies hold a characteristic flora and fauna which is very sensitive to anthropogenic interference. Since alpine streams appear to be low anthropogenically impacted they can be counted to ecosystems where slightest environmental changes can be recorded easily (Hannah et al., 2007). Especially the rise in temperature will cause some alterations of the inhabiting alpine species compositions (Hannah et al., 2007). In the past century the temperature in the Alps has increased up to 2° C which is the threefold of the global average temperature increase (Beniston et al., 2011). In consequence the precipitation patterns will shift which inflicts change of the alpine water bodies (Alcamo et al., 2007; García-Ruiz et al., 2011; Hannah et al., 2007; Jasper et al., 2004).

Stream systems represent very complex ecosystems which are shaped by many various environmental factors (Hannah et al., 2007; Luis et al., 2015; Suren, 1996). They form interconnected systems which are characterised by structural and functional connectivity where the spatial structure is combined with the change of spatiotemporal processes (Figure 1) (Fritz et al., 2018; Heino and Virtanen, 2006). Among those are physico-chemical factors such as underlaying geology, water temperature, electrolytic conductivity, water pH, turbulence and nutrient levels (Ceschin et al., 2015; Luis et al., 2015; Tremp et al., 2012). Those environmental factors shape the inhabiting species associated with lotic systems (Luis et al., 2015). Organisms which are crucial important for those systems are aquatic bryophytes. They form a large autotrophic biomass and are an important ecological player of stream systems (Ceschin et al., 2015; Monteiro and Vieira, 2017; Stream Bryophyte Group, 1999; Tessler et al., 2014). This important role and the physiological adaption which is needed to get established in stream systems will be discussed in the next chapter.

3 Aquatic bryophytes

Aquatic bryophytes occupy stream habitats which are spatially and temporally heterogenous defined by high disturbance and connectivity among them (Heino and Virtanen, 2006). Aquatic bryophytes are poikilohydric plants that are only metabolically active when hydrated (Frahm 2001). Their water and nutrient uptake takes place at their surface (Augusto *et al.* 2013, Frahm 2001). They belong to the C_3 plants which perform the photosynthesis in two spatially separated steps (Tuba et al., 2011). Their photosynthetic activity depends on their hydration and reaches its optimum in plant with full turgescence. Hence assimilation rates get drastically reduced under water stress, especially in aquatic bryophytes (Suren 1993, Frahm 2001). In contrast to other aquatic macrophytes aquatic bryophytes cannot use bicarbonate (HCO_3) as inorganic carbon source but use dissolved carbon dioxide (CO_2) instead (Stream Bryophyte Group, 1999; Tuba et al., 2011). In consequence they are found in turbulent, oligotrophic streams, where the water column is well mixed by the water movement and enriched with atmospheric CO_2 (Frahm 2001). An enhanced flow velocity increases also the nutrient uptake and additionally input of mineral substances occur by atmospheric deposition (Stream Bryophyte Group, 1999, Frahm 2001). Since aquatic bryophytes are most of the time in contact with water, they lack in comparison to terrestrial species external capillary fringes. Their physiology is adapted to the mechanical impact of the flowing water conditions in streams. They exhibit adaption as strong leave-nerves (e.g. *Hygroamblystegium sp.*), coarse cellnet-structure (e.g. *Fontinalis sp.*) or enforced leaf edges like found in *Cinclidotus sp.* (Frahm 2001).

Their main dispersal method is hydrochoric by which they proliferate vegetative by plant fragments which get transported with the water flow in downstream direction. More rarely they reproduce generatively via sexual gamets which development is triggered by certain temperature (Stream Bryophyte Group 1999; Frahm 2001, Tuba et al. 2011). They tend to grow on large stable substrate of the stream bed which are more likely to be exposed to air for longer period which allows the plant to establish, whereas smaller substrate is more likely to be submersed and is prone to be unstable (Monteiro and Vieira, 2017; Scarlett and O'Hare, 2006; Suren, 1993).

Submersed and bryophytes along the water line create important ecological niches for other aquatic organisms. They form substrate for epiphytically algal growth, collect organic detritus and provide shelter for macro-zoobenthos against water current and predators (Rosa et al., 2011; Suren, 1993). Especially in streams with strong water flow they are a sought habitat for benthic invertebrates (Stream Bryophyte Group, 1999). They act as a refugia during and after anthropogenic disturbance events such as an restoration for benthic invertebrates (Korsu, 2004).

4 Role of aquatic bryophytes as bioindicators

Aquatic bryophytes are found as very useful model organisms for assessing water quality and stream integrity (Augusto et al., 2013; Commission, 2000; Lang and Murphy, 2012). They grow constantly and accumulate therefore continually over the year substances such as pollutants found in the water (Thiébaut, 2009; Tremp et al., 2012). Additionally, they are globally distributed and easily macroscopically identifiable (Frahm 2001). They can be applied as active and as passive bioindicator (Gecheva and Yurukova, 2014). Active bioindicator are, for example 'moss bags' by which aquatic bryophytes had been transplanted and exposed to assess the environmental status of the waterbody (Roy et al., 1996). Another method of detecting environmental pollutants is to use them as passive bioindicator. Thereby the species which are observed in their natural habitat deliver information about the environmental status. The water quality impacts on the presence of certain bryophyte species (Frahm 2001).

Aquatic bryophytes tend to accumulate pollutants in their tissue, also referred as bioaccumulation, and can be helpful in pollutant source location (Frahm 2001, Augusto *et al.* 2013). According to Augusto *et al.* (2013) PAHs concentrations in the aquatic bryophyte correlate to the concentration found in the water. Further they are applied as bioaccumulators for heavy metals (Debén et al., 2015; Rudolf et al., 2012; Thiébaut, 2009).

A common bioindindicator mentioned in various studies is *Hygrohypnum luridum* (Ceschin et al., 2015; Hilfiker and Bergamini, 2005; Jamieson, 1976; Lang and Murphy, 2012; Rudolf et al., 2012). Since its representative characteristics as indicator species it was chosen as the species which this study was focused on.

5 *Hygrohypnum luridum*

Hygrohypnum luridum is a pleurocarpous, facultative aquatic bryophyte and belongs to the family Amblystegiaceae. Its growth form is moderate standing to carpet turf-like and its falcate shaped leaves are highly varying but can be used for taxonomic determination (Jamieson, 1976; Lang and Murphy, 2012). It has inflated alar cells which are short rectangular to quadrat shaped (Jamieson, 1976). It belongs to the group of is intermediate strategists determined by intermediate substrate stability and intermediate habitat disturbance. In contrast to other representatives of its genera it prefers base-rich, calcareous water chemistry (Lang and Murphy, 2012). Its presence can be mostly linked to cool, turbulent waters and found along the splash zone of boulders (Ceschin et al., 2015).

Since *Hygrohypnum luridum* and many other bryophytes can be correlated to the physico-chemical factors of the water body and reflect the water quality (Abati et al., 2016; Lang and Murphy, 2012;

Monteiro and Vieira, 2017; Tessler et al., 2014). Markert et al. (2003) states that *Hygrohypnum luridum* the species is an indicator for α-mesosaprobic water quality which implies a moderately oxygenated water with considerable dissolved organic content.

6 Research question

The aim of this master thesis was to examine the environmental variables which impact the bryophyte community composition in selected streams of South Tyrol (Figure 1 of the manuscript). To make predictions for the aquatic bryophytic assemblage following variables were taken into the account: elevation, water temperature, pH, electrolytic conductivity, total nitrogen and total phosphorus content. The hypothesis was that with similar environmental conditions resembling community compositions are found at the sampled sites. The center of this study was the species *Hygrohypnum luridum* with the ambition to assess its autecology in South Tyrol. This area was chosen since the study of environmental drivers determining the aquatic bryophytes community composition of waterbodies in South Tyrol is sparsely investigated and additionally the location of the area contributes to specific biogeographic conditions which may result in unexpected findings for the occurrence of *Hygrohypnum luridum*.

In the following 'Manuscript for publication' the implemented study with its discussed results is described in more detail. The manuscript was handed in at the journal 'Aquatic Botany' for publication.

7 Manuscript for publication

Which environmental factors shape the aquatic bryophyte community in selected mountain streams of the Eastern Alps?

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Abstract

Aquatic bryophytes are important players in mountain stream habitats and are potential indicators for climatic change. Despite their significance for freshwater ecosystems the impacting environmental factors for the bryophyte community composition of mountain streams are not well studied yet. To tackle this under-investigated field, we studied thirteen selected mountain streams in South Tyrol (Eastern Alps) and correlated the sampled species to the measured environmental factors. To determine the abiotic factor which best described the species community composition we performed a partial canonical correspondence analysis (pCCA). Additionally, we were interested if the same factors which impact the species composition determine the occurrence of single species. Therefore, we predicted the occurrence of the ten most dominant bryophyte species by the means of generalized linear mixed models (GLMMS) based on the measured abiotic factors and the computed mean Ellenberg indicator values. We found that the species community is shaped by elevation, electrolytic conductivity, water temperature and pH. Moreover, the results of the models suggested that the environmental factors predicting the occurrence of single species were varying amongst the species. Furthermore, we found that for the prediction of the occurrence of single species the indicator values have been better applicable.

Key Words: *Bryophytes, Freshwater habitat, Community predictors, Climate change, Indicator values, South Tyrol*

1. Introduction

Streams originating in mountain regions have a high impact on the industry, agriculture and tourism of adjacent lowland regions (Alcamo et al., 2007; Zekollari et al., 2019). Despite this economic importance, mountain streams are less strongly anthropogenically disturbed than lowland rivers and provide habitats for a specialized fauna and flora (Ceschin et al., 2015; Hannah et al., 2007). However, mountain streams are highly sensitive to changes in abiotic conditions making them a valuable indicator system for the effects of a warming climate (Hannah et al., 2007). In alpine regions of the European Alps temperature increases during the 20th century were about the threefold of the global average (Beniston et al., 2011). Such elevated temperatures cause shifts in precipitation pattern (Alcamo et al., 2007) which, in turn, changes the annual flow regimes of mountain streams. Earlier and less intense snowmelt runoff in spring, extended low water flow in summer and an increase of the frequency of irregular runoff during winter likely culminate in an overall reduced average streamflow (García-Ruiz et al., 2011) and influence the organisms living in these ecosystems.

Aquatic bryophytes are frequently used to monitor the water quality and stability of mountain streams and are, hence, acknowledged as biological reference-organisms by the European Water Framework Directives (Commission, 2000; Gecheva and Yurukova, 2014). Several traits qualify them as important bioindicators (Stream Bryophyte Group, 1999): The species composition of bryophytes communities is directly related to physico-chemical properties of the waterbody (Commission, 2000; Thiébaut, 2009). Bryophytes constitute a large portion of the aquatic autotrophic biomass and play a crucial role in stream ecology, especially in smaller alpine streams (Stream Bryophyte Group 1999; Monteiro and Vieira 2017). In addition, their longevity allows bryophytes to aggregate the conditions of the waterbody over a long time period (Tremp et al., 2012). Due to their lack of roots and a pronounced cuticle or epidermis, they absorb macro- and microelements through their entire surface (Bes et al., 2018) and are able to accumulate nutrients and heavy metals in their tissue (Frahm 2001). Although they hold a great capacity to evaluate the environmental status of a water body (Monteiro and Vieira, 2017) environmental conservation and management policies base their decision making rather on ecological needs of vascular plants, neglecting the specific demands of bryophytes (Vellak et al., 2010). Mountain streams require particular physiological and morphological adaptations of the species colonizing them (Fritz et al., 2018; Lang and Murphy, 2012; Luis et al., 2015). Aquatic bryophytes have a low temperature optimum for growth (Stream Bryophyte Group, 1999) matching the low and only marginally fluctuating water temperatures in mountain streams (Ceschin et al., 2015). The small growth habit of aquatic bryophytes can be seen as response to the rapid and strongly turbulent water flow (Ceschin et al., 2015; Tremp et al., 2012) caused by the mainly steep and rocky stream bed and the seasonally varying hydrological drainage (Brittain and Milner 2001). These turbulences capture atmospheric CO_2 which is crucial for the photosynthetic activity of aquatic bryophytes (Monteiro and

Vieira, 2017). Beyond these general characteristics of mountain streams, additional factors such as pH, electrolytic conductivity and nutrient content – all strongly affected by the geology of the catchment – are likely to co-determine the species composition of bryophyte communities (Lang and Murphy, 2012; Tessler et al., 2014; Tremp et al., 2012). For instant, Lang and Murphy (2012) identified two distinctive bryophyte communities representing calcareous and acidic stream water catchments. Furthermore, Abati *et al.* (2016) found bryophyte communities to depend on flow regulation. Another attempt to describe environmental conditions was made by (Spitale et al., 2020) by associating life-forms of bryophytes to land cover types. However, despite their potential in reflecting the environmental status of a habitat and being and informative organism group for conservational purposes (Monteiro and Vieira, 2017), the understanding of the autecology of aquatic stream bryophytes in the Eastern Alps remains rather unexplored. Obtaining a conclusive picture of the environmental drivers of the species composition in aquatic bryophyte community is therefore highly required.

In this study we aim at identifying the most important environmental determinants of bryophyte communities in mountain streams of South Tyrol, Italy. A set of physico-chemical variables obtained for 65 sampling sites by *in situ* and lab measurements is related to the species composition and the occurrence of the most common single species. In addition, the latter is related to a set of indices (i.e. indicator values; Ellenberg *et al.* (2001)) obtained from the detected species composition. In particular we answer the following questions: i) Which environmental variables are the most relevant drivers of aquatic bryophyte communities? ii) Are the same variables relevant in explaining the species composition and the occurrence of the dominant species in these communities?

2. Methods

2.1. Study area and sampling

We selected 13 sections across the stream network of South Tyrol, Italy (Figure 1). Per section five sampling sites were established to cover upper-, mid- and lower reaches of smaller streams (Table 1). These sections are further referred to as streams for simplicity. Sampling sites were visited between May to September 2019. At each site we measured the elevation (EL; GPS), the water temperature (WT) and the electrolytic conductivity (EC; conductivity meter 524 of Crison) and the pH (with pH Meter *330i* of *WTW) in situ*. Surface water samples were collected in sterile polyethylene bottles, kept cool during the transport to the lab ('Biologische Labor' in Laives, South Tyrol) and stored at -20° C until further treatment. In the lab we measured the total nitrogen content with a TOC analysist (*Shimadzu TOC-V CPN*). The total phosphorus content was determined using Vogler's phosphorus determination method (Vogler 1996) and results were obtained by photospectrometric analysis (with UV-VIS spectrometer *Shimadzu UV-1800*). Information on the geology of the catchment area and the geological stream bed composition of streams (Table 1) were compiled from GIS layers (GIS layers provided by Geobrowser3© product of the Provincia autonoma di Bolzano - Alto Adige, 2020, http://gis2.provinz.bz.it/geobrowser/; Provincia autonoma die Bolzano - Alto Adige 2009).

Additionally, we aimed at inventorying all submerse and riparian bryophytes in the selected streams at segments of 40 meters in length and centered around each sampling site. We collected species samples from all types of rocks in the stream bed and covering the gradient from the center of the stream to its splash zone at both banks. Thereby, we collected a minimum of one to a maximum of 16 samples per site. Samples were determined to the species level using Frahm and Frey (2004), Hedenäs *et al.* (2014) and Atherton *et al.* (2010). Nomenclature follows the *Checklist of Austrian Bryophytes* (Köckinger *et al.* 2020). For each bryophyte assemblage means of Ellenberg indicator values (Ellenberg *et al.* 2001) for light (eL), temperature (eT), continentality (eK), moisture (eF) and soil reaction (eR) were computed. These indicator values reflect the ecological requirements of the species and allow a characterization of the ecological conditions at sampling sites (Ellenberg *et al.* 2001).

2.2. Data analysis

All analyses were done using RStudio 3.6.1 (https://rstudio.com/) based on the statistical programing environment R (R Core Team 2016). Canonical Correspondence Analyses (CCA; Braak 1986) allow for non-linear and even non-monotonic (unimodal) relationships between species occurrences and environmental gradients and perform well when not all relevant environmental factors were determined (Palmer, 1993). To assess the effects of abiotic variables on the species composition of bryophyte assemblages a partial CCA (pCCA) as implemented in the function 'cca' of the 'vegan' package (Oksanen *et al.* 2019) was applied. Species with only one occurrence in the community data were removed to reduce the noise in the data. Normality of the abiotic variables was assessed by means of Shapiro-Wilk tests and Box-Cox transformations were applied if needed. In addition, abiotic variables were standardized to zero mean and unit variance prior to the analysis. To remove the spatial component of the abiotic variables (Borcard *et al.* 1992) coordinates were used as co-variables. Multicollinearity of environmental variables and co-variables was assessed by determining the variance inflation factors (VIF; function 'vif') (James et al. 2014). As all VIF were <5 all variables were kept in the pCCA. Subsequently, the effect of each abiotic variable on species composition was tested for significance using an ANOVA-like permutation test (function 'anova.cca') with 999 permutations of the residuals after removing the effects of the coordinates. Because this test is sensitive to the order of variables we provide an analysis of variance tables containing values averaged across all permutations (i.e. 720) of the variables.

We tested the effects of environmental variables on the occurrence of the species occurring in at least 20% of sampling sites, (i.e. *Amblystegium riparium, Amblystegium tenax, Brachythecium rivulare, Bryum pseudotriquetrum, Cratoneuron filicinum, Hygrohypnum duriusculum, Hygrohypnum luridum, Palustriella communtata var falcata, Platyhypnidium riparioides and Schistidium rivulare)* by means of Generalised Linear Mixed-effects Models (GLMMs) with canonical logit link-functions fitted in a Bayesian setting as implemented in the function 'bglmer' of the package 'blme'; Chung *et al.* 2013). Thereby, the default prior settings were used. As we have two sets of scaled environmental variables (abiotic variables derived and mean Ellenberg indicator values obtained by direct measurements and derived from the bryophyte species composition, respectively), which partly overlap in their representation of environmental conditions (e.g. water temperature or pH overlap with indicator values for temperature and soil reaction), we applied two separate GLMMs, both without interactions among fixed effect predictors. Since five sampling sites were observed at each stream, we accounted for the potential effects of this dependence by using stream as a grouping variable and allowing for a random intercept for each group. For each GLMM the effect of each fixed effect predictor (i.e. abiotic variables and indicator values) was quantified by means of an automated model selection using function 'dredge' implemented in the package 'MuMIn' (Barton 2020). Thereby, a candidate model was computed for each combination of fixed effect predictors in the global model (i.e. models ranging from a null model including only the intercept to the global model itself, which contains all predictors). The second order Akaike Information Criterion (AICc; Sugiura 1978), which includes a second-order bias correction appropriate for small sample sizes (Burnham and Anderson 2002), was used to evaluate the candidate model. Subsequently, the effect of each predictor was quantified as the sum of Akaike weights (Burnham and Anderson 2004) of candidate models containing the respective predictor (function 'importance ' of the package 'MuMIn ').

3. Results

3.1. Data overview

We recorded a total of 77 species. Twenty-four of these species are obligate aquatic bryophytes (Frahm and Frey 2004). Fifteen species belong to Marchantiophyta and 62 to Bryophyta, respectively. Within the Bryophyta acrocarpous bryophytes (34 species) were more frequent than pleurocarpous species (28). About half of species (41) occurring only at one sampling site and were, hence, discarded from analyses. The remaining species and their frequencies can be found in Table 2. The elevation (EL) of the surveyed sites ranged from 312 to 2240 m.a.s.l., the electrolytic conductivity (EC) values ranged from 34.8 and 515 µS, the measured water temperature (WT) ranged from 2.9 to 18.3° C, the pH varied from 6.05 to 8.3. The observed nutrient values ranged from 109 to 741 µg/l for total nitrogen (TN) and from 1 to 59.6 µg/l for total phosphorus (TP) (Table 1).

3.2. Community structure according to results of pCCA

Applying the pCCA, 6.8%, 15.5% and 77.7% of the total variance in the bryophyte species composition of 13 streams in South Tyrol were explained by their spatial position (coordinates), the abiotic variables and remained unexplained, respectively. The first axis of the pCCA was mainly determined by gradients of EL and WT pointing in nearly opposite directions (Figure 2). The second axis is determined by EL and to a lesser degree by pH. These four variables were significantly related to the species composition (Table 2) in contrast to TN and TP, which were correlated to WT (Figure 2). Bryophyte species formed a homogenous cluster, except for *Sciuro-hypnum plumosum* being separated along the second axis.

3.3. Occurrence of dominant species according to results of GLMMs

Our GLMM analyses identified eK, eL and eR as environmental variables each being relevant for the occurrence of about one third of the most common bryophyte species. These variables have high Akaike weights (mostly ≥0.9) and were significant predictors in the global models (Table 3). In addition, the majority of other environmental variables (i.e., eF, pH, TP, EL and EC) significantly explained the occurrence of one or two species but had lower Akaike weights. In contrast, WT, TN and eT were irrelevant for the occurrence of the analysed bryophyte species. *Hygrohypnum luridum, Palustriella communtata var falcata* and *Platyhypnidium riparioides* were explained by the most, i.e., four out of the nine, environmental variables. The occurrence of *Brachythecium rivulare, Bryum pseudotriquetrum, Cratoneuron filicinum* and *Amblystegium riparium* was related to one or two variables while those of *Amblystegium tenax, Hygrohypnum duriusculum* and *Schistidium rivulare* were explained by none of them. In general, variable importance derived from Akaike Weights was very congruent with the pattern of significant predictors in global models (compare Table 3) except for TP being significant in *Palustriella communtata var falcata* despite the low Akaike Weight of 0.33 and the non-significant eT in *Hygrohypnum duriusculum* despite an Akaike weight of 0.87.

4. Discussion

This study highlights the linkage of abiotic factors to the bryophyte community composition in mountain streams of the Eastern Alps, supporting previous studies which indicated the impact of environmental drivers shaping bryophyte communities (Ceschin et al., 2015; Lang and Murphy, 2012; Luis et al., 2015). Our findings suggest that the bryophyte community composition can be primarily linked to elevation and electrolytic conductivity. The former finding explained the species gradient along the first axis of the pCCA, which is shifted toward the right of the plot, indicating a higher species richness with increasing elevation. The same pattern was also found by Spitale (2016) regarding the same study area, although he focused on terrestrial bryophytes of alpine forest. Scarlett and O'Hare (2006) noticed as well that headwaters are especially rich in bryophytes. Further can elevation indicate various climatic and topographic settings (Bes et al., 2018) which may also influence the occurrence of bryophytes. This evidenced also Düll-Wunder (2008), who revised the highest elevation of occurrence of bryophytes species in South Tyrol. Amongst them was also an aquatic bryophyte (*Conocephalum conicum*) which implicated that bryophytes already reacted to climate warming, migrating toward higher elevation to follow their temperature optimum. In addition, predicted Spitale (2016) that in case of a warming scenario of 2°C in the Alps, the functional diversity of terrestrial bryophytes would decrease by 10%. Conveying this projection onto the species community of streams this would implicate large alterations of the species assemblage, affecting other organisms of the aquatic habitat (Tuba et al., 2011).

In addition, we found that electrolytic conductivity determined the bryophyte community composition. Various other studies confirmed the important role of conductivity for stream bryophyte communities (Bes et al., 2018; Lang and Murphy, 2012; Manolaki and Papastergiadou, 2013). Suren (1996) states that EC can be accounted as a surrogate of the proportion of soft sedimentary underlaying rock, which reflects our measurements of streams with substrate composition containing conglomerate, sandstone and dolomite were characterized by higher conductivity. Coherent to this type of lithology in our study could be associated calcicolous species such as *Hygrohypnum luridum* and *Palustriella commutata var falcata*, corresponding also with the findings of previous studies (Ceschin et al., 2015; Gecheva et al., 2013). This affinity to certain type of lithology can be affiliated by different physiological capacity in cation exchange (Bes et al., 2018). Nevertheless, the results of the models showed no significant impact of conductivity on those two species.

Inversely related to the elevation was the water temperature, which distinguishes the species found left side of the pCCA plot. Water temperature thriving the aquatic macrophyte composition was also found by Manolaki and Papastergiadou (2013). Additionally, they underlined that it had a seasonable impact, with summer as the significant time. Although their study was accomplished in a water body located in Greece and characterised by Mediterranean climate, the same effect could have higher water temperature during summer in mountain streams. Our sampling was implemented during spring-summer and the overall mean water temperature lied around 10.0°C, which reflects the low temperature optimum for the growth of stream bryophytes suggested by Stream Bryophyte Group (1999). Moreover water temperature did not only shape the bryophyte community but also had an effect on species associated with aquatic bryophytes such as macroinvertbrates and diatoms (Turunen et al., 2020).

Surprisingly, did water temperature (WT) and the indicator value for temperature (eT) not show an effect at all in our models. Despite the expected representative overlapping of measured environmental conditions and indicator values we concluded that they coincided only partly regarding the occurrence of dominant species. For example, the effect of the measured pH and the indicator value for soil reaction (eR) were both relevant, although for different species and hence not overlapping regarding their expected predictive overlap. An exception to this different relevance was *Plathyhypnidium riparoides*, which occurrence was impacted by both predictors (pH and eR). According to Lang and Murphy (2012) it belongs to the 'core' species of high-latitude streams. They grouped this 'core' species combined with *Hygrohypnum luridum* and *Palustriella commutata var falcata* as a characteristically association for base-rich water quality. We found that the indicator value for eR played for the same above-mentioned species an important role. In addition, our species community composition shifted along the pH gradient. This underlines the relevance of this abiotic factor, since the pH levels impact the availability of dissolved CO_2 in aquatic environments (Luis et al., 2015), which is considered as an important carbon source for aquatic bryophytes (Stream Bryophyte Group, 1999).

Despite our expectations of nitrogen and phosphorus being limiting elements in aquatic systems (Elser et al., 2007) and therefore responsible drivers of our bryophyte community composition, we detected no significant influence by them. Although we found the nutrient content in our streams to be inversely related to elevation and we noticed a shift of the species composition toward the right side of the pCCA plot, indicating sample sites defined by higher elevation. This same pattern was found by *Tessler et al.* (2014) who correlated low levels phosphorus positively to species abundance and richness. Nevertheless the recorded nutrient levels were low which indicate good water quality of the sampled streams hence coherent with habitat requirements of aquatic bryophytes (Stream Bryophyte Group, 1999). Despite the irrelevance of the nitrogen levels for the species community, we found that for the prediction of the occurrence of *Hygrohypnum luridum* and *Palustriella communtata var falcata* phosphorus was determinant.

Regarding the contradictory results of the models leads us to the conclusion that the indicator values had a higher relevance in explaining the ecological drivers of the occurrence of single species. Furthermore they reflect not only the momentary ecological preferences of species, but include the environmental long-term setting (Schaffers and Sýkora, 2000). Whereas the measured abiotic variables were more suitable to describe the whole community composition, although the variance explained by the pCCA needs to be interpreted critically, since it covers a rather small fraction (15.5%) of the variance in the species composition. On the one hand this low value could derive form the fact that the sampled abiotic factors represented only a snapshot of the flow conditions at that moment, which only partially represent the physico-chemical constitution of the sampled water body. On the other hand, this suggests that stochastic processes are more likely to form the species composition. To the same conclusion came Nascimbene *et al.* (2011), albeit they investigated the congruencies of various autotrophic groups inhabiting springs in the Italian Alps. Further it could be attributed to the spatial heterogeneity of stream habitats (Wohl, 2016). This underlines again the complexity of a stream ecosystems and urges the further need of investigating on a spatial and temporal scale. Thereby, environmental factors on various scales, such as on a macroscale (i.e. elevation, climate, geology), on a mesoscale (i.e. hydrology, water quality) and on a microscale (turbulence, substrate size and stability), should be taken into consideration. All these spatial processes wield their influence over different time period, from years to several days (Stream Bryophyte Group, 1999). Therefore, including both spatial and temporal aspects into prospective studies, could help to gather a better understanding of the ecological requirements of bryophyte communities in streams. Respectively of the future ecological changes caused by rising temperatures (Tuba et al., 2011), these demanded requirements gain an even larger importance. Based on the floristic knowledge obtained from this type of studies, future decisions should be incorporated in biodiversity management and conservation policies, regarding mountain streams in the Alps.

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Tab. 1: General characterisation of the 13 study streams as illustrated in Fig. 1. Stream regime codes: g: glacial, np: nivo-pluvial (Provincia autonoma die Bolzano - Alto Adige 2009); Geological substrate codes: ab: amphibolite, Bf: Bellerophon formation, cms: calcareous mica schist, do: dolomite, di: diorite, ig: ignimbrite, ms: mica schist, mb: metabasite, gr: granit, og: orthogneiss, pg: paragneiss, qp: quart-phyllite, sa: sandstone, co: conglomerate, SC: Schneeberg Complex, to: tonalite, Wf: Werfen formation (Provincia autonoma di Bolzano - Alto Adige 2009). Further shown is the elevation (EL: m.a.s.l.) range of the sample sites and average values of abiotic variables measured at each sample site of the surveyed streams; Codes of abiotic variables: EC (electrolytic conductivity: µS), WT (water temperature: °C), pH, TP (total phosphorus: µg/l), TN (Total nitrogen: µg/l).

						Abiotic variables					
Name	**Catchment area [km²]**	**Stream length [km]**	**Elevation of catchment area [m]**	**Stream regime**	**Geological substrate**	**EL range**	**EC**	**WT**	**pH**	**TP**	**TN**
Rio di Silandro	54	14	670 - 3369	np	ms, pg	743 - 2210	236.8	10.08	6.61	4.7	205.2
Rio di Sesto	110	16	1170 - 3145	np	co, sa	1204 - 1584	347.	8.92	7.61	14.2	295.4
Rio di Slingia	40	12	1040 - 3162	np	ms, pg	1108 - 2115	192.3	8.76	7.2	5.62	214.6
Rio di Tires	65	15	310 - 3002	np	Bf, do, Wf	397 - 1578	362.6	16.1	8.18	5.16	582.4
Rio Fleres	75	15	1060 - 3267	g	do, pg	1082 - 1662	95.06	10.54	6.82	5.78	339.8
Rio Gardena	200	26	470 - 3179	np	do	660 - 1904	291.2	9.86	7.7	6.78	422.6
Rio Nero	41	13	389 - 2499	np	do	804 - 1742	352.2	7.24	7.73	12.98	329.2
Rio Saldura	100	22	900 - 3738	g	ms, pg	1380 - 2240	214.9	7.72	7.24	30.76	273.0
Rio Vallarsa	29	14	230 - 2120	np	ig	312 - 1564	458.4	8.38	7.8	17.48	535.8
Torrente Aurino	629	50	810 - 3498	g to np	cms, mb, ms, og, pg	830 - 1951	118.66	12.24	7.11	7.2	194.0
Torrente Passirio	428	52	295 - 3481	g to np	ab, ms, og, pg, SC	345 - 2228	135.38	10.9	6.28	3.54	215.4
Torrente Talvera	429	46	260 - 2781	np	di, gr, ig, qp, to	465 - 1768	73.8	10.92	6.96	7.3	355.8
Torrente Valsura	300	42	265 - 3443	np	ms, pg	987 - 1990	103.38	7.82	7.32	10.82	288.8

Tab. 2: Thirty-six bryophyte species and their frequencies found in at least two out of 65 sampling sites at 13 streams in South Tyrol, Italy. Nomenclature follows Köckinger et al. (2020).

Species name	Species code	Frequency
Amblystegium fluviatile (Sw. ex Hedw.) Schimp.	AmFl	6
Amblystegium riparium (L. ex Hedw.) Schimp.	AmRi	14
Amblystegium tenax (Hedw.) C.E.O.Jensen	AmTe	14
Blindia acuta (Hedw.) Bruch & Schimp.	BlAc	3
Brachythecium albicans (Neck. ex Hedw.) Schimp.	BrAl	2
Brachythecium rivulare Schimp.	BrRi	33
Brachythecium salebrosum (Hoffm. ex F.Weber & D.Mohr) Schimp.	BrSa	2
Bryoerythrophyllum recurvirostrum (Hedw.) P.C.Chen var. recurvirostrum	BrRe	2
Bryum pseudotriquetrum (Hedw.) P.Gaertn., E.Mey. & Scherb.	BrPs	25
Bryum schleicheri DC. var. schleicheri	BrSc	4
Campylium stellatum (Schreb. ex Hedw.) Lange & C.E.O.Jensen	CaSt	4
Campylopus flexuosus (Hedw.) Brid.	CaFl	4
Cinclidotus fontinaloides (Hedw.) P.Beauv.	CiFo	7
Conocephalum conicum (L.) Dumort.	CoCo	7
Cratoneuron filicinum (L. ex Hedw.) Spruce	CrFi	16
Dichodontium pellucidum (Hedw.) Schimp.	DiPe	8
Didymodon fallax (Hedw.) R.H.Zander	DiFa	3
Fontinalis antipyretica L. ex Hedw.	FoAn	4
Grimmia longirostris Hook.	GrLo	2
Hygrohypnum duriusculum (De Not.) D.W.Jamieson	HyDu	14
Hygrohypnum luridum (Hedw.) Jenn.	HyLu	37
Jungermannia obovata Nees	JuOb	3
Palustriella communtata var. falcata (Brid.) Ochyra	PaCovFa	16
Palustriella commutata (Hedw.) Ochyra var. commutata	PaCo	4
Philonotis caespitosa Jur.	PhCa	7
Plagiochila asplenioides (L. emend. Taylor) Dumort.	PlAs	2
Plagiochila porelloides (Torr. ex Nees) Lindenb.	PlPo	3
Platyhypnidium riparioides (Hedw.) Dixon	PlRi	28
Racomitrium aquaticum (Brid. ex Schrad.) Brid.	RaAq	2
Rhizomnium punctatum (Hedw.) T.J.Kop.	RhPu	6
Sanionia uncinata (Hedw.) Loeske	SaUn	5
Scapania subalpina (Nees ex Lindenb.) Dumort.	ScSu	2
Scapania undulata (L.) Dumort.	ScUn	2
Schistidium apocarpum (Hedw.) Bruch & Schimp.	ScAp	4
Schistidium rivulare (Brid.) Podp.	ScRi	25
Sciuro-hypnum plumosum (Hedw.) Ignatov & Huttunen	ScPl	3

Tab. 3: Relative importance of environmental variables for the occurrence of the most common bryophyte species expressed as summed Akaike weights. The Akaike weight gives the probability that a given model explains species occurrence best among the set of candidate models comprising each combination of environmental variables (i.e., models ranging from a null model including only the intercept to a global model, which contains all variables). Values in the tables represent the sum of Akaike weights of all models containing the respective variable. Asterisks indicate the significance of a variable in the full model (i.e. a model including all variables of either the abiotic measurements or the Ellenberg indicators at the levels $p<0.05$ (*), $p<0.01$ (**). Two sets of environmental variables were analysed separately: abiotic variables derived from technical measurements and mean Ellenberg indicator values (Ellenberg *et al.* 2001) inferred from the bryophyte species composition. Species occurring in at least 20% of sampling sites were included in the table. For codes of abiotic variables refer to table 1. Codes Indicator values: eL (light-regime indicator value), eT (temperature indicator value), eK (continentality indicator value), eF (soil moister indicator values), eR (soil reaction indicator value i.e. acidity/lime content).

	Abiotic variables						Ellenberg indicator indices				
	EL	EC	WT	pH	TP	TN	eL	eT	eK	eF	eR
Amblystegium riparium	0.26	0.53	0.48	0.61	0.24	0.29	**0.80***	0.57	0.25	0.26	0.26
Amblystegium tenax	0.42	0.23	0.26	0.24	0.52	0.27	0.29	0.50	0.24	0.30	0.25
Brachythecium rivulare	0.25	0.26	0.28	**0.80***	0.43	0.29	0.25	0.35	**0.95***	0.45	0.24
Bryum pseudotriquetrum	0.47	0.25	0.28	0.36	0.43	0.78	**1.00****	0.24	0.30	0.27	0.24
Cratoneuron filicinum	0.39	0.23	0.49	0.23	0.50	0.25	**0.96***	0.63	0.42	0.28	**0.97****
Hygrohypnum duriusculum	0.64	0.71	0.34	0.68	0.24	0.26	0.49	0.87	0.24	0.66	0.54
Hygrohypnum luridum	0.65	0.30	0.33	0.36	**0.74***	0.31	**0.99****	0.31	**0.95***	0.64	**0.90***
Palustriella communtata var falcata	**0.99***	0.60	0.26	0.43	**0.33***	0.24	0.55	0.27	**0.90***	0.34	**0.97****
Platyhypnidium riparioides	0.85	**0.70***	0.44	**0.80***	0.25	0.26	0.32	0.31	0.38	**0.99****	**0.95***
Schistidium rivulare	0.28	0.41	0.38	0.80	0.37	0.30	0.31	0.26	0.25	0.26	0.51

Tab. 4: Analysis of Variance table derived from a permutation test of the significance of abiotic variables used as constraints in a partial canonical correspondence analysis to explain the variance in bryophyte assemblages of 65 sampling sites located at 13 streams in South Tyrol, Italy. This test is sensitive to the order of variables and we, hence, present the mean of 720 permutations of the six variables. Significance p-values are indicated by asterixis p<0.05 (*), p<0.01 (**), p<0.001 (***).

Variable	ChiSquare	F-ratio	p-value
Elevation	0.19	2.41	**0.001*** **
Electrolytic conductivity	0.18	2.31	**0.001*** **
Water temperature	0.14	1.82	**0.008** **
pH	0.13	1.64	**0.015* **
Total phosphorus	0.11	1.41	0.082
Total nitrogen	0.12	1.54	0.089

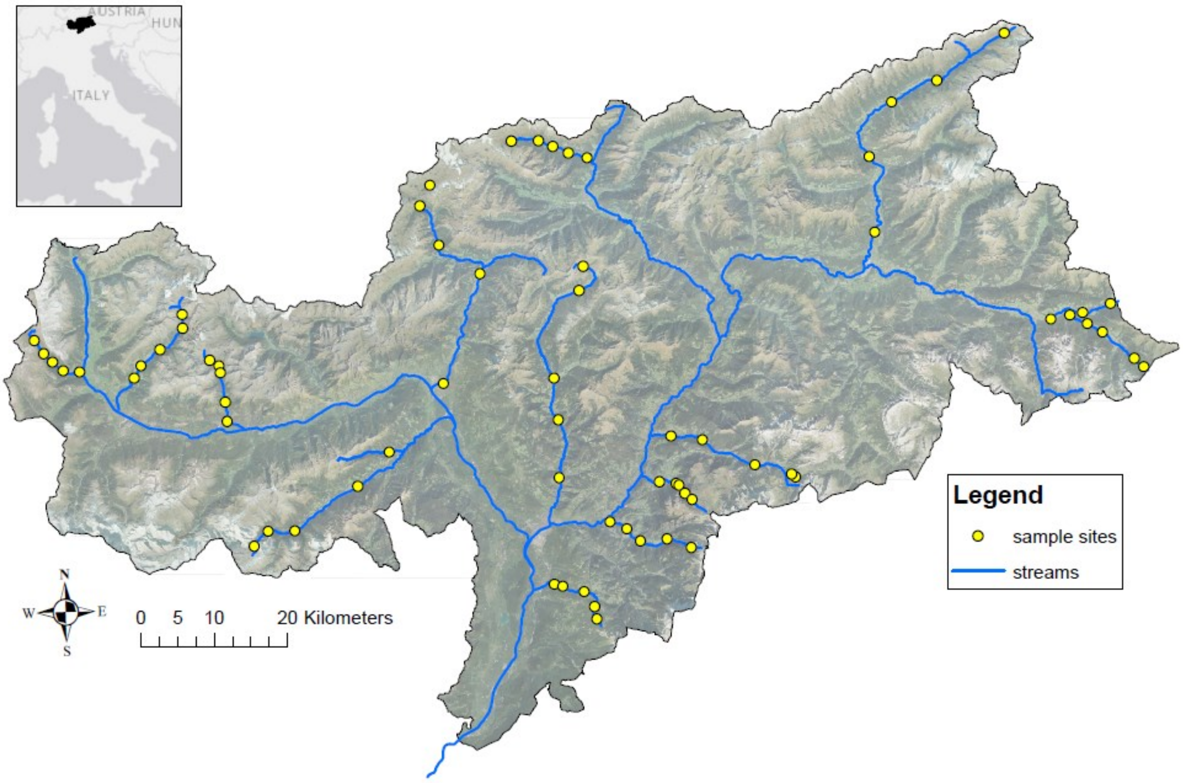

Fig. 1: Thirteen streams (dark blue) within the stream network of South Tyrol, Italy. Each comprising five sampling sites (dots), selected to investigate abiotic factors shaping aquatic bryophyte assemblages. Mapcredits: South Tyrol: Geobrowser3©2020, Basemap: Esri, HERE, Garmin, ©OpenStreetMap contributors, and the GIS user community).

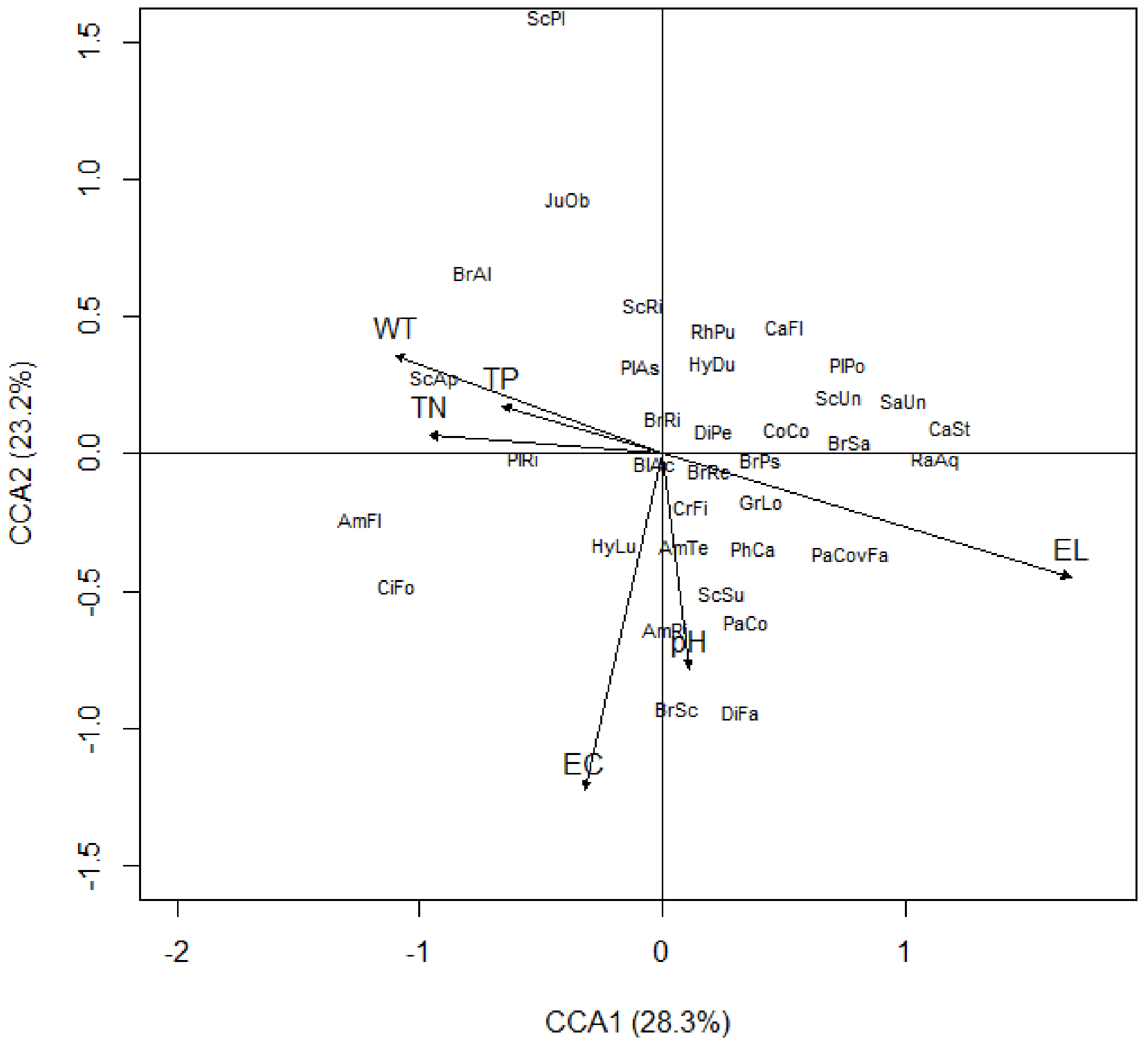

Fig. 2: Partial canonical correspondence analysis depicting the effects of abiotic variables on the species composition of 36 species bryophyte assemblages collected along 13 streams in South Tyrol, Italy. Proportion of variance explained by the first and second ordination axis on the total of 15.5% of variance explained by all abiotic variables are given in parentheses. For abiotic variables codes refer to table 1; for species codes refer to Table 2.

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8 Findings for *Hygrohypnum luridum*

The initial research question altered through the workflow of the manuscript for the publication. Nevertheless, I would like to present some results regarding the species *Hygrohypnum luridum*, which was the species I was originally focusing on. It was the commonest species with an occurrence at 54% of the sampled sites (Table 2). The species occurred in sites characterized by lower elevation (mean 1996 m.a.s.l.) hence higher water temperature (mean 10.5°C). Further the preferences of *Hygrohypnum luridum* in respect to the water quality are following: it preferred sites defined by higher pH levels (mean 7.36), lower nutrient levels (mean total phosphorus levels of 7.63 µg/l and nitrogen levels with a mean of 338.18 µg/l) and sites with an electrolytic conductivity which lied around 244 µS (Figure 2). For the modelled occurrence of the species the total phosphorus (TP) played an important role (Table 3 of manuscript). In addition, for each site means of Ellenberg indicator values were computed (Ellenberg *et al.* 2001). For the occurrence of *Hygrohypnum luridum* the indicator values for light regime (eL), continentality (eK) and soil reaction (eR) were driving factors (Table 3 of manuscript). Furthermore, the effect plots displayed the predicted values for the presence of the species (Figure 3). According to them its probability of occurrence was increasing with lower elevation, higher temperature, higher pH levels and higher conductivity. Furthermore, the species probability of occurrence increased with low phosphorus and nitrogen levels.

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10 Appendix

Zusammenfassung

In der vorliegenden Studie wurde die Fragestellung, welcher abiotische Faktor das Vorkommen von *Hygrohypnum lurid*um (Hedw.) Jenn. und anderen aquatischen Bryophyten am meisten beeinflusst, untersucht. Dafür wurden ausgewählte Fließgewässer in Südtirol (Provinz in Nord Italien) auf folgende Umweltfaktoren beprobt: Höhenlage, Wassertemperatur, elektrische Leitfähigkeit, pH, Gesamtphosphor- und Gesamtstickstoffgehalt. An den jeweiligen Wasserprobenahme-Stellen wurden innerhalb eines 40m Transekts eine geschichtete Zufallsstichprobennahme von Moosbelegen, die im Uferbereich und submers vorkamen, genommen. Insgesamt konnten 77 Arten erhoben werden, darunter befanden sich 16 obligate aquatische Bryophyten. Zu den drei häufigsten Arten zählten *Hygrohypnum luridum* (54% Probenahmestellen), *Brachythecium rivulare* Schimp (48% Probenahmenstellen) and *Platyhypnidium riparioides* (Hedw.) Dixon (42% Probenahmestellen).
Zur Auswertung der abiotischen Faktoren, die auf die Artengarnitur einwirkten, wurde eine partielle kanonische Korrespondenzanalyse (pCCA) durchgeführt. Dabei konnte festgestellt werden, dass Höhenlage, Leitfähigkeit, Wassertemperatur und pH die Artgemeinschaft ausschlaggebend beeinflussten. Allerdings muss festgehalten werden, dass die erklärte Varianz nur teilweise (19.5%) die Artengarnitur erklärt. Weiters wurde das Vorkommen der 10 häufigsten Bryophyten anhand generalisierter linear gemischter Modelle (GLMMs) analysiert. Dazu wurden einerseits die erhobenen abiotischen Faktoren und anderseits die Mittelwerte von Ellenberg Zeigewerten für die Artgemeinschaft an den jeweiligen Probenahmestellen als formgebende Prädiktoren eingesetzt. Die Aussagen von den gemessenen Werten und von ermittelten Zeigerwerten bezieht sich teilweise auf dieselben abiotischen Faktoren, wie pH und Reaktionszahl oder Temperatur und Temperaturzahl. Die Auswertung der Modelle ergab, dass für das Vorkommen von *Hygrohypnum luridum* der Gesamtphosphor, Licht-, Kontinentalitäts- und Reaktionszahl ausschlaggebend waren. Die Ergebnisse der Modelle zeigen, dass sich dieselben Arten nur teilweise die gemessenen abiotischen Faktoren und die Zeigerwerte für das Vorkommen überschneiden. Dabei wiesen die Zeigerwerte höhere Signifikanzen in den Modellen auf. Schlussfolgernd wurde anhand dieser Untersuchung festgestellt, dass für die Beschreibung der Artengarnitur die gemessenen abiotischen Faktoren besser geeignet sind und das Vorkommen von Einzelarten besser anhand von Zeigerwerten erklärt werden kann.

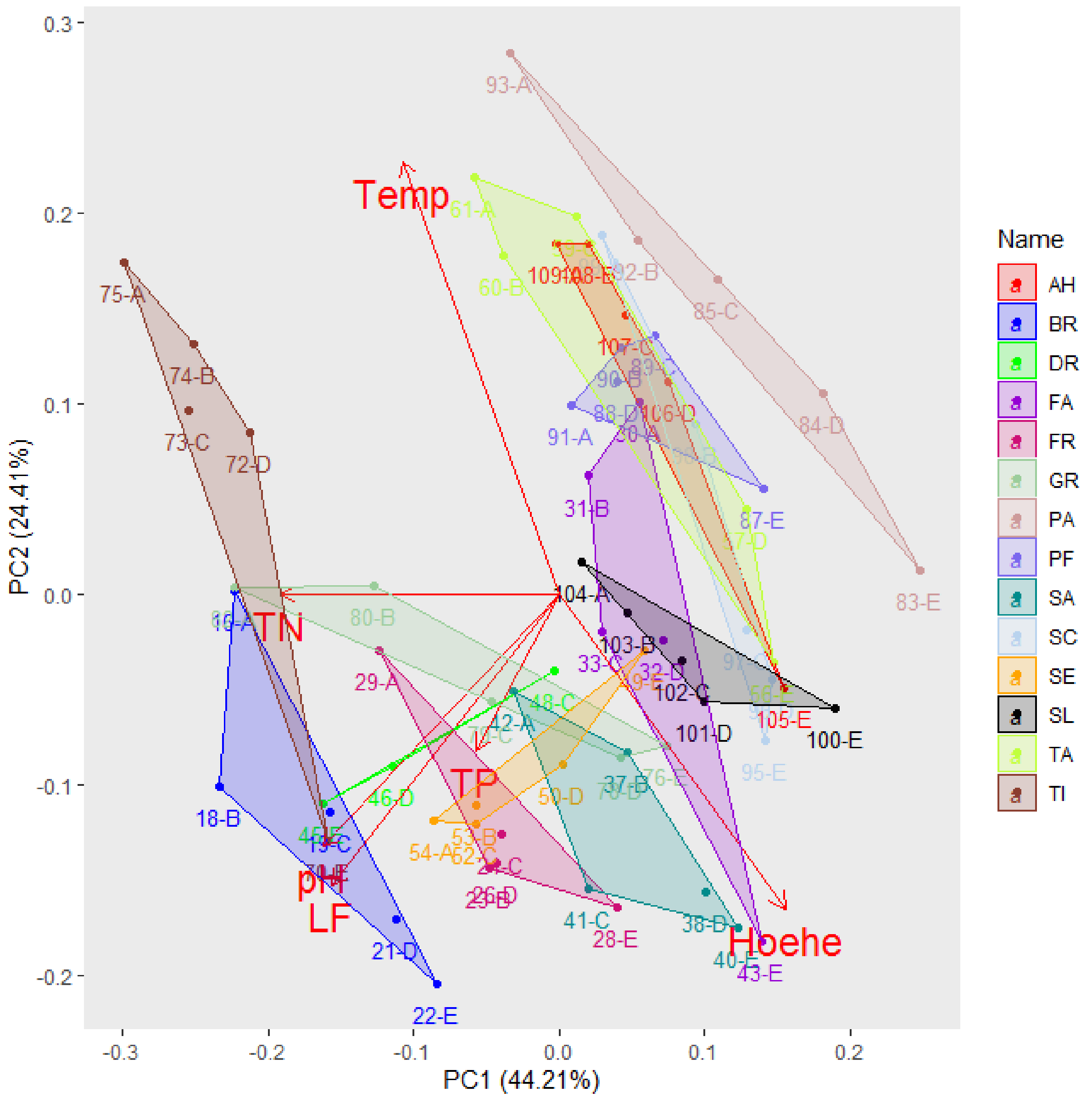

Fig 1: Principal component analysis (PCA) depicting the correlation between sample sites and measured environmental variables indicates the connectivity of the stream systems. Stream codes: AH (Ahr), BR (Brantentalbach), DR (Drau), FA (Fallschauer), FR (schwarzgriesbach), GR (Grödner Bach), PA (Passer), PF (Pflerscherbach), SA (Saldurbach), SC (Schlienigerbach), SE (Sextnerbach), SL (Schlandraunbach), TA (Talfer), TI (Tierserbach), Sample site codes: A (upper reach), B, C, D (mid reach), E (lower reach).

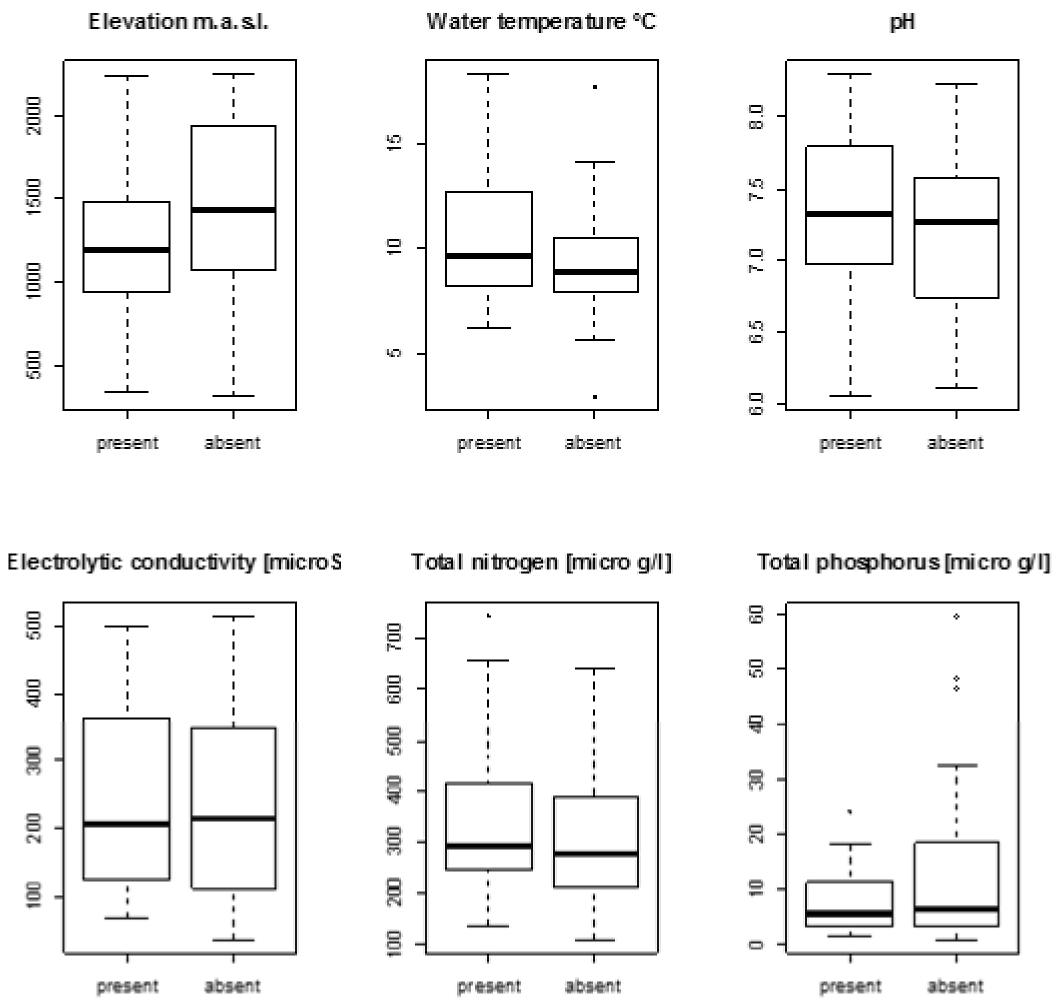

Fig. 2: Boxplots depicting the range of various measured environmental variables comparing site where the species *Hygrohypnum luridum* occurred to sites where the species was absent.

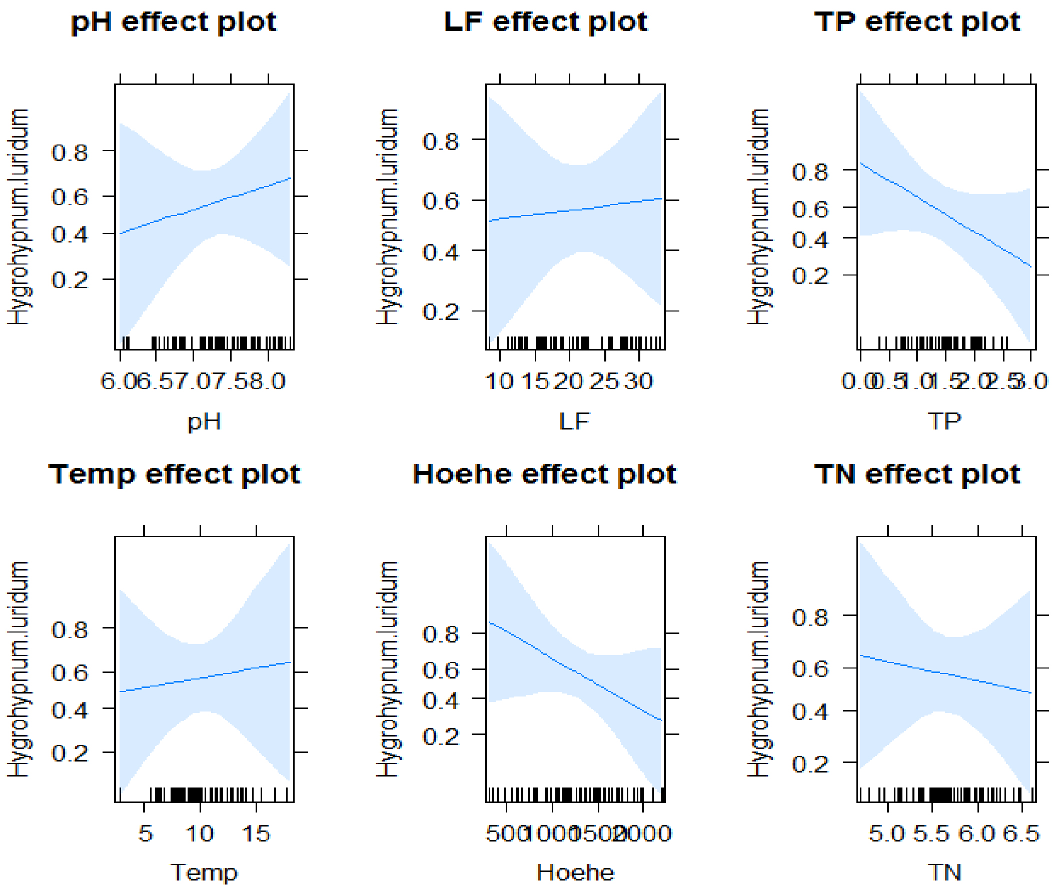

Fig. 3: Effects plots depicting the predicted occurrence of *Hygrohypnum luridum* in correlation to the various environmental variables. Environmental variables codes: pH, electrolytic conductivity (LF), total phosphorus (TP), water temperature (Temp), elevation (Hoehe) and total nitrogen (TN).

Tab. 1: Nomenclature follows Köckinger et al. (2020) and abbreviations of species found at the various sample sites in South Tyrol.

Species name	**Abbreviation**
Amblystegium fluviatile (Sw. ex Hedw.) Schimp.	A. fluviatile
Amblystegium tenax (Hedw.) C.E.O.Jensen	A. tenax
Amblystegium varium (Hedw.) Lindb.	A. varium
Barbilophozia barbata (Schmidel ex Schreb.) Loeske	B. barbata
Blindia acuta (Hedw.) Bruch & Schimp.	B. acuta
Brachythecium albicans (Neck. ex Hedw.) Schimp.	B. albicans
Sciuro-hypnum plumosum (Hedw.) Ignatov & Huttunen	S. plumosum
Sciuro-hypnum populeum (Hedw.) Ignatov & Huttunen	S. populeum
Brachythecium rivulare Schimp.	B. rivulare
Brachythecium salebrosum (Hoffm. ex F.Weber & D.Mohr) Schimp.	B. salebrosum
Bryoerythrophyllum recurvirostrum (Hedw.) P.C.Chen var. recurvirostrum	B. recurvirostrum
Bryum capillare Hedw.	B. capillare
Bryum pseudotriquetrum (Hedw.) P.Gaertn., E.Mey. & Scherb.	B. pseudotriquetrum
Bryum schleicheri DC. var. schleicheri	B. schleicheri
Calliergonella cuspidata (L. ex Hedw.) Loeske	C. cuspidata
Campylium stellatum (Schreb. ex Hedw.) Lange & C.E.O.Jensen	C. stellatum
Campylopus flexuosus (Hedw.) Brid.	C. flexuosus
Campylopus subulatus Schimp. ex Milde var. Subulatus	C. subulatus
Cinclidotus fontinaloides (Hedw.) P.Beauv.	C. fontinaloides
Conocephalum conicum (L.) Dumort.	C. conicum
Cratoneuron filicinum (L. ex Hedw.) Spruce	C. filicinum
Dichelyma capillaceum (Dicks.) Myr.	D. capillaceum
Dichodontium pellucidum (Hedw.) Schimp.	D. pellucidum
Didymodon fallax (Hedw.) R.H.Zander	D. fallax
Didymodon luridus Hornsch.	D. luridus
Didymodon spadiceus (Mitt.) Limpr.	D. spadiceus
Didymodon tophaceus (Brid.) Lisa	D. tophaceus
Encalypta streptocarpa Hedw.	E. streptocarpa
Eucladium verticillatum (With.) Bruch & Schimp.	E. verticillatum
Fissidens adianthoides Hedw.	F. adianthoides
Fissidens crassipes Wilson ex Bruch & Schimp.	F. crassipes

Fontinalis antipyretica L. ex Hedw.	F. antipyretica
Grimmia longirostris Hook.	G. longirostris
Homalothecium sericeum (Hedw.) Schimp.	H. sericeum
Hygrohypnum alpestre (Sw. ex Hedw.) Loeske	H. alpestre
Hygrohypnum duriusculum (De Not.) D.W.Jamieson	H. duriusculum
Hygrohypnum luridum (Hedw.) Jenn.	H. luridum
Hygrohypnum smithii (Sw.) Broth.	H. smithii
Hypnum lindbergii Mitt.	H. lindbergii
Jungermannia exsertifolia subsp. cordifolia (Dumort.) Váña	J. exsertifolia ssp. cordifolia
Jungermannia obovata Nees	J. obovata
Amblystegium riparium (L. ex Hedw.) Schimp.	A. riparium
Marchantia polymorpha L. subsp. polymorpha	M. polymorpha
Mnium thomsonii Schimp.	M. thomsonii
Nardia scalaris Gray	N. scalaris
Palustriella communtata var. falcata (Brid.) Ochyra	P. communtata var. falcata
Palustriella commutata (Hedw.) Ochyra var. commutata	P. commutata
Pellia endiviifolia (Dicks.) Dumort.	P. endiviifolia
Philonotis caespitosa Jur.	P. caespitosa
Philonotis seriata Mitt.	P. seriata
Plagiochila asplenioides (L. emend. Taylor) Dumort.	P. asplenioides
Plagiochila porelloides (Torr. ex Nees) Lindenb.	P. porelloides
Plagiomnium cuspidatum (Hedw.) T.J.Kop.	P. cuspidatum
Plagiomnium ellipticum (Brid.) T.J.Kop.	P. ellipticum
Plagiomnium rostratum (Schrad.) T.J.Kop.	P. rostratum
Platyhypnidium riparioides (Hedw.) Dixon	P. riparioides
Pohlia ludwigii (Spreng. ex Schwägr.) Broth.	P. ludwigii
Racomitrium aquaticum (Brid. ex Schrad.) Brid.	R. aquaticum
Racomitrium canescens (Timm. ex Hedw.) Brid. subsp. Canescens	R. canescens
Racomitrium elongatum Ehrh. ex Frisvoll	R. elongatum
Racomitrium ericoides (Brid.) Brid.	R. ericoides
Rhizomnium punctatum (Hedw.) T.J.Kop.	R. punctatum
Rhynchostegium confertum (Dicks.) Schimp.	R. confertum
Rhytidiadelphus squarrosus (L. ex Hedw.) Warnst.	R. squarrosus
Sanionia uncinata (Hedw.) Loeske	S. uncinata
Scapania aequiloba (Schwägr.) Dumort.	S. aequiloba

Scapania irrigua (Nees) Nees subsp. Irrigua	S. irrigua
Scapania nemorea (L.) Grolle	S. nemorea
Scapania subalpina (Nees ex Lindenb.) Dumort.	S. subalpina
Scapania uliginosa (Sw. ex Lindenb.) Dumort.	S. uliginosa
Scapania undulata (L.) Dumort.	S. undulata
Schistidium apocarpum (Hedw.) Bruch & Schimp.	S. apocarpum
Schistidium rivulare (Brid.) Podp.	S. rivulare
Tortella tortuosa (Ehrh. ex Hedw.) Limpr.	T. tortuosa
Warnstorfia sarmentosa (Wahlenb.) Hedenäs	W. sarmentosa

Tab 2: Occurrence data of sampled bryophyte species at sampled sites in South Tyrol. 1 signifies the presence of a species, 2 indicates the species in its fertile state (with sporophytes), abbreviations for nomenclature are found in Tab. 1.

ID	A. fluviatile	A. tenax	A. varium	B. acuta	B. albicans	B. barbata	B. capillare	S. plumosum	S. populeum	B. pseudotriquetrum	B. recurvirostrum	B. rivulare	B. salebrosum	B. schleicheri	C. conicum	C. cuspidata	C. filicinum	C. flexuosus	C. fontinaloides	C. stellatum	C. subulatus	D. capillaceum
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18	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
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24	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
28	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.
29	1	.	.	.	1	.	.	.	.	1	1	1	.	.	.	.	1	.	1	.	.	.
30	.	.	.	.	2	.	.	.	.	1	.	2	.	.	.	.	.	1	.	.	.	.
31	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
32	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
33	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	2	.	.	.	.	.
37	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.
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40	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
41	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	1	.	.	.	.
42	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
43	.	1	.	.	.	1	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.
44	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.
45	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.
46	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.
47	1	.	1	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
48	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	1	.	.	.	.	.
49	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.
50	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
51	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
52	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
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55	.	.	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	1	.	1	.	.
56	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	1	.	1	.	1	.	.
57	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
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ID	A. fluviatile	A. tenax	A. varium	B. acuta	B. albicans	B. barbata	B. capillare	B. plumosum	B. populeum	B. pseudotriquetrum	B. recurvirostrum	B. rivulare	B. salebrosum	B. schleicheri	C. conicum	C. cuspidata	C. filicinum	C. flexuosus	C. fontinaloides	C. stellatum	C. subulatus	D. capillaceum
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ID	D. capillaceum	D. fallax	D. luridus	D. pellucidum	D. spadiceus	D. tophaceus	E. streptocarpa	E. verticillatum	F. adianthoides	F. antipyretica	F. crassipes	G. longirostris	H. alpestre	H. duriusculum	H. luridum	H. lindbergii	H. sericeum	H. smithii	J. exsertifolia ssp. cordifolia	J. obovata	A. riparium
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ID	D. capillaceum	D. fallax	D. luridus	D. pellucidum	D. spadiceus	D. tophaceus	E. streptocarpa	E. verticillatum	F. adianthoides	F. antipyretica	F. crassipes	G. longirostris	H. alpestre	H. duriusculum	H. luridum	H. lindbergii	H. sericeum	H. smithii	J. exsertifolia ssp. cordifolia	J. obovata	A. riparium
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ID	M. polymorpha	M. thomsonii	N. scalaris	P. asplenioides	P. commutata	P. communtata var. falcata	P. caespitosa	P. cuspidatum	P. ellipticum	P. endiviifolia	P. ludwigii	P. porelloides	P. rostratum	P. seriata	R. canescens	R. aquaticum	R. confertum	R. elongatum	R. ericoides	R. punctatum	P. riparioides	R. squarrosus
16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
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ID	M. polymorpha	M. thomsonii	N. scalaris	P. asplenioides	P. commutata	P. communtata var. falcata	P. caespitosa	P. cuspidatum	P. ellipticum	P. endiviifolia	P. ludwigii	P. porelloides	P. rostratum	P. seriata	R. canescens	R. aquaticum	R. confertum	R. elongatum	R. ericoides	R. punctatum	P. riparioides	R. squarrosus
70	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
72	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
73	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
74	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
75	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
76	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	1	.	.
77	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
78	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
79	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.
80	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.
82	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
83	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	.	.	1	.	.	.	.
84	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.
85	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
86	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
87	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
88	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
89	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
90	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	.	1	.	.	.	.	.
91	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
92	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
93	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.
94	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.
95	.	.	.	1	.	.	.	.	.	1	.	1	.	.	.	.	1	.	.	.	.	.
96	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
97	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
98	.	.	.	.	.	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.
99	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
100	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	.	1	.	.	.	.	.
101	.	1	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
102	.	1	.	.	.	.	.	.	.	.	.	1	.	1	.	.	1	.	.	.	.	.
103	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	1	.	.	.	.	.
104	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
105	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.
106	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.
107	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.
108	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.
109	.	.	.	.	.	.	.	1	.	1	.	1	.	.	.	.	1	.	.	.	.	.

ID	S. aequiloba	S. apocarpum	S. irrigua	S. nemorea	S. subalpina	S. uncinata	S. undulata	S. uliginosa	S. rivulare	T. tortuosa	W. sarmentosa
16	.	1	.	.	.	.	.	.	.	.	.
18	.	.	.	.	.	.	.	.	.	.	.
19	.	.	.	.	.	.	.	.	.	.	.
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29	.	.	.	.	.	.	.	.	1	.	.
30	.	1	.	.	.	.	.	.	.	.	.
31	.	.	.	.	.	.	.	.	1	.	.
32	.	.	.	.	.	2	.	.	1	.	.
33	.	.	.	.	.	.	.	.	2	.	.
37	.	.	.	.	1	1	.	.	1	.	.
38	.	.	.	.	.	.	.	.	.	.	.
40	.	.	.	.	.	.	.	.	.	.	.
41	1	.	.	.	.	.	.	.	1	.	.
42	.	1	.	.	.	.	.	.	2	.	.
43	.	.	.	.	.	.	.	.	.	.	.
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55	.	.	.	.	.	1	.	1	1	.	.
56	.	.	.	.	2	.	1	.	1	.	.
57	.	.	.	.	.	.	.	.	1	.	.
58	.	.	.	.	.	.	.	.	1	.	.
59	.	.	.	.	.	.	.	.	1	.	.
60	.	.	.	.	.	.	.	.	1	.	.
61	.	.	.	.	.	.	.	.	1	.	.
68	.	1	.	.	.	1	.	.	1	.	.
70	.	.	.	.	.	.	.	.	.	.	.

ID	S. aequiloba	S. apocarpum	S. irrigua	S. nemorea	S. subalpina	S. uncinata	S. undulata	S. uliginosa	S. rivulare	T. tortuosa	W. sarmentosa
72	.	.	.	.	.	.	.	.	.	.	.
73	.	.	.	.	.	.	.	.	.	.	.
74	.	1	.	.	.	.	.	.	.	.	.
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83	.	.	.	1	.	.	.	.	2	.	1
84	.	.	.	.	.	.	.	.	2	.	.
85	.	.	.	.	.	.	.	.	.	.	.
86	.	.	.	.	.	.	.	.	2	.	.
87	.	.	.	.	.	.	1	.	.	.	.
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93	.	.	.	.	.	.	.	.	.	.	.
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95	.	.	1	.	.	1	.	.	1	.	.
96	.	.	.	.	.	.	.	.	.	.	.
97	.	.	.	.	.	.	.	.	2	.	.
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106	.	.	.	.	.	.	.	.	2	.	.
107	.	.	.	.	.	.	.	.	1	.	.
108	.	.	.	.	.	.	.	.	1	.	.
109	.	.	.	.	.	.	.	.	1	.	.