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Drivers of Alpine Mire Vegetation at Their Range Limit

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Abstract

Mires are fragile ecosystems in which plant communities are structured by complex interactions among hydrological regimes and groundwater properties. Although extensively studied in boreal and temperate regions, their environmental drivers in southern European mountains remain poorly understood. We investigated five complex mires in the Pyrenees, sampling 156 plots of vascular plants and bryophytes while measuring water table dynamics and groundwater chemistry over two years. Vegetation was classified into six main groups, including acid and alkaline fens, transition mires and *Sphagnum* hummocks. Ordination analyses (tb-PCA and RDA) revealed that mean water table depth, groundwater calcium and silicon content, and pH were the most important determinants of floristic composition. Bryophytes responded primarily to pH, whereas vascular plants were more influenced by water table variables, reflecting functional trait differences. Despite these environmental effects, spatial structure explained a comparable or greater proportion of variance, especially for vascular plants, underscoring the roles of local species pools, dispersal limitation, and site history in shaping community patterns. Establishing a reliable baseline is crucial for interpreting the distribution patterns of mire vegetation. Our results demonstrate that both environmental gradients and spatial processes are fundamental to understanding mire vegetation and highlight the importance of analyzing plant taxonomic groups separately.

Keywords: bogs; fens; environmental gradients; Pyrenees; peatlands; vegetation

Academic Editor: Michael Wink

Received: 5 September 2025
Revised: 29 September 2025
Accepted: 6 October 2025
Published: 8 October 2025

Citation: Pérez-Haase, A.; Ninot, J.M. Drivers of Alpine Mire Vegetation at Their Range Limit. *Diversity* **2025**, *17*, 702. https://doi.org/10.3390/d17100702

1. Introduction

In the Iberian Pyrenees, mire vegetation (fens and bogs) typical of cold and temperate regions occurs between 1300 and 2700 m a.s.l., with optimum distribution in the subalpine belt [1]. In high-mountain landscapes, mires always occupy small, isolated areas linked to glacial tarns, slope springs, or seepages. Nevertheless, their vegetation is highly diverse and characterized by plant species specialized to withstand prolonged flooding [1–3].

The distribution of mountain mire flora and vegetation follows strong ecological gradients related to water chemistry and water table depth [4–8]. Most available information on these gradients and vegetation patterns comes from boreal and temperate Atlantic regions [9–12]. Although knowledge of these patterns in southern European mountain ranges has increased considerably in the last 25 years [13–17], most information remains biased toward colder regions [18–20]. Based on hydrological regime, four main categories of mires have been recognized [21]: ombrogenous (fed by atmospheric precipitation), topogenous (influenced by stagnant groundwater), soligenous (fed by flowing waters, with inclined water tables) and limnogenous (under permanent influence of lakes or slow streams). The last three categories are geogenous mires, i.e., those fed by mineral-enriched waters after contact with mineral substrates. Geogenous mires are the most widespread in the Pyrenees [1,3]. As for water chemistry, several authors have identified the poor–rich gradient as a key determinant of floristic composition, acting through its direct effects on nutrient availability and water chemistry, which subsequently determine the plant communities that can establish [20,22–24]. This complex gradient is always linked to base richness, particularly to calcium and magnesium concentration and to pH [5,13,25,26].

Despite this ecological background, the Pyrenees remain an exception. The diversity of communities and flora is relatively well known [2,3,16], but few studies have assessed their relationship with the main ecological gradients. Moreover, in southern European mountain ranges, plant species often show variation in their ecological requirements compared to central and northern Europe. These variations include, for example, broader ecological niches, which may lead to changes in the relative importance of key ecological determinants [27–29].

Moreover, not all taxonomic groups (bryophytes, vascular plants, diatoms, etc.) are expected to respond in the same way to ecological gradients, as they differ considerably in their functional traits. Several studies have therefore emphasized the importance of analyzing different organism groups separately in relation to ecological gradients [30–34].

Mountain mire biodiversity is fragile due to fragmentation and island-like biogeographical processes. Current climate change and land-use changes are altering plant species composition and ecosystem functioning, placing additional pressure on these oligotrophic ecosystems [29,35,36]. Mountain mires are threatened by global warming, prolonged summer droughts, habitat loss, groundwater depletion, and overgrazing [37–40]. Nevertheless, vegetation in mountain mires changes slowly, exhibiting what Gorham [41] termed "biological inertia," whereby such ecosystems may persist long after the conditions suitable for their establishment have disappeared, thereby obscuring biodiversity responses.

In southern European mountains, there is a gap in knowledge regarding the roles of variables related to the water table compared with the better-established poor–rich gradient, as well as a lack of comparative analyses of these gradients in relation to vascular plant and bryophyte patterns. This is key to better understanding vegetation patterns and processes, as well as improving management policies for such vulnerable ecosystems.

For all these reasons, the main aim of this study is to develop a robust understanding of Pyrenean mountain mires through a detailed investigation of five complex mire sites. Establishing a reliable ecological baseline is essential to interpret future changes in the distribution of mire vegetation and to evaluate their ecological condition. Each mire includes a wide diversity of plant communities and shows pronounced variation in the associated environmental variables, encompassing differences in microtopography, hydrology, and groundwater chemistry. This internal heterogeneity provides a valuable natural framework for disentangling the drivers of vegetation patterns, as it allows the coexistence of contrasting ecological conditions within relatively short spatial distances. While there is notable overlap among them in vegetation composition and environmental conditions, taken together, they provide a comprehensive representation of Pyrenean mountain mires. Specifically, we aim (i) to identify the main gradients affecting mire vegetation and assess their relative weight in the distribution of plant communities, and (ii) to evaluate the relative importance of environmental determinants for the distribution of vascular plants and bryophytes, comparing the responses of these two groups separately. Based on previous evidence, we hypothesized that the main environmental drivers will be related to groundwater properties, and that vascular plants and bryophytes will respond differently to environmental conditions.

2. Materials and Methods

2.1. Study Sites

The five mires studied are located in the subalpine belt of the Pyrenees, differing in elevation (1857–2305 m a.s.l.) and relative position within the range (Figure 1). Siscaró and Prat Fondal are situated in the eastern Pyrenees, whereas Beret, Bassa Nera, and Filià are in the central Pyrenees. These five sites are representative of high-mountain Pyrenean mires, all of which have previously been visited by botanists for this reason. Their main characteristics are summarized in Table 1.

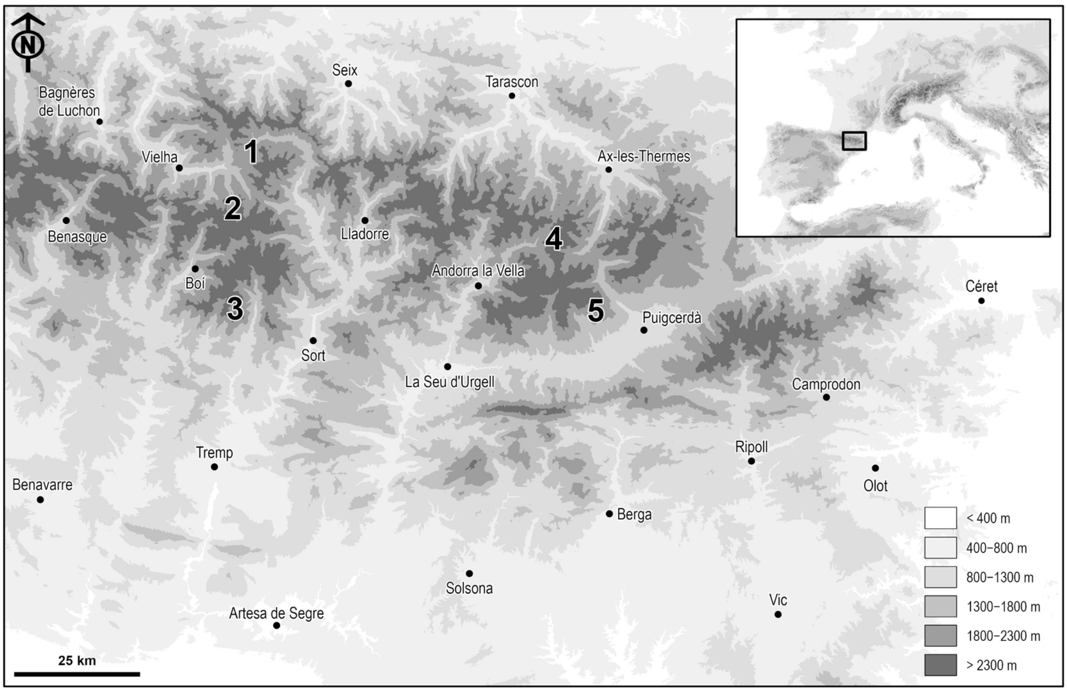


Figure 1. Distribution of the five localities studied in the Pyrenees. 1—Beret; 2—Bassa Nera; 3—Filià; 4—Siscaró; 5—Prat Fondal.

Table 1. Main characteristics of the five mires studied. Check marks denote the sites at which hydrological types are present.

	Beret	**Bassa Nera**	**Filià**	**Siscaró**	**Prat Fondal**
Geographical coordinates (long., lat.)	0.95358, 42.71462	0.92421, 42.63818	0.95196, 42.45417	1.70454, 42.59528	1.79272, 42.47692
Number of plots	32	35	29	30	22
Mire size (ha)	4.8	1.9	3.9	4.6	3.1
Elevation (m a.s.l.)	1857–1875	1889–1893	2050–2122	2142–2149	2304–2305
Mean annual precipitation (mm)	1004	1063	1435	1221	1056
Mean annual temperature (°C)	4.8	4.6	4.2	4.9	3.2
Mean July temperature (°C)	11.6	12.9	12.2	12.8	10.6
Bedrock	Schists and limestones	Granites	Lutites and limestones	Gneiss	Granites
Main hydrological types					
Topogenous	✓	✓	✓	✓	✓
Soligenous	✓	✓	✓	✓	✓
Limnogenous		✓			
Ombrogenous (*Sphagnum* hummocks)	✓	✓	✓	✓	

All sites were geogenous mires with sphagnum hummocks marking transitions to ombrogenous systems. Among the geogenous mires, topogenous and soligenous subtypes are well represented, while at Bassa Nera, quaking limnogenous *Sphagnum* carpets also occur.

The vegetation surrounding the five mires is typical of Pyrenean subalpine belt. In all of them, mesophilous pastures are prominent, and forests of mountain pine (*Pinus uncinata*) and alpenrose (*Rhododendron ferrugineum*) heathlands are also important components of the landscape.

2.2. Study of Environmental Variables and Vegetation

2.2.1. Sampling Plots

We established an irregular network of plots in each mire, with the dual aim of including at least three examples of each physiognomic type (based on the height of dominant species) and capturing the diversity of hydrological conditions (Table 1). Depending on the size and complexity of each mire, 22–36 plots were set up. A total of 156 plots were established. At each plot, we vertically inserted into the substrate a PVC pipe, 16 mm in diameter and 1 m long, perforated every 5 cm to allow groundwater inflow. All plots were georeferenced, and their elevation and slope were determined by a topographic survey using a total station.

2.2.2. Vegetation Relevés

In the second half of July 2005, at each plot, we carried out a vegetation relevé of 2.5 × 2.5 m (6.25 m^2), a size large enough to capture vegetation composition [42] while small enough to be characterized by local environmental measurements. Each relevé consisted of a complete list of vascular plants and bryophytes, with projected cover for each species recorded using the Domin scale [43]. Plant nomenclature follows [44] for vascular plants and [45] for bryophytes.

2.2.3. Water Table Depth

In 2004 and 2005, water levels were monitored in the PVC pipes of all plots. Measurements were taken every 15 (±4) days during the growing season (June–October), from snowmelt until plant senescence. Water table depth was linearly interpolated between dates, and from this dataset we derived: (1) percentage of time during which the water table was: (a) above the soil surface (flooded); (b) between the soil surface and -10 cm; (c) between -10 and -25 cm; (d) between -25 and -50 cm; (e) between -50 and -75 cm; (2) mean water table depth (cm); (3) maximum (shallowest) water level (cm); (4) minimum (deepest) water level reached (cm). Lower (more negative) values of water table depth indicate a deeper water table, i.e., farther below the soil surface, whereas positive values indicate flooding (water table above the surface).

2.2.4. Water Chemistry

In July 2005 we collected groundwater samples from inside the PVC pipes. For each water sample, we measured pH and electrical conductivity with a portable WTW meter. Following Sjörs [9], we corrected the conductivity by subtracting the contribution of H^+. In addition, we measured total cation concentrations (in ppm) of calcium, aluminum, magnesium, phosphorus, sulfur, iron, sodium, silicon, zinc, and manganese by inductively coupled plasma mass spectrometry (ICP-MS). All samples were previously filtered through a 0.20 µm pore-diameter filter.

Finally, we indirectly estimated plot productivity potential from the Ellenberg fertility indicator value (N) of species in each relevé [46]. For each relevé, we calculated the mean N value as the cover-weighted average of species values (weights log-transformed). Ellenberg N values for vascular species were obtained from [47], and that for bryophytes from [48].

2.3. Statistical Analyses

2.3.1. Numerical Classification

The vegetation relevés were classified using beta-flexible hierarchical clustering ($\beta = -0.25$) and Hellinger distance [49,50]. First, we converted the Domin cover scale to percentage cover (midpoints of each class; [43]) and log-transformed to reduce the relative weight of the abundant species. We cut the clustering tree into 2 to 11 groups. To determine the optimal cluster level, we applied three stopping criteria: (1) Calinski–Harabasz index (CHI), a geometric method [51]; (2) classification stability [52]; (3) OptimClass method [53]. The latter two are non-geometric methods [51]. Stability was measured as the frequency with which objects were repeatedly classified into the same group. OptimClass quantified the number of ecologically significant species per level, defined as species with indicator values [54] greater than 0.3 and a *p*-value below 0.01 (therefore dismissing those species that were more weakly related to a group, despite being significantly linked to it). Cluster levels were ranked by each index, ranks summed across methods, and the level with the lowest overall value selected. This combined geometric and non-geometric criteria, balancing structural soundness with stability and ecological information. In addition, we tested for differences in environmental variables among groups using a non-parametric permutation test of independence implemented in the R package coin. This framework allowed us to assess whether differences among vegetation groups were statistically significant, while explicitly accounting for the hierarchical structure of the data (i.e., samples nested within sites).

2.3.2. Ordination Analyses

To ordinate the vegetation relevés by floristic composition, we performed a principal component analysis (tb-PCA) [49] on log-transformed, Hellinger-standardized species cover data [55].

To evaluate and compare environmental determinants of vegetation composition, we conducted redundancy analysis (RDA) [49] for vascular plants, bryophytes and the combined dataset. Stepwise forward selection was used to identify significant variables, ordered by adjusted R^2 and tested by permutation ($p < 0.05$). For variable selection, we first chose those cations above the instrumental detection threshold for more than 1/3 of the samples. Second, we removed one of each highly correlated pair of environmental variables ($r \geq 0.70$). In addition, some variables were log-transformed to achieve symmetric distributions. Quadratic terms of key variables were included to detect unimodal species responses [49].

To account for spatial structure, Moran's eigenvector maps (MEMs) [49] were computed and significant vectors (selected by stepwise procedures) included as covariables in RDAs. This allowed partitioning of spatial vs. environmental effects. Fertility (Ellenberg N) was projected post hoc into the ordination space, since it is a derived rather than directly measured variable [46,56].

Variance partitioning was then performed [49] to assess the relative contributions of groundwater mineralization (e.g., pH, Ca), hydrological regime (e.g., water table depth, maximum water level), and spatial structure (MEM). Separate analyses were conducted for the combined dataset, vascular plants, and bryophytes.

All analyses were performed in R v. 4.4.1 [57] using the packages agricolae v. 1.3-7, coin v. 1.4-3, cluster v. 2.1.6, indicspecies v. 1.7.5, and vegan v. 2.6-6.1 [58–62].

3. Results

3.1. Plant Vegetation Types

We classified the 156 relevés and found that the optimal clustering level corresponded to pruning the classification tree into six groups. This level ranked first in all three indices, with the following values: Calinski–Harabasz Index (CHI) = 12.683; stability, modified $\lambda = 0.766$; OptimClass, 87 indicator species. The most faithful species for each group are listed in Table A1, and the environmental characterization of each group is shown in Figure 2. Based on the composition of the relevés, the indicator species, and the abiotic characteristics of the habitats, we interpreted the six groups as follows:

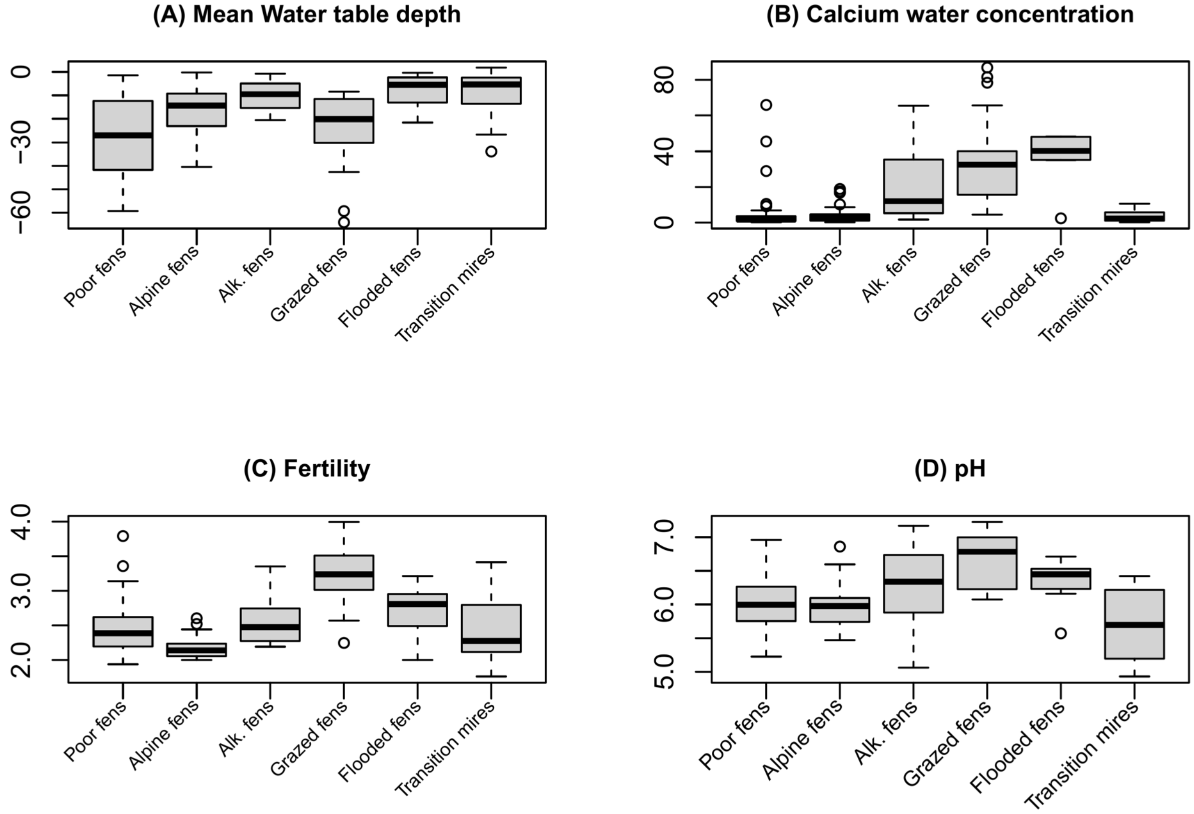


Figure 2. Boxplots of key environmental variables for the groups resulting from the vegetation classification. In all four cases, the non-parametric permutation test of independence was significant ($p < 0.05$).

Group 1—Acid fens (38 relevés from 3 sites).

Poor acid fens (EUNIS Q22—"poor fen"; alliance *Caricion fuscae*). The most frequent species are *Carex nigra*, *Festuca nigrescens*, *Epikeros pyrenaeus*, *Nardus stricta*, *Carex echinata* and *Aulacomnium palustre*. Faithful species include *Festuca nigrescens*, *Carex echinata*, *Viola palustris*, *Nardus stricta*, *Pedicularis pyrenaica* and *Aulacomnium palustre*, all typical of sub-alpine acid fens. Some samples are transitional to incipient *Sphagnum* hummocks, with notable cover of *Sphagnum* spp. (*S. russowii*, *S. capillifolium*, etc.) and other bog species (*Eriophorum vaginatum*, *Polytrichum strictum*, etc.). These mires tend to have fluctuating water tables, shallow during snowmelt and deep in mid-summer, and were found in both eastern and central Pyrenees.

Group 2—Acid fens with alpine character (hereafter, Alpine fens; 34 relevés from 4 sites).

Poor acid fens related to Group 1, also assignable to EUNIS Q22. Differ floristically by the much higher frequence of *Agrostis canina*, *Sphagnum subsecundum*, *Eriophorum an-*

gustifolium and *Festuca airoides*, among others. Mean water table is higher than in Group 1, and fluctuation more moderate. Most relevés come from the Prat Fondal site, the highest in elevation (2300 m), which confers on them an alpine character, though the group occurs in both the eastern and central Pyrenean sites.

Group 3—Alkaline soligenous fens (hereafter, Alkaline fens; 28 relevés from 3 sites).

Alkaline fens with surface water flow—at least during part of the summer—either diffusely or in small rivulets. Attributable to the EUNIS Q41 "alkaline, calcareous, carbonate-rich small-sedge spring fen" (and to alliance *Caricion davallianae*). The most frequent species are *Carex davalliana*, *Carex nigra*, *Primula farinosa*, *Carex panicea*, *Potentilla erecta*, and *Parnassia palustris*. This group occurs in both eastern and central Pyrenean sites.

Group 4—Grazed fens (22 relevés from 2 sites).

Close to rich alkaline fens (EUNIS Q41) but disturbed by livestock grazing and trampling. It cannot be clearly assigned to any described phytosociological vegetation-type. Floristically, the relevés are well characterized by the frequent presence of *Poa supina*, *Scorzoneroides carpetana* subsp. *duboisii*, *Carex nigra*, *Trifolium repens*, *Veronica serpyllifolia*, and *Ranunculus acris*. These are also the most productive fens studied, with the most calcium-rich waters and the highest pH. Restricted to the central Pyrenean sites.

Group 5—Flooded alkaline fens (hereafter Flooded fens; 11 relevés from 2 sites).

Fens with a distinctive floristic composition, close to EUNIS Q42 "extremely rich moss-sedge fen" (and to *Caricion davallianae* alliance). The most frequent species are *Comarum palustris*, *Carex nigra*, *Eleocharis quinqueflora*, *Calliergonella cuspidate*, *Juncus articulatus*, and *Scorpidium cossonii*. Occur both in eastern and central Pyrenean sites.

Group 6—Transition mires and *Sphagnum* hummocks (hereafter Transition mires; 23 relevés from 1 site).

Sphagnum hummocks transitional to raised bogs (related to EUNIS Q11 Raised bog) and *Carex lasiocarpa*-dominated transition mires (chiefly EUNIS Q24 "intermediate fen and soft-water spring mire"). Among the *Sphagnum* mires, it includes both ombrogenous hummocks and limnogenous floating carpets. Assignable to *Caricion lasiocarpae* and *Sphagnion medii* alliances. Rare species in the Pyrenees are abundant in this group, such as *Carex lasiocarpa*, *Equisetum fluviatile*, *Drosera longifolia*, *Sphagnum divinum*, etc. This group is represented only at Bassa Nera site.

3.2. tb-PCA and RDA Ordinations

The first two axes of the transformed-based principal components analysis (tb-PCA) accounted for 23.0% of variance (Figure 3). Species most strongly correlated with the first four axes (together explaining 37.9%) are listed in Table A2. Most of these species also proved to be indicators of the classification groups (Table A1). Along the first tb-PCA axis, the negative end included *Equisetum fluviatile*, *Menyanthes trifoliata*, *Carex lasiocarpa*, etc., species of flooded habitats, while the positive end included species of non-flooded habitats, such as *Festuca nigrescens*, *Nardus stricta*, *Epikeros pyrenaeum*, etc. The second axis placed the characteristic species of overgrazed mires at the positive values (*Trifolium repens*, *Poa supina*, *Veronica serpyllifolia*, etc.), along with calcicolous species (*Calliergonella cuspidata*, *Palustriella falcata*, *Scorpidium cossonii*), whereas acidophilous and alpine species (*Trichophorum cespitosum*, *Straminergon stramineum*, *Aulacomnium palustre*) were on the negative side. Interestingly, typical calcicolous plants (*Carex davalliana*, *Primula farinosa*, *Tofieldia calyculata*, *Selaginella selaginoides*) loaded highest on the fourth axis.

For RDA, after removing collinear variables (Table A3), we retained the predictors: calcium concentration (Ca) and its square (Ca^2), aluminum concentration (Al), sulfur concentration (S), iron concentration (Fe), sodium concentration (Na), silicon concentration (Si), manganese concentration (Mn), pH and its square (pH^2), mean water table depth

(Mean_WTD) and its square (Mean_WTD^2), percentage of time with the water table: (i) above ground level (WTD_above0); (ii) between −10 and −25 cm (WTD_10_25), between −25 and −50 cm (WTD_25_50), between −50 and −75 cm (WTD_50_75), maximum water table level (Max_WTD), and Slope of the plot in degrees (inclination). Overall, the main determinants were mean water table depth, pH, calcium concentration and silicon concentration, with some significant quadratic terms, indicating unimodal species responses (Figure 4 and Table 2). Nevertheless, other variables had weaker but significant effects (Table A4). Only Al, WTD_above0, WTD_10_25, and Slope were never significant. Determinants differed between taxonomic groups: vascular plants were driven mainly by water table variables, whereas bryophytes responded primarily to pH. The combined dataset reflected vascular-plant patterns, consistent with their greater weight (inertia: 6.66 for vascular plants vs. 2.91 for bryophytes, total = 9.57).

In the three RDA (without considering covariables), environmental determinants explained 22% of variance at most (Table 3). Including spatial structure caused the variance to range from 13.6% (bryophytes) to 18.8% (all data). In all datasets, spatial structure was as important as the environmental determinants. Significant MEM corresponded to coarser spatial scales, capturing site history and inter-site proximity.

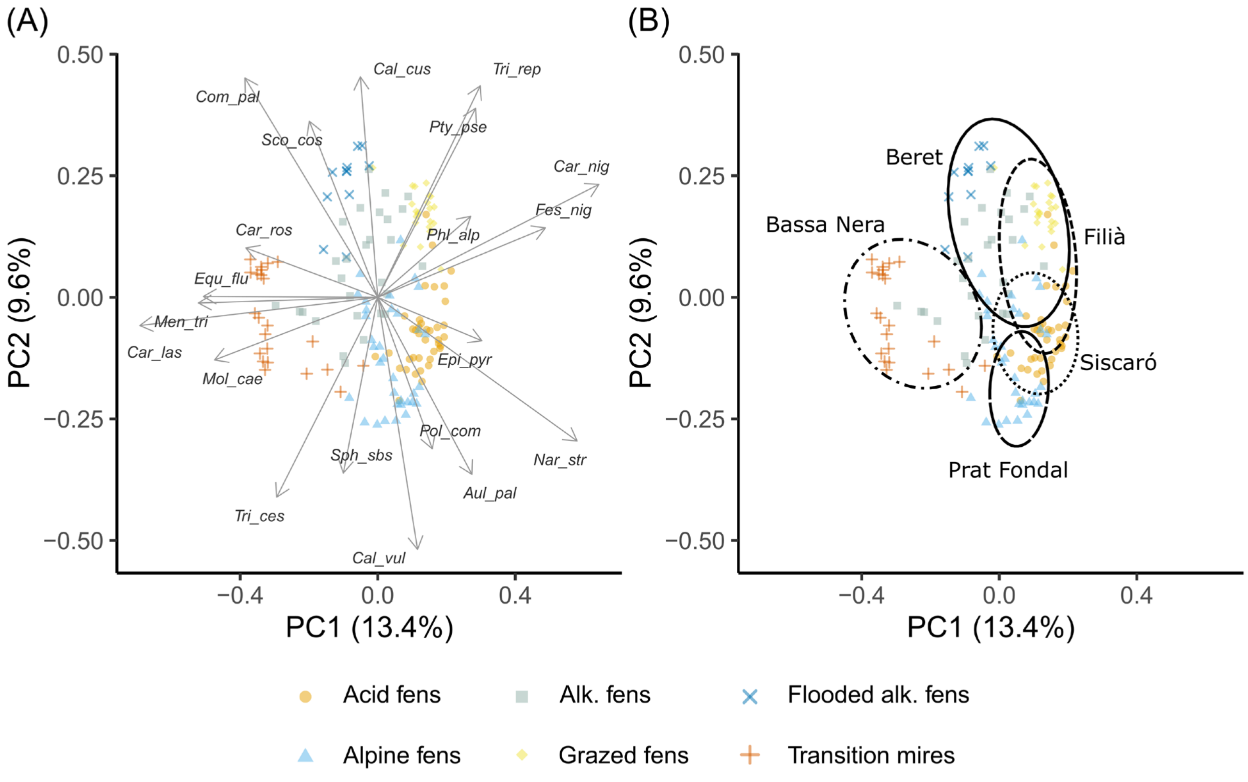
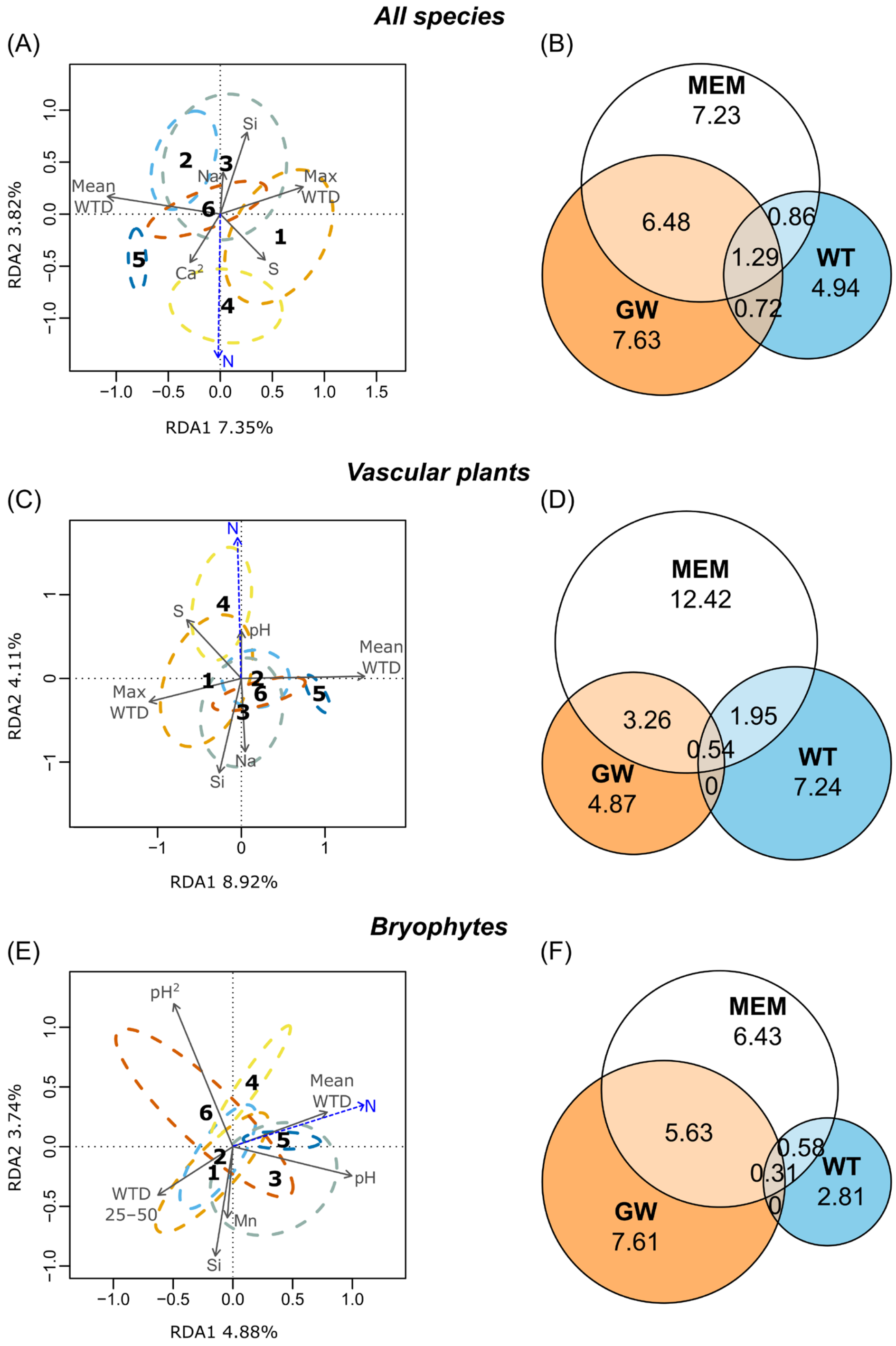


Figure 3. Ordination of floristic relevés along the first two axes of the tb-PCA. Symbols of different colors identify the vegetation groups, as indicated at the bottom of the figure. (**A**) The 10% species with highest fit are represented by abbreviations: Aul_pal, *Aulacomnium palustre*; Cal_cus, *Calliergonella cuspidata*; Cal_vul, *Calluna vulgaris*; Car_las, *Carex lasiocarpa*; Car_nig, *Carex nigra*; Car_ros, *Carex rostrata*; Com_pal, *Comarum palustre*; Epi_pyr, *Epikeros pyrenaeus*; Equ_flu, *Equisetum fluviatile*; Fes_nig, *Festuca nigrescens*; Men_tri, *Menyanthes trifoliata*; Mol_cae, *Molinia caerulea*; Nar_str, *Nardus stricta*; Phl_alp, *Phleum alpinum*; Pol_com, *Polytrichum commune*; Pty_pse, *Ptychostomum pseudotriquetrum*; Sco_cos, *Scorpidium cossonii*; Sph_sbs, *Sphagnum subsecundum*; Tri_ces, *Trichophorum cespitosum*; Tri_rep, *Trifolium repens*. (**B**) The five mire sites are represented through ellipses with confidence limit of 95% on the same tb-PCA ordination.



All species

Vascular plants

Bryophytes

Figure 4. RDA ordinations and variance partitioning. (**A**) Combined dataset (RDA); (**B**) variance partitioning (Euler diagram); (**C**) vascular plants (RDA); (**D**) variance partitioning; (**E**) bryophytes (RDA); (**F**) variance partitioning. In (**A**,**C**,**E**): arrows = variables with $p < 0.001$ (stepwise RDA, correlation with axis 1 or 2 > 30%); dashed line = Ellenberg's N (fertility) fit on first two axes ($p < 0.001$); centroids of groups are shown with ellipses = SD of distances among relevés. Variable codes: Ca = groundwater Ca; Max_WTD = max. water table depth; Mean_WTD = mean water table depth; Na = groundwater Na; S = groundwater S; Si = groundwater Si. In Euler diagrams: GW = groundwater variables selected in RDA; WT = water table variables; MEM = Moran's eigenvector maps (spatial structure). Vegetation group codes: 1 = Acid fens; 2 = Alpine fens; 3 = Alkaline fens; 4 = Grazed fens; 5 = Flooded fens; 6 = Transition mires.

Table 2. Results of the selection of explanatory variables by forward stepwise entry in three RDA analyses (only the first five variables are shown). The first includes all species, the second only vascular plants, and the last only bryophytes. Variables are ordered according to explained variance (adjusted R^2). Only the most ecologically significant variables are shown (*** = $p \leq 0.001$).

Explanatory Variables	**Adjusted R^2**	**Pseudo-F Ratio**
Combined dataset		
Mean_WTD	0.041	8293 ***
Si	0.018	4.37 ***
Ca	0.014	3.531 ***
Mean_WTD^2	0.010	2.948 ***
pH	0.008	2.506 ***
Vascular plants		
Mean_WTD	0.054	11.28 ***
Si	0.021	4.96 ***
Ca	0.012	3.31 ***
S	0.012	3.35 ***
Mean_WTD^2	0.011	3.09 ***
Bryophytes		
pH	0.027	5.62 ***
pH^2	0.019	4.28 ***
Mean_WTD	0.018	4.11 ***
Si	0.013	3.30 ***
Fe	0.010	2.74 ***

Table 3. Variance structure (conditional, constrained, and unconstrained) in the three RDA analyses (combined dataset, vascular plants only, bryophytes only), and in the variance partitioning of the selected variables in these analyses (constrained without covariables, and intersection of constrained and conditional fractions). The conditional fraction refers to the variance explained by the covariables, in all cases the MEM selected by stepwise procedures. The constrained fraction refers to the variance explained by the environmental variables selected through stepwise procedures. The unconstrained fraction corresponds to the variance not explained either by the spatial covariables (conditional variance) or by the environmental variables (constrained variance). The constrained (without covariables) fraction refers to the variance explained by environmental variables when no covariables are included in the RDA model. Finally, the intersection between the constrained and conditional fractions indicates the variance jointly explained by both sets of variables (environmental and spatial).

	Type	**Adjusted R^2 (%)**
Combined dataset	Conditioned	17.6
	Constrained	18.8
	Unconstrained	63.6
	Conditioned (without controlling for covariates)	22.0
	Intersection (Constrained and conditioned parts)	8.6
Vascular plants	Conditioned	19.8
	Constrained	16.4
	Unconstrained	63.7
	Conditioned (without controlling for covariates)	20.2
	Intersection (Constrained and conditioned parts)	7.3
Bryophytes	Conditioned	14.7
	Constrained	13.6
	Unconstrained	71.6
	Conditioned (without controlling for covariates)	16.7
	Intersection (Constrained and conditioned parts)	6.5

Variance partitioning showed that, in the combined dataset, groundwater mineralization and spatial structure accounted for the largest fractions of explained variance (21.3% and 17.6%), while water table variables explained 9.7% (Figure 4B). Bryophytes showed similar results but with even less contribution from water table-related variables (4.9%; Figure 4E). For vascular plants, spatial structure explained 19.8% and water table variables 11.5% (Figure 4D). In no case did the combined environmental determinants and spatial structure exceed 31% of the variance. After removing intersections among groups of variables, vascular plants were explained mainly by spatial data (12.4%), reflecting inter-site differences, whereas bryophytes were explained more by mineralization (7.61%) than spatial structure (6.43%).

4. Discussion

4.1. Vegetation Types

The clusters differed in key environmental variables, thereby underscoring the ecological basis of the numerical classification. These include the mean water table depth, which is related to soil hypoxia, groundwater calcium content and pH, primarily related to nutrient availability, and fertility, which is associated with growth capacity and community competition for light and soil resources. All of them have consistently been identified in previous studies as the main factors structuring plant communities in mires [5,16,25,63,64], and thus they play similar roles in the Pyrenees.

Regarding previous classification proposals of Pyrenean mire vegetation, our results are partially inconsistent with the classification proposed in previous works [2,3,16]. The main factor responsible for these discrepancies is the role of locally abundant and ubiquitous species (related to the local species pool), which causes the classification to also reflect the site of origin of the relevés. For instance, group 6 included vegetation of the quaking, flooded transition mires (regardless of being alkaline or acid) alongside the vegetation related to raised *Sphagnum* hummocks, which, in contrast, is characterized by a markedly deeper water table depth. All the relevés in group 6 came from Bassa Nera, where *Carex lasiocarpa*, among other distinctive elements, occurred in almost all samples (while absent from other sites). Such cases contributed to the numerical classification, likely reflecting local metacommunity stochastic processes—chiefly homogenizing dispersal and mass effects [65,66]—that grouped together alkaline and acid mires as well as geogenous and ombrogenous types. Similarly, the other relevés corresponding to *Sphagnum* hummocks clustered in group 1, together with acid mires. Thus, although the classification reflected the main ecological gradients, it was also shaped by floristic differences among sites. These differences are driven both by the regional species pool (eastern vs. central Pyrenees) and by variation in the local species pool across sites [67].

4.2. Environmental Drivers of the Plant Communities

In the combined dataset, mean water table depth emerged as the main environmental factor governing floristic composition in high-mountain mires. This is evident in the RDA ordination and is consistent with the tb-PCA, where the species were ordered from more to less hygrophilous along the first axis. Previous studies, mostly in oceanic temperate or boreal systems, have also emphasized the key role of water table depth [6,22,24,25], but often found sample ordinations primarily structured by the poor–rich gradient [6,16,23,29]. This likely reflects the fact that many of those studies were conducted in mires with relatively homogeneous water table depth [5,24]. By contrast, where the water table gradient is large, anoxia stress from soil water saturation becomes the dominant determinant of floristic composition [4,33,68]. In this regard, Pyrenean mires represent a distinctive model, as they are subject to pronounced fluctuations in water table depth, caused by reduced summer precipitation and higher insolation compared to the main distribution areas of such vegetation types [38]. These patterns are linked to Mediterranean climatic influence during summer (reduced precipitation and higher insolation) and to the lower latitude of the Pyrenees. In addition, the complex microtopography typical of high-mountain environments accentuates water table variation over short distances. Despite the central role of water table depth, our results also highlight the importance of the groundwater mineralization. Both calcium (highly correlated to electrical conductivity) and pH significantly affected vegetation composition, and when comparing water table-related versus mineralization-related variables, mineralization overall emerged as the stronger determinant of floristic composition.

Furthermore, among the results obtained, we found the consistent role of silicon as a determinant of floristic composition. Silicon, which until recently had received little attention from ecologists [69–72], can influence vegetation in multiple ways: it affects plant growth and vigor, organic matter decomposition, C/N/P stoichiometry and pH, and mitigates the toxic effects of iron and aluminum [73–76]. Moreover, its role in wetlands has been increasingly emphasized [74,76–79]. Among the plant groups known to accumulate silicon, Poales—comprising the main vascular species in mires—and bryophytes stand out. Evidence suggests that silicon may be limiting in wetlands [79–81], particularly since peatlands contain some of the lowest soil silicon concentrations among terrestrial ecosystems [77]. Silicon has also been proposed as an indicator of ombrotrophic conditions [13]. In addition, silicon accumulation provides defense against herbivores and pathogens; under grazing pressure, as in most Pyrenean mires, silicon-accumulating species may be favored [82]. It may also contribute to the formation of elevated tussocks typical of tall graminoids in inundated habitats [74]. In line with these findings, our results suggest a significant role of silicon in determining floristic composition. Concentrations ranged from 0.9 to 24.4 ppm (mean 5.7 ppm), consistent with reported values [77,83]. However, the specific mechanisms by which silicon influences floristic composition, and their relative importance, remain unclear, and we cannot rule out that it is caused by correlation to other variables. In mires, silicon sometimes shows a negative correlation with nitrogen [32], a pattern also found in our data, suggesting that part of the variance explained by silicon may be linked to fertility. Alongside silicon, sulfur and iron were also significant in the RDAs, their concentrations typically reflecting the redox gradient, which drives changes in soil and water chemistry and can lead to mutual interactions [26,27].

Regarding plant productivity and soil fertility, our results indicate that fertility plays a significant role in determining floristic composition and acts independently of groundwater mineralization (i.e., the poor–rich gradient, represented in our data by pH and calcium concentration). In fact, within the classification groups, we can distinguish alkaline fens (groups 3 and 5), where species typical of livestock-enriched habitats are scarce, from more nitrophilous communities that belong to the group 4 (grazed fens). Additionally, the second tb-PCA axis is strongly influenced by species most demanding of fertile conditions. Nevertheless, a dedicated study would be required to disentangle the effects of fertility from those of trampling and grazing. Other authors have likewise concluded that the fertility gradient is independent of base richness [5,10,13,26], though this relationship may vary with geographic region and with increasing atmospheric nitrogen deposition [25]. Moreover, the effects of fertility have often been underestimated in previous studies of Pyrenean mire vegetation. Authors addressing this issue emphasized above all the type of hydrological regime (geogenous vs. ombrogenous) and the degree of water mineralization [2,17,42]. By contrast, our results highlight a stronger role of fertility, although currently inseparable from livestock trampling and grazing. The numerical classification further suggests that certain vegetation types (e.g., group 4, grazed fens) related to the fertility gradient have been overlooked in previous studies.

4.3. Comparison of Ecological Drivers of Vascular Plants and Bryophytes

Regarding the patterns exhibited by vascular plants and bryophytes, clear differences were observed, consistent with previous studies [13,23,32]. Although bryophytes are also sensitive to water table depth, their distribution responded more strongly to variation in pH. The two groups possess distinct functional traits that shape their ability to inhabit mires. In vascular plants, the root system and presence of aerenchyma condition their response to environmental variables, particularly water table depth and the redox gradient [4,24,42,84]. In contrast, bryophytes lack roots and are therefore not directly affected by deep soil redox conditions. Because they form a layer in intimate contact with the peat, bryophytes respond readily to differences in groundwater and soil chemistry, such as pH. This is especially evident in the variance partitioning, which shows the limited explanatory power of water table-related variables for bryophyte composition.

4.4. The Role of Spatial Structure on Vegetation Patterns

As indicated by the variables related to spatial structure (MEM) and by the floristic classification, plant community composition varied strongly among sites. Several studies highlight the importance of colonization dynamics and other stochastic processes in shaping community composition [85–88], which can generate vegetation patterns that differ among sites beyond those explained by environmental gradients. In addition, historical biogeographical processes may have influenced the species pool available at a site and the relative abundances of its species [89,90]. Together with unique abiotic and biotic characteristics at each site [3], these aspects help explain the role of spatial structure in the mires studied. For bryophytes, spatial structure accounted for the smallest proportion of variance (compared with drivers related to groundwater, water table, or vascular plant patterns), reflecting primarily regional-scale variation among sites. This finding is consistent with the high dispersal capacity of bryophytes [91,92], which, being more ubiquitous at the regional scale, exhibit lower floristic variability among sites than vascular plants. Conversely, the relatively limited dispersal capacity of vascular plants may represent a key biological trait underlying spatial structure, particularly in terrestrial island ecosystems such as mountain mires.

4.5. Future Trajectories of Pyrenean Mires

Anticipating vegetation changes under climate and land-use pressures requires an understanding of ecological responses. In the Pyrenees, projected environmental changes are multidimensional and include altered precipitation patterns, higher temperatures, earlier snowmelt, more frequent dry spells, and land-use changes [38,93,94]. Reduced summer precipitation will lower water tables and is expected to alter vascular plant composition, likely favoring the encroachment of shrubs and more competitive, thermophilous grassland species into mires [95,96]. Increased productivity on the vascular plant layers would, in turn, trigger cascading effects across all biodiversity compartments, notably bryophytes, which are likely to be outcompeted [95,97,98].

5. Conclusions

Our results contribute to the ecological foundations of vegetation distribution in alpine mountain mires, particularly at their rear edge. They underscore the need to view mires—isolated patches in the landscape—within a regional framework that integrates historical and biogeographical processes with environmental determinants. Different taxonomic groups respond differently: contrary to our hypothesis, vascular plants were more sensitive to fluctuations in water table depth than to groundwater mineralization, whereas bryophytes were more strongly influenced by water and soil chemistry. This suggests vascular plants may be especially vulnerable to climate change, as water table drawdown is expected, with secondary effects on soil reaction and plant–bryophyte interactions.

The study, conducted in 2004–2005 before major recent climate shifts, provides reference conditions for future comparisons. The sharp variation observed within and among Pyrenean sites evidences vegetation responses to environmental gradients, using a space-for-time approximation. Looking ahead, monitoring mire vegetation responses to climate change, and accounting for interactions among taxonomic groups, will be crucial.

Author Contributions: A.P.-H. and J.M.N. contributed to all stages of the research (from conceptualization to reviewing and editing the manuscript). All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the LIFE Programme of the European Union (LIFE Limnopirineus—LIFE13 NAT/ES/001210, LIFE—Resque Alpyr LIFE20 NAT/ES/000369 and LIFE22-IPC-ES-LIFE PYRENEES4CLIMA), and by the Spanish National Parks MTERD/OAPN program (BIOOCULT, 2413/2017).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Data collected during this research are available upon request.

Acknowledgments: We thank all field assistants for their help, and Víctor Lecegui and Eulàlia Pladevall-Izard for help in the preparation the final version of the figures. We sincerely thank the reviewers for their valuable comments, which helped us to improve the manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Indicator species (phi coeficient > 0.3 and p-value < 0.01) for each classification group.

Taxon	Group	Phi Coefficient	Taxon	Group	Phi Coefficient
Festuca nigrescens	1. Poor fens	0.67	*Anthoxanthum odoratum*	3. Alk. fens	0.52
Carex echinata	1. Poor fens	0.67	*Eriophorum latifolium*	3. Alk. fens	0.52
Viola palustris	1. Poor fens	0.64	*Pinguicula grandiflora*	3. Alk. fens	0.46
Nardus stricta	1. Poor fens	0.63	*Pedicularis pyrenaica*	3. Alk. fens	0.46
Pedicularis pyrenaica	1. Poor fens	0.62	*Juncus pyrenaeus*	3. Alk. fens	0.45
Aulacomnium palustre	1. Poor fens	0.6	*Alchemilla vulgaris*	3. Alk. fens	0.44
Luzula sudetica	1. Poor fens	0.59	*Caltha palustris*	3. Alk. fens	0.43
Trifolium alpinum	1. Poor fens	0.56	*Thalictrum alpinum*	3. Alk. fens	0.42
Potentilla erecta	1. Poor fens	0.55	*Tomentypnum nitens*	3. Alk. fens	0.41
Trifolium spadiceum	1. Poor fens	0.51	*Riccardia chamaedryfolia*	3. Alk. fens	0.38
Trifolium pratense	1. Poor fens	0.51	*Trifolium repens*	4. Grazed fens	0.8
Dactylorhiza maculata	1. Poor fens	0.5	*Ptytochosmum pseudotriquetrum*	4. Grazed fens	0.75
Dicranum bonjeanii	1. Poor fens	0.47	*Ranunculus acris*	4. Grazed fens	0.73
Gentiana pyrenaica	1. Poor fens	0.47	*Scorzoneroides carpetana* subsp. *duboisii*	4. Grazed fens	0.64
Euphrasia stricta	1. Poor fens	0.46	*Agrostis capillaris*	4. Grazed fens	0.61
Scapania irrigua	1. Poor fens	0.46	*Palustriella falcata*	4. Grazed fens	0.59
Sphagnum russowii	1. Poor fens	0.43	*Phleum alpinum*	4. Grazed fens	0.56
Juncus filiformis	1. Poor fens	0.42	*Poa annua*	4. Grazed fens	0.56
Rhinanthus minor	1. Poor fens	0.4	*Plantago media*	4. Grazed fens	0.55
Agrostis canina	2. Alpine fens	0.87	*Veronica serpyllifolia*	4. Grazed fens	0.53
Festuca airoides	2. Alpine fens	0.75	*Carex nigra*	4. Grazed fens	0.49
Pinguicula vulgaris	2. Alpine fens	0.71	*Gentiana verna*	4. Grazed fens	0.48
Ranunculus pyrenaeus	2. Alpine fens	0.69	*Philonotis calcarea*	4. Grazed fens	0.43
Eriophorum angustifolium	2. Alpine fens	0.67	*Galium uliginosum*	4. Grazed fens	0.41
Primula integrifolia	2. Alpine fens	0.63	*Cerastium fontanum*	4. Grazed fens	0.41
Polytrichum commune	2. Alpine fens	0.61	*Comarum palustre*	5. Flooded fens	0.84
Sphagnum subsecundum	2. Alpine fens	0.57	*Calliergonella cuspidata*	5. Flooded fens	0.78
Straminergon stramineum	2. Alpine fens	0.51	*Eleocharis quinqueflora*	5. Flooded fens	0.67
Sarmentypnum exannulatum	2. Alpine fens	0.49	*Scorpidium cossonii*	5. Flooded fens	0.59
Euphrasia minima	2. Alpine fens	0.48	*Juncus articulatus*	5. Flooded fens	0.55
Cetraria islandica	2. Alpine fens	0.44	*Epilobium palustre*	5. Flooded fens	0.46
Salix lapponum	2. Alpine fens	0.4	*Carex lasiocarpa*	6. Transition mires	0.95
Carex davalliana	3. Alk. fens	0.9	*Equisetum fluviatile*	6. Transition mires	0.87
Primula farinosa	3. Alk. fens	0.85	*Menyanthes trifoliata*	6. Transition mires	0.81
Briza media	3. Alk. fens	0.79	*Molinia caerulea*	6. Transition mires	0.65
Bartsia alpina	3. Alk. fens	0.75	*Sphagnum papillosum*	6. Transition mires	0.64
Campylium stellatum	3. Alk. fens	0.7	*Sphagnum divinum*	6. Transition mires	0.63

Table A1. *Cont.*

Taxon	Group	Phi Coefficient	Taxon	Group	Phi Coefficient
Tofieldia calyculata	3. Alk. fens	0.68	*Sphagnum subnitens*	6. Transition mires	0.55
Valeriana dioica	3. Alk. fens	0.63	*Drosera anglica*	6. Transition mires	0.53
Carex panicea	3. Alk. fens	0.63	*Drosera rotundifolia*	6. Transition mires	0.48
Succisa pratensis	3. Alk. fens	0.61	*Melampyrum pratense*	6. Transition mires	0.42
Selaginella selaginoides	3. Alk. fens	0.58	*Utricularia minor*	6. Transition mires	0.42
Prunella vulgaris	3. Alk. fens	0.56	*Sphagnum angustifolium*	6. Transition mires	0.42
Sphagnum warnstorfii	3. Alk. fens	0.53	*Vaccinium myrtillus*	6. Transition mires	0.41

Table A2. Species scores on the first four axes of the tb-PCA. Only species with values greater than $|0.5|$ on at least one of the first four axes are shown.

Species	PC1	PC2	PC3	PC4
Agrostis canina	0.095	−0.469	0.633	−0.387
Aulacomnium palustre	0.453	−0.653	0.256	0.250
Calliergonella cuspidata	−0.084	0.814	0.484	−0.107
Calluna vulgaris	0.191	−0.930	−0.163	−0.311
Campylium stellatum	−0.226	0.123	−0.402	−0.627
Carex davalliana	−0.171	0.344	−0.733	−0.929
Carex flava agg.	0.157	0.232	0.185	−0.817
Carex lasiocarpa	−1.144	−0.104	−0.173	0.654
Carex nigra	1.064	0.417	0.718	−0.582
Carex panicea	−0.201	0.339	−0.488	−0.795
Carex rostrata	−0.635	0.182	0.358	0.421
Comarum palustre	−0.639	0.810	0.775	0.419
Eleocharis quinqueflora	−0.020	0.489	0.208	−0.690
Epikeros pyrenaeum	0.501	−0.160	−0.155	−0.069
Equisetum fluviatile	−0.839	0.003	−0.068	0.523
Eriophorum angustifolium	−0.076	−0.475	0.404	−0.572
Festuca airoides	0.138	−0.536	0.638	−0.423
Festuca nigrescens	0.806	0.256	−0.691	0.669
Menyanthes trifoliata	−0.863	−0.021	0.109	0.673
Molinia caerulea	−0.785	−0.231	−0.599	0.034
Nardus stricta	0.959	−0.530	−0.363	0.881
Palustriella falcata	0.203	0.503	0.049	−0.183
Polytrichum commune	0.262	−0.559	0.520	−0.116
Potentilla erecta	0.365	−0.341	−1.099	0.185
Ptychostomum pseudotriquetrum	0.471	0.698	−0.098	0.095
Scorpidium cossonii	−0.329	0.650	−0.098	−0.671
Sphagnum subsecundum	−0.166	−0.648	0.580	−0.108
Sphagnum warnstorfii	0.042	−0.129	−0.539	−0.275
Straminergon stramineum	−0.045	−0.503	0.318	−0.047
Succisa pratensis	0.193	−0.282	−0.903	0.061
Trichophorum cespitosum	−0.486	−0.738	−0.791	−0.620
Trifolium repens	0.493	0.780	−0.128	0.442

Table A3. Pearson correlation between environmental variables.

Variable	Ca	Al	Mg	P	S	Fe	Na	Si	Zn	Mn	pH	EC	WTD Above0	WTD 0_10	WTD 10_25	WTD 25_50	WTD 50_75	Mean WTD	Min WTD	Max WTD	WT_ Fluctuation	Slope	Lon
Ca	1.00	−0.09	0.75	−0.09	0.37	−0.03	0.25	−0.36	−0.22	0.10	0.69	0.90	−0.12	0.19	0.00	−0.16	−0.08	0.15	−0.10	−0.05	−0.09	0.33	−0.45
Al	−0.09	1.00	−0.09	0.19	0.20	0.21	0.33	0.02	0.11	0.02	−0.04	0.11	−0.07	−0.27	−0.03	0.29	0.24	−0.38	0.48	0.15	0.47	0.07	0.01
Mg	0.75	−0.09	1.00	−0.09	0.63	−0.07	0.05	−0.25	−0.20	0.18	0.65	0.68	−0.08	0.14	−0.08	−0.04	0.03	0.07	−0.05	0.01	−0.06	0.21	−0.39
P	−0.09	0.19	−0.09	1.00	0.01	0.11	0.13	0.07	0.07	−0.04	−0.20	0.01	−0.04	−0.21	0.03	0.30	0.02	−0.19	0.20	0.19	0.16	−0.02	0.03
S	0.37	0.20	0.63	0.01	1.00	−0.12	0.13	−0.20	−0.02	0.03	0.35	0.41	0.01	−0.02	−0.18	0.18	0.14	−0.15	0.18	0.09	0.16	0.22	−0.17
Fe	−0.03	0.21	−0.07	0.11	−0.12	1.00	0.17	0.31	−0.02	−0.04	−0.17	0.07	0.02	−0.14	0.06	0.08	0.12	−0.12	0.19	−0.05	0.22	−0.01	0.11
Na	0.25	0.33	0.05	0.13	0.13	0.17	1.00	0.01	0.14	0.00	0.17	0.46	−0.08	−0.10	−0.04	0.12	0.14	−0.17	0.29	0.13	0.27	−0.12	−0.07
Si	−0.36	0.02	−0.25	0.07	−0.20	0.31	0.01	1.00	0.32	−0.09	−0.29	−0.25	−0.03	−0.34	0.03	0.27	0.40	−0.37	0.29	0.15	0.27	−0.21	0.59
Zn	−0.22	0.11	−0.20	0.07	−0.02	−0.02	0.14	0.32	1.00	−0.05	−0.11	−0.14	−0.05	−0.24	0.11	0.18	0.03	−0.19	0.21	0.00	0.23	−0.23	0.52
Mn	0.10	0.02	0.18	−0.04	0.03	−0.04	0.00	−0.09	−0.05	1.00	0.14	0.09	−0.03	−0.08	0.07	0.04	0.04	−0.07	0.08	−0.06	0.11	0.03	−0.10
pH	0.69	−0.04	0.65	−0.20	0.35	−0.17	0.17	−0.29	−0.11	0.14	1.00	0.66	−0.02	0.08	−0.03	−0.09	−0.01	0.03	−0.01	−0.09	0.01	0.30	−0.33
EC	0.90	0.11	0.68	0.01	0.41	0.07	0.46	−0.25	−0.14	0.09	0.66	1.00	−0.10	0.11	−0.04	−0.07	0.03	0.03	0.07	−0.04	0.09	0.25	−0.41
WTD_above0	−0.12	−0.07	−0.08	−0.04	0.01	0.02	−0.08	−0.03	−0.05	−0.03	−0.02	−0.10	1.00	0.05	−0.21	−0.14	−0.11	0.24	−0.21	−0.34	−0.12	−0.09	0.02
WTD_0_10	0.19	−0.27	0.14	−0.21	−0.02	−0.14	−0.10	−0.34	−0.24	−0.08	0.08	0.11	0.05	1.00	−0.57	−0.63	−0.42	0.77	−0.70	−0.57	−0.58	−0.05	−0.32
WTD_10_25	0.00	−0.03	−0.08	0.03	−0.18	0.06	−0.04	0.03	0.11	0.07	−0.03	−0.04	−0.21	−0.57	1.00	−0.10	−0.17	−0.07	0.08	0.21	0.02	0.17	−0.02
WTD_25_50	−0.16	0.29	−0.04	0.30	0.18	0.08	0.12	0.27	0.18	0.04	−0.09	−0.07	−0.14	−0.63	−0.10	1.00	0.34	−0.68	0.60	0.65	0.44	−0.07	0.32
WTD_50_75	−0.08	0.24	0.03	0.02	0.14	0.12	0.14	0.40	0.03	0.04	−0.01	0.03	−0.11	−0.42	−0.17	0.34	1.00	−0.76	0.73	0.27	0.69	−0.04	0.23
Mean_WTD	0.15	−0.38	0.07	−0.19	−0.15	−0.12	−0.17	−0.37	−0.19	−0.07	0.03	0.03	0.24	0.77	−0.07	−0.68	−0.76	1.00	−0.90	−0.54	−0.79	0.00	−0.33
Min_WTD	−0.10	0.48	−0.05	0.20	0.18	0.19	0.29	0.29	0.21	0.08	−0.01	0.07	−0.21	−0.70	0.08	0.60	0.73	−0.90	1.00	0.35	0.96	−0.04	0.29
Max_WTD	−0.05	0.15	0.01	0.19	0.09	−0.05	0.13	0.15	0.00	−0.06	−0.09	−0.04	−0.34	−0.57	0.21	0.65	0.27	−0.54	0.35	1.00	0.08	0.04	0.05
WT_fluctuation	−0.09	0.47	−0.06	0.16	0.16	0.22	0.27	0.27	0.23	0.11	0.01	0.09	−0.12	−0.58	0.02	0.44	0.69	−0.79	0.96	0.08	1.00	−0.05	0.29
Slope	0.33	0.07	0.21	−0.02	0.22	−0.01	−0.12	−0.21	−0.23	0.03	0.30	0.25	−0.09	−0.05	0.17	−0.07	−0.04	0.00	−0.04	0.04	−0.05	1.00	−0.19
Lon	−0.45	0.01	−0.39	0.03	−0.17	0.11	−0.07	0.59	0.52	−0.10	−0.33	−0.41	0.02	−0.32	−0.02	0.32	0.23	−0.33	0.29	0.05	0.29	−0.19	1.00

Table A4. Results of the selection of explanatory variables by the stepwise method in three RDA analyses. The first includes all species, the second only vascular plants, and the last only bryophytes. Variables are ordered according to explained variance (adjusted R^2). F—pseudo-F ratio; Mean—mean depth of the water table; Between −10 and −25 cm and Between −25 and −50 cm—percentage of time with the water table within the indicated depth intervals.

Forward Selection Steps	**Variable**	**Adjusted R^2**	**Pseudo-F Ratio**	***p*-Value**
Combined dataset				
1	Mean_WTD	0.041	8.292	0.001
2	Si	0.059	4.377	0.001
3	Ca	0.073	3.531	0.001
4	Mean_WTD^2	0.083	2.948	0.001
5	pH	0.091	2.506	0.001
6	pH2	0.100	2.579	0.001
7	S	0.107	2.411	0.001
8	Na	0.114	2.295	0.002
9	Fe	0.120	2.064	0.001
10	Max_WTD	0.125	1.938	0.004
11	Ca^2	0.129	1.769	0.010
12	Mn	0.133	1.764	0.008
Vascular plants				
1	Mean_WTD	0.055	11.281	0.001
2	Si	0.075	4.961	0.001
3	Ca	0.087	3.307	0.001
4	S	0.099	3.353	0.001
5	Mean_WTD^2	0.110	3.089	0.001
6	pH	0.118	2.603	0.002
7	Na	0.124	2.264	0.005
8	Max_WTD	0.129	2.062	0.008
Bryophytes				
1	pH	0.027	5.619	0.001
2	pH^2	0.046	4.282	0.001
3	Mean_WTD	0.064	4.114	0.001
4	Si	0.077	3.300	0.001
5	Fe	0.086	2.738	0.001
6	WTD_25_50	0.094	2.439	0.004
7	Mn	0.102	2.287	0.003

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