PLANT ZONATION PATTERNS ALONG THE WATER-LEVEL GRADIENT IN TWO HIGH-ELEVATION WETLANDS UNDER DIFFERENT MACROCLIMATES

José Antonio Molina[1] and Gonzalo Navarro[2]

Abstract: Plant zonation patterns along a water-level gradient were compared in two high-elevation wetlands, one under a tropical climate and the other under an extratropical climate. Numerical classification showed that each zonation followed an analogous internal distribution of vegetation physiognomy types. Correspondence Analyses related both zonations to life-form distribution patterns. Habitats with a longer period of flooding were dominated by helophytes and hydrophytes, and habitats with a shorter period of flooding were dominated primarily by hemicryptophytes. The most distinct vegetation belts were those on marshlands. Extratropical intermediate zonation included rhizomatous geophytes as the dominant life form while pulvinate chamaephytes characterized the tropical zonation.

Keywords: flooding gradient, high mountain wetland, vegetation zonation, plant life forms, fens

High-elevation wetlands (HEWs) are unique and extremely fragile habitats (Catalan et al., 2006; Xu et al., 2024). They are characterized by highly diluted waters and environments with low temperatures and high UV radiation. They include not only water bodies such as lakes, ponds, and rivers, but also marshlands, mires, and humid grasslands (Snethlage, 2015). Lands fringing wetlands have been commonly used as pasture for cattle grazing (Middleton, 2016; Biró et al., 2019). HEWs provide a plethora of ecosystem services, such as storing carbon, which contributes to climate regulation, which in turn are related to the functional traits of dominant plants (Mitsch et al., 2015; Chatanga et al., 2020). They are especially fragile habitats that are highly sensitive to global change (Schmeller et al., 2022). Furthermore, HEWs are witnesses to climate change and other human activities, and thus they can be considered sentinels of change (Gerdol et al., 1998; Gignac et al., 1998; Catalan et al., 2006). In this context, the identification of the baseline state in high mountain wetlands is important for assessing the health and stability of such habitats.

Environmental gradients are responsible for structuring plant communities and their indicators (Čarni et al., 2011; Rahman et al., 2020). Specifically, wetland vegetation zoning is dependent on the terrain morphology, depth and duration of flooding, and water chemistry (Hirvnák, 2005; Lou et al., 2013; Sánchez-Higueredo et al., 2025). Wetland vegetation has been considered as azonal as it occurs across several biomes/zones (Mucina et al., 2016). The distribution and composition of wetland plant communities have also been related to climate (Malmer, 1986; Bragazza, 1999; Miserere et al., 2003), hence, wetland vegetation has been regarded as intrazonal (Sieben, 2019). The usefulness of considering life and growth forms as a standardized basis for comparison of floras among regions has been highlighted in biodiversity analyses (Taylor et al., 2023). The differences among life forms are crucial for understanding the differences between aquatic and terrestrial plants and their habitat heterogeneity (Santamaría, 2002; Molina, 2017). In this work, for the first time, we investigate how different vegetation types are arranged and respond to the flooding gradient under different climates using plant life-form distribution as a comparative zonation pattern. Specifically, we compare two high-mountain complex wetlands under different macroclimates, namely tropical and temperate. This knowledge will shed light on global patterns in those ecosystems and thus provide valuable information to monitor simultaneously ecosystem changes in equivalent habitats.

Materials and Methods

Study Area

Two high mountain wetland areas, one located in southwestern Europe (Pyrenees, Spain, Northern Hemisphere) and the other in central South America (Tunari, Bolivia, Southern Hemisphere) were chosen to carry out our study. The surveyed area was about 5 km^2 in both cases and included a system of lakes and small rivulets. They share an oligotrophic soil environment and some comparable climatic features, such as the mean annual temperature. The European site is in the Central Pyrenees (northeastern Spain) in the high basin of the Esera River where the average altitude of the relevés was 2,200 m. The

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1 Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, c/ José Antonio Novais 12, 28040-Madrid, Spain. jmabril@ucm.es
2 Unidad Académica Regional Cochabamba, Carrera de Ingeniería Ambiental, Universidad Católica Boliviana «San Pablo», Cochabamba, Bolivia.

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	Elevation	Geographic coordinates	P	T	Ic	M	m	Itc	Tp	Io
Fanlo (Huesca, Spain)	2,215 m	42°39’ N, 0°0’ E	1,682	4.4	14.3	2.2	-5.7	9	549	22.1
Ulla-Ulla (Franz Tamayo, Bolivia)	4,460 m	15º03’ S, 69º16’ W	495	4.4	3.3	11.8	-6.8		528	9.36

P = annual precipitation; T = annual mean temperature; Continentality Index (Ic) = interval between the highest and lowest monthly average temperatures of the year; M = mean maximum temperature of coldest month; m = mean minimum temperature of coldest month; Thermicity Index (It) = (T + M + m)10; annual positive temperature (Tp) = sum of monthly mean temperature higher than 0ºC; Ombrothermic Index (Io) = 10(Pp/Tp).

Table 1: Climatic and bioclimatic data obtained from the closest weather stations to the studied sites

headwaters have moderate mineralization with an EC of 150 µS/cm (CHE, 2002). Lithologically, the area consists of acidic plutonic rocks (Aranguren and Suárez, 1973). The South American site is in the Tunari Range (central Bolivia) with an average altitude of 4,200 m. This area has base-poor Paleozoic lithologies. The wetlands have water with an EC< 50 µS; they are neutral or somewhat acidic and hypomineralized (Maldonado and Goitia, 2003). Table 1 shows the climatic data obtained from the closest and most representative weather stations to the study areas and the bioclimatic indexes determined according to Rivas-Martínez et al. (1999). From this, it can be inferred that the bioclimatic characterization of the stations is Orotemperate Oceanic Hyperhumid for the Pyrenean site and Orotropical Pluviseasonal Humid for the tropical site. It is noteworthy, as mentioned above, that the sites have a similar mean annual temperature (about 4 C) and a similar positive temperature. In contrast, the Pyrenean area is about four times rainier and more continental than the Bolivian area.

Methods

Relevés were taken using the phytosociological method (Braun-Blanquet, 1979). In the field sampling, the average height of the dominant plants was determined as a surrogate for vegetation structure, and the relative elevation above the water table (relative altitude) served as a surrogate for the duration of flooding (Molina et al., 2004). Two tables were obtained: the Pyrenean table with 17 relevés and 61 taxa (Table 2), and the Andean table with 30 relevés and 60 taxa (Table 3). All the species were also assigned suitable life forms according to the Raunkiaer (1934) life-form classification. Data are available on request from the data custodians (jmabril@ucm.es; gonzalonavarrosanchez@gmail.com), in the BOVEDA database (Andean inventories), and in the VEGAS database (Pyrenean inventories) (GIVD).

The matrices of the data obtained from the species cover values have been analyzed numerically with cluster analysis using the Syn-tax Program (Podani, 2001). Thus, by using the average linkage method (UPGMA) and the chord distance as a distance algorithm, it was possible to classify the relevés and delimit the plant communities. Cluster analysis of the Bolivian relevés has already been published (Molina et al., 2007). Syntaxonomical typology follows Mucina et al. (2016) for European plant communities and to Galán de Mera et al. (2025) for Bolivian ones. A syntaxonomical synopsis of the study vegetation is included in Appendix 1.

In order to determine the degree of similarity in plant life forms between site zonations, a correspondence analysis and subsequently a cluster analysis were performed with SPAD 3.5 software (CISIA-CERESTA, 1998) Cluster analysis was carried out on the factorial coordinates of the levels in the first three factors, which cover 95% of the total variance. Classification analysis used Euclidean distance to compute the distance between each pair of samples, and Ward’s method as distance-optimizing clustering method.

RESULTS

Pyrenean Zonation

Seven plant communities were identified in the Pyrenean site (Table 2). The sequence of plant communities along a hydric gradient was the following: *Nardus stricta* humid grasslands (cervunal), *Juncus alpinoarticulatus* Community, *Tricophorum cespitosum* Community, *Carex nigra* Community, *Eriophorum angustifolium* Community, *Carex rostrata* Community and *Sparganium angustifolium* Community.

Species richness increased mainly with relative altitude (Table 4). The plant community height increased from terrestrial to helophytic and aquatic communities. From a physiognomic point of view, the Pyrenean zonation had the following characteristics: the upper belt consisted of grasslands dominated by the caespitose hemicryptophytes; the belts with intermediate flooding had the rhizomatous geophyte as the dominant biotype, although they also had a relatively high proportion of hemicryptophytes and mosses in their composition; and finally, the aquatic niches were mostly occupied by helophytes and hydrophytes, depending on the depth of the water.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Nardus stricta L.	3	3	2						1	2							
Plantago alpina L.	2	2	1						+								
Juncus alpinoarticulatus Chaix				5			1	2	+		1				1		
Trichophorum cespitosum (L.) Hartm.					3	5	5	5	5	4	1				1		
Carex nigra (L.) Reichard				+				1		1	4	5					
Eriophorum angustifolium Honck.					2	2	1				2		4	3	4		
Carex rostrata Stokes													1			5	
Sparganium angustifolium Michx.																	5
Carex echinata Murray						2	3		1	3	2	2					
Pinguicula vulgaris L.					1		1	2	1								
Festuca nigrescens Lam.	+	2	+														
Jasione laevis Lam.	1	+	1														
Carex macrostyla Lapeyr.	+	2	2														
Potentilla erecta (L.) Raeusch.	1		+					+									
Calliergonella cuspidata (Hedw.) Loeske										1	2	2					
Trifolium alpinum L.		3	4														
Galium cespitosum Lam.	+	+															
Scorzoneroides pyrenaica (Gouan) Holub	+	+															
Pilosella lactucella (Wallr.) P.D. Sell & C. West	1		+														
Poa alpina L.		1	1														
Calluna vulgaris (L.) Hill		+	+														
Sphagnum capillifolium (Ehrh.) Hedw.				+						2							
Leontodon duboisii Sennen							1		1								
Ptychostomum pseudotriquetrum (Hedw.) J.R.Spence & H.P.Ramsay							+			1							
Primula integrifolia L.								1	1								
Caltha palustris L.								1		2							
Festuca rubra L.								+		1							
Carex demissa Hornem.											+				1		
Dichodontium palustre (Dicks.) M.Stech													1	1			
Euphrasia minima Jacq. ex DC.	2																
Carex caryophyllea Latourr.	2																
Trifolium pratense L.	+																
Pilosella officinarum Vaill.	+																
Ranunculus bulbosus L.	+																
Thymus pulegioides L.	+																
Phyteuma hemisphaericum L.	+																
Scorzoneroides hispidula (Delile) Greuter & Talavera	+																
Antennaria dioica (L.) Gaertn	+																
Phleum alpinum L.		+															

Table 2 continued

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Angelica pyrenaea (L.) Spreng.		+															
Atocion rupestre (L.) Oxelman		+															
Gentiana acaulis L.		+															
Lotus alpinus (Ser.) Schleich. ex Ramond			+														
Meum athamanticum Jacq.			+														
Polytrichum sp.				+													
Sphaghum sp.				+													
Armeria bubanii G.H.M. Lawr.							1										
Brachythecium Schimp. sp.							+										
Pedicularis mixta Gren.								1									
Parnassia palustris L.								r									
Bartsia alpina L.									1								
Carex frigida All.									1								
Aulacomnium palustre (Hedw.) Schwägr.										1							
Chiloscyphus polyanthos (L.) Corda										1							
Scapania undulata (L.) Dumort.										1							
Juncus filiformis L.											+						
Philonotis fontana (Hedw.) Brid													1				
Sanionia Loeske sp.														1			
Fontinalis antipyretica Hedw.														1			
Micranthes stellaris (L.) Galasso, Banfi & Soldano															1		
Poa supina Schrad.															+		

Localities: Spain, Pyrenees, Maladeta Massif, Ibón de la Renclusa and surrounding wetlands, 42º40’03” N 0º38’34”.

TABLE 2: Detailed table of the Pyrenean relevés (columns). 1-3 Nardus stricta humid grassland (cervunal); 4 J*uncus alpinoarticulatus* Community; 5-10 *Tricophorum cespitosum* Community; 11-12 *Carex nigra* Community; 13-15 *Eriophorum angustifolium* Community; 16 *Carex rostrata* Community; 17 *Sparganium angustifolium* Community.

	Dominant species	**Number of relevés**	**Species richness**	**Community height (cm)**	**Dominant biotype**	**Relative altitude* (cm)**	**Soil type****
Pyrenean zonation	*Nardus stricta,* *Plantago alpina*	3	15	25	caespitose hemicryptophyte	+10	Humic Umbrisols
	Juncus alpinoarticulatus	1	4	15	rhizomatous geophyte	+5	Gleysols
	Tricophorum cespitosum	6	8	9	rhizomatous geophyte	0	Gleysols
	Carex nigra	2	6	17	rhizomatous geophyte	-2.5	Fibric-Dystric Histosols
	Eriophorum angustifolium	3	5	45	rhizomatous geophyte	-5	Histosols
	Carex rostrata	1	1	56	helophyte	-30	Oligotrophic Gyttja
	Sparganium angustifolium	1	1	100	radicant hydrophyte	-70	Oligotrophic Gyttja
Andean zonation	*Festuca humilior,* *Eleocharis albibracteata,* *Festuca dolichophylla*	3	16	30	caespitose hemicryptophyte	+30	Dystric-Umbric Gleysols
	Plantago tubulosa	11	10	4	rosulate hemicryptophyte	+7	Fibric Histosols
	Distichia muscoides, *Cinnagrostis jamesonii*	5	8	45	pulvinulate chamaephyte	-5	Fibric Histosols+ Terric Histosols (in depth)
	Cinnagrostis orbygniana *Deschampsia eminens*	2	7	45	caespitose hemicryptophyte	-12	Oligotrophic Gyttja
	Lilaeopsis occidentalis *Cotula mexicana*	5	5	5	radicant hydrophyte	-3	Oligotrophic Gyttja
	Ranunculus flagelliformis, *Callitriche heteropoda*	4	4	30	radicant hydrophyte	-28	Oligotrophic Gyttja

* Symbols mean above (+) or below (-) relative elevation in relation to the water table

** Soil nomenclature follows the WRB system of soil classification [IUSS Working Group WRB. 2022. World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps. 4th edition. International Union

TABLE 3: Geobotanical features of the Pyrenean and Andean zonations.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Festuca humilior Nees & Meyen	3	2	4																											
Eleocharis albibracteata Nees & Meyen ex Kunth	2	3	1	+		+			1		3	2																		
Festuca gr. dolichophylla	3	2	1																											
Plantago tubulosa Decne.	1	+	+	5	5	5	5	5	5	5	5	5	5	5	2	1	1	2	1	3				+						
Distichia muscoides Nees & Meyen				+	+	+	+	1	+						5	5	5	5	5		2	1	1							
Cinnagrostis jamesonii (Steud.) P.M. Peterson, Soreng, Romasch. & Barberá						+				+					2	2	1		2			+								
Cinnagrostis orbignyana (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá																				3	1									
Deschampsia eminens (J.Presl) Saarela																				1	2									
Lilaeopsis occidentalis J.M.Coult. & Rose															1	+						3	4	4	3	3	+	1		
Cotula mexicana (DC.) Cabrera																			+			3	1		2	3				
Ranunculus flagelliformis Sm.																							1	+	1		3	2	3	3
Callitriche heteropoda Engelm. ex Hegelm.																											3	2	3	3
Isoetes L. sp.																								2		2	3	3		3
Gentiana postrata Haenke		+	2	1	1	1		2	2	1		2	2		+	1	1				+									
Hypochaeris taraxacoides (Loisel.) O.Hoffm.	1		2	+	1	+	+	1		2	1	1		1																
Cinnagrostis rigescens (J.Presl) P.M. Peterson, Soreng, Romasch. & Barberá		+	1	3	1		2	2	2				2	1		+	+													
Werneria pygmaea Gillies ex Hook. & Arn.	2			2	1	1	3			1			2	1			2			1										
Gentianella primuloides (Gilg) J.S.Pringle				1	1	1	1	2	1					1	1	1			+											
Cinnagrostis curvula (Wedd.) P.M.Peterson, Soreng, Romasch. & Barberá	2			1	1		1		+		+				1	2		+												
Myrosmodes paludosa (Rchb.f.) P.Ortiz				1		1	+							1	1	+	1	+	+											
Alchemilla diplophylla Diels				+			1			+	3	1											+	3	1	2				
Castilleja pumila (Benth.) Wedd.				+	+		1			1		1		+	+															
Alopecurus aequalis Sobol.			+																			+	+				1	+	2	
Oritrophium limnophilum (Sch.Bip.) Cuatrec.				1	+	2		1							+							+								

Table 4 continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Phlegmariurus saururus (Lam.) B.Øllg.				1	+	1			+				+					+												
Aciachne pulvinata Benth.	2	1								1		+	+																	
Luzula racemosa Desv.	2			1		+		1																						
Alchemilla pinnata Ruiz&Pav.	1	1	2															1												
Hypochoeris meyeniana (Walp.) Benth. & Hook. f. ex Griseb.	1	1	1																											
Novenia acaulis (Benth. & Hook. f. ex B.D. Jacks.) S.E. Freire & F.H. Hellwig				2	1			+																						
Lysipomia pumila (Wedd.) E.Wimm.										1	1	2																		
Azorella biloba (Schltdl.) Wedd.	1	1																												
Fesctuca rigescens (J.Presl) Kunth		2																		2										
Trifolium amabile Kunth			2								1																			
Juncus ebracteatus E.Mey.			1								1																			
Cinnagrostis brevifolia (J.Presl) P.M. Peterson, Soreng, Romasch. & Barberá									+				1																	
Carex bonplandii Kunth																				1	+									
Perezia poeppigii Less.	2																													
Cinnagrostis filifolia (Wedd.) P.M.Peterson, Soreng, Romasch. & Barberá var. trichophylla	2																													
Stipa hansmeyeri Pilg.	1																													
Poa kurtzii R.E.Fr.	1																													
Cinnagrostis heterophylla (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá	1																													
Gentianella aff. boliviana (Pax) J.S.Pringle	1																													
Cyperus seslerioides Kunth		1																												
Calandrinia acaulis Kunth		1																												
Gomphrena meyeniana Walp.		1																												
Paranephelius ovatus Wedd.		1																												
Lobelia nana Kunth			1																											

Table 4 continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Gamochaeta purpurea (L.) Cabrera			1																											
Hordeum muticum J.Presl			1																											
Cerastium arvense subsp. *strictum* Gaudin			1																											
Baccharis alpina Kunth				1																										
Sisyrinchium L. sp.				+																										
Poa perligulata Pilg.							1																							
Werneria heteroloba Wedd.									2																					
Plantago orbignyana Steinh. ex Decne.											+																			
Viola pygmaea Juss. ex Poir.												2																		
Cinnagrostis tarmensis (Pilg.) P.M.Peterson, Soreng, Romasch. & Barberá																				1										
Deschampsia chrysantha (J.Presl) Saarela																					1									
Myriophyllum quitense Kunth																											1			
Localities: Bolivia, Tunari ranges, wetlands between 17º14’S-17º15’S and 66º18’-66º21’W.																														

TABLE 4: Detailed table of the Andean relevés (columns). 1-3 Eleocharis albibracteata-Festuca humilior humid grassland (pajonal); 4-14 Gentianella primuloidis-Plantago tubulosa Community (flat peat-bog, bofedal plano); 15-19 Cinnagrostis jamesonii-Distichia muscoidis Community (cushion-like peat bog, bofedal pulvinular); 20-21Cinnagrostis orbygniana-Deschampsia eminens Community (bunch-grassland swamp, pajonal inundado); 22-26 Cotula mexicana-Lilaeopsis occidentalis Community (submerged aquatic vegetation in temporary waters); 27-30 Ranunculus flagelliformis Community (submerged aquatic vegetation in permanent waters).

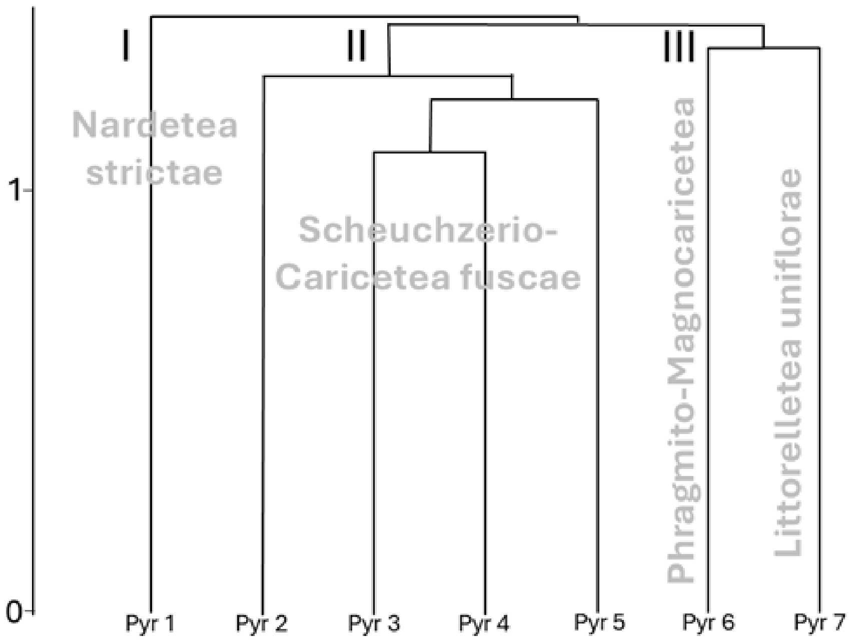

FIGURE 1:Vegetation classification of Pyrenean zonation. Nardetea strictae: Species-rich Nardus grassland, on siliceous substrates in mountain areas; S*cheuchzerio palustris-Caricetea fuscae*: mire and fen vegetation; *Phragmito-Magnocaricetea*: helophytic and sedge vegetation; *Littorelletea uniflorae*: soft-water amphibious vegetation.

Andean Zonation

Six plant communities were identified in the Andean site (Table 3). They showed the following distribution: *Eleocharis albibracteata-Festuca humilior* humid grassland (pajonal higrofítico), *Gentianella primuloides-Plantago tubulosa* Community (flat peat bog, bofedal plano), *Cinnagrostis jamesonii-Distichia muscoides* Community (cushion-like peat bog, bofedal pulvinular), *Cinnagrostis orbygniana-Deschampsia eminens* Community (bunch-grassland swamp, pajonal inundado), and submerged aquatic vegetation (*Cotula mexicana-Lilaeopsis occidentalis* Community in temporary waters; *Ranunculus flagelliformis* Community in permanent waters).

Species richness increased clearly with the relative altitude of the plant community as in the Pyrenean zonation, and the upland vegetation again showed the highest species richness (Table 4). Monospecific plant communities were not found in this zonation. Marginal vegetation in the border water communities reached a greater size, specifically in *Cinnagrostis jamesonii-Distichia muscoidis* Community and *Cinnagrostis orbygniana-Deschampsia eminens* Community. Physiognomically, the upper belt was dominated by caespitose hemicryptophytes; the belts of intermediate flooding consisted of plant communities dominated by hemicryptophytes (rosulate or caespitose) or pulvinulate chamaephytes; and the aquatic habitats were composed of radicant hydrophytes. There were no helophytes found in the study area, but helophytic vegetation, such as *Schoenoplectus tatora* stands (totorales), is common in Andean high mountains (De la Barra, 2003).

Vegetation Classification

The classification dendrogram of Pyrenean vegetation diversity showed three main groups (Fig. 1). Group I encompassed humid grasslands (*Nardetea strictae* Rivas Goday et Borja Carbonell in Rivas Goday et Mayor López 1966), group II gathered different types of sedges (*Scheuchzerio palustris-Caricetea fuscae* Tx. 1937) and group III included swamps of *Scheuchzerio palustris-Caricetea fuscae* Tx. 1937, helophytic vegetation of Phragmito-Magnocaricetea Klika in Klika and Novak 1941 and aquatic communities of *Littorelletea uniflorae* Br.-Bl. et Tx. ex Westhoff et al. 1946. The Andean numerical classification also showed two main groups (Molina et al., 2007), one gathering humid grasslands and mire and bog vegetation (*Plantagini rigidae-Distichietea muscoidis* Rivas-Martínez & Tovar 1982), and another including aquatic vegetation (*Limoselletea australis* Galán, Campos, Linares, Montoya, Torres & Vicente 2021). Both classifications, Pyrenean and Andean, show a similar cluster structure in the types of wetland vegetation. This suggests that there is a similar internal organization within zonations across different macroclimates: the zonation starts with aquatic plant communities, which give way to mire vegetation and then to humid grasslands. The most important soil difference

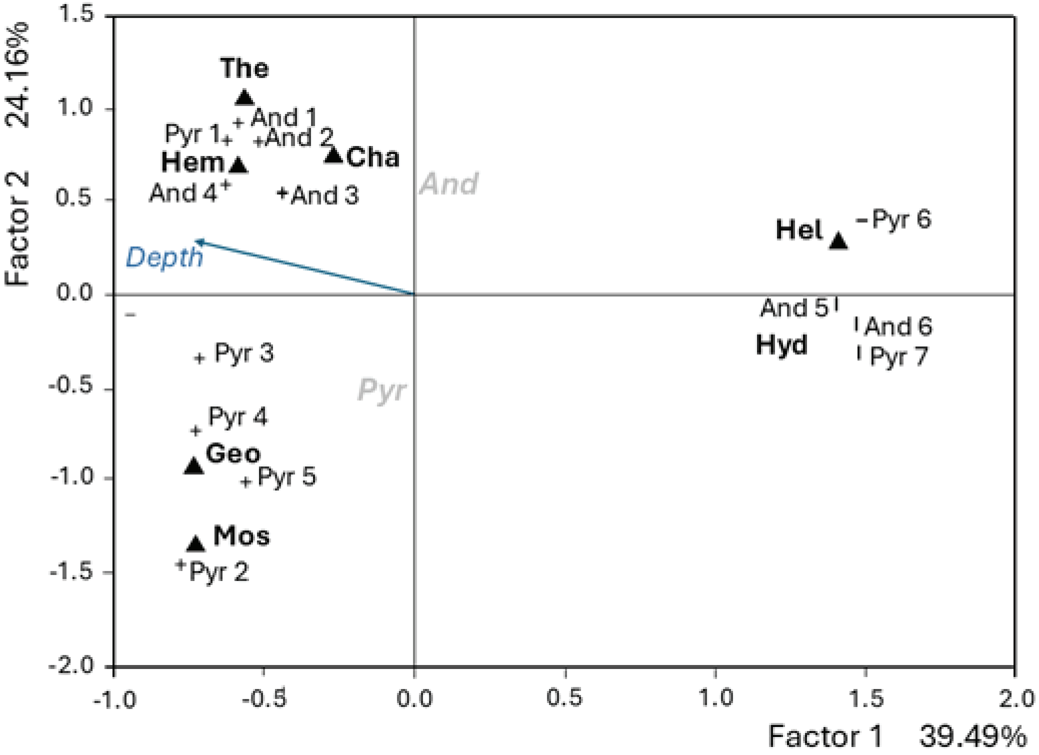

Figure 2: Correspondence Analysis biplot of zonation habitats and the clusters generated in the classification. The eigenvalues of axis 1 (horizontally) and axis 3(vertically) are 0.87 and 0.53; the eigenvalue of axis 2 (not shown) is 0.70. Groups obtained from the clustering analysis are represented as crosshairs (group 1), horizontal mark (group 2) and vertical marks (group 3). The biotypes are abbreviated to the part in italics as follows: *Cha*maeophytes, *The*rophytes, *Hemicryptophytes*, *Geo*phytes, Mosses. Plant communities are labelled as follows: And 1, *Eleocharis albibracteata-Festuca humilior* Community; And 2, *Gentianella primuloides-Plantago tubulosa* Community; And 3, *Cinnagrostis jamesonii-Distichia muscoides* Community; And 4, *Cinnagrostis orbygniana-Deschampsia eminens* Community; And 5, *Cotula mexicana-Lilaeopsis occidentalis* Community; And 6, *Ranunculus flagelliformis* Community; Pyr 1, *Nardus stricta* humid grasslands, Pyr 2, *Tricophorum cespitosum* Community; Pyr 3, *Juncus alpinoarticulatus* Community; Pyr 4, *Carex nigra* Community; Pyr 5, *Eriophorum angustifolium* Community; Pyr 6, *Carex rostrata* Community; Pyr 7, *Sparganium angustifolium* Community.

in the segregation of vegetation types is that which separates aquatic plant communities growing on gyttja from the other hygrophilous plant communities developing on histosols and gleysols (Table 4).

Zonation Comparison

The degree to which both zonations are correlated was examined using correspondence analysis. Figure 2 displays Factor 1 compared to Factor 3, and the location of life forms, plant communities, and sites, and clusters from the classification results. Axis 1 explained 39.49% of the inertia, and Axis 3 explained 24.16%. The first axis distinguished the plant communities in which the dominant biotypes were helophytes or hydrophytes from the others. Thus, this factor is highly correlated with the depth of flooding. The aquatic communities corresponded to both Andean and Pyrenean localities. The second axis separated the Andean vegetation from the Pyrenean one. The groups were characterized by geophytes and mosses for the Pyrenean site and by chamaephytes and hemicryptophytes for the Andean site. This factor is related to geographical features.

Discussion

Species richness of freshwater shorelines is controlled by abiotic factors in the frequently flooded zone (Lenssen et al., 1999). A decrease in species richness has been described towards deeper water (Fu et al., 2014). According to our results, vegetation zonation in subalpine wetlands under different macroclimates included a similar number of plant communities. Regardless of the zonation studied, our results also supported a decreasing pattern in species richness from terrestrial to aquatic habitats. In comparison to terrestrial habitats, aquatic habitats represent a stressful environment for plants, which is characterized by low carbon availability, sediment anoxia, and significant restrictions to sexual reproduction, among others (Santamaría, 2002). Thus, the shift from terrestrial to aquatic habitats represents environmental filtering that favors stress-tolerant taxa with wide plasticity, such as aquatic plants. This may explain the reduction in species richness found in the plant zonation pattern along the water-level gradient. Zonation is also known to be primarily structured by competition in shallow water and by physiological flooding tolerance in deep water (Sorrell et al., 2012). Moreover, seed germination requirements can help to explain community assembly along a hydroperiod gradient (Rosbakh et al., 2020). Nevertheless, comparing both catenas, the Bolivian wetland zonation showed an overall higher species richness than the European ones. This is in line with the importance of the Neotropics as one of the world's richest hotspots for macrophyte diversity (Murphy et al., 2019).

An important step in the vegetation zonation along the flood gradient is the transition between permanent aquatic habitats and those subjected to fluctuating water table influence (Molina et al., 2007). In both zonations, our multivariate analyses revealed a clear floristic differentiation between aquatic and swamp vegetation, on the one hand, and marsh and wet grassland vegetation, on the other. The same physiognomic patterns were found in aquatic habitats; the submerged habitats consisted of plant communities growing on oligotrophic gyttja sediments dominated by helophytes in shallower waters and by radicant hydrophytes in deeper or more permanent waters. Both helophytes and hydrophytes are widely distributed plants (Santamaría, 2002) although with different geographic patterns in which water-related environmental variables have a greater impact on the phylogenetic diversity of hydrophytes than those of helophytes (Zhou et al., 2023). Our study also showed that wetland zonations share a fringing vegetation belt composed of caespitose hemicryptophytes with vegetation dominated by cespitose grasses. Reduced snow and ice in mountains due to climate change pose threats to high-altitude wetlands (Joyce et al., 2016; Vento et al., 2024).

According to our results, the most obvious differences in plant life forms between the two zonations occurred in the intermediate flooding vegetation belts. Specifically, Orotemperate marshes were characterized by a high proportion of rhizomatous geophytes, whereas Orotropical marshes were characterized by pulvinulate chamaephytic vegetation were dominated by cushion plants. Morphology at the community level is correlated with environmental factors for alpine vegetation (Halloy and Mark, 1996). Geophytes inhabit cooler, and more thermally variable climates compared to non-geophytes, with temperature likely being a driving force in rhizome evolution (Howard et al., 2019). It may be inferred that geophytes are plant forms that are better adapted to more continental environments, such the Alpine high mountain, compared with the Andean mountains. Andean high-mountain peatlands characteristically host cushion plants, a unique plant life form (Navarro and Maldonado, 2002; Galán de Mera et al., 2003; Martínez-Amigo and Jaramillo, 2024). Cushion plants, initially associated with high-altitude and cold ecosystems (Aubert et al., 2014), exert a protective effect on guild-dependent plants in high-altitude peatlands (Raevel et al., 2018). Moreover, peatland cushion-plants create a microtopographic pattern of hollows and hummocks (Martínez-Amigo and Jaramillo, 2024) constituting an intermediate phase in the natural succession process between the hollows occupied by open water and aquatic plants and the grasslands still associated with wet conditions towards the edge of peatlands. One possible explanation for the occurrence of this distinct plant life form in high Andean mountains may be related to different environmental conditions such as a less continental and a higher UV radiation in the high-mountain Neotropics compared to Holarctic mountains.

Literature Cited

Aranguren, F., and J. Suárez. 1973. *Mapa Geológico de la Península Ibérica*. I.G.M.E.

Aubert, S., F. Boucher, S. Lavergne, J. Renaud, and P. Choler. 2014. 1914–2014: A revised worldwide catalogue of cushion plants 100 years after Hauri and Schröter. Alpine Botany 124: 59–70. https://doi.org/10.1007/s00035-014-0127-x

Biró, M., Z. Molnár, D. Babai, A. Dénes, A. Fehér, S. Barta, L. Sáfián, K. Szabados, A. Kiš, L. Demeter, and K. Öllerer. 2019. Reviewing historical traditional knowledge for innovative conservation management: A re-evaluation of wetland grazing. Science of the Total Environment 666: 1114–1125.

Bragazza, L. 1999. Spatial patterns of plant species in a poor mire on the Southern Alps (Italy). Plant Biosystems 133: 83–92. https://doi.org/10.1080/11263509909381535

Braun-Blanquet, J. 1979. *Fitosociología. Bases para el estudio de las comunidades vegetales*. Herman Blume, Madrid.

Čarni, A., N. Juvan, P. Košir, A. Marinšek, A. Paušič, and U. Šilc. 2011. Plant communities in gradients. Plant Biosystems 145: 54–64. https://doi.org/10.1080/11263504.2011.602730

Catalan, J., L. Camarero, M. Felip, S. Pla, M. Ventura, T. Buchaca, F. Bartumeus, G. de Mendoza, A. Miró, E. O. Casamayor, J. M. Medina-Sánchez, M. Bacardit, M. Altuna, M. Bartrons, and D. Díaz de Quijano. 2006. High mountain lakes: extreme habitats and witnesses of environmental changes. Limnetica 25: 551–584.

Chatanga, P., D. C. Kotze, T. W. Okello, and E. J. J. Sieben. 2020. Ecosystem services of high-altitude Afromontane palustrine wetlands in Lesotho. Ecosystem Services, 45: 101185.

CHE. 2002. *Estudio de la calidad ecológica integral de los tramos fluviales más importantes del río Cinca. Comisaría de Aguas (Ministerio de Medio Ambiente). Informe de Síntesis río Cinca.* Vol. 2. Confederación Hidrográfica del Ebro.

CISIA-CERESTA. 1998. *SPAD Version 3: Manuel de Prise En*

Main. CISIA-CERESTA, Montreuil, France.

De La Barra, N. 2003. Clasificación ecológica de la vegetación acuática en ambientes lacustres de Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 13: 65–93.

Fu, H., J. Zhong, G. Yuan, P. Xie, L. Guo, X. Zhang, J. Xu, Z. Li, W. Li, M. Zhang, T. Cao, and L. Ni. 2014. Trait-based community assembly of aquatic macrophytes along a water depth gradient in a freshwater lake. Freshwater Biology 59: 2462–2471. https://doi.org/10.1111/fwb.12443

Galán de Mera, A., C. Cáceres, and A. González. 2003. La vegetación de la alta montaña andina del sur del Perú. Acta Botanica Malacitana 28: 121–147.

Galán de Mera, A., H. Beltrán, J. Campos, E. Linares, J. Montoya, C. Trujillo, and J. Orellana. 2025. Diversidad de comunidades vegetales del Perú. Una revisión a través de una clasificación fitosociológica. Arnaldoa 31: 211–239. https://doi.org/10.22497/arnaldoa.312.31201

Gerdol R., A. Bonora, R. Marchenisi, R. Gualanchi, and S. Pancaldi. 1998. Growth response of *Sphagnum capillifolium* to nighttime temperature and nutrient level: Mechanisms and implications for global change. Arctic and Alpine Research 30: 388–395.

Gignac, L. D., B. J. Nicholson, and S. E. Bayley. 1998. The utilization of bryophytes in bioclimatic modeling: Predicted northward migration of mires in the Mackenzie River Basin, Canada, as a result of global warming. Bryologist 101: 572–587.

Halloy, S. R. P., and A. F. Mark. 1996. Comparative leaf morphology spectra of plant communities in New Zealand, the Andes and the European Alps. Journal of the Royal Society of New Zealand 26: 41–78.

Howard, C. C., R. A. Folk, J. M. Beaulieu, and N. Cellinese. 2019. The monocotyledonous underground: global climatic and phylogenetic patterns of geophyte diversity. American Journal of Botany 106: 850–863.

Hrivnák, R. 2005. Effect of ecological factors on the zonation of wetland vegetation. Acta Societatis Botanicorum Poloniae 74: 73–81.

Joyce, C. B., M. Simpson, and M. Casanova. 2016. Future wet grasslands: ecological implications of climate change. *Ecosystem Health and Sustainability* 2(9): e01240. https://doi.org/10.1002/ehs2.1240

Lenssen, J., F. Menting, W. van der Putten, and K. Blom. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. Oikos 86: 523–534. https://doi.org/10.2307/3546656

Lou, Y., G. Wang, X. Lu, M. Jiang, and K. Zhao. 2013. Zonation of plant cover and environmental factors in wetlands of the Sanjiang Plain, northeast China. Nordic Journal of Botany 31: 748–756. https://doi.org/10.1111/j.1756-1051.2013.01721.x

Maldonado, M., and E. Goitia. 2003. Las hidroecoregiones del Departamento de Cochabamba. Revista boliviana de ecología y conservación ambiental 13: 117–141.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Canadian Journal of Botany 64: 375–383.

Martínez-Amigo, V., and R. Jaramillo. 2024. Cushion plants from the Andes — an overview of current knowledge and some research needs. Wetland Science and Practice 42: 97–103.

Middleton, B. 2016. Cattle grazing in wetlands. Pages 1–16 in C. M. Finlayson, M. Everard, K. Irvine, R. J. McInnes, B. A. Middleton, A. A. van Dam, and N. C. Davidson, editors, *The Wetland Book*. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-6172-8_60–2

Miserere, L., F. Montacchini, and G. Buffa. 2003. Ecology of some mire and bog plant communities in the Western Italian Alps. Journal of Limnology 62: 88–96.

Mitsch, W. J., B. Bernal, and M. E. Hernandez. 2015. Ecosystem services of wetlands. International Journal of Biodiversity Science, Ecosystem Services & Management 11: 1–4. https://doi.org/10.1080/21513732.2015.1006250

Molina, J. A. 2017. Aquatic and wetland vegetation of the Iberian Peninsula. Pages 355–396 in J. Loidi, editor, *The Vegetation of the Iberian Peninsula.* Vol 2. Springer, Cham. https://doi.org/10.1007/978-3-319-54867-8_7

Molina, J. A., C. Pertíñez, A. Díez, and M. A. Casermeiro. 2004. Vegetation composition and zonation of a Mediterranean braided river floodplain. Belgian Journal of Botany 137: 140–154. https://www.jstor.org/stable/20794548

Molina, J. A., G. Navarro, N. De la Barra, and A. Lumbreras. 2007. Andean aquatic vegetation in central Bolivia. Phytocoenologia 37: 753–768. https://doi.org/10.1127/0340-269X/2007/0037-0753

Mucina, L., H. Bültmann, K. Dierssen, J.-P. Theurillat, T. Raus, A. Čarni, K. Sumberová, W. Willner, J. Dengler, R. Gavilán, M. Chytrý, M. Hájek, R. Di Pietro, D. Iakushenko, J. Pallas, F. J. A. Daniëls, E. Bergmeier, A. Santos Guerra, N. Ermakov, M. Valachovič, J. H. J. Schaminée, T. Lysenko, Y. P. Didukh, S. Pignatti, J. S. Rodwell, J. Capelo, H. E. Weber, A. Solomeshch, P. Dimopoulos, C. Aguiar, S. M. Hennekens, and L. Tichý. 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19: 3–264. https://doi.org/10.1111/avsc.12257

Murphy, K., A. Efremov, T. A. Davidson, E. Molina-Navarro, K. Fidanza, T. C. Crivelari Betiol, P. Chambers, J. Tapia Grimaldo, S. Varandas Martins, I. Springuel, M. Kennedy, R. P. Mormul, E. Dibble, D. Hofstra, B. A. Lukács, D. Gebler, L. Baastrup-Spohr, and J. Urrutia-Estrada. 2019. World distribution, diversity and endemism of aquatic macrophytes. Aquatic Botany 158: 103127.

Navarro, G., and M. Maldonado. 2002. *Geografía ecológica de Bolivia. Vegetación y ambientes acuáticos*. Fundación Simón I. Patiño, Cochabamba.

Podani, J. 2001. *Syn-TAX 2000. Computer Program for Data Analysis in Ecology and Systematics. User's Manual*. Scientia Publishing, Budapest, Hungary.

Raevel, V., F. Anthelme, R. I. Meneses, and F. Munoz. 2018. Cushion-plant protection determines guild-dependent plant strategies in high-elevation peatlands of the Cordillera Real, Bolivian Andes. Perspectives in Plant Ecology, Evolution and Systematics 30: 103–114. https://doi.org/10.1016/j.ppees.2017.09.006

Rahman, I. U., A. Afzal, Z. Iqbal, R. W. Bussmann, H. Alsamadany, E. Soares Calixto, G. M. Shah, R. Kausar, M. Shah, N. Ali, and F. Ijaz. 2020. Ecological gradients hosting plant communities in Himalayan subalpine pastures: Application of multivariate approaches to identify indicator species. Ecological Informatics 60: 101162. https://doi.org/10.1016/j.ecoinf.2020.101162

Raunkiaer, C. 1934. *The Life Forms of Plants and Statistical Plant Geography*. Oxford University Press.

Rivas-Martínez, S., D. Sánchez-Mata, and M. Costa. 1999. North American boreal and western temperate forest vegetation. Itinera Geobotanica 12: 5–316.

Rosbakh, S., S. S. Phartyal, and P. Poschlod. 2020. Seed germination traits shape community assembly along a hydroperiod gradient. Annals of Botany 125: 67–78.

Sánchez-Higueredo, L. E., J. A. Ramos-Leal, J. Morán-Ramírez, P. Moreno-Casasola, D. Lithgow, S. González de León, and L.A. Peralta-Pelaez. 2025. Wetland vegetation zoning as a response to groundwater complex systems. Science of the Total Environment 958: 177893.

Santamaría, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. Acta Oecologica 23: 137–154.

Schmeller, D. S., D. Urbach, K. Bates, J. Catalan, D. Cogălniceanu, M. C. Fisher, J. Friesen, L. Füreder, V. Gaube, M. Haver, D. Jacobsen, G. Le Roux, Y.-P. Lin, A. Loyau, O. Machate, A. Mayer, I. Palomo, C. Plutzar, H. Sentenac, R. Sommaruga, R. Tiberti, and W. J. Ripple. 2022. Scientists' warning of threats to mountains. Science of the Total Environment 853: 158611. https://doi.org/10.1016/j.scitotenv.2022.158611

Sieben, E. J. J. 2019. Zonal and azonal vegetation revisited: How is wetland vegetation distributed across different zonobiomes. Austral Ecology 44: 449–460. https://doi.org/10.1111/aec.12679

Snethlage, M. 2015. Short topic assessment: Integrated approaches for wetland conservation and management. France: European Topic Centre on Biological Diversity.https://www.eionet.europa.eu/etcs/etc-bd/products/etc-bd-reports/short_topic_assessment_wetlands

Sorrell, B. K., C. C. Tanner, and H. Brix. 2012. Regression analysis of growth responses to water depth in three wetland plant species. AoB Plants 2012: pls043. https://doi.org/10.1093/aobpla/pls043

Taylor, A., P. Weigelt, P. Denelle, L. Cai, and H. Kreft. 2023. The contribution of plant life and growth forms to global gradients of vascular plant diversity. New Phytologist 240: 1548–1560. https://doi.org/10.1111/nph.19011

Vento, B., J. Rivera, and M. Ontivero. 2024. Climate influence on future suitability of high-altitude wetlands in two natural protected areas from the Central Andes of Argentina. Perspectives in Ecology and Conservation 22: 240–249. https://doi.org/10.1016/j.pecon.2024.04.006.

Xu, G., X. Kang, F. Wang, W. Zhuang, W. Yan, and K. Zhang. 2024. Alpine wetlands degradation leads to soil nutrient imbalances that affect plant growth and microbial diversity. Communications Earth & Environment 5: 397. https://doi.org/10.1038/s43247-024-01562-w

Zhou, Y.-D., H. Qian, K.-Y. Xiao, Q.-F. Wang, and X. Yan. 2023. Geographic patterns and environmental correlates of taxonomic and phylogenetic diversity of aquatic plants in China. Journal of Systematics and Evolution 61: 979–989. https://doi.org/10.1111/jse.12939

APPENDIX I
SYNTAXONOMICAL SYNOPSIS

1. Intrazonal boreo-temperate European grasslands
Nardetea strictae Rivas Goday et Borja Carbonell in Rivas Goday et Mayor López 1966
  Nardetalia strictae Oberdeorfer ex Preising 1949
    Nardion strictae Br. Bl. In Br. Bl. & Jenny 1926
      Nardus stricta humid grassland (cervunal)
2. Azonal vegetation of Eurasian wetlands
2.1. Vegetation of bogs and fens
Scheuchzerio palustris-Caricetea fuscae Tx. 1937
  Caricetalia fuscae Koch 1926
    Caricion fuscae Koch 1926
      Tricophorum cespitosum Community
      Carex nigra Community
      Eriophorum angustifolium Community
      Carex rostrata Community
2.2 Vegetation of freshwater springs, shorelines and swamps
Littorelletea uniflorae Br.-Bl. et Tx. ex Westhoff et al. 1946
  Littorelletalia uniflorae Koch ex Tx. 1937
    Littorellion uniflorae Koch ex Klika 1935
      Sparganium angustifoliuwm Community
3. Vegetation of high-elevation peatlands of the tropical Andes
Plantagini rigidae-Distichietea muscoidis Rivas- Martínez & Tovar 1982
  Calamagrostietalia nitidulae Galán, Cáceres & González 2003
    Festuca humilior alliance
      Eleocharis albibracteata-Festuca humilior Community
  Plantaginetalia tubulosae Gutte 1985
      Gentianella primuloidis-Plantago tubulosa Community
  Calamagrostio jamesoni-Distichietalia muscoidis Rivas-Martínez & Tovar 1982
  Calamagrostion chrysanthae Rivas-Martínez & Tovar 1982
      Deschampsia chrysantha-Deschampsia eminens Community
      Cinnagrostis jamesonii-Distichia muscoidis Community
4. Sof-water vegetation of high-elevation Andean wetlands
Limoselletea australis Galán, Campos, Linares, Montoya, Torres & Vicente 2021
  Crassuletalia venezuelensis Cleef 1981
    Ditricho submersi-Isoetion lechleri Galán de Mera, Beltrán, Campos, Linares, Montoya, Trujillo & J.Orellana 2024
      Ranunculus flagelliformis Community