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*Original article*

# Key abiotic parameters for the management of the richness of bryolichenic communities in bogs of North Patagonia (Chile)

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## ABSTRACT

Peatlands are ecosystems that play a special role in conserving biodiversity because they are refugia for unusual wetland-dependent species. Nevertheless, these ecosystems are threatened in southern South America by the overharvesting of *Sphagnum* moss, used in horticulture as substrate. Moreover, the biodiversity measurement as species richness has not been considered in management practices. Thus, our purpose was to study the bryophyte and lichen diversity and abiotic factors of Chiloé peatlands to distinguish habitat preferences and key abiotic factors to improve peatland management. The study was conducted in eight peatlands of Chiloé Island in Chile (42-43° S and 75-73° W). We found good predictors to overall species richness and each organism group. The observed patterns of cryptogamic species richness are well explained by microtopographic variables and moisture, increasing in tree base, and decreasing in saturated substrate and carpet. We highly recommend conserving "tree base" microtopographic areas as reservoirs of species richness in intervened areas by harvesting. Furthermore, we also suggest monitoring water chemistry variables such as pH or ionic ratio (IR), to provide information to predict impacts on the biodiversity of peatlands under *Sphagnum* harvesting. These recommendations give rise to sustainable management and to transforming moss into a renewable resource for farmers.

**Keywords:** Chiloé, peatlands, bryo-lichen flora, richness, diversity

## Introduction

Peatlands are ecosystems that play a special role in conserving global biodiversity because they constitute the refugia of some of the rarest and most unusual wetland-dependent species (Rydin & Jeglum 2006). Nevertheless, these areas have been generally considered to be stressed ecosystems and to present relatively low species richness (Vitt *et al*. 1995; Roig & Roig 2004; Minayeva 2008). The harsh environmental conditions constrain plant life to evolutionary adaptation under certain conditions such as cold and soils permanently saturated with water, high soil acidity and a low supply of essential macronutrients (Rydin & Jeglum 2006; Kleinebecker *et al*. 2010). Although peatlands, especially bogs, have long been considered communities

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poor in species, bryophytes are surprisingly diverse in many types of peatland. Moreover, some keystone species for ecosystem function are found within this botanical group, as *Sphagnum* spp., have been considered ecosystem engineers (Norby *et al*. 2019).

The floristic variation within peatland of the northern hemisphere is mainly controlled by three ecological gradients: acidity-alkalinity, availability of nutrients, and water table depth (Bragazza & Gerdol 1996; Hájková & Hájek 2004; Tousignant *et al*. 2010). The acidity of peatlands depends on the balance of metallic cations and strong acid anions, which in turn depends upon the composition of their water sources and the capacity of these to buffer acidity produced endogenously by plants, especially *Sphagnum* spp. (Clymo 1984; Wheeler & Proctor 2000). Furthermore, depth to the water table from the ground surface has one of the strongest relationships with vegetation gradients in peatlands, dividing mires into microtopographic or microstructural levels along the water table gradient (Rydin & Jeglum 2006). On the other hand, although abiotic factors explain the variability of species richness, human disturbances are important in structuring vegetation in peatlands (Tousignant *et al*. 2010) and have an influence on species assemblages in this kind of ecosystem (Lachance *et al*. 2004).

The knowledge of floristic variation within the peatland of southern South America is limited. However, León *et al*. (2018) reported that water chemistry is considered a key factor for plant composition of peatland ecosystems. Their showed that ombrotrophic to transitional conditions associated with ionic ratio (IR) and pH, strongly influence on species occurrence. Nevertheless, we still do not know a clear relationship between abiotic variables and the richness of bryophytes and lichens in peatland ecosystems.

*Sphagnum* moss, a natural resource from peatlands, is mainly used in horticulture and gardening as substrate and nutrient retainer. The main importing countries are Taiwan, China, and the USA (ODEPA 2019). The commercialization of Chilean *Sphagnum* moss is relevant globally; in 2018 exports of Chilean *Sphagnum* had a market share of 64 % in Taiwan (Taiwan Bureau of Foreign Trade 2019) and 58 % in Japan (Japan Ministry of Finance 2019).

Peatlands in southern South America have just begun to be considered due to the interest generated by the extraction and international trade of *Sphagnum* moss as a commodity. *Sphagnum* fibers are currently the most important non-timber forest product in Chile (INFOR 2020) and extraction is an important source of employment during the summer months in rural communities of southern Chile (Domínguez 2014). Nevertheless, the increased demand for moss and the weak legislation to regulate this activity have led to excessive extraction without sustainable protocols. This can be seen in many localities where overharvesting is evident; the moss does not regenerate. Considering this problem, several studies in the last 15 years (Díaz & Silva 2012; Díaz *et al*. 2012; Oberpaur *et al*. 2018) have developed protocols for sustainable extraction of *Sphagnum* and best management practices. However, the measurement of biodiversity as species richness has not been considered.

Graham *et al*. (2019) explained that to protect the environment, including its biodiversity, we need methods and warnings that indicate when the habitat/environment is coming close to being irreparably damaged. Thus, to distinguish habitat preferences and key abiotic factors can be useful to improve understanding of the habitat requirements, and the management and conservation of Chilean peatlands. Our purpose in this paper is to study the bryophyte and lichen diversity and abiotic factors of Chiloé peatlands to answer the following questions: What are the main abiotic factors that explain and predict the variation in species richness? and how do different species respond to pH and IR? We hypothesized that: (i) microhabitat heterogeneity and pH can be used to predict site biodiversity (Vitt *et al*. 1995); and (ii) different organism groups will show different responses to pH and IR, expecting that liverworts will dominate under the poorest nutrient conditions, whereas mosses and lichens will increase with improving nutrient supply (Kleinebecker *et al*. 2010).

## Materials and methods

### *Study area*

The eight study sites are located in the Isla Grande de Chiloé, Región de Los Lagos, Chile (42-43° S and 73-75° W). The prevailing climate is wet temperate with a strong oceanic influence (di Castri & Hajek 1976). The total annual rainfall is about 2,300 mm (CONAF 2009), with a mean summer temperature of 10.2 °C and a mean winter temperature of 6.2 °C (Pérez *et al*. 2003).

We selected eight sites from two kinds of *Sphagnum* peatlands, defined according to their origin and their characteristic vegetation (Díaz *et al*. 2008). The first type, natural peatland, originated after the last glaciation. The second type, anthropogenic peatland, corresponds to flooded areas colonized by *Sphagnum* moss after the burning or logging of forests in areas with poor-drainage soils (Zegers *et al*. 2006; Díaz *et al*. 2008). The three study areas representing the natural peatland type were Río Negro (RN), Los Caulles (CA) and Púlpito (PL); whereas the five study areas representing the natural peatlands: PL, Púlpito y CA, Caulles, RN, Rio Negro; anthropogenic peatlands: SD, Senda Darwin; CH, Chepu; PM, Pumanzano; LC, Lecam y TG, Teguel (Fig. 1).

### *Sampling and laboratory analysis*

Cryptogamic vegetation (bryophytes and lichens) of the sites was quantitatively sampled by extracting blocks from the surface layer of 20 × 20 × 10 cm. At each site, three linear transects of 50 m were established. In each transect, three equidistant samples were performed and, in each plot, a block was extracted (n = 72). We evaluated species richness and biomass following Bullock's harvest method (1997).

Specimens were carefully determined according to morphological characters, and their characteristics were compared with the literature, type specimens, and/or other herbarium specimens. For lichens, chemical characters were also used. Lichen substances were identified using thin-layer

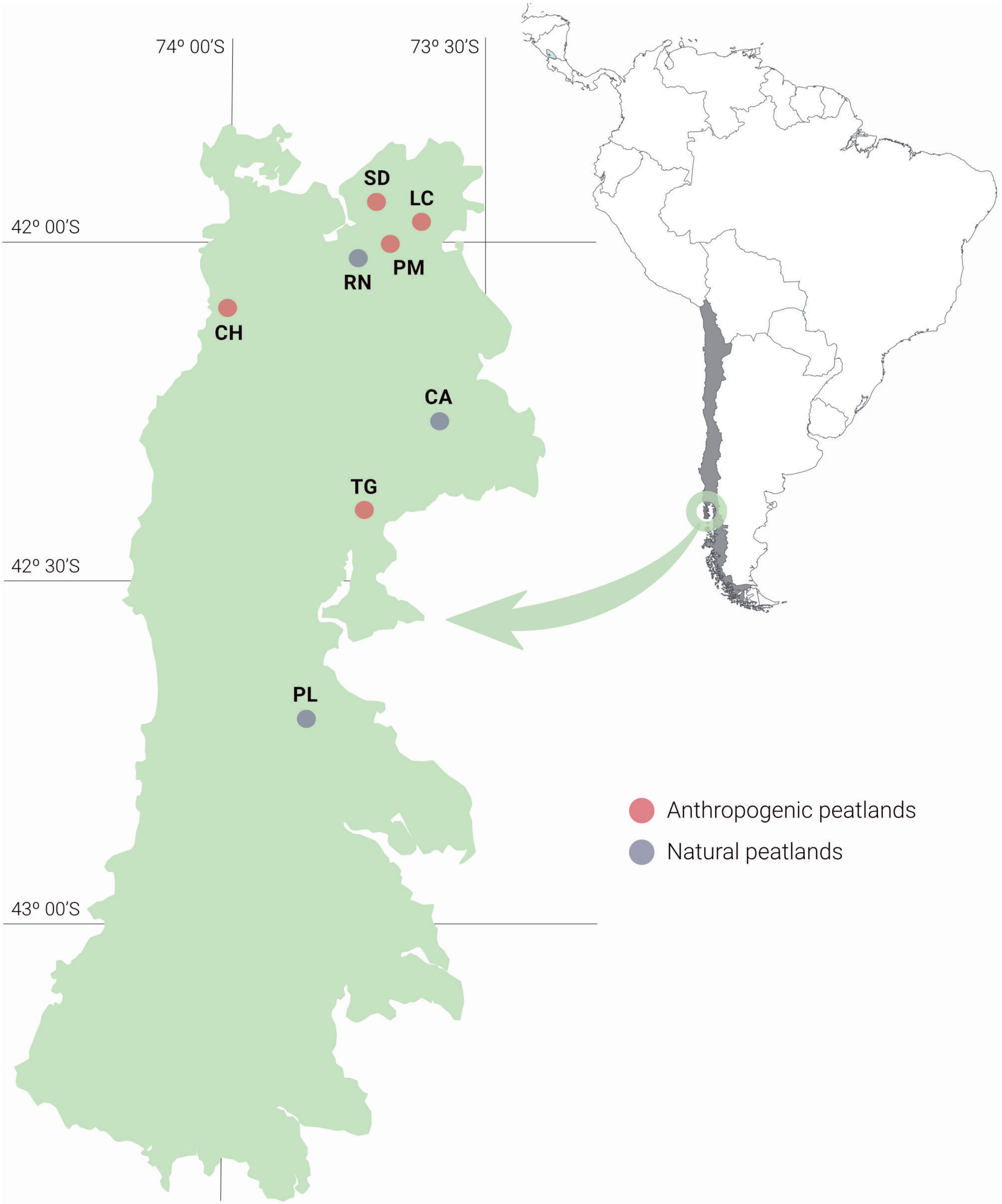

**Figure 1.** Location of eight peatlands sites in Chiloé. Natural peatlands: PL, Púlpito; CA, Caulles; RN, Rio Negro. Anthropogenic peatlands: SD, Senda Darwin; CH, Chepu; PM, Pumanzano; LC, Lecam; TG, Teguel.

chromatography (TLC), following the protocol of White & James (1985). Specimens were deposited in MACB and CONC herbaria. The nomenclature is as follows: Müller (2009) for mosses, except for Racomitrium geronticum Müll. Hal. (Larraín 2012), Hässel de Menéndez & Rubies (2009) for liverworts, and Galloway & Quilhot (1998), Feuerer (2012) and Index Herbariorum (CABI Bioscience *et al*. 2012) for lichens. Table S1 provides a list of the species collected (Supplementary material).

Water samples for each plot (n = 72) were collected in 1000 mL polystyrene bottles and stored at 4 °C for chemical analysis. We measured conductivity and pH *in situ* using an HI 98129 meter. Surface water samples were analyzed for minerals (Ca, Mg, Na, Cl) and nutrients (N and K), following Sadzawka *et al*. (2006). These analyses were performed at the INIA *Laboratorio de Suelo* (soil laboratory) in Chile.

We used Ionic Ratio (IR) as an indicator for water sources. It is calculated as 2(Ca)/(1 (Ca)+ (Cl)). On a scale from 0 to 1, this value indicates similarity to groundwater versus rain- and seawater. Groundwater is characterized by a high IR due to the dissolution of $CaCO_3$ in the mineral soil. Rainwater and, at very high mineral levels, seawater, are characterized by a low IR due to the dominance of Cl in both seawater and rain. Intermediate values represent a mixture of groundwater and rainwater (Hedenäs 2003).

Additionally, each plot was assigned a microtopographic category (NAN1: Hummock, NAN2: Lawn, NAN3: Carpet, NAN4: tree base) and moisture as an indirect measure of the water table (MOI1: Dry, MOI2: moderately wet, MOI3: saturated). Each locality was assigned an accompanying vascular plants category (TS_R, small trees, and shrubs or rushes), the source of peatland (S_P, natural or anthropogenic peatland), anthropic impact (HAR, harvested peatland or without harvest), and drainage (DRA, drained peatland or without drainage).

### Data analysis

To evaluate the effect of abiotic parameters on species richness, partial least squares regressions (PLSR) were used. This technique is an extension of multiple regression analysis in which the effects of linear combinations of several predictors on a response variable (or multiple response variables) are analyzed (Carrascal *et al*. 2009). PLSR is useful when there are few replicates, many predictors or when predictors show high collinearity (Maestre 2004). PLSR reduces a set of explanatory variables into a few components that have maximum covariance with the dependent variable (Maestre 2004). Cross-validation was used to estimate the significance and number of components to include in the regression model (Garthwaite 1994). Kolmogorov-Smirnov and Shapiro-Wilk tests were used to test for normal distribution of residuals. Categorical variables were transformed into dummy variables.

We generated response curves of species relative to pH and IR with the use of generalized additive models (GAM) (Zuur *et al*. 2007) assuming a Poisson distribution. The fitted model was compared with the null model. Only species or functional groups with significant responses were considered. Smooth term complexity was selected using the Akaike information criterion (AIC) (Lepš & Šmilauer 2003; Kleinebecker *et al*. 2010). We employed CANOCO for Windows 4.5 (ter Braak & Šmilauer 2002) for GAM modelling. STATISTICA 7.0 (StatSoft 2004) was used for the PLSR and Kruskal-Wallis H test.

## Results

### Species richness and abiotic parameters

The total richness of species per plot was related to abiotic parameters. PLSR analyses provide a single significant component explaining 52.3 % of the original variance in the response variable (Tab. 1). Considering the weights attained by the variables, the component is negatively associated with 'carpet' and 'saturated substrate'. Moreover, this component is positively related to 'tree base'. In the case of anthropogenic peatlands, the significant component explained 59.3 % of the variance and is also related to 'carpet', 'saturated substrate', and 'tree base'. The significant component of natural peatlands explained 53.3 % of the variance and is positively related to 'tree base' and 'saturated substrate'.

PLSR analyses per group showed different trends. Total moss species richness presents a single significant component with 45.2 % of variance explained. This component is positively related to pH and is negatively correlated with N-Total and K. The model of *Sphagnum* species richness also shows a single significant component explaining 46.3 % of the variance. This component is mainly associated with the distance to the sea and the altitude, being both of them negatively correlated with richness. In the case of moss species richness (excluding *Sphagnum*), the results of PLSR analysis provide a single significant component explaining 42.4 % of the variance. The microtopographic category 'carpet' and the saturated substrate are the main factors that are negatively correlated with species richness. The significant component of liverwort explained 46.1 % of the variance and is positively related to 'tree base' and 'dry substrate'. Meanwhile, lichens showed a single significant component explaining 26.5 % of the variance. This component is negatively associated with Na, the microtopographic category 'carpet', and 'saturated substrate' (Tab. 1).

As seen in the results of the PLSR analyses, microtopographic categories (Fig. 2A) and moisture are the key factors for species richness. We found a significant difference ($p<0.001$) in species richness among microtopographic categories and soil moisture levels (Fig. 2B, C), considering all species richness, species richness

**Table 1.** Results of the partial least squares regression analysis (PLSR) carried out with total richness, moss richness, *Sphagnum* richness, and moss (No *Sphagnum*) richness. Species richness is expressed as the number of species per sample point. W COMP1: weight of each variable in the first PLSR component. $R^2$: proportion of variance in the response accounted for by component of the PLSR. Only significant PLS models are shown. PLSR weights whose squares are larger than 0.3 are shown in the table.

| Dependent variable | Independent variable | W COMP1 | $R^2$ |
|---|---|---|---|
| All Peatland<br>Total Richness<br>(Mean of species number by plot = 4.72 ± 2.76) | Nan 3 | -0.347 | 0.523 |
| | Nan 4 | 0.450 | |
| | Moi 3 | -0.347 | |
| Anthropogenic Peatlands<br>Total Richness<br>(Mean of species number by plot = 4.96 ± 3.10) | Nan 3 | -0.341 | 0.593 |
| | Nan 4 | 0.349 | |
| | Moi 3 | -0.341 | |
| Natural Peatlands<br>Total Richness<br>(Mean of species number by plot = 4.3 ± 2.08) | Nan 4 | 0.581 | 0.533 |
| | Moi 3 | -0.345 | |
| Moss richness<br>(Mean of species number by plot = 2.08 ± 1.17) | pH | 0.417 | 0.452 |
| | K | -0.365 | |
| | N-TOTAL | -0.347 | |
| *Sphagnum* richness<br>(Mean of species number by plot = 1.36 ± 0.68) | C_D | -0.360 | 0.463 |
| | ALT | -0.487 | |
| Moss (No *Sphagnum*) richness<br>(Mean of species number by plot = 0.72 ± 0.91) | Nan 3 | -0.382 | 0.424 |
| | Moi 3 | -0.382 | |
| Liverwort richness<br>(Mean of species number by plot = 1.83 ± 1.64) | Nan 4 | 0.658 | 0.461 |
| | Moi 1 | 0.437 | |
| Lichen richness<br>(Mean of species number by plot = 0.81 ± 1.33) | Na | -0.348 | 0.265 |
| | Nan 3 | -0.345 | |
| | Moi 3 | -0.345 | |

of natural peatland and anthropogenic peatlands. The same trend can be observed separately in mosses, liverworts, and lichens (Fig. 3A, B).

### *Response of species to pH and IR*

The response curves of species showed differentiation according to their ecological niches. This could be observed at the pH and IR gradient (Fig. 4, 5). On the IR gradient, the abundance of mosses (Fig. 4A, B) showed clear differences, especially in *Sphagnum* species. *Sphagnum falcatulum* increases at low IR, *Sphagnum magellanicum* increases at close to 0.4, and *Sphagnum fimbriatum* peaks at high IR. Liverworts were concentrated at the extremes of the gradient (Fig. 4C). The abundance of *Riccardia floribunda*, *Herbertus runcinatus*, *Kurzia setiformis*, and *Lepicolea ochroleuca* showed increases at low IR. On the contrary, *Jamesoniella colorata* increased at higher IR values. Lichens showed a similar pattern. *Cladonia* subgen. *Cladina* and *Cladonia squamosa* were more abundant, close to 0.2, while *Cladonia gracilis* showed greater abundance at close to 0.6.

On the pH gradient, important differences among species were observed. *Sphagnum magellanicum* was more abundant at lower pH, whereas *Sphagnum fimbriatum* increased at the extremes of the gradient, especially at high pH values (Fig. 5A). *Polytrichastrum longisetum* showed an abundance peak close to pH 5 (Fig. 5B). On the other hand, liverworts were more abundant at a pH above 4 (Fig. 5C), and *Cladonia gracilis* exhibited greater abundance close to pH 5 (Fig. 5D).

## Discussion

### *Species richness*

The results of the analyses presented here show that the abiotic variables studied are clearly related to cryptogamic species richness. Tousignant *et al.* (2010) found that disturbances had detrimental effects on bryophyte species richness, but abiotic conditions are still predominant in controlling the overall plant composition. They show that while human disturbances are important in structuring vegetation in bogs, they do not override the prevalence of local abiotic conditions. This is in accordance with our observations, which showed that species richness is affected more by abiotic parameters than by human disturbance.

We found good predictors to overall species richness and for each organism group. The observed patterns of cryptogamic species richness are well explained by microtopographic variables and moisture, increasing in ‘tree base’ and decreasing in ‘saturated substrate’ and ‘carpet’. When analyzing our hypothesis, only microhabitat was confirmed as a predictor. According to our results, moisture becomes more relevant compared to pH. Nevertheless, pH is useful to understand the response of each of the species, as will be seen in the next section. Moreover, we found the same trends between natural and anthropogenic peatlands. These results are consistent with those of León *et al.* (2018) who found peatland origin (natural or anthropic) was not

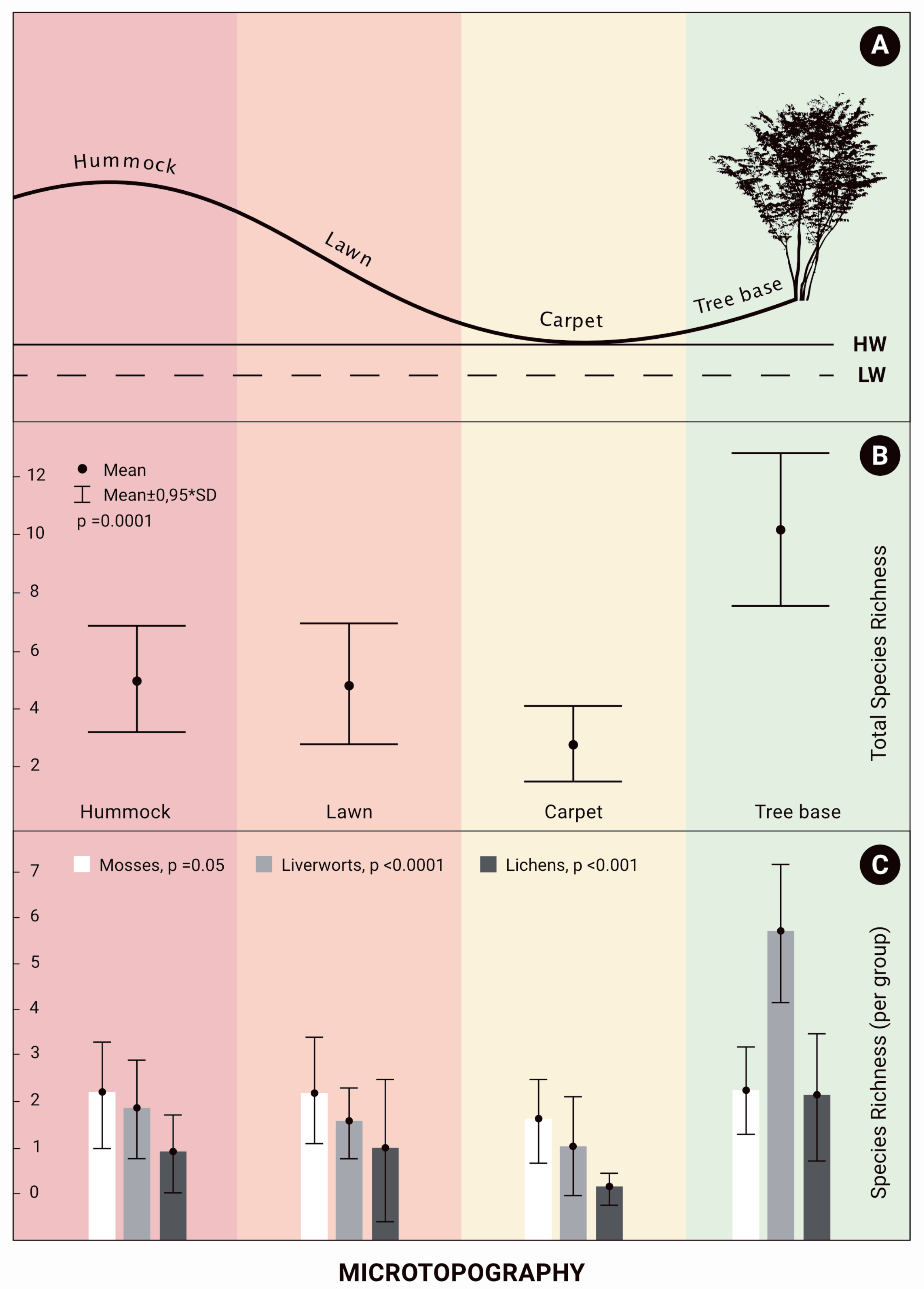

**Figure 2.** Species richness in different microtopography types (**A**): Total richness vs. microtopography (**B**) and richness per each botanical group vs. microtopography (**C**). Species richness is expressed as a number of species per sample point.

the most significant factor accounting for changes in floristic composition among peatlands.

Although our research could not provide detailed information about water table level, we did indirect measures of this factor because it is important in determining the occurrence of species on peatlands (Wheeler & Proctor 2000; Charman 2002; Rydin & Jeglum 2006). The results showed that species richness decreased in 'saturated substrate' (Fig. 3). These results agree with those reported by Whitehouse & Bayley (2005) in peatlands of Canada. They presented that communities of peatlands were distributed across a wet-to-dry gradient. Another important factor involved in species richness is the microtopographical variation associated with the water table. In this vertical zonation along the hummock-hollow gradient, the species may occupy different positions along this gradient at different sites (Andrus *et al*. 1983; Wheeler 1993; Wheeler & Proctor 2000; Rydin & Jeglum 2006). According to our results, this trend is confirmed; this gradient shows how species richness varies relative to microtopography. Moreover, in contrast to peatlands of the Northern Hemisphere, where lawns seem to have the greatest richness (Rydin & Jeglum 2006), our results show that the greatest richness is found in the bases of *Tepualia stipularis* (Myrtaceae). This is an endemic tree (5-10 m in height) highly abundant in the peatlands of Chiloé (Villagrán 2002).

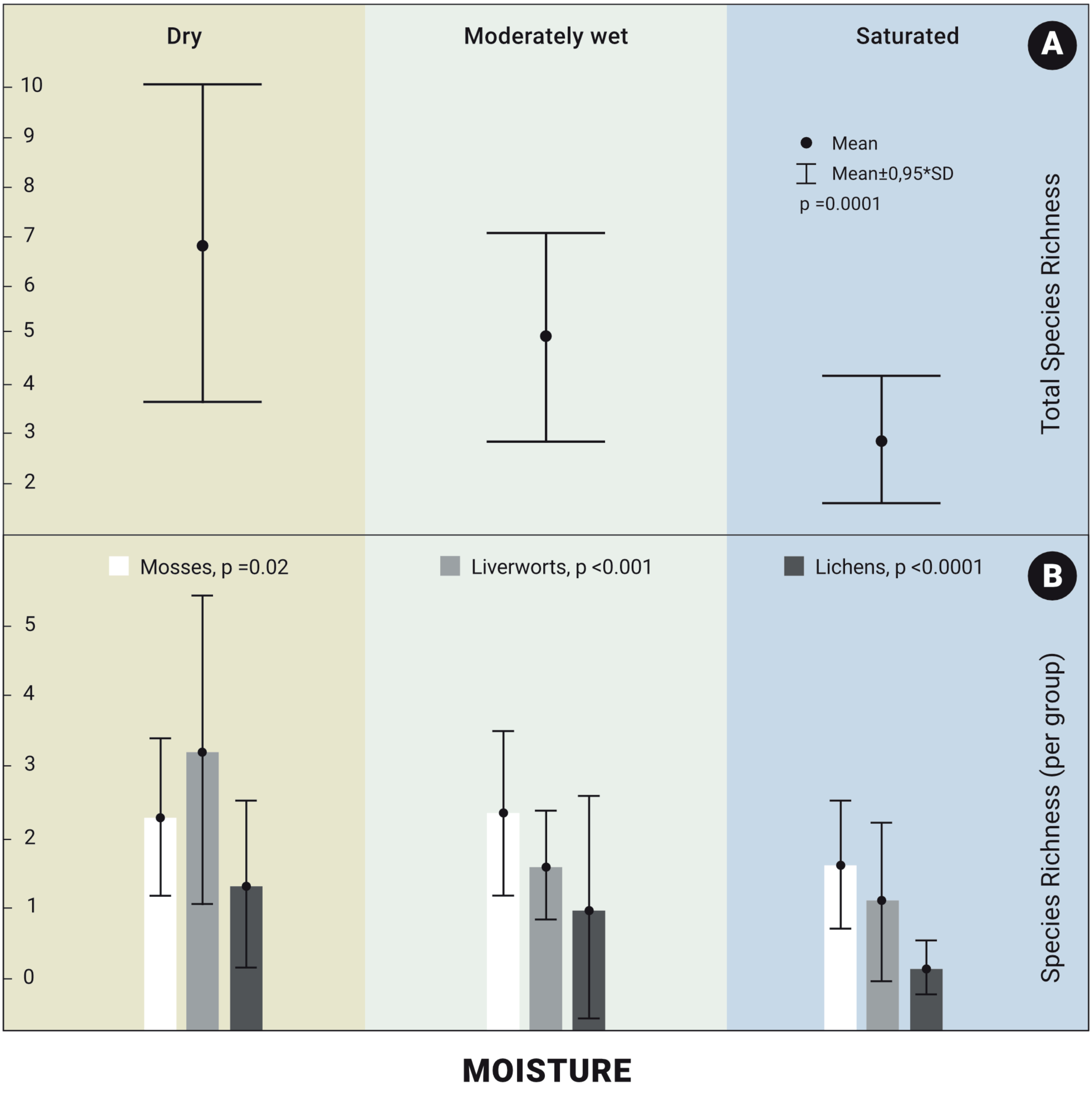

**Figure 3.** Species richness in different moisture conditions: **A**) Total richness vs. moisture, and **B**) Richness per each botanical group vs. moisture. Species richness is expressed as the number of species per sample point.

### *IR and pH*

Our results show clear differences in the response of species to environmental parameters such as IR and pH. These parameters are widely considered to be of primary importance in the classification of peatlands and they are relevant in determining the occurrence of species (Daniels & Eddy 1985; Vitt *et al*. 1995; Wheeler & Proctor 2000; Hedenäs 2003; Rydin & Jeglum 2006). Among bryophytes, *Sphagnum* species are well separated along different environmental gradients. These species are important ecological indicators and are often used in the classification of peatland vegetation and habitats. The high indicative value of *Sphagnum* species is increased by intense competition among closely related species, which leads to marked niche differentiation (Hájková & Hájek 2004).

In this work, IR curves reported a distinct separation of the species, particularly remarkable for the species of *Sphagnum*, which occupy different ecological niches along the gradient. Daniels & Eddy (1985) described the chemical status of water in peatlands (amount of dissolved ions and degree of acidity) as one of the main factors influencing the distribution of species. We found that taxa such as *Sphagnum falcatulum*, *Riccardia floribunda*, *Herbertus*

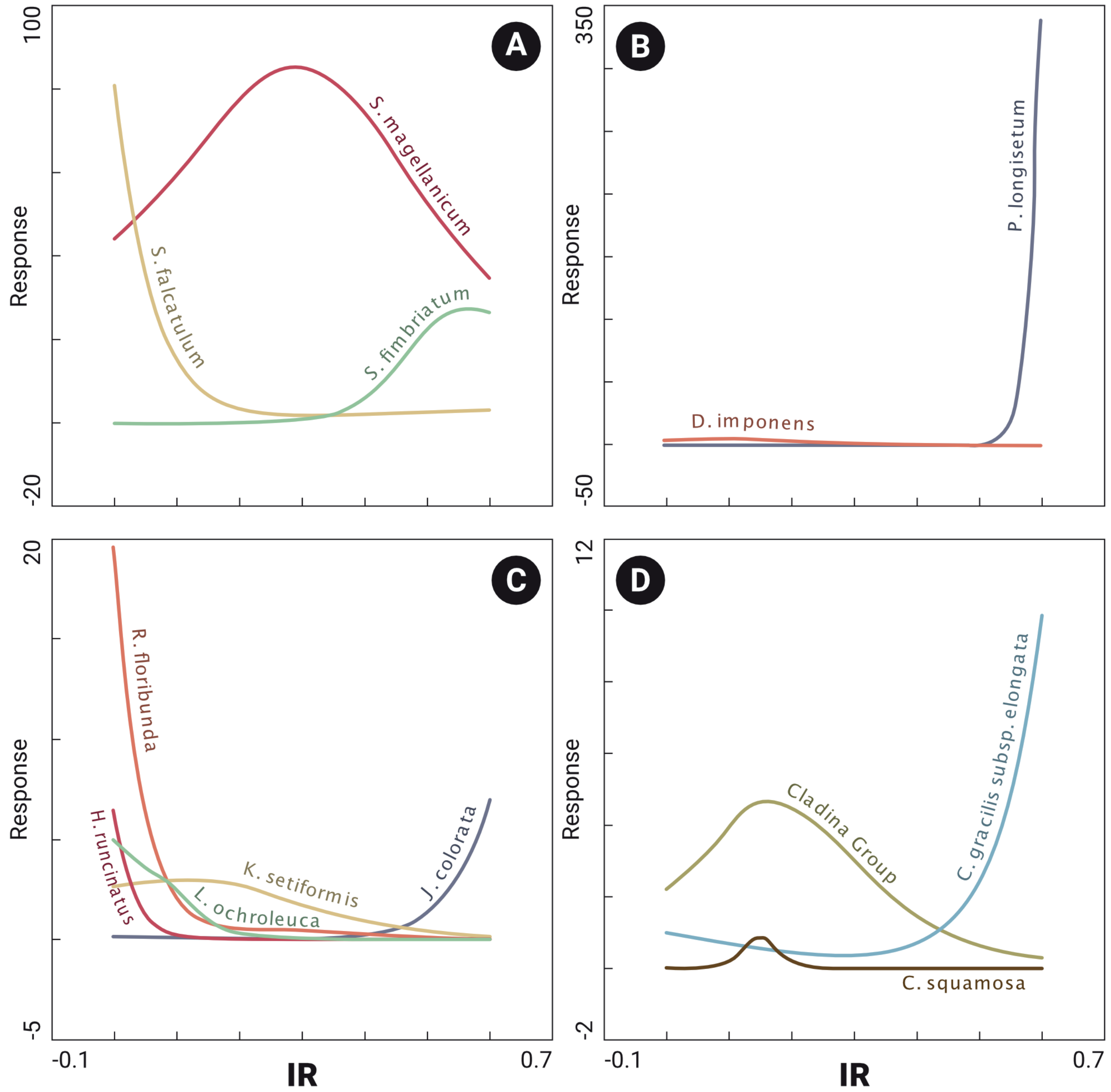

**Figure 4.** GAM response curves to ionic ratio (IR) in **A**) *Sphagnum* species, **B**) moss species (except *Sphagnum*), **C**) liverwort species and **D**) *Cladonia* species. We only considered species with the significant response and not eliminated by the Akaike information criterion (AIC). The response is presented as dry biomass per sample plot.

*runcinatus*, *Lepicolea ochroleuca*, *Cladonia* subgen. *Cladina*, and *Cladonia squamosa* are related to ombrotrophic habitats, as they are mostly present in sites with an IR close to 0.2. In contrast, species such as *Sphagnum fimbriatum*, *Polytrichastrum longisetum*, *Cladonia gracilis*, and *Jamesoniella colorata* are associated with transitional-minerotrophic conditions. Preliminarily, the presence of these species could be indicative of certain environmental conditions. The pH curves also reported a distinct separation of the species. *S. magellanicum* increased at lower pH, while *S. fimbriatum* increased when the pH was higher. These results are consistent with those of other studies performed in the northern hemisphere. These studies note that *S. fimbriatum* grow in mesotrophic to eutrophic areas, while *S. magellanicum* prefers oligotrophic habitats (Daniels & Eddy 1985; Hájková & Hájek 2004; Wojtuń *et al*. 2013). In conclusion, according to these results, we rejected the hypothesis ii, because each organism group (liverworts, mosses, and lichens) do not show the same response to pH and IR.

All this ecological information is highly relevant to the management of peatlands, especially considering the

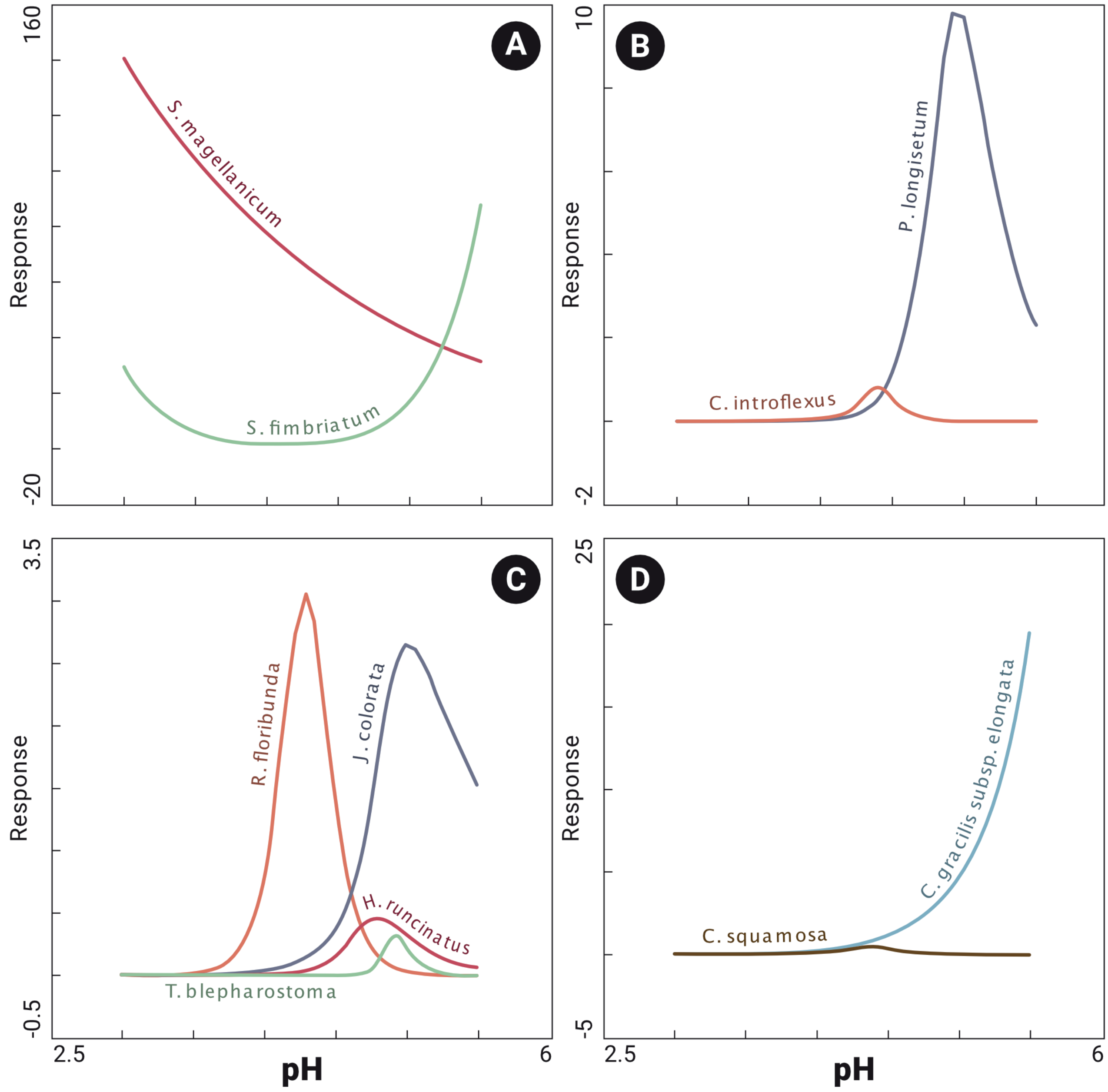

**Figure 5.** GAM response curves to pH in **A**) *Sphagnum* species, **B**) moss species (except *Sphagnum*), **C**) liverwort species and **D**) *Cladonia* species. We only considered species with significant response and not eliminated by the Akaike information criterion (AIC). Response is presented as dry biomass per sample plot.

extractive activities performed in southern Chile. Studies that have developed harvesting techniques suggest manual extraction by plot, removing only the first 12 cm of moss, and replanting after harvest to ensure *Sphagnum* regeneration and conservation peatlands (Díaz & Silva 2012; Díaz *et al*. 2012; Délano *et al*. 2013; Oberpaur *et al*. 2018). In addition, the new legal regulation (Decree 25 of the Ministry of Agriculture) requires conserving a minimum of 30 % of moss cover without harvesting the total area (Ministerio de Agricultura 2017). However, no recommendations have been established for protecting the accompanying flora or parameters for managing biodiversity.

Taking into consideration our results, we highly recommend conserving 'tree base' micrograph areas as reservoirs of species richness in the untouched areas. In addition, this could have implications for colonization by protecting nurse plants for moss. However, this is a subject that requires specific studies. Another open question for future research is what happens to species richness after harvesting *Sphagnum*.

Finally, we also suggest monitoring water chemistry variables such as pH or IR that are easily measurable. These parameters would provide us valuable information to predict impacts on the biodiversity of peatlands under harvesting of *Sphagnum*. Moreover, the study provided a scientific basis to consider that sustainable extraction of *Sphagnum* moss is plausible.

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