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# Fine-scale vegetation mosaics in Pyrenean mires are driven by complex hydrological regimes and threatened by extreme weather events

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**Abstract**

Holarctic mires are systems of great ecological value and limited alpine distribution. Their southernmost European boundary borders the Mediterranean region. Understanding how environmental factors influence the plant community distribution and its response to disturbances, especially in the water regime, is a key step for their management and conservation. Here, we report our study of the main ecological gradients that determine the distribution of different plant community types in the Trescuro mire system and their response to variations in the environmental conditions such as summer drought. We set up 30 sampling points across the vegetation mosaic where pH, electrical conductivity, water table depth, and ion concentration were recorded during the 2014 and 2015 summers. The results revealed that variation in the water table level is what most drives the vegetation distribution at the local scale, followed by the ion concentration. Soligenous communities, which are highly dependent on water run-off, were the most affected by the drought event in 2015. Because these communities are generally situated in the marginal parts of mire systems, summer drought periods may facilitate invasion by trees into the areas they occupy, which may eventually lead to a reduction of mire area. This study contributes to the understanding of the dynamics of these unique and complex systems through elucidating the relationship between the vegetation and climatic variations.

**KEYWORDS**

alpine mountains, bryophyte communities, environmental gradients, habitat disturbance, mires, protected areas, Pyrenees, vascular plant communities

## 1 | INTRODUCTION

Mires are fairly common ecosystems in Europe, especially in boreal regions, which contain more than 60% of the 187,000 km<sup>2</sup> of European peatlands (Čivić & Jones-walters, 2010; Raeymaekers, 2000). At southern latitudes, these habitats are far less widespread, being chiefly restricted to special topographic alpine positions. The Pyrenees represent the south-western distribution limit of these ecosystems, facing the Mediterranean region.

Mires have a wide range of ecosystem functions, such as carbon storage, acting as energy and water buffers, providing specific habitats for flora and fauna, etc. (Chimner, Lemly, & Cooper, 2010; Joosten, Tanneberger, & Moen, 2017). They host plant species and form habitats that are of great interest (Council Directive 92/43/EEC; Whittaker, 1970), especially within the Pyrenees and similar ranges, due to their regional scarcity. The loss and degradation of mires that has occurred over recent decades, mainly due to human activity, has led to a decrease of 70% in the total mire surface in Europe (Raeymaekers, 2000); as a

result, mires and bogs are the most threatened groups of habitats in the European Union (Janssen et al., 2016). All these characteristics make mire conservation and restoration a major priority on European and national agendas.

The shortage of nutrients and extreme hydrological conditions (flooding, water flushing, or overflow) in mires act as strong limiting factors for many species (Bridgham, Pastor, Janssens, Chapin, & Malterer, 1996). For this reason, the biotic communities of these areas are highly specialized and often include a high rate of unique and rare species that deserve high-conservation status (Jimenez-Alfaro et al., 2014). Moreover, due to this specialization, mire species are very sensitive to environmental changes that may lead to disturbance of the system. Particularly, they are sensitive to oscillations in the water regime associated with climate variations, such as decreasing precipitation and rising temperatures, or due to anthropogenic activity, such as water management by hydroelectric facilities. These disturbances could lead to a loss of mire habitats (Essl, Dullinger, Moser, Rabitsch, & Kleinbauer, 2012) in the lower mountain areas and restrict their distribution to higher alpine areas. Thus, understanding the response of mire vegetation to hydroecological conditions, especially during extreme weather events, is a key step in setting mire management and conservation within a context of global climate change.

In the Pyrenees, most mires are situated in basins exploited through hydroelectric power stations, which have directly destroyed some of these ecosystems in the past and are still a threat and a source of artificial disturbance. Nevertheless, the presence of dams and the possibility to ecologically regulate the hydrological regime could provide an opportunity to improve the state of conservation of these habitats.

The mire vegetation communities in southern European massifs have been studied over the last few decades (Aldasoro et al., 1996; Bragazza & Gerdol, 1999; Carrillo et al., 2008; Pérez-Haase, Batriu, & Ninot, 2012; Pérez-Haase & Ninot, 2017). Nevertheless, we are still far from the level of knowledge of Atlantic and boreal mires, which have been studied in depth and monitored for a long time. The vegetation of Pyrenean mires is mainly dominated by sedge-moss fen communities, in places including small ombrotrophic *Sphagnum* hummocks, and horsetail or tall-herb stands. Due to the physiographic and bioclimatic conditions, their optimal development is in the subalpine zone (Pérez-Haase et al., 2012).

Distribution patterns of mire communities along ecological gradients have been studied in different areas around the world (Bridgham et al., 1996; Castelli, Chambers, & Tausch, 2000; Sjörs & Gunnarsson, 2002). The main gradients that have been found to determine vegetation distribution are water table depth (hereafter, WTD); (Malmer, 1986; Negishi, 2014; Pérez-Haase & Ninot, 2017; Sekulová, Hájek, & Syrovátka, 2013), richness of nutrients and fertility (Gredol, 1995; Okland, 1989), and water acidity (Sekulová et al., 2013; Wheeler & Proctor, 2000). These gradients act together in mires and determine the composition and characteristics of the vegetation found at each point. Apart from isolated cases (Pérez-Haase, Batriu, Carrillo, & Ninot, 2011; Pérez-Haase & Ninot, 2017), Pyrenean mires have been poorly studied in terms of the relationship between environmental gradients and the distribution of plant communities. This study focuses on the Trescuro mires, which constitute a unique system, because of both its hydrological structure and the high degree of diversity of rare

species and valuable wetland habitats (Carrillo et al., 2008). It is a unique feature also the combination of so distinct habitats in a complex mire mosaic, which, in the Pyrenees, occurs only in few locations (Pérez-Haase & Ninot, 2017). Moreover, the Trescuro lakes and mires are included in an integral reserve within the Aigüestortes i Estany de Sant Maurici National Park, which has helped to keep it remarkably untouched and in a good state of conservation, despite the presence of hydroelectric dams in the basin and also pressures from human activity and cattle grazing.

This paper has two main objectives: (a) to evaluate the main ecological gradients that determine the distribution of different types of vegetation in the Trescuro mires, and (b) to analyse how different vegetation community types respond to variations in environmental conditions, paying special attention to a drought occurred in summer, 2015.

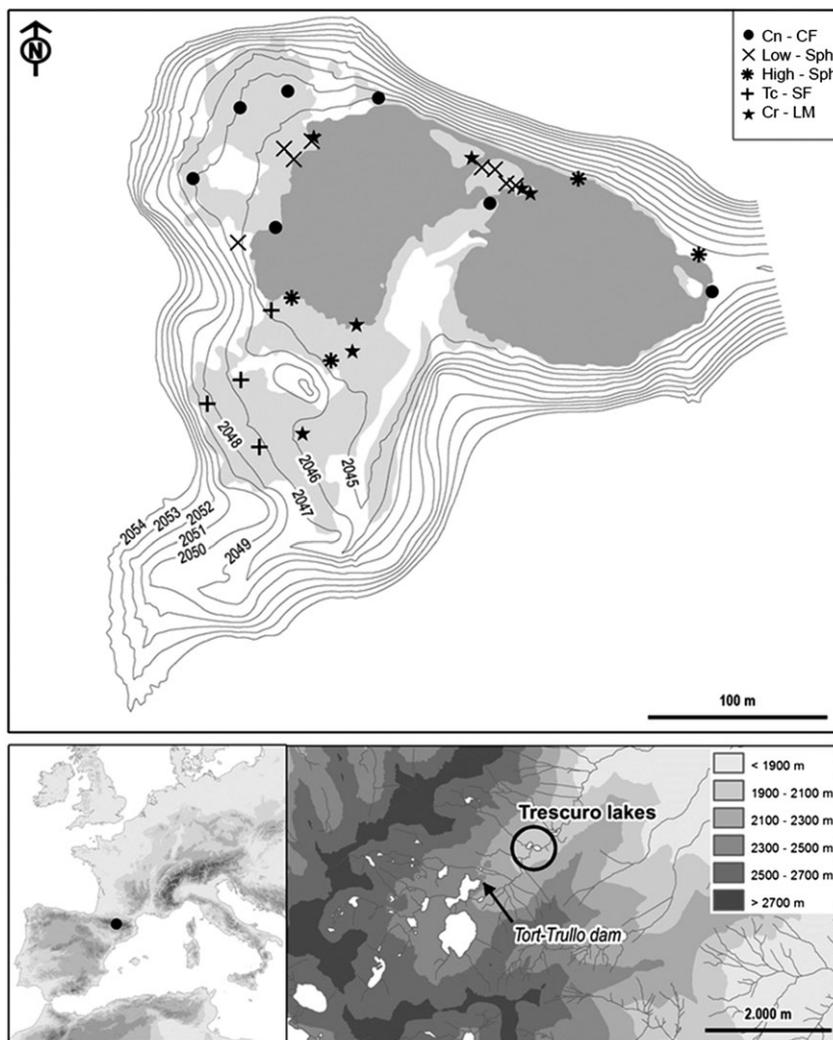
## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The Trescuro lakes and their surrounding mire complex are located in the Aigüestortes i Estany de Sant Maurici National Park, in central Catalan Pyrenees, NE Spain. The area is situated at 2,045 m a.s.l., and experiences a high mountain climate (cold-axeric bioclimate, following de Bolòs, Vigo, Masalles, & Ninot, 2005). The mean annual temperature is 5.3°C, and the average annual precipitation of the last 15 years is 1,150 mm with spring and autumn peaks (SMC [Servei Meteorològic de Catalunya], 2016).

The lentic complex consists of two small lakes 5.7 and 5.4 m deep with surface areas of 0.8 and 0.7 ha, and a total volume of 21,139 and 17,709 m<sup>3</sup> located on granitic substrate (Gacia et al., 1994; Generalitat de Catalunya, 2007). The two water bodies are well connected (Figure 1), and the main water inlet comes from the main river in the valley, which flows into the right lake; water is mainly supplied to the left lake through small rivulets. The topographic representation of the area (Figure 1) shows gentle relief surrounding the left lake, which promotes the development of mire communities. In contrast, the margins of the right lake are much steeper and mostly covered by *Pinus uncinata* woodlands.

Although nowadays the area is protected, water flow was artificially altered in the mid-20th century by the construction of hydroelectric dams and several subterranean channels upstream. Hydroelectric regulation is still ongoing and thus conditions the fluvial dynamics. As a whole, the lentic system is rich in plant biodiversity and habitats. Carrillo et al. (2008) reported up to 10 distinct CORINE Biotopes. Some rare and remarkable plant communities are found in the transition mires (*Sphagnum* quaking mires with *Carex rostrata* along the lake margins), bog woodland of mountain pine (*P. uncinata*), and the active raised bogs with *Sphagnum* and *Ericaceae*. The latter two units are classified as priority habitats of community interest (HCI) by the EC legislation (Council Directive 92/43/EEC; Whittaker, 1970). As a whole, it could be classified as a mixed mire, with both calcicolous and acidophilic vegetation. Regarding the hydrological conditions, a great part of the mire is situated on a gentle slope with soligenous conditions created by several streams and the surface water circulation. But, in the lower areas, there are numerous



**FIGURE 1** Location of the study site and sampling points, classified according to the vegetation type. In the main figure, dark grey represents lake surface, and light grey represents the main mire area. Abbreviations stand for *Carex nigra* fens (Cn-AF), *Trichophorum cespitosum* fens (Tc-SF), *Carex rostrata* beds (Cr-LM), Low *Sphagnum* hummocks (Low-Sph), and High *Sphagnum* hummocks (High-Sph)

*Sphagnum* ombrotrophic bogs, some of them raised more than 1 m above the surface. The extension and density of the bog woodland has changed over time, partly due to human activity. During the last decades, the density of the mountain pine population in the mire system has clearly increased in detriment of other mire units (Figure S1), which may be envisaged as a thread for mire conservation. The landscape surrounding the lentic system is dominated by forests of mountain pine (*P. uncinata*) with *Rhododendron ferrugineum*. Higher on the slopes of the basin, the forest gives way to a landscape of *Festuca eskia* and *Nardus stricta* grasslands and rocky areas (Carrillo et al., 2008).

## 2.2 | Vegetation, groundwater, and soil sampling

We first identified the main hydrological regimes of the mire and the main physiognomic vegetation types in it. We set up 30 sampling points spread across the study area, which covered all the hydrological conditions and all physiognomic vegetation types with at least three points each.

At each sampling point, we installed a longitudinally perforated Poly Vinyl Chloride (PVC) pipe sunk vertically 1 m into the mire, in order to monitor Water Table Depth (WTD) and to collect samples of groundwater for subsequent chemical analysis. Around each PVC pipe, we carried out a vegetation inventory in an area of 2.5 × 2.5 m.

These consisted of exhaustive floristic records of vascular plants and bryophytes. Each species was assigned a value on the Domin scale ranging from 1 to 10, according to its projected cover (Rodwell, 1991; van der Maarel, 1979). The names of the vascular plants followed de Bolòs et al. (2005), except for *Trichophorum cespitosum* (L.) Hartm., and those of bryophytes followed Casas, Brugués, Cros, and Sérgio (2006) and Casas, Brugués, Cros, Sérgio, and Infante (2009).

Water sampling was carried out fortnightly during 2014 and 2015 growing seasons (from June 18 to October 9, 2014 and from June 2 to October 30, 2015). It included field measurements of WTD (both seasons) and, in the summer of 2014, the collection of water from each pipe in order to measure pH and electrical conductivity. Then, WTD, electric conductivity, and pH were measured again in June 2016 by means of a portable instrument. Water samples were stored frozen until analysis. Once in the laboratory, we first filtered the water (pore diameter, 20 μm), and then the concentrations of calcium, silicon, sodium, iron, aluminium, sulphur, zinc, copper, potassium, phosphorus, magnesium, and manganese were analysed using inductively coupled plasma mass spectrometry.

In order to measure the water levels of the lakes continuously, an automatic data logger was installed in each lake. The loggers measured the water levels every hour over the entire study period in 2014 and 2015.

In addition, we dug out a soil core by means of a steel bore at each sampling point for the purpose of characterizing the upper soil layers (~20 cm) in terms of peat depth and other characteristics.

## 2.3 | Data analysis

In order to classify the vegetation relevés numerically, the values of plant cover were transformed into the Combined scale (van der Maabel, 1979). We then computed the Hellinger distance matrix of the species data (Borcard, Gillet, & Legendre, 2011a) to calculate the floristic relationships between plots, and we performed beta-flexible hierarchical clustering on them (beta value = -0.25; Borcard, Gillet, & Legendre, 2011b; Legendre & de Cáceres, 2013). When beta is set at -0.25, the beta-flexible clustering optimally represents distances among samples (Legendre & Legendre, 1998).

Once the dendrogram was obtained from the hierarchical clustering, the number of ecologically significant species for each cluster level (from level 2 to 10) was calculated by means of indicator values. This quantitative index measures the statistical correspondence of species to each of the classes forming a classification (de Cáceres & Legendre, 2009). We used the highest number of indicator species as a stopping criterion for selecting the cluster level (Tichý, Chytrý, Hájek, Talbot, & Botta-Dukát, 2010).

At the same time, in order to analyse the relationship between the environmental variables and the distribution of the vegetation, we carried out a canonical correspondence analysis (CCA), using the software CANOCO (Lepš & Smilauer, 2003). To select the significant explanatory variables in the model ( $p$  value <0.05 in a Monte Carlo permutation test), we used a stepwise selection procedure. The metric coordinates of each point were analysed as covariables in order to factor out the effect of spatial autocorrelation.

Before the analysis was run, we performed some transformations on the data. Regarding the electrical conductivity, when the pH is below 5, proton conductivity becomes a significant component of the measured conductivity and it has been shown that corrected conductivity data correlate better with vegetation distribution (Rydin & John, 2006; Sjörs, 1950). So that, we eliminated the conductivity component following Sjörs (1950). Also, we calculated Pearson

correlation coefficients between the explanatory variables. When the correlation between two variables was above 0.75, we discarded one of them.

Finally, the ecological data from different vegetation community types were compared using analysis of variance (ANOVA) for the normally distributed variables. The variables with a non-normal distribution were log-transformed, and those that still presented a non-normal distribution after the transformation were analysed with the Kruskal–Wallis test. ANOVA and Kruskal–Wallis analyses were performed with R (R Core Team, 2013), using the packages “vegan” (Oksanen et al., 2015) and “cluster” (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2016) for the hierarchical clustering classification and the dendrogram representation and “indicspecies” (de Cáceres & Jansen, 2016) for the species associated in each group.

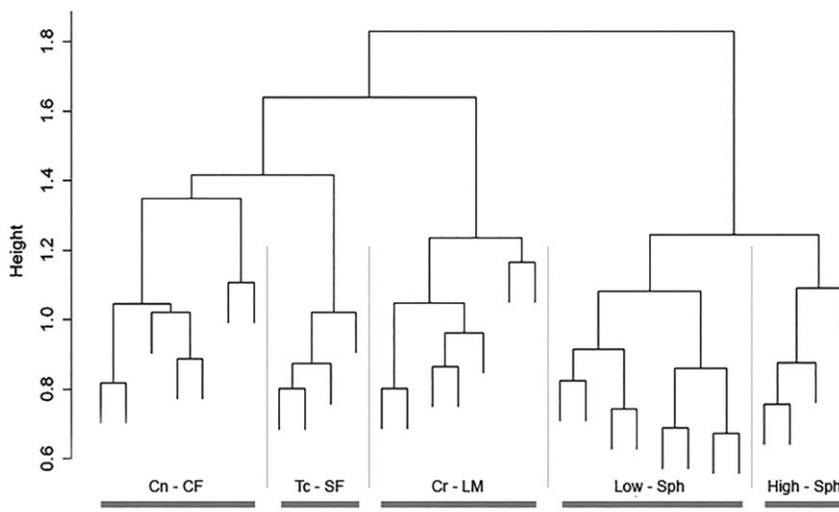
## 3 | RESULTS

### 3.1 | Vegetation

From the 30 sampling points, 108 species were recorded, of which 62 were vascular plants and 46 were bryophytes. Eight species were found in more than 50% of the 30 sampling points, although the cover of these species was highly variable. Only four species had a mean cover of more than 10%: two Cyperaceae (*C. rostrata* and *T. cespitosum*), one Rosaceae (*Potentilla erecta*) and one sphagnum moss (*Sphagnum capillifolium*).

In the first step, the clustering of vegetation samples (Figure 2) yielded four vegetation groups (or vegetation types), which corresponded to the best cluster level with 62 indicator species. However, we subsequently divided one of these groups, the *Sphagnum* hummocks, into two subgroups, low and high hummocks, due to the heterogeneity and complexity of the group. This partition also obtained the maximum number of indicator species statistically associated with each vegetation group.

The five groups were named according to their species composition and characteristics. The first one, *Carex nigra* fens, includes vegetation plots dominated by *C. nigra* and a number of species that are characteristic of alkaline fens such as *Carex davalliana* or *Swertia*



**FIGURE 2** Vegetation plots grouped by hierarchical clustering. Each group is named according to its composition and the characteristics of the vegetation. The plant community types are identified as in Figure 1

*perennis*. The *T. cespitosum* fens were mostly soligenous fens situated on gentle slopes with a constant surface or subsurface water flow. The *C. rostrata* beds were situated along the lake margins and frequently remained covered by the lake water. Low-*Sphagnum* hummocks were only slightly raised above the surrounding fens. Some hygrophilous plants like *Viola palustris* and *C. rostrata* were found there among the most abundant *Calluna vulgaris* and *Potentilla erecta*. Also, low hummocks showed covering of *Sphagnum* species, mainly *S. magellanicum*, *S. russowii*, and *S. teres*. High-*Sphagnum* hummocks included higher bogs, which resulted into a deeper water table position with respect to the hummock top. They were characterized by species that are unable to thrive in flooded substrata, like *Vaccinium myrtillus*, *R. ferrugineum*, or *P. uncinata*, and exhibited high-cover percentages of *Sphagnum capillifolium*.

As for soil types, all sampling points have a hystic horizon situated above a sandy layer including coarse grains. However, the thickness of the hystic horizon is variable between plant communities (Table S3). Low and high-*Sphagnum* hummocks are always peaty (i.e., hystic horizon or peat  $\geq 30$  cm), whereas other vegetation types are not necessarily peaty. Alkaline and soligenous fens showed the lowest mean peat thickness (33 and 41 cm, respectively). In relation to soil saturation, for all vegetation types, the mean minimum WTD was higher than the mean peat depth.

### 3.2 | Relationship between vegetation and environmental variables

The correlation matrix (Table S1) revealed correlations higher than 0.75 or lower than -0.75 between some of the variables; for this

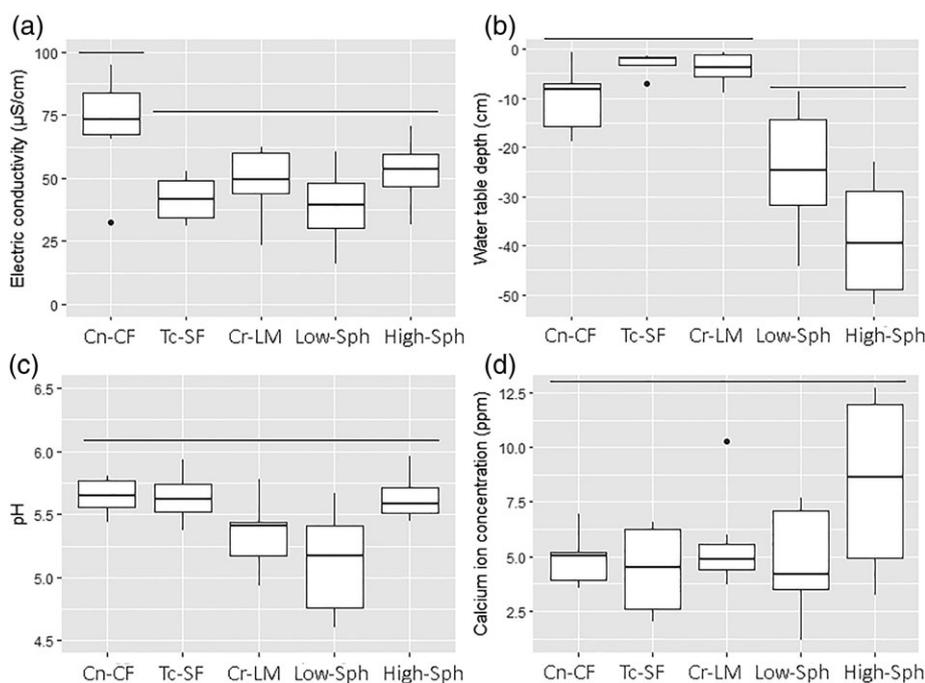
reason maximum WTD, minimum WTD, days of WTD under -30 cm, and Sulphur concentration were discarded, whereas the rest of variables showed in Table S1 were included in the analysis.

The main environmental variables showed interesting trends within the vegetation studied, although clear differences between plant community types were scarce (Figure 3). The electrical conductivity values of *C. nigra* fens were significantly higher than the rest of the communities (ANOVA;  $F = 4.12$ ;  $p = 0.011$ ; Figure 3a). There were no significant differences in pH found between the mires (ANOVA;  $F = 2.75$ ;  $p = 0.108$ ; Figure 3b).

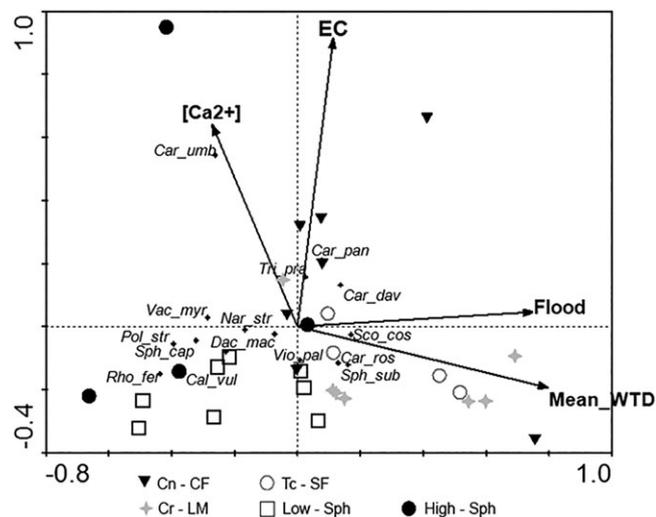
The mean WTD in the two *Sphagnum* communities (Low Sph and High Sph) was found to be significantly deeper than in the other communities (Kruskal-Wallis;  $K = 2.02$ ;  $p = 0.002$ ; Figure 3c). The high-*Sphagnum* hummock community had the lowest levels, which averaged 40 cm under the surface.

Calcium was the most abundant ion; the mean value for the whole system was 5.56 ppm, but the differences between communities were not significant (ANOVA;  $F = 3.54$ ;  $p = 0.124$ ; Figure 3d and Table S1). In most cases, copper, zinc, and phosphorus had values below the detection threshold of the method used (0.2 ppm for P and 0.01 ppm for Cu and Zn). For this reason, their concentrations were not included in the statistical analysis.

In order to summarize the main environmental gradients describing the vegetation variability in the mire, we performed a step-wise CCA (Figure 4). The first two axes had eigenvalues of 0.39 and 0.28, respectively, and together accounted for 17.2% of the total variance (10.0% on the first axis and 7.2% on the second axis). In the figure, the sampling points are identified as symbols and appeared mostly spread along the first axis of variation. This axis is strongly related to water table variables, such as mean WTD level and total number of



**FIGURE 3** Box plots of the main ecological variables: electric conductivity (a), pH (b), water table depth (c), and calcium concentration (d; measured from the 1 m deep PVC pipes). The plant community types are identified as in Figure 1. Horizontal lines group non-significantly different vegetation types following ANOVA/Kruskal Wallis tests; see text for more details on the statistical procedure



**FIGURE 4** Canonical correspondence analysis ordination showing the sampling points and the most frequent species, with respect to the significant variables (EC, Electric conductivity; [Ca2+], Calcium concentration; Flood, number of flooding days, and Mean\_WTD, Mean water table depth). The plant community types are identified on the legend as in Figure 1. The 15 species with best fit to the ordination are shown. Their abbreviated names correspond to (in alphabetical order): *Calluna vulgaris*, *Carex davalliana*, *Carex panicea*, *Carex rostrata*, *Carex umbrosa ssp. huetiana*, *Dactylorhiza maculata*, *Nardus stricta*, *Polytrichum strictum*, *Rhododendron ferrugineum*, *Scorpidium cossonii*, *Sphagnum capillifolium*, *Sphagnum subsecundum*, *Trifolium pratense*, *Vaccinium myrtillus*, and *Viola palustris*

flooded days, whereas the second axis is related to water mineral content and nutrient richness variables, such as electric conductivity and calcium concentration.

### 3.3 | Hydrological regime

Because mean WTD was found to be the variable with the greatest influence on the vegetation distribution, we carried out a more detailed analysis of hydrological data in each community type.

WTD oscillated from  $-44$  cm in the highest areas and in *Sphagnum* hummocks to positive values (12 cm), which indicate flooding, along the lake and rivulet margins. Areas with a deeper mean WTD often corresponded to raised bogs produced by peat accumulation and therefore do not necessarily correspond to marginal areas of the mire system.

There was a slightly lower mean WTD in 2015 than in 2014 at all the points sampled, although the differences were not significant (Kruskal–Wallis;  $K = 3.02$ ;  $p = 0.082$ ), and the water level of the lakes (recorded by automatic data loggers) were also higher in 2014. Likewise, the oscillation amplitude of the measurements was higher in 2015 than in 2014 at all the sampling points, but the differences were not significant (Kruskal–Wallis;  $K = 1.81$ ;  $p = 0.178$ ).

### 3.4 | System response to precipitation

In order to determine the response of each type of vegetation to changes in water intake, the oscillations of WTD were compared with precipitation data recorded at the closest weather station (Figure 5),

situated less than 2 km away from Trescuro, at 2,519 m a.s.l. During the 122 days of the 2014 study period (from June 18 to October 9, 2014), there were rain events on 51 days, with a total precipitation of 602.4 mm. During the 121 days of the 2015 period (from June 2 to October 30), there were 46 rainy days, with a total of 594.5 mm. In spite of the similarity of these raw data from one year to the next, the summer of 2015 included a noticeable dry period: Between mid-June and mid-July, when there were only two rain events, totalling just 19.1 mm. This drought episode, highlighted in grey in Figure 5, provided a great opportunity to evaluate the response of the different community types to extreme events.

During 2014, mean WTD was significantly different for all the vegetation groups (Kruskal–Wallis;  $K = 423.38$ ;  $p = 0.00$ ) except between the lake margins and the *T. cespitosum* fens; whereas in 2015, all the vegetation groups were significantly different in this aspect (Kruskal–Wallis;  $K = 220.46$ ,  $p = 0.01$ ). No significant differences were found between the 2 years of study within community types (Kruskal–Wallis;  $K = 312.31$ ,  $p = 0.081$ ). Nevertheless, the amplitude of WTD was significantly higher in 2015 than in 2014, indicating higher variability during 2015, when the drought period occurred (Figure 6). During the drought period, the community type that suffered the largest decrease in WTD was the *T. cespitosum* fen, which dropped from  $-6.5$  cm to  $-25.9$  cm (Figure 5).

Regarding the lake water level oscillation, a small delay in the response to the precipitation events of the left lake was detected, because it took longer there than in the right lake for the level to increase after a precipitation episode. In 2014, the amplitude of water level registered was of 13.8 cm in the left lake and 16.0 cm in the right lake, whereas in 2015, the amplitudes were 25.0 and 25.1 cm, respectively.

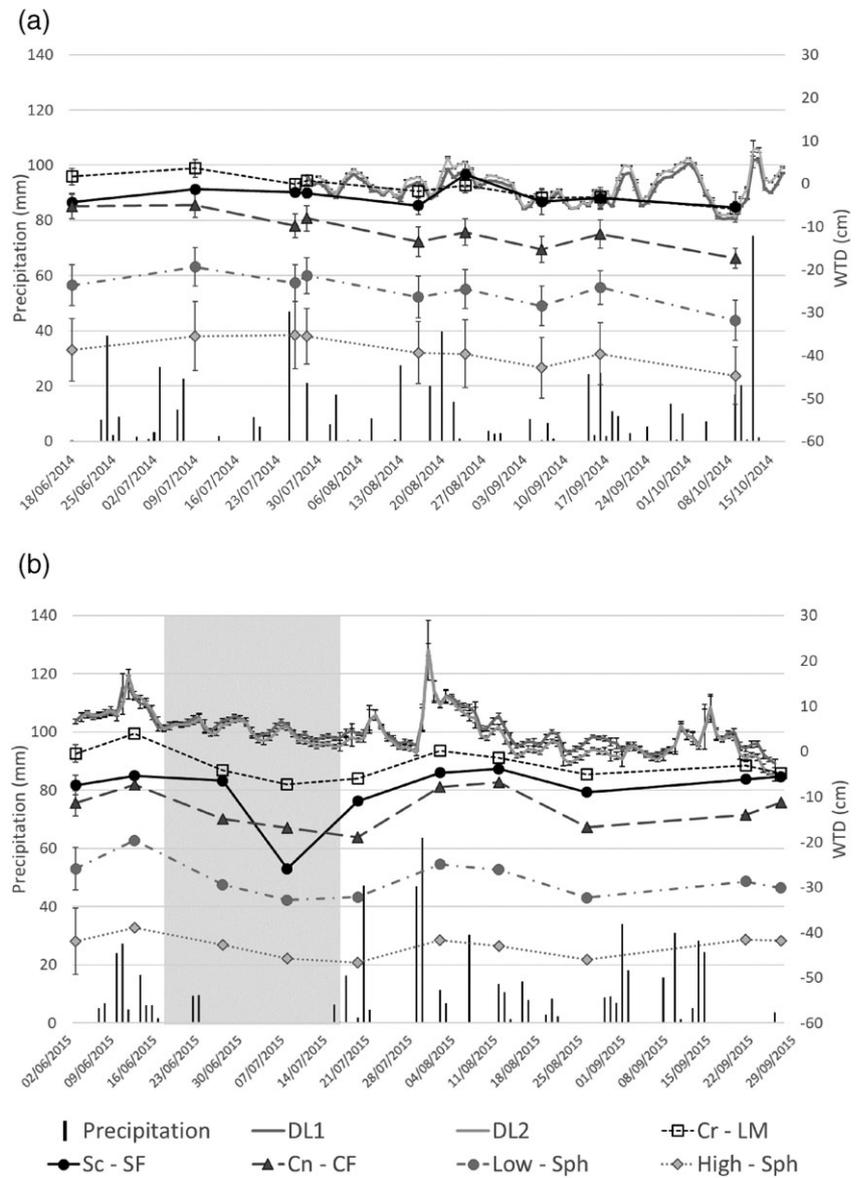
## 4 | DISCUSSION

### 4.1 | Vegetation and ecological gradients

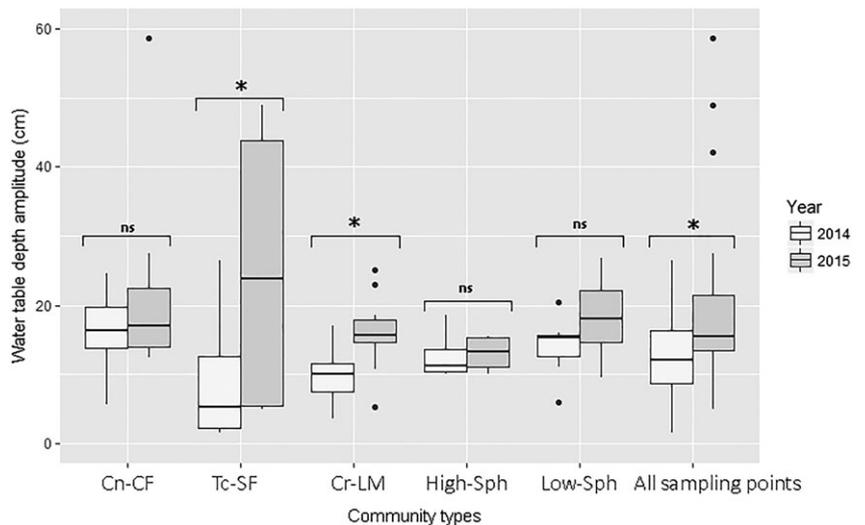
The classification of the mire vegetation into five community types (Figure 2) is a result of the contrasting species composition found in the mire vegetation and may be understood as the plant response to environmental gradients. Moreover, it is consistent with the previous description of the vegetation in the area using a more straightforward phytosociological method (Carrillo & Ninot, 1992).

The WTD (mean WTD and number of flooded days) was the main ecological gradient explaining the variance in the vegetation. Similar results in previous studies (Bragazza, Rydin, & Gerdol, 2005; Castelli et al., 2000; McIlroy & Allen-Diaz, 2012) also support the idea that at detailed scales, mean WTD and WTD oscillation is the most important ecological gradient that determines vegetation composition and distribution (Raulings, Morris, Roache, & Boon, 2010), especially in high-mountain mires (Pérez-Haase & Ninot, 2017).

As a secondary driver, water mineral content (evaluated through ion concentration) represented a relevant gradient, as in other alpine mires (Gredol, 1995). In contrast, the groundwater pH gradient was not selected as a determinant ecological gradient for the vegetation in the Trescuro mires, although there were relevant differences



**FIGURE 5** Water table depth variation in the communities studied (identified as in Figure 1) and variation in the water surface level of the two lakes (DL1, left lake; DL2, right lake); and precipitation registered during the study period, 2014 (a) and 2015 (b). The grey shading corresponds to the 2015 drought period



**FIGURE 6** Amplitude of the water table depth in the community types sampled for 2014 and 2015. The plant community types are identified as in Figure 1. Asterisks denote significantly different amplitudes between both years ( $P < 0.05$ ) and *ns* not significant differences

between the community types. The reason why pH did not appear as a significant gradient could be the similarity of the effects with the water mineral content, which could in part mask the pH effects in the stepwise selection of variables in the CCA ordination.

*Carex rostrata* beds, situated along the lake margins, were characterized by their thriving at the highest water table level, with some days of flooding. *Trichophorum cespitosum* and *C. nigra* fens presented much more variable WTD, depending on the location of each plot in relation to the streams and lake margins. Regarding both low and high-*Sphagnum* hummocks, they have a permanent low-water level as they are raised up from the rest of the mire. The values of WTD and pH, and the area covered by the communities, leads them to be included in “bog hummocks” and “fen carpets,” respectively, following the terminology proposed in Wheeler and Proctor (2000) and Okland, Okland, and Rydgren (2001). Nevertheless, the great variability in the concentrations of calcium found in the high hummocks does not fit with either of these categories. This variability is most probably due to the fact that the 1-m long-sampling pipes took water from lower depths than the bottom of the hummocks, which are influenced by the water in the surrounding array of *Trichophorum* fens, whereas the higher parts of the hummocks are almost exclusively influenced by rainwater. Therefore, hummocks have transitional conditions between the minerotrophic fen at the base and the ombrotrophic conditions of the hummock top (Rydin & John, 2006). Pyrenean *Sphagnum* bogs represent the southernmost location of this community type, so they are on the verge of extinction from a geographical perspective (Harrison, Berry, Butt, & New, 2006; Joosten et al., 2017). The high dependence of these bogs on precipitation contributions means that the decrease in precipitation southwards in Europe could become a relevant threat for these valuable habitats (Hedwall, Brunet, & Rydin, 2017; Strack, 2008).

Nevertheless, it is also important to take into consideration that at different study scales, the gradients that drive vegetation distribution in mires could vary. In studies where ecological gradients have been considered at a local scale, WTD and the water mineral content have been shown to be the main drivers of vegetation distribution (Rydin & John, 2006) and it describes the hydrological conditions better than other measures, such as the soil moisture, determined by the capillary properties of the soil (Sekulová et al., 2013). However, in regional scale studies, climate variables and pH gradients were the most relevant (Okland, 1989; Sekulová et al., 2013).

## 4.2 | System response to water input variations

Over the last 50 years, there has been an increase in climate irregularities and, especially, a higher frequency of periods of drought during the summer months. The summer temperature has risen 0.4°C per decade, and precipitation has decreased by around 28 mm per decade. Moreover, these trends are very likely to increase throughout central Europe and the Mediterranean area in the coming decades (IPPC [Intergovernmental Panel on Climate Change], 2013). In the Pyrenees, particularly in the eastern Iberian watersheds (where Trescuro is located), there is a strong evidence of a significant reduction in summer rainfall (OPCC [Observatori Pirinenc del Canvi Climàtic], 2014; Serra, Burgueño, Martínez, & Lana, 2006).

Mires are highly sensitive to these climate variations, and summer drought periods have a negative impact on the hydrological regime (Fenner & Freeman, 2011; Romanowicz, Siegel, & Glaser, 1993) and subsequently on vegetation, especially on communities that are dependent on a shallow-water table and surface run-off (Breeuwer et al., 2009). Moreover, recently, Jassey et al. (2018) found that when the WTD fell below the tipping point of -24 cm, the peatland respiration increased significantly (through increased fungal activity). Nevertheless, the response of the different community types in a mire system to this drought is not fully understood, partly due to the varying resilience of the plant species and the different habitats.

A great opportunity to analyse the response of mire vegetation to such a disturbance arose following the drought period that occurred in the summer of 2015, consisting of 22 days of no precipitation and with very low levels of atmospheric humidity. Moreover, the average monthly temperature was 3.5°C higher than a previous 30-year average July temperature (period 1961–1990; Servei Meteorològic de Catalunya, 2015).

This case study is very significant because drought events represent a real threat to Pyrenean mires. According to the hydrological response recorded at the 30 sampling points in the Trescuro mire, distinct plant community types responded in a similar way to the regular water intake and outlet. However, during extreme weather events such as severe drought periods, different vegetation types may respond in distinct consistent ways to the variations (Breeuwer et al., 2009; Harrison et al., 2006).

*Carex rostrata* lake margins are highly correlated with lake water level oscillations. Thus, during the drought event, WTD dropped a mean of 5 cm.

*Carex nigra* fens, situated near streams or even near the lakeshore, showed greater water buffering capacity and resistance to drought, maintaining a relatively constant WTD through the 2014 and 2015 summers. This may be partly due to the higher water retention capacity of these fen soils, which are finer-textured and peaty.

The *Sphagnum* hummocks, especially the highest ones, have a transition of hydrological characteristics from minerotrophic conditions in the lower parts to ombrotrophy at the top. This structure leads to precipitation water being retained (van Breemen, 1995) and taking more time to reach the underground water. Therefore, the water level depth remained locally more stable, with the lowest amplitude values even during 2015, when the drought event occurred (Figure 5).

Meanwhile, the *T. cespitosum* soligenous fens are highly related to flowing surface water, which is highly dependent on the precipitation regime. In the Trescuro system, they are mostly situated in the peripheral area of the mire, which is the most sensitive area to drought episodes (Hose, Bailey, Stumpp, & Fryirs, 2014). During the first days of the 2015 drought period, mean WTD of this community maintained similar levels as it was receiving run-off water. Nevertheless, when a critical drought threshold was reached, the surface intake stopped, and WTD dropped more than 20 cm on average. Some of the pipes became completely dry, indicating that the water level was below 100 cm. These characteristics make this community type the most sensitive to summer drought episodes.

On peaty soils, capillary fringe keeps soil water-saturated above the WTD (Wheeler, 1999). This keeps the anoxic (or hypoxic) conditions in the main rooting zone, and consequently, it may have a

determinant role on vegetation. However, in the *Trichophorum* soligenous fen plots—the most peripheral within the mire mosaic—capillary fringe is unlikely to influence the rooting zone because WTD was too deep. Therefore, we expect ecological processes related to water table drawdown not to be buffered by capillary fringe in those sampling points showing extreme low values.

Regarding root hypoxia, the rooting zone in mires is usually above the mean WTD (Fan, Miguez-Macho, Jobbagy, Jackson, & Otero-Casal, 2017), except for *C. rostrata* lake margins, which are adapted to flood. Consequently, sharp water table drawdown may lead to a decrease in stress by waterlogging on roots, which could be especially relevant to plants not adapted to saturated soils. In summary, our data indicate that mires are resilient to environmental changes up to a certain level of disturbance, but they may shift to new states when a critical point is reached, as described by Heijmans (2013). This could potentially lead to colonization by vascular plants adapted to more xeric conditions, such as ericaceous shrubs and other woody plants (Belyea & Baird, 2006; Breeuwer et al., 2009; Dise, 2009). So, a higher frequency of drought periods will lead to greater soil oxygenation, thereby weakening fen species and allowing the settlement of woody species, such as *P. uncinata* and *Ericaceae* (Heijmans, Van der Knaap, Holmgren, & Limpens, 2013). Because the resulting forested peatland has higher evapotranspiration than do open mires, positive feedback may operate by enhancing further encroachment by woody plants, and thus a reduction in the size of the mire (Hedwall et al., 2017; Holmgren et al., 2015). This could be operating in the Trescuro system, where over the last decades, the tree cover has increased from 20% to almost 35% (See Figure S1).

Although all the Trescuro mire system is interconnected, the differences recorded in the hydrological functioning between the two lakes suggest that there are site-specific responses within the system following extreme events. Because the main river enters exclusively into the right lake, increases in flow produces rapid rises in its water level in response. Such peak level values occurred after strong rainfall events (Figure 5) and following generalized snow melt at the beginning of summer. The connections between the two lakes through narrow water channels imply that the effects of flash floods in the main river are far less noticeable on the left lake. Similarly, as this left lake is mostly fed by small surface streams (Figure 1), the water level both in this lake and in the surrounding mires is less sensitive to water shortages in the main river. This suggests that any significant disturbance due to variation in the river flow, whether caused by a downpour or by variations in the dam water management, would affect the mires depending on the right lake more critically than those situated around the left lake.

### 4.3 | Concluding remarks

This study has determined that the hydrological regime, specifically, variations in WTD, is the most significant ecological gradient for the mire vegetation distribution at the local scale. The comparative dynamics of the water level in the lakes and in the mire units presented here contribute to a better understanding of the functioning of alpine mires. Our results show that the response to extreme events

depends on the vegetation community types, and on the situation of each community within the mire, generating a complex mosaic of vegetation typologies and environmental conditions at the fine scale that suggests that the mire system partially resists extreme events such as those measured within this study. Nevertheless, if the frequency of such events increases, as climate models predict, Pyrenean mires are likely to suffer severe consequences and even end up disappearing. In Trescuro, we found that soligenous communities depending on flowing surface water, often situated at the edges of the mire, are the most sensitive units to drought events. Such events may enhance invasion by trees and subsequently the reduction of the mire area. Our study suggests that in southern mountain ranges, scientists and land managers can assess drought events effects on mires by detailed monitoring of peripheral soligenous fens depending on run-off waters.

We hope that this case study will contribute to building good approaches to mire management and conservation strategies in a context of global climate change. This is particularly important in south European mountain landscapes, where mountain mires are at their biogeographical limit and subject to very restrictive conditions.

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