LIFE+ LIMNOPIRINEUS: CONSERVATION OF AQUATIC HABITATS AND SPECIES IN HIGH MOUNTAINS OF THE PYRENEES

TECHNICAL REPORT

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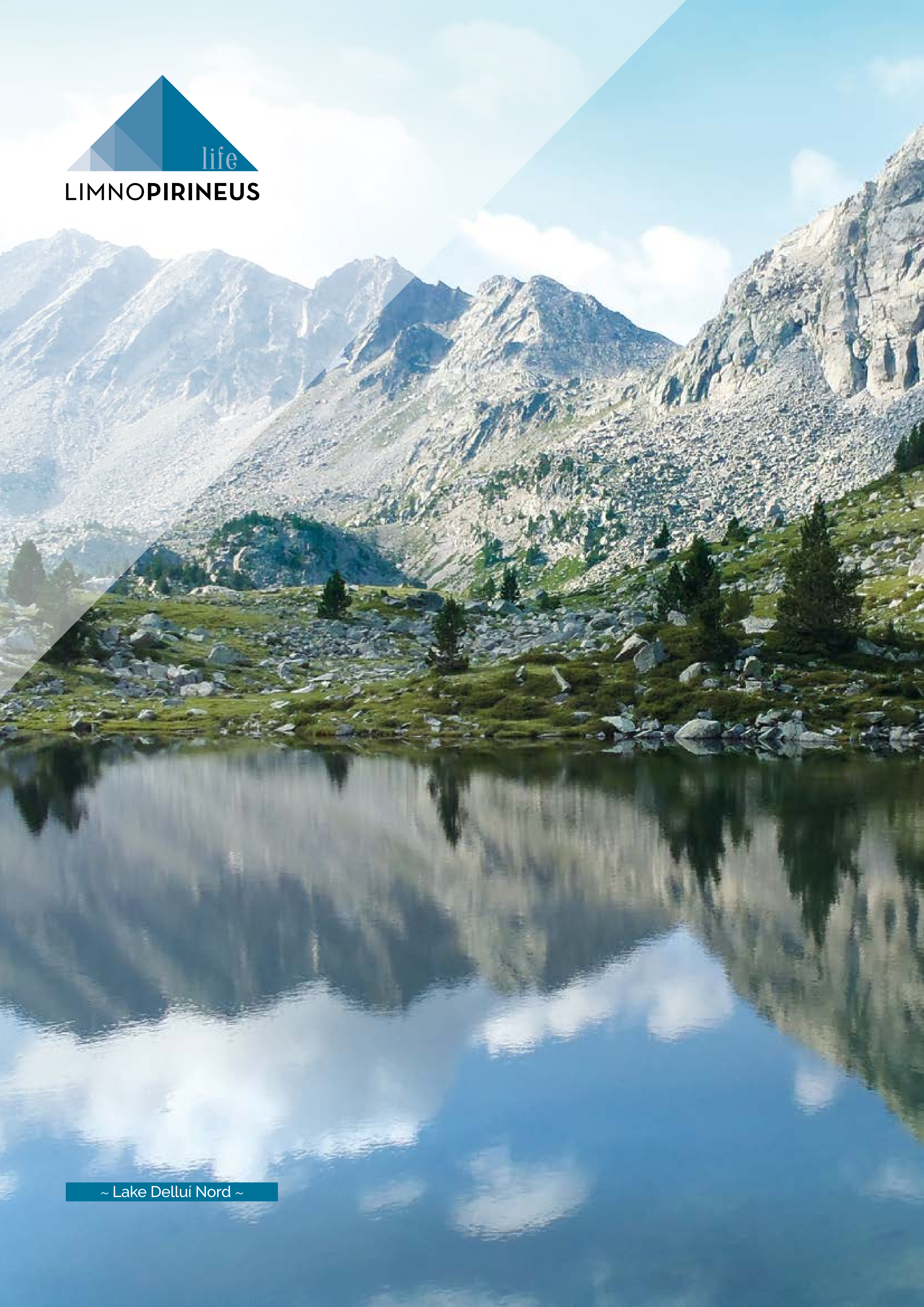

~ Lake Delluí Nord ~

THE TRESCURO MIRE SYSTEM: HOW SHARP ENVIRONMENTAL GRADIENTS AND CLIMATIC EVENTS CONSTRAIN THE LOCAL DISTRIBUTION OF PLANT COMMUNITY TYPES

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RESUM

Mire ecosystems found in Alpine mountains are of great ecological value, since their distribution is very limited by rough physiography and by Mediterranean climatic influence. Understanding how environmental factors together with varying water regime drive the vegetation patterns is a key step for the management and conservation of vulnerable mire systems. Here, we analyse the relationship between these abiotic drivers and the distribution of different plant community types in the Trescuro mire system. 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 evidenced that variation in the water table level is the main driver for small-scale vegetation distribution, followed by the ion concentration. Soligenous communities, which are highly dependent on water runoff, were the most affected by drought events, and thus the most sensitive to eventual invasion by trees.

INTRODUCTION

Mires are fairly common ecosystems in Europe, especially in boreal regions which contain more than 60% of the 187,000 km^2 of European peatlands (Jones-Walters & Summary 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. (Joosten *et al.* 2017). They host plant species and form habitats that are of great interest (Council Directive 92/43/EEC), 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 *et al.* 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 *et al.* 2012) in the lower mountain areas and restrict their distribution more 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 that are 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 regulating 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 *et al.* 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 *et al.* 2000; Sjörs 2002). The main gradients that have been found to determine vegetation are water table depth (Malmer 1986; Sekulová *et al.* 2013; Pérez-Haase & Ninot 2017), 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 & 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). 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 (Figure 1).

This paper has two main objectives: (1) to evaluate the main ecological gradients that determine the distribution of different types of vegetation in the Trescuro mires, and (2) to analyse how different vegetation community types respond to variations in environmental conditions, paying special attention to a drought event occurred in summer, 2015.

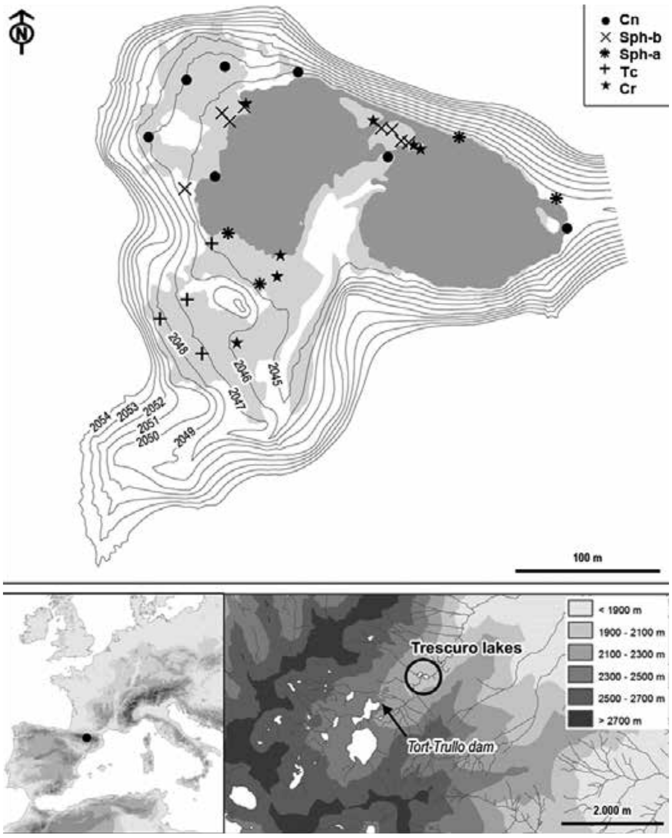
Figure 1. General view of the Trescuro site. The mire system develops as a complex vegetation mosaic on the gentle areas surrounding the two small lakes.

MATERIALS AND METHODS

Study area

The Trescuro lakes and their surrounding mire complex, located in the central Pyrenees, are situated at 2,045 m a.s.l., and experience a high mountain climate The mean annual temperature is 5.3 °C and the average annual precipitation is 1,150 mm with spring and autumn peaks (SMC 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^3 located on granitic substrate (Generalitat de Catalunya 2007). The two water bodies are well connected (Figure 2) 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 2) 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.



▲ **Figure 2.** Location of the study site and sampling points, classified according 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), *Trichophorum cespitosum* fens (Tc), *Carex rostrata* beds (Cr), Low *Sphagnum* hummocks (Sph-b) and High *Sphagnum* hummocks (Sph-a).

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 practiced 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 (*Pinus 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). 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 the several streams and the surface water circulation. But in the lower areas there are numerous *Sphagnum* ombrotrophic bogs, some of them raised more than 1m above the surface. The extension and density of the patches of 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 been clearly increasing in detriment of other mire units, which may be envisaged as a thread for mire conservation. The landscape surrounding the lentic system is dominated by forests of mountain pine (*Pinus 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).

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 PVC pipe sunk vertically 1 m into the mire, in order to monitor the water table depth and to collect samples of groundwater for subsequent chemical analysis.

Around each PVC pipe, we carried out a vegetation relevé in an area of 2.5 × 2.5 m, namely an exhaustive floristic record 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.

In the summer of 2014 we collected water from each pipe in order to measure pH and electrical conductivity by means of a portable instrument, and to perform further chemical analyses in the laboratory. After filtering these water samples (pore diameter, 20 µm), the concentrations of calcium, silicon, sodium, iron, aluminium, sulphur, zinc, copper, potassium, phosphorus, magnesium and manganese were analysed using inductively coupled plasma mass spectrometry (ICP-MS).

Water table depth (hereafter, WTD) was measured fortnightly during the 2014 and 2015 growing seasons (from 18th June to 9th October 2014, and from 2nd June to 30th October 2015). In parallel, we assessed the water level of the lakes by means of an automatic data logger installed in each lake.

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

Data analysis

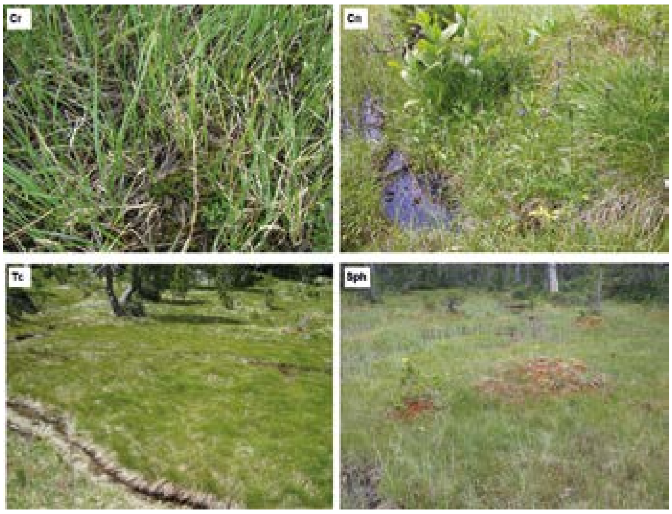
In order to classify the vegetation relevés numerically, we computed a distance matrix of the species data and finally produced a dendrogram to evidence the main vegetation groups or community types (for further details, see Colomer *et al.* 2019).

At the same time, we analysed the relationship between the environmental variables and the distribution of the vegetation through a canonical correspondence analysis (CCA), using the software CANOCO (Lepš & Smilauer 2003). The significant explanatory variables in the model (p-value<0.05 in a Monte Carlo permutation test) were selected by means of 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 corrected the data of electrical conductivity when the pH was below 5, to eliminate the measured acidity corresponding to proton conductivity, following Sjörs (1950), since corrected conductivity data correlate better with vegetation distribution. 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 ANOVA for the normally distributed variables. The other variables 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 package vegan (Oksanen *et al.* 2015).

The numerical classification of the vegetation samples yielded five vegetation types (Figure 3). The first one, *Carex nigra* fens, includes vegetation plots dominated by *Carex nigra* and a number of species that are characteristic of alkaline fens such as *Carex davalliana* or *Swertia perennis*. The *Trichophorum cespitosum* fens were mostly soligenous fens situated on gentle slopes with a constant surface or sub-surface water flow. The *Carex rostrata* beds were species-poor communities situated along the lake margins and frequently remained covered by the lake water. Low *Sphagnum* hummocks were only slightly raised above the surrounding fens. They were mainly formed by *Sphagnum* species, mainly *S. magellanicum*, *S. russowii* and *S. teres*, and included both some hygrophilous plants like *Viola palustris* and *Carex rostrata,* together with the most abundant *Calluna vulgaris* and *Potentilla erecta*. 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, Rhododendron ferrugineum* or *Pinus uncinata,* and exhibited high cover percentages of *Sphagnum capillifolium*.



▲ **Figure 3.** Examples of the vegetation types evidenced: *Carex rostrata* bed with *Sphagnum* (Cr), *Carex nigra* fen (Cn), *Trichophorum cespitosum* fen (Tc), and *Sphagnum* hummocks (Sph).

RESULTS

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 (*Carex rostrata* and *Trichophorum cespitosum*), one Rosaceae (*Potentilla erecta*) and one sphagnum moss (*Sphagnum capillifolium*).

As for soil types, all sampling points had a hystic horizon of variable thickness between plant communities, situated above a sandy layer including coarse grains. Low and High Sphagnum hummocks were always peaty (i.e. hystic horizon or peat ≥30 cm), whereas other vegetation types were 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.

Relationship between vegetation and environmental variables

The main environmental variables showed interesting trends within the vegetation studied, although clear differences between plant community-types were scarce (Figure 4). The electrical conductivity values in *Carex nigra* fens were significantly higher than in the rest of the communities (ANOVA; F=4.12; p=0.011) (Figure 4a). There were no significant differences in pH found between the vegetation types (ANOVA; F=2.75; p=0.108) (Figure 4b).

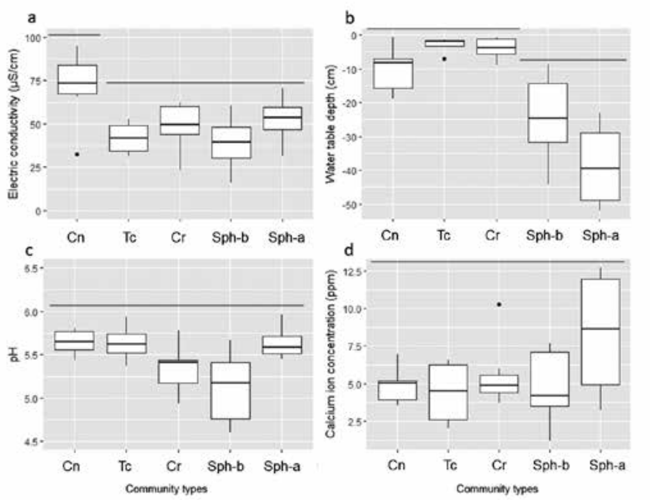


Figure 4. Box plots of the main ecological variables: electric conductivity (a), pH (b), water table depth (c) and Ca^+ concentration (d) (measured from the 1 m deep PVC pipes). The plant community types are identified as in Fig. 2.

The mean WTD in the two *Sphagnum* communities (Low-Sph and High Sph) was significantly deeper than in the other communities (Kruskal-Wallis; K=2.02; p= 0.002), the High *Sphagnum* hummocks experiencing the lowest levels, which averaged 40 cm under the surface (Figure 4c).

Calcium (Ca^{2+}) was the most abundant ion; the mean value for the whole system was 5.56 ppm, with non significant differences between community types (ANOVA; F=3.54; p= 0.124) (Figure 4d). 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), and thus their concentrations were not included in the statistical analysis.

The main environmental gradients describing the vegetation variability in the mire were evidenced through a step-wise CCA (Figure 5). The first two axes 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 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 flooding days, whereas the second axis is related to water mineral content and nutrient richness variables, such as electric conductivity and calcium concentration.

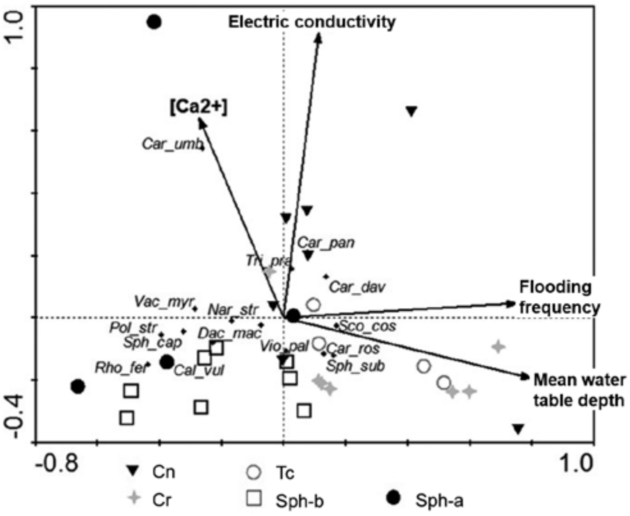


Figure 5. Canonical correspondence analysis (CCA) ordination showing the sampling points and the most frequent species, with respect to the significant variables. The plant community types (symbols) are identified on the legend as in Fig. 2. The 15 species with best fit to the ordination are shown through their abbreviated names, and 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.*

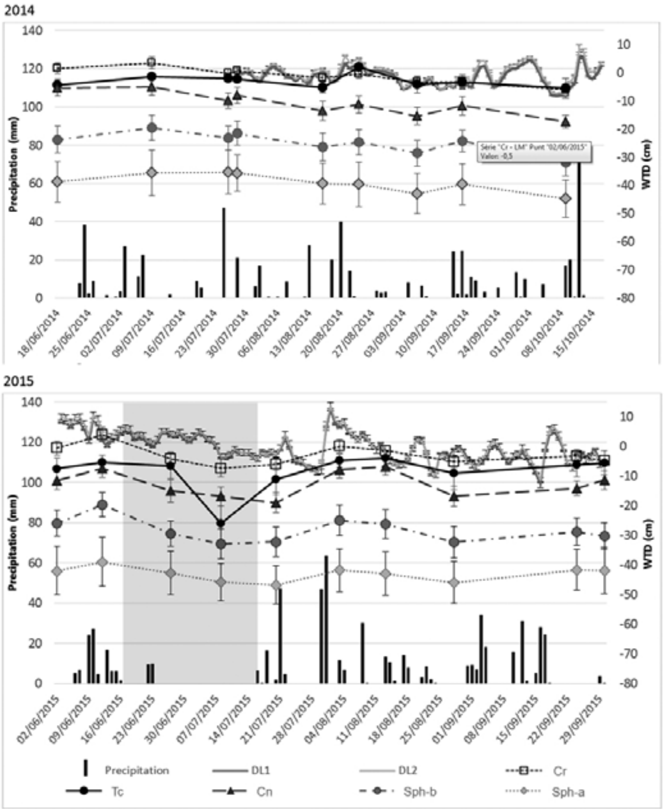
Hydrological regime

Water table depth –the most influencing variable on vegetation distribution– 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.

System response to precipitation

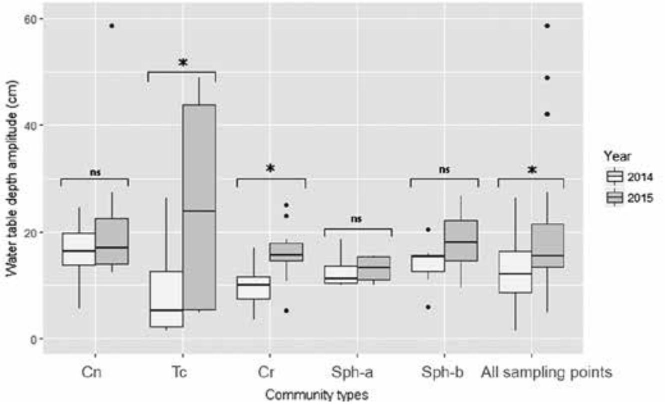
In order to determine the response of each type of vegetation to changes in water intake, we compared the oscillations of WTD during the growing period to precipitation data recorded at the closest weather station (two km away and about 500 m higher elevation) (Figure 6). During the 122 days of the 2014 study period there were rain events on 51 days, with a total precipitation of 602.4 mm. During the 121 days of the 2015 period 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, there were only two rain events, totalling just 19.1 mm. This drought episode, highlighted in grey in Figure 6, provided a great opportunity to evaluate the response of the different community types to extreme events.



▲ **Figure 6.** Water table depth variation in the communities studied (identified as in Fig. 2) and variation in the water surface level of the two lakes (DL1, left lake; DL2, right lake); and precipitation registered during the study period, in 2014 and 2015. The grey shading corresponds to the 2015 drought period.

During 2014, mean WTD was significantly different for all the vegetation groups (Kruskal-Wallis; K = 423.38; p = 0.00) except between the *Carex rostrata* beds and the *Trichophorum cespitosum* fens; while, 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 two years of study within community types (Kruskal-Wallis; K = 312.31, p = 0.081). Nevertheless, the amplitude of WTD was significantly higher in 2015 that in 2014, indicating higher variability during 2015, when the drought period occurred (Figure 7). During the drought period, the community type that suffered the largest decrease in WTD was the *Trichophorum cespitosum* fen, which dropped from −6.5 cm to −25.9 cm (Figure 6).

Regarding the lake water level oscillation, a small delay in the response to the precipitation events of the left lake was detected, since 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, while in 2015 the amplitudes were 25.0 and 25.1 cm respectively.



▲ **Figure 7.** Amplitude of the water table depth in the community types sampled for 2014 and 2015. The plant community types are identified as in Fig. 2. Asterisks denote significantly different amplitudes between both years ($P < 0.05$) and *ns* not significant differences.

DISCUSSION

Vegetation and ecological gradients

The classification of the mire vegetation into five community types is consistent with the previous description of the vegetation in the area using the phytosociological method (Carrillo & Ninot 1992). Both classifications may be understood as the plant response to environmental gradients, since they are the result of the contrasting species composition found in the mire vegetation mosaic.

The WTD (mean WTD and number of flooding days) was the main ecological gradient explaining the variance in the vegetation. Similar results in previous studies (Bragazza *et al.* 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, especially in high mountain mires (Pérez-Haase & Ninot 2017; Raulings *et al.* 2010).

As a secondary driver, water mineral content (evaluated through ion concentration) represented a relevant gradient, as in other alpine mires (Gredol 1995). The groundwater pH values gave also relevant differences between the community types. However, the pH gradient was not included as a determinant ecological gradient in the stepwise selection of variables, probably because its effects on vegetation could be masked by those of the mineral content.

The relevance of WTD and the water mineral content in the Trescuro system is in accordance with that found in other studies at local scales in mountain areas, while in regional-scale studies, climate variables and pH gradients were the most relevant drivers (Okland 1989; Sekulová *et al.* 2013).

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 *Carex 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 & Proctor (2000) and Okland *et al.* (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 because the water in the surrounding fens influences the bottom parts of the hummocks, while the higher parts are almost exclusively influenced by rainwater. Therefore, hummocks have transitional conditions between minerotrophic and ombrotrophic conditions (Rydin & John 2006). Pyrenean *Sphagnum* bogs represent the southern-most location of this community type, so they are on the verge of extinction from a geographical perspective (Harrison *et al.* 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 *et al.* 2017; Strack 2008).

System response to water input variations

Over the last 50 years, there has been a rising 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 (OPCC 2014; Serra *et al.* 2006). Moreover, these trends are very likely to increase throughout central Europe and the Mediterranean area in the coming decades (IPPC 2013).

Mires are highly sensitive to these climate variations, chiefly to the negative impact that summer drought periods have on the hydrological regime (Fenner & Freeman 2011; Romanowicz *et al.* 1993) and subsequently on vegetation depending on a shallow water table and surface runoff (Breeuwer *et al.* 2009). Moreover, when the WTD falls below the tipping point of -24 cm the peatland respiration increased significantly through increased fungal activity (Jassey *et al.* 2018). Nevertheless, the response of the different community types in a mire system to drought should vary according to the particular resilience of the plant species and the vegetation types (Breeuwer *et al.* 2009; Harrison *et al.* 2006).

The drought period that occurred in the summer of 2015, consisting of 22 days with no precipitation and with very low levels of atmospheric humidity, was a great opportunity to analyse the response of mire vegetation to such disturbance. Moreover, the average monthly temperature was 3.5°C higher than a previous 30-year average July temperature (period 1961 to 1990) (SMC 2015). This case study is very significant, since 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, they showed noticeable differences after the extreme drought considered. *Carex rostrata* beds in the lake margins were highly correlated with lake water level oscillations, and thus WTD dropped a mean of 5 cm during the drought event.

Carex nigra fens, situated near streams or even near the lakeshore, showed greater water buffering capacity and resistance to drought, since they maintained 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 6).

Meanwhile, the *Trichophorum 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. During the first days of the 2015 drought period, mean WTD of this community maintained similar levels as when it was receiving runoff 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 most affected *Trichophorum* soligenous fen plots, capillary fringe is unlikely to influence the rooting zone since WTD was too deep. Therefore, ecological processes related to water table drawdown, such as peat depletion, would affect the areas showing extreme low values of WTD.

Moreover, 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. This could potentially lead to colonization by plant species not adapted to waterlogging, such as ericaceous shrubs and other woody plants (Belyea & Baird 2006; Breeuwer *et al.* 2009; Dise 2009). Therefore, 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 *Pinus uncinata* and *Ericaceae* (Heijmans *et al.* 2013). Since the resulting forested peatland has higher evapotranspiration than open mires, positive feedback may enhance 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% (Figure 8). 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 *et al.* (2013).

Although all the Trescuro mire system is interconnected, there were site-specific responses within the system following extreme events. Since the main river enters exclusively into the right lake, increases in flow occurred after strong rainfall events (Figure 6) or following generalized snow melt at the beginning of summer produces rapid rises in its water level. The effects of flash floods in the main river are far less noticeable on the left lake, which is mostly fed by small surface streams (Figure 2) and thus more influenced by current precipitation regime. This suggests that the mires related to the right lake would be more sensitive to significant variations in the river flow, whether caused by a downpour or by variations in the dam water management, whereas those situated in peripheral areas around the left lake would be more affected by drought events.

CONCLUSIONS

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. The response to extreme events depends on the vegetation community types, but also on the situation of each community within fine scale mosaic of the mire, that suggests that the mire system partially resists extreme events such as those measured within this study.

▲ **Figure 8.** The Trescuro system includes small patches of bog woodland, which during the last decades densify and expand through the encroachment of juveniles of *Pinus uncinata* on *Sphagnum* hummocks.

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. Therefore, detailed monitoring of fens depending on runoff waters would be very valuable as an assessment of drought events effects on mires in southern Alpine ranges.

This case study is a science-based contribution to 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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