Intricate spatial soil carbon distribution in four Pyrenean mires

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SUMMARY

Alpine mires in the Pyrenees are remarkable ecosystems for the singularity of their plant communities and for their occurrence at a southern distribution limit. However, the structure of their organic soils and their contribution to carbon (C) dynamics are largely unknown. In this study, we aimed to map and quantify organic C stocks and peat thickness in Pyrenean mires for the first time. In four mire sites located on the Iberian side of the central Pyrenees, we took more than a hundred soil core samples encompassing the vegetation mosaics found at each site and analysed their organic matter content along the soil profile. We then mapped overall C stock and peat thickness in the sites using interpolation techniques and analysed the relationship between soil properties and vegetation units. Peat thickness and organic C stocks varied greatly within and amongst mires, with average values increasing with elevation from 31.1 to 43.2 cm and from 14 to 21.3 kg m^{-2}, respectively. Only part of the peat layer in each mire was thicker than 30 cm, and this part increased with elevation. Our results showed that the variation within and among sites is related to the complexity of the alpine physiography, where some drivers (like topoclimatic variables) operate at larger scale and others (such as topography and hydrology) at smaller scales coupled with complex vegetation mosaics. The complexity of the spatial patterns in C stocks observed, along with their relationship to vegetation, highlights the need for future research in mountain peatlands focused on disentangling the distinct factors that contribute to peat formation.

KEY WORDS: alpine landscape, habitats, mapping, peatland, SOC, soil organic matter, SOM

INTRODUCTION

Peatlands are key ecosystems for the global carbon (C) cycle due to their capacity for storing large amounts of soil organic matter which is subject to very slow mineralisation. Indeed, although they cover only around 3 % of the world's land area, peatlands contain roughly 21 % of the total soil organic C (SOC) (Joosten 2010, Scharlemann *et al.* 2014). Under increasing exploitation, drained peatlands are responsible for ~5 % of the anthropogenic C emissions contributing to climate change (Joosten 2015, Leifeld & Menichetti 2018). Because of their capacity to store C, the restoration and conservation of peatlands has become a focal point for scientific research and nature conservation, particularly within the nature-based climate solutions framework aimed at limiting global temperature rise (UNEP 2019, Loisel *et al.* 2021). In order to reduce greenhouse gas emissions, it is a top priority to acquire deeper and broader knowledge on peatlands and on the related mire ecosystems. Since, at present, we have better spatial knowledge on mire ecosystems than on peatland properties (Moen *et al*. 2017), unveiling the relationships between mire types and peat characteristics becomes a promising way to improve our peatland knowledge.

In this respect, SOC mapping has become a crucial tool to identify, quantify and evaluate the contribution of mire ecosystems to global C storage (Jiménez-Alfaro *et al*. 2023). Peat thickness and its C content - both being highly variable in space - are still unknown for most mire ecosystems, which limits the accuracy of C stock estimations (Weissert & Disney 2013). Since most peatland cover estimates are made at a global scale (Minasny *et al*. 2019), translating these values to local and regional scales results in large uncertainties. Therefore, understanding the spatial variability of SOC at local scale is essential for assessing soil quality, C dynamics and ecosystem functioning, as well as for natural resource management (Zhang *et al*. 2018).

In the European context, and particularly in recent decades, there has been a growing focus on mapping and quantifying C stocks and greenhouse gas emissions in peatlands and mires (Tanneberger *et al*. 2017a). Acquiring this knowledge poses increasing difficulties when shifting from Boreal or Atlantic regions to mountain regions in southern Europe, since their high environmental and biogeographic heterogeneity leads to a variety of distinct mire types. In parallel, these mountain mires have rarely been studied in terms of peatland properties and functioning (Moen *et al*. 2017).

In the case of mountain mires such as those in the Pyrenees or the Alps, the rough physiography found at mid and high elevations leads to the formation of a large variety of mire habitats with distinct hydrological and ecological characteristics, including valley-bottom and spring fens, *Sphagnum* bogs, quaking mires and wet meadows. These mire habitats may be isolated like small islands within drier landscapes, or combined into mosaics of hydrophilic vegetation showing sharp gradients over short distances. Furthermore, as mountain ecosystems, these mires are subject to geomorphic dynamics. In any given case, parts of the mire may be slowly growing into ponds or alpine lakes through loamy-sandy shorelines, while other parts may be undergoing erosion by stream courses or drying out due to hydrological changes (Pérez-Haase & Ninot 2017, Colomer *et al.* 2019). Therefore, the thickness of the peat layer may not be coupled with the vegetation of mountain mires at fine scale. Understanding the relationship between mire vegetation and peat properties is a current research gap within mountain ecology. In this regard, and given the poor knowledge currently available on peat extent in mountain mire systems, we use the term 'mire' primarily for ecosystems bearing mire vegetation. Following established criteria (cf. Joosten *et al.* 2017), we consider peatland to be an area where peat forms a layer at least 30 cm thick, and we define a soil layer with at least 30 % dry mass of organic matter as peat.

Pyrenean mires occur scattered throughout the subalpine and alpine vegetation belts (i.e., 1600–2700 m a.s.l.), being favoured by mild to cold bioclimates and by alpine topography, and profiting from ancient infilling lakes, moraine-related springs and seepages, and rivulet margins (Ninot *et al*. 2017). These mountain mires are well-known in terms of vegetation and habitat characterisation, as well as their main drivers, which include water chemistry, hydrology and bioclimate (e.g., Cholet & Magnon 2010, Pérez-Haase *et al*. 2012, Carreras *et al.* 2015, Pérez-Haase & Ninot 2017, Peralta *et al*. 2018). Biogeographically, Pyrenean mire vegetation belongs to the Boreal and Atlantic type - the plant communities are classified as fens of the Scheuchzerio-Caricetea class and bogs of the Oxycocco-Sphagnetea class - and are considered to be relict assemblages remaining from the cold Pleistocene periods (Jiménez-Alfaro *et al.* 2012). Pyrenean mires are mostly small landscape units, yet they include distinct habitats in the form of complex mosaics or systems dominated by cyperaceous fens (Pérez-Haase & Ninot 2017). For instance, in a 1:10,000 habitat map of the Catalan Pyrenees, more than 4,500 mire patches pooled together barely reach 277 ha, and only a dozen of the patches exceed 5 ha. The most highly represented habitats are the Acidic *Carex nigra* fens (91 ha) and the Rich fens with *Carex davalliana* (51 ha) (data from GEOVEG 2023). Given the small area covered by these mire systems, their diversification in terms of habitat type, and their location at the southernmost range limits of most of the habitats and specialist species, Pyrenean mire systems have acquired great conservation priority within the EU Natura 2000 network and the Ramsar Convention (Carreras *et al*. 2015, Julve & Muller 2017, Ramil-Rego & Rodríguez Guitián 2017).

In contrast to the good knowledge of plant species composition and regional distribution in Pyrenean mire systems, their soil properties remain under-studied, even compared to mires in other alpine regions (Bortoluzzi *et al*. 2006, Tanneberger *et al.* 2017a, Tanneberger *et al.* 2017b, D'Angelo *et al*. 2021). Both the SOC distribution and the extent to which the mire vegetation actually corresponds to peatland are largely unknown. This knowledge gap hampers our understanding of their contribution to C dynamics at local and regional scales. Although alpine mires do not occupy large areas, and the related peaty soils do not reach notable depths, they are relatively frequent in the central sector of the Pyrenean range (Pérez-Haase *et al.* 2020), and thus their contribution to the C dynamics at regional scale should not be neglected. Moreover, alpine mires exhibit greater plant diversity and soil properties at the landscape level compared to similar ecosystems in higher latitudes. This makes analysing their response to climatic variations and predicting their future under current climate change critically important (Colomer *et al.* 2019, Carbognani *et al.* 2023).

The aim of this study was to determine the distribution of SOC in typical Pyrenean mire systems. More specifically, we wanted to:

a) quantify SOC stocks in four Pyrenean mire systems which are examples of the mires found in the central Iberian Pyrenees where plant communities and ecological drivers are well known;

b) describe peat and SOC distribution and extent in these mire systems; and

c) search for patterns of SOC distribution related to habitat types and physiographic variables.

METHODS

The mire sites studied

We selected four sites that are representative of the larger mire systems on the Iberian side of the central Pyrenees (GEOVEG 2023). Three of them - Pallerols, Rubió and Sotllo - lie on Cambro-Ordovician acidic pelite and sandstone, making the soils mostly siliceous and base poor. The fourth site, Estanyeres, is surrounded by colluvial calcium-rich slate (ICGC 2023; Table 1). The selected mires occupy flat or gently sloping areas associated with spring and stream systems, and thus are fed by minerotrophic waters. We based site delimitation on the cover of mire vegetation units. Although the sizes of these mires (ranging from 10,888 to 25,906 m^2) are moderate, each of them encompasses strong variation in hydrological conditions and vegetation units (Pérez-Haase *et al*. 2020, and own data from the projects GREEN 2023 and LIMNOPIRINEUS 2023). The dominant vegetation in all of them corresponds to Cyperaceae fens, which vary between sites and include patches of specific units (Figure 1). Altogether, we sampled six habitat types, namely:

1) acidic *Carex nigra* fens, dominant in Pallerols and Rubió;
2) acidic *Trichophorum cespitosum* fens, dominant in Sotllo;
3) rich fens with *Carex davalliana*, dominant in Estanyeres;
4) *Sphagnum* hummocks, sparsely present in all of the sites except Pallerols;
5) semi-aquatic habitats (i.e., Glycerio-Sparganion and transitional communities); and
6) meso-hygrophile grasslands co-occurring with and densely interspersed within the previous units.

Another vegetation unit - *Pinus uncinata* bog woodland - is occasional in Estanyeres and notable in Rubió; but since this habitat corresponds to open pine stands interspersed within herbaceous mire communities, we positioned our sampling points in the herbaceous communities. The study sites span the altitude range from low to high subalpine belt (1670–2186 m a.s.l.), where the potential vegetation is (mesophile) mountain pine (*P. uncinata*) forest.

Table 1. Main descriptors of the mire sites studied. The water properties (water table level, pH and electrical conductivity) are averages of July data collected at some sampling points for each site (n = 7–12); plant growth period is derived from local topoclimatic variables (cf. Ninot *et al*. 2013); standing biomass refers to dry weight of aboveground parts of higher plants at end of summer in plots with grazing excluded. High standard deviation values (in brackets) indicate the high within-site variability in water table depth and standing biomass. Ecological data come from the previous projects LIFE+ Limnopirineus and POCTEFA Green (GREEN 2023, LIMNOPIRINEUS 2023). The value for standing biomass in the last column does not come from Sotllo, but from a location at similar elevation in a nearby valley; thus it is only indicative.

Descriptors	Pallerols	Rubió	Estanyeres	Sotllo
Elevation (m a.s.l.)	1,670	1,980	1,937	2,186
Coordinates (E, N)	1.72355332, 42.39937169	1.23940609, 42.41211623	1.05999704, 42.60840519	1.38132411, 42.64399035
Size (m^2)	10,888	18,005	12,438	25,906
Bedrock	Acidic pelite and sandstone	Acidic pelite and sandstone	Lime slate	Acidic pelite and sandstone
Water table depth (cm)	-4.9 (±4.4)	-16.5 (±11.1)	-13.6 (±16.5)	-5.7 (±8.2)
pH	6.1 (±0.4)	6.1 (±0.5)	6.2 (±0.6)	5.0 (±0.2)
Conductivity (µS cm^{-1})	133.4 (±62.2)	175.6 (±66.6)	249.6 (±76.2)	63.4 (±24.5)
Main habitat	Acidic fen of *Carex nigra*	Acidic fen of *Carex nigra*	Rich fen with *Carex davalliana*	Acidic fen of *Trichophorum cespitosum*
Plant growth period (months)	6.5	6	5	5
Standing biomass (g m^{-2})	360 (±84)	278 (±63)	253 (±103)	226 (±65)

Indeed, Rubió and Pallerols are surrounded by pine forest, and the other two sites are not far from forest patches. In any case, the mires are surrounded by slopes with drier soils, and are covered by diverse grassland vegetation types together with pinewoods (GEOVEG 2023; Figures A1 to A4 in the Appendix).

Most Pyrenean mires have been subject to anthropogenic grazing since ancient times, but grazing by cattle and horses has become more intense in some areas during recent decades. At present, livestock herding occurs only sporadically at Sotllo (the most remote of our study sites) and more

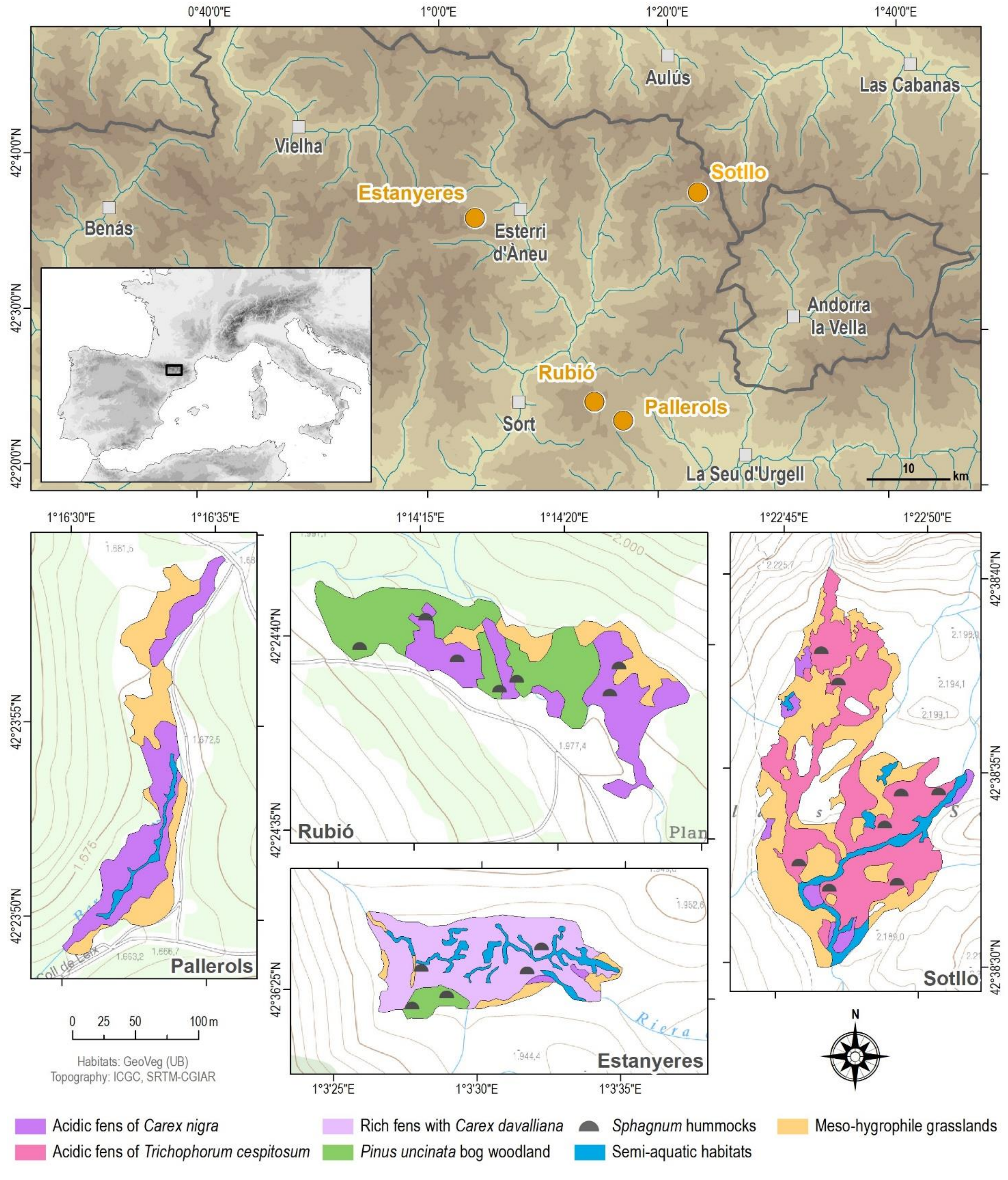

Figure 1. Locations of the four mire systems in the Pyrenees and cover of the main habitats in each study site.

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frequently at the other three sites. Within the mire conservation projects mentioned above, the four study sites have been previously assessed in terms of vegetation (i.e., species composition, cover, height), plus water table level, pH and conductivity (Table 1).

Sampling and laboratory procedures

In each study site we took numerous soil samples to encompass the variety of plant communities and hydrological units found within the mire mosaic. Most (65–87 %) of the samples were collected from the predominant habitat and two or three in each less-common habitat. Nearly half of the sampling points coincided with plots that were previously assessed for hydrological and vegetation features (i.e., water table level, pH, electrical conductivity and plant species composition). Overall, we took 104 soil core samples distributed across the distinct mire habitat types (see Table 2). We took a few additional cores from peripheral mesophile grassland units to inform adjustments to the cartographic distribution of peat variables. All of the sampling points were classified in terms of habitat type and percentage cover of *Sphagnum* or other mosses, and their geographic coordinates were recorded.

We extracted soil samples using a semi-cylindrical gouge with diameter 25 mm and length 1 m (Eijkelkamp single gouge auger). Thus, we could reach the whole of the peat layer when its depth was less than 85–90 cm. In the vast majority of cases, the samples obtained were shorter and included the entire peaty soil profile plus part of the deeper mineral layer. At the a few sampling points where the peat layer was thicker, the total peat depth was incompletely sampled. In the field we cut and sorted, from each semi-cylindrical sample, up to seven subsamples from the following depths: 0 to -5 cm, -5 to -10 cm, -10 to -15 cm, -20 to -30 cm, -40 to -50 cm, -60 to -70 cm and -80 to -90 cm (labelled, respectively, as a, b, c, d, e, f and g; see Figure A5). The subsamples were stored in sealed plastic bags in a portable coolbox until laboratory processing.

The original volume of each subsample was calculated as the product of its length and the near-semi-circular area delivered by the gouge (6.3 cm^2). Where the deepest subsample obtained was incomplete, we measured and used its actual length. Since the gouge sampling introduced apparent compression of the upper soil layer in most cases, we carefully re-shaped this part of the sample to its original length prior to cutting and separating the subsamples.

In the laboratory, we oven-dried the soil subsamples at 105 °C for at least 72 hours and weighed them (in g). This dry mass was the basis for calculating the bulk density (BD) and the proportions of organic matter and C for each subsample. We then put the subsamples into a muffle furnace at 450 °C for four hours to burn off the organic matter (loss on ignition method following Bisutti *et al*. 2004) and thus obtain the proportion of soil organic matter (SOM, in g kg^{-1}). In addition, we sieved the remaining (mineral) part of each subsample through a 2 mm mesh to remove gravel, and deducted the gravel mass from the initial dry mass for the calculations of SOM.

Data elaboration

For each subsample we estimated the total SOC as 0.5 of SOM, following general soil science procedures and specific peat-related studies (Schumacher 2002, Bisutti *et al*. 2004, Klingenfuß *et al*. 2014). Using the values of SOM, SOC and BD for the subsamples analysed, we calculated the same metrics for the discarded intermediate segments of each core by interpolating between the two adjacent subsamples. Finally, we calculated the organic C stock per unit area at each sampling point (in kg m^{-2}) as the sum of C stocks (the product of SOC in kg kg^{-1} and dry mass in kg) for all (retained and discarded) core segments divided by the area drilled (6.3×10^{-4} m^2).

To standardise further calculations, and following generalised definitions of peat (Joosten & Clarke 2002, Rydin & Jeglum 2013), we classified as peat those subsamples with SOM > 300 g kg^{-1} and thus with SOC >150 g kg^{-1} (i.e., greater than 30 % and 15 % of dry mass, respectively). This allowed us to estimate the peat thickness at each sampling point from the SOM values per subsample and their variation with depth. While SOM decreased from one subsample to the next deeper one in most cores, for a few sampling points the SOM values revealed intermediate non-peat layers between shallower and deeper peat. In these cases, we calculated peat thickness as the sum of the peat layers, discarding the SOM-poor intermediate material.

We converted the SOC and peat thickness data into maps to visualise the spatial variation of peat characteristics within each mire site studied. To do this and derive a global estimate for each of the sites, we used the deterministic spatial interpolation method 'Inverse Distance Weighted' (IDW). IDW is one of the most widely applied interpolation techniques in soil science (Bhunia *et al*. 2018), and was considered as optimal for our study given the density and spatial distribution of the sampling points. Its estimates are based on known nearby locations, where closer points are afforded more weight than distant points. Moreover, IDW adjusts the relative weighting of the nearby points in each interpolation, which makes this method appropriate for distinct data types and non-uniform spatial distributions. Calculations of IDW were performed in the Geostatistical analyst extension of ArcGIS software (ArcGIS Pro 2023). The accuracy of interpolation was estimated in terms of the Root Mean Square Error (RMSE), which evaluates the average deviation of predicted values from measured ones.

Based on the spatial distribution of C stock values (in kg m^{-2}) for each mire site, we stratified the mire area into categories with each category corresponding to one interval of 5 kg m^{-2}. We then calculated the average C stock value for the area covered by each category, multiplied this value by the category area to obtain the corresponding partial C stock value, and calculated the C stock for the entire mire as the sum of the partial values.

Statistical analyses

First, we looked for relationships between SOC and habitat type or mire site. For this we used SOC values for the upper soil layers (the average of a, b and c subsample values per core) as the response variable, as these shallower levels are most closely related to the functioning of extant vegetation. Since the normality assumption was not met for some (habitat type or site) groups, we opted for a non-parametric test for differences between groups. Thus, we ran Kruskal-Wallis tests using the kruskal function from the agricolae package in R® 4.1.1. Then we performed post-hoc pairwise comparisons adjusted for multiple testing using the Bonferroni correction method to identify groups that differed significantly from one another.

To analyse the strength of the relationship between the variables measured for the soil subsamples, we constructed a similarity distance matrix based on the Pearson correlation index. For each sample we considered the variables obtained for all sampling points - specifically the SOC values for a, b, c and d subsamples because some cores did not include deeper levels, the C stock per unit area, and the peat thickness. Additionally, given the physiographical heterogeneity within each mire site, we added the terrain slope at each sampling point as a potential explanatory variable. We derived the slope data from a digital elevation model (DEM) with a resolution of 2 m per pixel provided by ICGC (2023).

Finally, we evaluated the relative influence of the soil variables on the habitat types. To do this we conducted a Principal Components Analysis (PCA) using all of the soil samples from all habitat types and mire sites. To obtain a more balanced result, we used in the PCA only one of the three more-strongly correlated variables (Pearson value ≥ 0.8) by retaining SOC at level a and discarding SOC at levels b and c. Additionally we log-transformed the values of the remaining variables. The ordination solution was computed using the precomp r- function of the stats package in R® 4.1.1, and we visualised it on the two first axes of the PCA.

RESULTS

Most of the core samples obtained reached mineral substrata at levels shallower than -85 cm, while only four (three from Pallerols and one from Estanyeres) were composed entirely of peat. Supplementary estimates of peat depth obtained by probing with a graduated steel rod at these two sites only rarely (in about 3 % of cases) indicated depths greater than 85 cm, with a maximum of 120 cm.

The main properties measured in the subsamples are presented in Tables S1 to S4 in the Supplement (Excel file), and average values are provided in Table 2. There was a general decreasing trend of SOC with increasing depth (Figure 2), and a strong inverse relationship between (decreasing) SOC and (increasing) BD (Figure A6), coupled with increasing depth. In most samples the shift occurred gradually through the peat layers, where SOC remained >15 % and BD < 0.25, then there was a sharp change to

Table 2. Summary of soil data for the mire sites studied, expressed as average values and standard deviations (in brackets) calculated from values measured for the individual soil samples.

Descriptors	Pallerols	Rubió	Estanyeres	Sotllo
Sample points	23	39	25	17
Bulk density (g cm^{-3})	0.315 (± 0.146)	0.299 (± 0.161)	0.179 (± 0.114)	0.173 (± 0.073)
SOC of the peat layer (g kg^{-1})	244.7 (± 53.8)	286.6 (± 64.6)	329.9 (± 67.9)	334.0 (± 62.0)
Peat thickness (cm)	31.1 (± 27.3)	32.6 (± 20.5)	44.3 (± 22.2)	43.2 (± 12.3)

higher BD and lower SOC when entering the deeper mineral layers. This sharp transition occurred between 25 and 40 cm depth in most cases, except at Pallerols where it mostly occurred between 10 and 20 cm depth. The Pallerols site also stands out because we found a mineral layer occurring between shallow and deep peat layers in nine out of 23 samples. This pattern was rarely found at Rubió and never found at the other two sites.

The primary data on organic matter derived from the soil samples showed an average peat thickness greater than 30 cm in all of the sites, and exceeding 40 cm in two of them (Table 2). Focusing on the SOC at shallower levels (from 0 to -15 cm), the Kruskal-Wallis and post hoc tests revealed significant differences between sites, with Pallerols and Rubió showing significantly lower values and greater within-site heterogeneity than the other two sites (Figure 3).

In fact, there was noticeable heterogeneity between the samples from each site in terms of SOC, BD and their variation with depth, as well as peat thickness (Tables S1–S4). This heterogeneity was evident when mapping the values of C stock per unit area (Figure 4) and even more obvious when mapping peat thickness (Figure A7), since each mire site tightly encompassed patches with shallow or weak peat layers, average areas and deeper deposits in favourable patches. Thus, in Pallerols and Rubió, peat thickness and C stocks showed higher values along parts of the main watercourse fed by diffuse water springs. These patches of thicker peat contrasted with the rest of the mire, which had developed on gentle slopes and where peat thickness was moderate or low. In Estanyeres the overall picture looked similar, with the thickest peat denoting the location of an infilled small alpine lake. The present rivulets were not related to peat and, in fact,

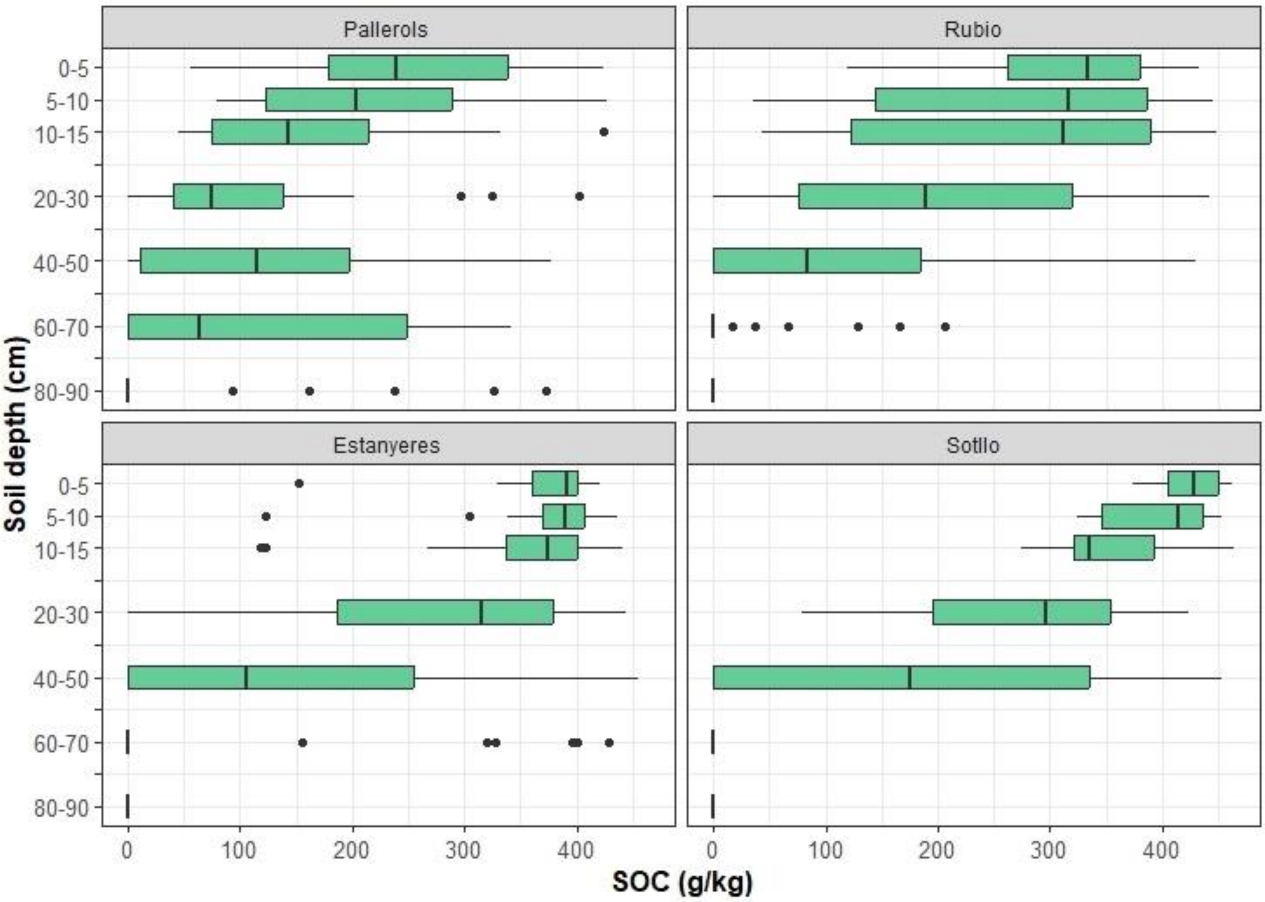

Figure 2. Distribution of soil organic carbon (SOC) proportion (g kg^{-1}) with depth in the samples obtained from the four mire systems. Zero values of SOC indicate missing sample segments, thus assumed to be mineral.

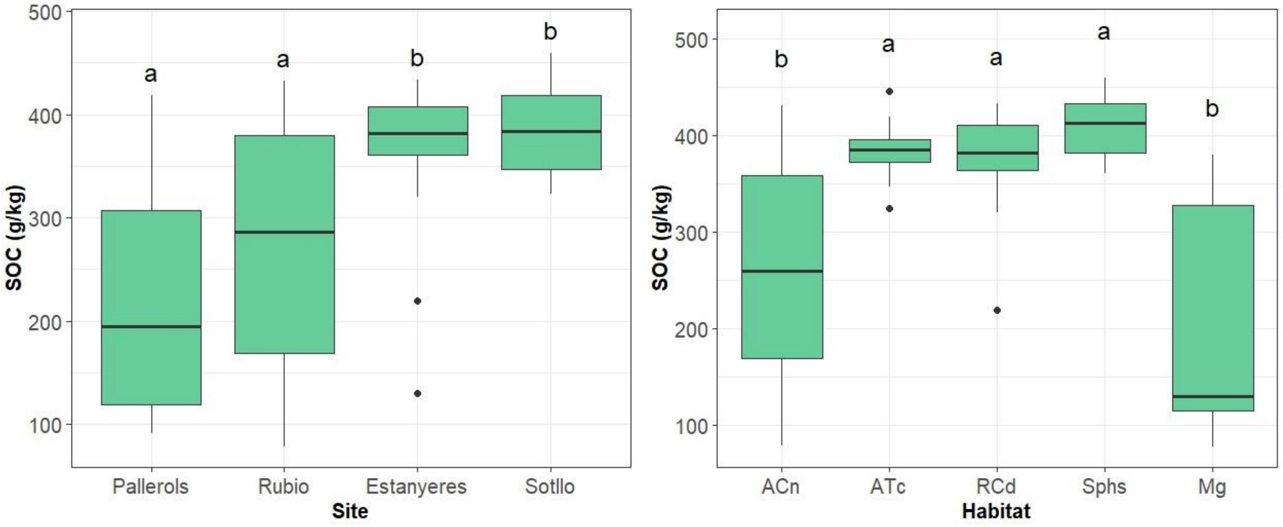

Figure 3. Soil organic carbon (SOC) proportion (g kg^{-1}) in the 0 to -15 cm soil layer; left: in the four mire sites studied, according to the samples analysed for each (in brackets): Pallerols (23), Rubió (39), Estanyeres (25) and Sotllo (17); right: in the five habitats considered, from the samples analysed for each habitat in different mires (in brackets): ACn, Acidic *Carex nigra* fen (52/2); ATc, Acidic *Trichophorum cespitosum* fen (10/1); RCd, Rich fen with *Carex davalliana* (19/1); Shs, *Sphagnum* hummocks (8/3); Mg, mesohygrophyle grasslands (13/4); the semi-aquatic habitats are not included because only two samples were available. Different letters indicate differences between sample groups according to the post-hoc significant difference test at $\alpha = 0.05$, between sites ($F = 32.7$, $p = 3.70e^{-07}$) and between habitats ($F = 39.92$, $p = 4.49e^{-08}$).

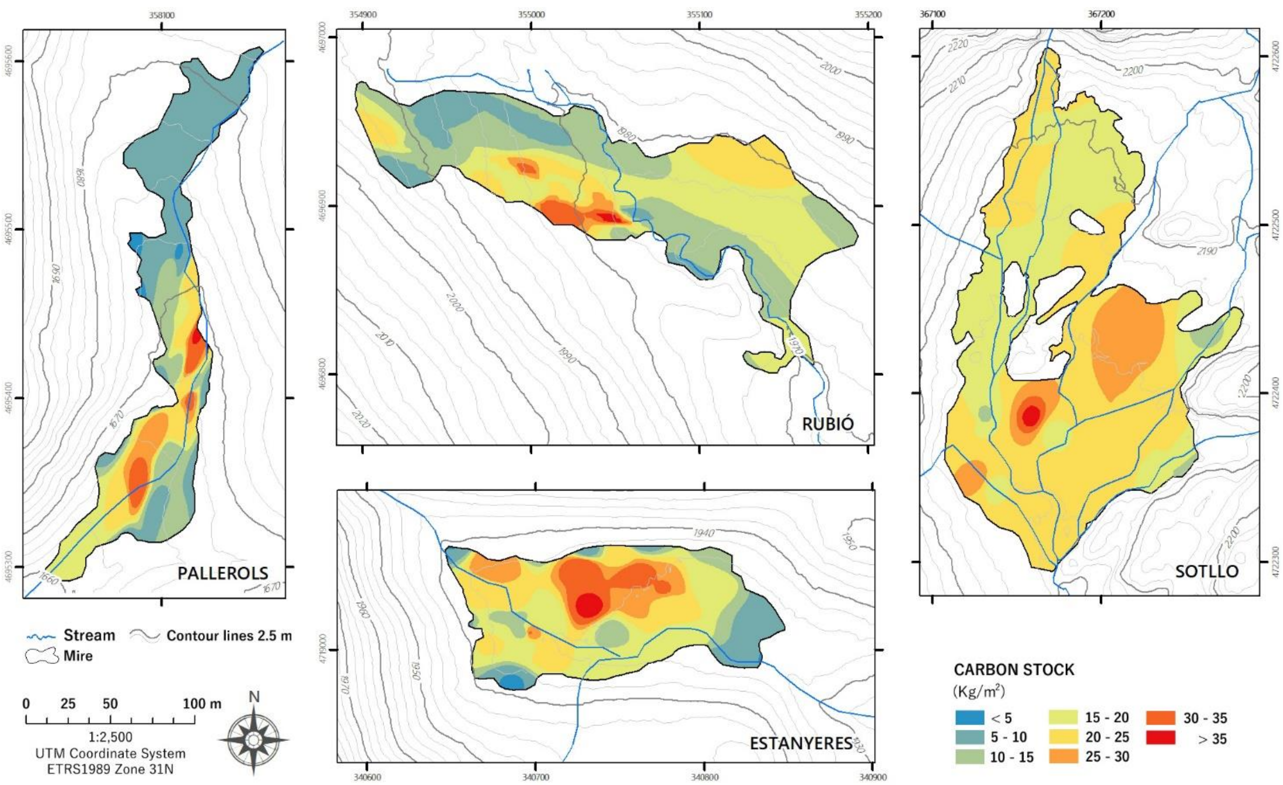

Figure 4. Distribution of soil C stock (in kg m^{-2}) in the four mire systems studied, showing sharp gradients within each system.

they seemed to partly prevent its development. Sotllo also included old small alpine lakes, but the peat development looked rather uniform, with moderate thickness and high C concentrations across most of the mire (Figures 4 and A7).

Mapping the soil data enabled us to obtain integrated values of the distributions of C and peat thickness in the mires (e.g., Table A1). In a rough comparison between the sites, the average values of SOC per unit area, which increase from Pallerols to Sotllo, and the relative peat extension within each site, which increases in the same direction, stand out (Table 3). In the case of peat extension, the higher percentage of peatland found in Estanyeres and Sotllo was due to the general increase of C concentration values and decrease of spatial heterogeneity (Figures 2 and 3).

The Pearson correlation tests revealed positive relationships between all the C-related variables, while the attribute terrain slope correlated negatively with all of them at similar strength (Table A2). The PCA performed to evaluate relationships among soil samples, soil variables and mire habitats after removing two of the most highly correlated variables (SOC of layers b and c) accumulated 62 % of the variance on the first axis and 15 % on the second axis (Figure 5).

Table 3. Global organic carbon and peat figures for the studied mires, according to GIS calculations.

Descriptors	Pallerols	Rubió	Estanyeres	Sotllo
C per area (kg m^{-2})	14.04	15.94	19.50	21.26
Total C stock (kg)	152,863	286,911	238,868	550,856
Peat area extent (%)	27	41	59	97

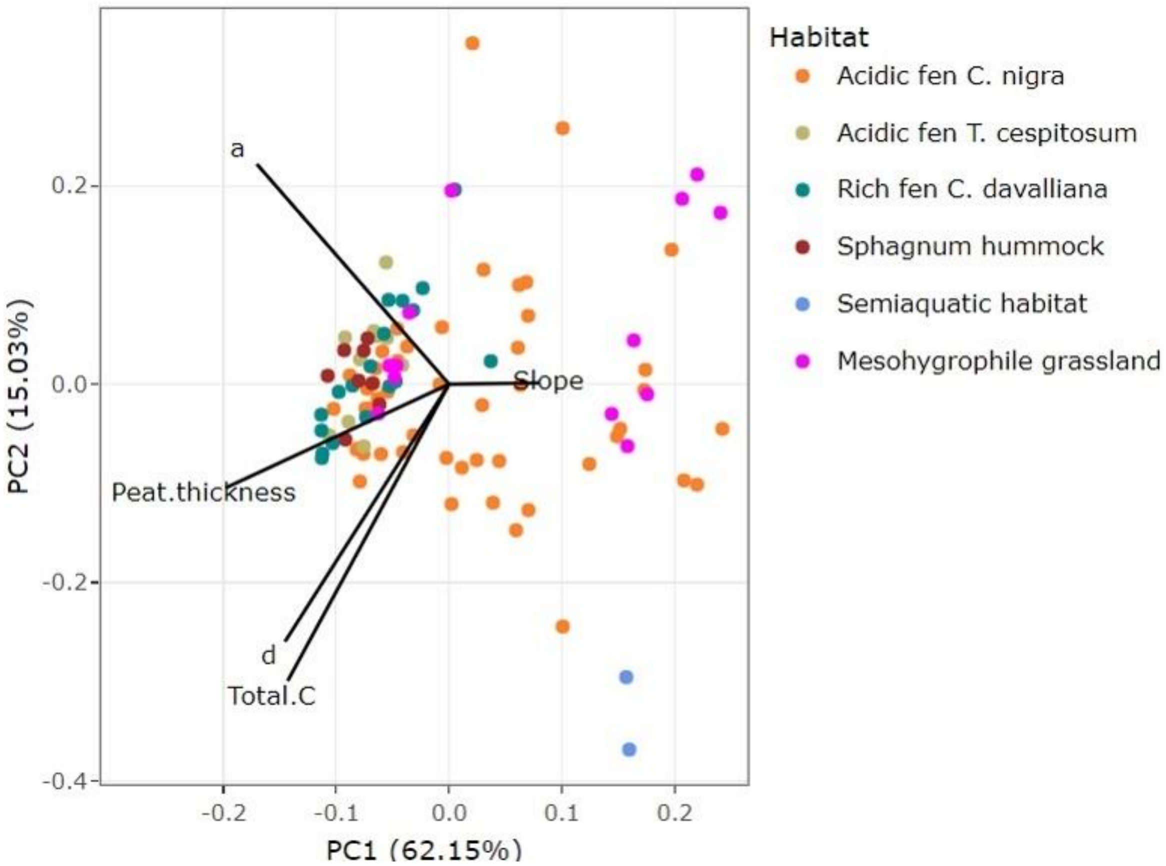

Figure 5. Principal Components Analysis (PCA) of the samples taken from the four mire systems, identified according to the habitat types by different colours. Vectors correspond to the factors used for the ordination: total C per area unit (Total.C), peat thickness, C proportion in the soil subsamples (a: 0 to -5 cm; d: -20 to -30 cm), and terrain slope.

Within this space, variables describing C-related soil properties were distributed through the negative part of Axis 1, from SOC at layer a (related to vegetation and recent processes) to SOC at layer d and total C (expressing deep - i.e., ancient - soil characteristics.

Referring to the six habitat types considered, we found significant differences in terms of soil characteristics. Three of the habitats were characterised by greater SOC in the shallow soil layers (Figure 3). These were: *Sphagnum* hummocks (average 409.3 g kg^{-1} at depth 0 to -15 cm); Acidic fens of *Trichophorum cespitosum* (383.7 g kg^{-1}); and Rich fens with *Carex davalliana* (375.4 g kg^{-1}). All of these corresponded to flat or poorly sloping areas with noticeable or great peat thickness (Figure 5). Acidic fens of *Carex nigra* and Meso-hygrophile grasslands exhibited lower and more heterogeneous SOC values in the shallow soil levels (261.54 g kg^{-1} and 215.44 g kg^{-1}, respectively) and occurred on flat to sloping areas - the first of these habitat types being found more frequently in flatter areas with thicker peat (Figure 5). In contrast, the two samples from semi-aquatic habitats were C-poor (68.5 g kg^{-1}).

As for the total moss cover, we found a weak positive correlation ($R^2 = 0.25$) with SOC in the shallow soil layers (Figure A8).

DISCUSSION

Peatland distribution and SOC at the locations studied and in the Pyrenees

In this study, we have estimated the total belowground organic C stocks in four typical Pyrenean mires. We measured SOC and peat thickness in many sampling points, and we spatially interpolated these variables for each mire site. The spatial distribution of SOC was very variable within each mire site depending on local physiographic and habitat characteristics. In fact, the indicator RMSE of the interpolation procedure for mapping C stocks showed relatively high values for the four mire systems (i.e., Pallerols, 10.21; Rubió, 9.04; Estanyeres, 11.39; Sotllo, 11.48; cf. Bhunia *et al.* 2018). This indicates that noticeable differences may occur even between neighbouring points, for instance between a flat fen area and a small *Sphagnum* hummock nearby. This variability also means that the studied mire systems qualify only partly as peatland (27–97 % of the area of mire vegetation in the study sites).

Although supported by only four cases, the variability in SOC and in peatland extent at fine scale may be extrapolated to most high-mountain Pyrenean mires that share similarly rugged physiography. In the Pyrenees, the extent of peatland seems to be neatly lower than that of mire vegetation, in contrast to other regions where peatland area exceeds the area of mire vegetation - mainly due to anthropic use of peatland as arable land or tree plantations (Tanneberger *et al.* 2017b). On the one hand, intensive anthropic uses of peatland, other than livestock herding, are scarce in high-mountain landscape. On the other hand, Pyrenean mires are dynamic systems where parts of the peat layer have not yet achieved sufficient thickness, depending on local physiography and hydrology. In this sense, it is likely that most Pyrenean mires became established in the mid-Holocene (i.e., 5000–7000 yr cal BP; Jalut *et al.* 1982, González-Sampériz *et al.* 2006), although some are much younger (Pérez-Obiol *et al.* 2012) and a few are older (Garcés-Pastor *et al.* 2017). Thus, their present condition is a product not only of the geomorphic dynamics characterising alpine systems, but also of current soil and peat building processes which vary at small scale within the mire mosaic as well as over time, such as litter accumulation, grazing, and erosion.

Our calculations of SOM may incorporate moderate underestimates for patches where the entire peat layer could not be sampled, which may represent less than 3 % of the peatland area. Moreover, we presume that some additional organic matter occurs in deeper non-peaty layers, i.e., in mineral layers harbouring older or migrated organic matter (Harrison *et al.* 2011 and own data). Nonetheless, we estimate that the reported mires contain 171.7 Mg ha^{-1} of SOC, with per-site values increasing from the lowest elevation (Pallerols: 140 Mg ha^{-1}) to the highest (Sotllo: 213 Mg ha^{-1}). These values are certainly much lower than for peatlands formed on gentler reliefs in arctic and subarctic regions, which average 1275 Mg ha^{-1} (Loisel *et al*. 2014); the Zoige peatlands on the high-elevation Tibetan Plateau, averaging about 1036 Mg ha^{-1} (Chen *et al*. 2014); or the deep German bogs with an average of 1400 Mg ha^{-1} (Roßkopf *et al*. 2015). Our Pyrenean values are very similar to those for shallow German bog soils, with 170 Mg ha^{-1} (Roßkopf *et al*. 2015); hill peatlands in the British Isle of Man, with range 147–224 Mg ha^{-1} (Weissert & Disney 2013); and peatlands in a north Italian alpine valley, approaching 210 Mg ha^{-1} (Agaba *et al*. 2024). On the other hand, a detailed study of a large alpine mire in the Austrian Tyrol gave an average value of only 40 Mg ha^{-1} (Egger *et al.* 2025). Compared with other high-altitude Pyrenean habitats, these mires had higher average SOC density than most grasslands, with range 59–299 Mg ha^{-1} and mean 153 Mg ha^{-1} (Garcia-Pausas *et al*. 2007); and certainly more SOC than the sparsely vegetated areas such as scree and rocky summits. The moderate C stock values for the mires we studied reinforce the impression that mountain relief prevents great peat accumulations, owing to more active erosive processes, lower propensity for regular flooding, and younger peatland systems (Liu *et al.* 2018, Agaba *et al.* 2024), in addition to reduced primary production under colder climates.

The soil C stock of Pyrenean mires represents only a small contribution to regional C storage, since the mires are small with dispersed occurrence across hydrological catchments, as is usual for these landscape units in alpine regions (Patterson & Cooper 2007, Chimner *et al*. 2010, Wüst-Galley *et al.* 2015). In the case of the Catalan Pyrenees, considering only the area of mire habitats mapped (277 ha) and the average C stock density estimated in this study, the regional C stock would amount to about 49,000 Mg (neglecting uncountable small and tiny mires). Therefore, although the upscaling from our case studies is still not reliable enough, the contribution of high mountain mires to the Pyrenean C budget is not negligible. In any case, the detailed knowledge of C dynamics in our alpine peatlands may be an indicator of the processes and patterns occurring in other high elevation peatlands occupying larger areas (e.g., Chen *et al*. 2014, Wüst-Galley *et al.* 2015).

Mire habitats and peat development

Some of the mire habitats included in our study showed a strong correspondence with peat characteristics (Figures 3 and 5). More specifically, the *Sphagnum* hummocks, the Acidic *Trichophorum cespitosum* fen and the Rich fen with *Carex davalliana* were usually found on noticeable peat layers where the shallower soil levels contained large proportions of organic matter (with SOC values mostly in the range 370–430 Mg ha^{-1}).

The *Sphagnum* hummocks, occurring in three of the four mires studied, always related to noticeable peaty soils, thus reinforcing the correlation of *Sphagnum*-dominated habitats with noticeable peat layers found in other studies, irrespective of the location (Weissert & Disney 2013). As the two fen types mentioned in the previous paragraph were found in only one mire site each, their peat characteristics may be partly due to particular site conditions. In contrast, the Acidic *Carex nigra* fen showed remarkable heterogeneity in peat characteristics and C stocks. Although mostly corresponding to peatland, it also developed in peat-poor soils. This could be due to the relatively ubiquitous nature of this fen type at various scales, since it is the most widespread fen type in the Central Pyrenees (GEOVEG 2023) and in our study. At fine scale, it was found on young developing peatland or, contrarily, as remaining plant cover on ancient peatland undergoing erosion (own observation and Tables S1 and S2 in the Supplement). The semi-aquatic vegetation units - only considered in Pallerols - occurred on peat-poor layers bordering small watercourses where fluvial dynamics would prevent peat accumulation. The meso-hygrophyle grassland was found mostly in marginal parts of all of the mires or in domed spots, and was thus related to peat-poor soils subject to less flooding. Therefore, the hydrological dynamics limit the spatial development of peatland in our study mires, through an irregular flooding regime in sloping or marginal parts or through erosive processes along small watercourses.

The relationship between moss cover and peat properties was weak, with no correspondence between SOC and moss cover in a number of samples (Figure A8). This finding may be partly due, firstly, to the diverse composition of the moss layer. While *Sphagnum* bogs and carpets are known to promote peat development, looser carpets of *Sphagnum* or other moss types - such as the brown mosses frequently found in our study (see Tables S1 to S4) - do not seem to exert this effect (Thormann *et al.* 1999, Weissert & Disney 2013, this study). Secondly, the moss cover may be both a driver for mire functioning and a response to the density of the herbaceous layer or the grazing intensity (Taylor *et al*. 2020). In three of the mires studied, monitoring during recent years has revealed that grazing prevents the development of dense cyperaceous swards and, thus, may indirectly favour the growth of non-*Sphagnum* moss carpets (own data, related to GREEN 2023).

In general terms, the moderate correspondence between vegetation units and peat accumulation (at least in the case of *Carex nigra* fen) may be explained by the contrast between a faster development of mire vegetation following environmental changes and a much slower development of peaty soils. In mountain areas, changes in hydrology such as slope colluvium dynamics or variations in the pathways of streams may have led to changes in the spatial distribution of mire plant species in a faster way than peat development and accumulation (Patterson & Cooper 2007, Ehnvall *et al*. 2024, Egger *et al*. 2025). Moreover, although we have no precise documentation on the development of peatland at the study sites, paleoecological studies in two Central Pyrenean mires (Pérez-Obiol *et al*. 2012, Garcés-Pastor *et al*. 2017) show intense anthropogenic landscape changes around these ecosystems. Apart from forest clearing by wildfires beginning seven millennia ago, grazing pressure would have affected the mires and neighbouring grasslands increasingly through time, mainly in the late Bronze era, in the Roman era, and in the Middle Ages. Suppression of the tree cover, together with grazing activity, could have changed the soil hydrology and favoured mire expansion from a few millennia ago to some decades ago. Presently, under a low-intensity grazing regime and surrounded by forest, mires in the Central Pyrenees experience a trend of area reduction by pine encroachment (own data from LIMNOPIRINEUS 2023).

Therefore, human activities in combination with mountain dynamics could explain why some of the mire vegetation was found on non-peat or peat-poor soils (Egger *et al*. 2025); and why soil layers that were very poor in organic matter - expression of colluvia or alluvia - were found covering older peat layers in some places. Evidence of fluvial dynamics driving changes, in the form of mineral soil layers covering older peat layers, was observed frequently in Pallerols (located in the mid-course of a mountain stream) and more rarely in Rubió (closer to a headwater area).

Peatland through Pyrenean landscapes

Hydrogeomorphology drives plant community composition and SOC distribution patterns in mires through multiple gradients operating at different spatial scales. Therefore, peat development and accumulation must be understood as a multifactorial result of several drivers, namely plant primary production, litter decay and mineralisation, and soil erosion (Bridgham *et al.* 1996, Chadde *et al.* 1998, Grootjans *et al*. 2006, Gerdol *et al.* 2011). The first driver largely depends on bioclimate, which mostly varies with elevation in mountain areas; the second comes from topoclimate and hydrology at local scale; and the third correlates with small-scale topography and hydrology, and is thus peculiar to the individual mire system. Analysing the different patterns of peat distribution found within the studied mire sites could help to disentangle the roles of these drivers in Pyrenean landscapes.

In Pallerols and Rubió, fluvial morphology may have shaped sharp gradients in soil C stocks. Patches with large peat thickness and C stock, coinciding with lateral diffuse water springs, may be found at short distances from peat-poor soils in the marginal parts of the mire where flooding vanishes through summer, or in the edges of water courses subject to erosive processes. However, the two sites showed different patterns, which we attribute partly to different locations within the fluvial network, and partly to differences in topoclimate. Thus, the higher temperatures and greater incorporation of new mineral sediment characterising Pallerols would explain a longer plant growth period and larger standing biomass (i.e., primary production, Table 1) than in Rubió, together with the absence of *Sphagnum* hummocks from Pallerols.

The sites Estanyeres and Sotllo, located in glacially-shaped valleys, are subject to colder topoclimates, which lead to lower primary production (Table 1) together with slower mineralisation of organic matter. Presumably, the second effect counterbalances the first, which in distinct alpine vegetation types leads to greater SOM accumulation with increasing elevations (Körner 2021). Indeed, our highest mire site (Sotllo) showed the most C-rich shallow soil layers, which were found even in the marginal parts of the mire. Moreover, both Estanyeres and Sotllo include old alpine ponds whose terrestrialisation would have contributed to peat accumulation over time (Chadde *et al*. 1998). Thus, in these two sites, the combination of colder bioclimates with glacial morphology (including former small lakes) would promote SOC accumulation.

While this study focuses on only four cases, it represents the first mapping effort based on peat distribution, C stocks and habitats, for Pyrenean mires. As a contribution to the understanding of SOC stocks and dynamics in southern European peatlands, it should be expanded through additional research that provides more data from such heterogeneous localities, under varying human influence. Our results reveal how peatland patterns and processes vary across the Pyrenean landscape, and help to improve our understanding of mire diversity and functioning at the southern edge of the Palaearctic temperate region.

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AUTHOR CONTRIBUTIONS

JMN originated and planned the work, conducted field sampling and laboratory work, wrote the first draft, and is the lead author; MM conducted field sampling and laboratory work, and performed all calculations for peat mapping; VMA performed the statistical analyses and contributed to the first draft; EC contributed to field sampling; EPI and APH contributed to planning of the work and in general assessment of the study. All authors contributed to building and revision of the manuscript.

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Appendix

Figure A1. General view of the Pallerols mire, bounding a mountain stream course and surrounded by *Pinus sylvestris* and *P. uncinata* woodland.

Figure A2. The Rubió mire is fed by a system of springs around a stream course. *Pinus uncinata* forms mesophile woodland on the slopes and swamp forest is interspersed in the mire.

Figure A3. Estanyeres, where the mire system has developed in the flat and gently sloping area, surrounded by mesophyle pasture and *Pinus uncinata* pinewood on more pronounced slopes.

Figure A4. Mire of Sotllo, in the flat bottom of an alpine valley, interspersed with rocky landscape units and sloping mesophyle pasture and woodland.

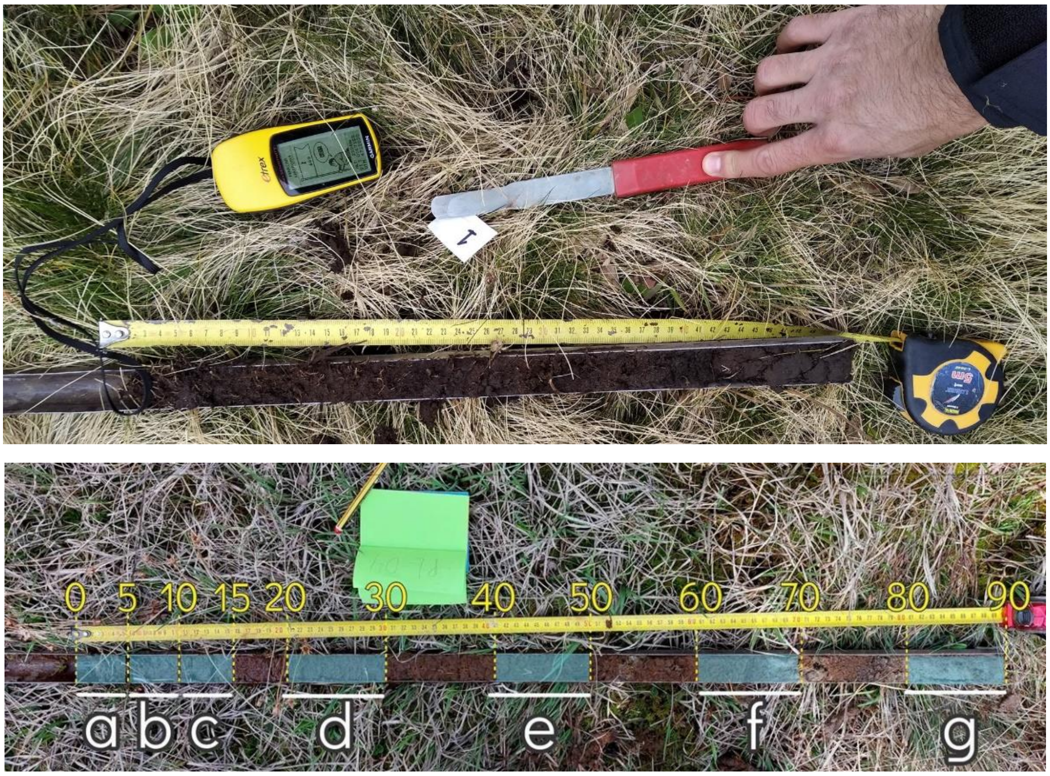

Figure A5. Sampling procedure. Top: at each sampling point, we recorded geographic coordinates and ecological features (habitat type, moss cover). Bottom: from each soil sample (core), we separated in the field a number of subsamples, of which the shallower ones (a, b, c) were 5 cm long and contiguous, and the deeper ones (e, f, g) were 10 cm long and separated from one another by 10 cm.

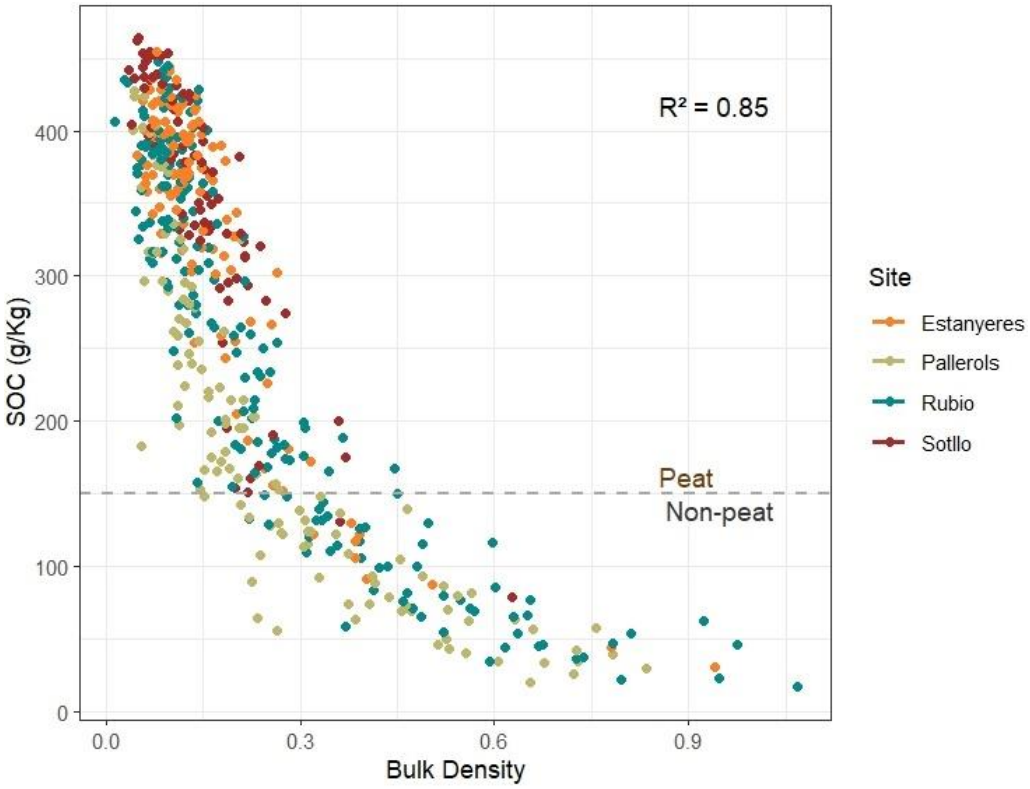

Figure A6. Relationship between bulk density and C proportion in the soil subsamples taken in the four mires (R^2 = 0.8494, p < 2.25e^{-16}). The dashed line at SOC = 150 separates the non-peat subsamples (below) from the peat subsamples (above).

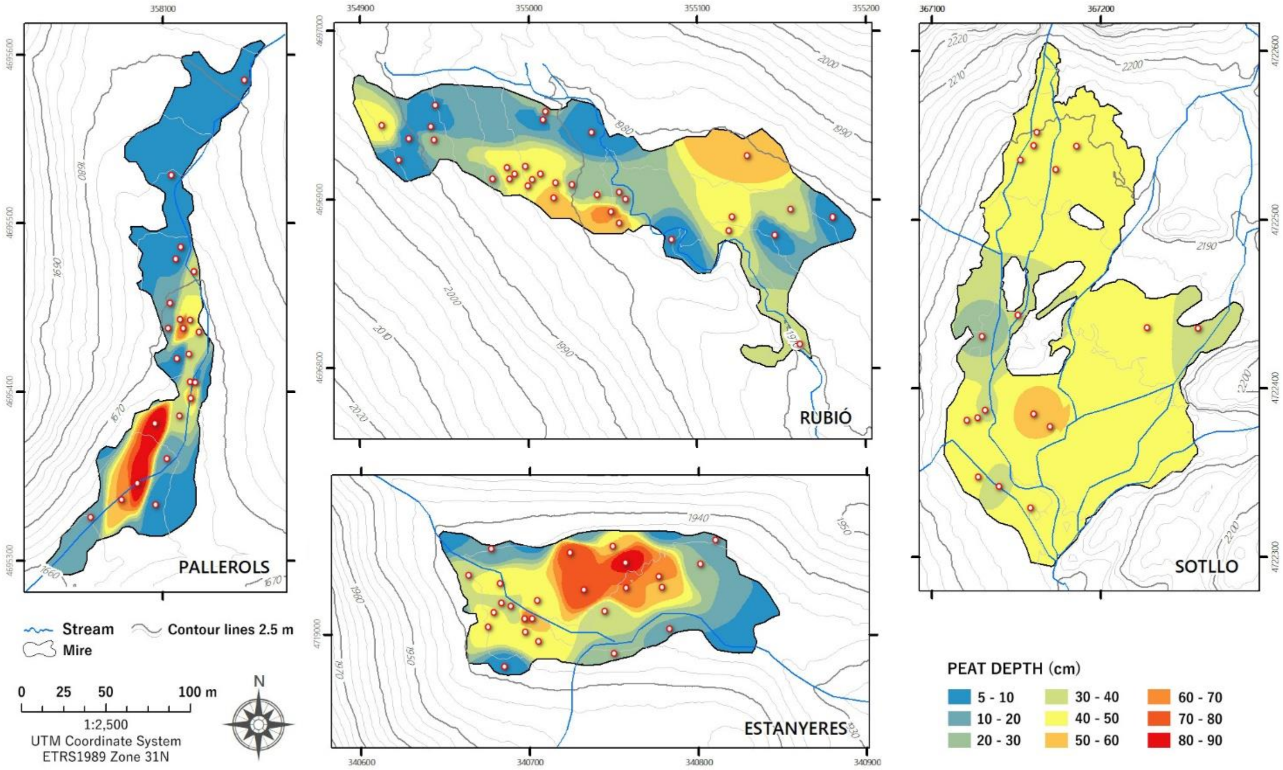

Figure A7. Thickness of the peat layer in the four mire systems studied. The dots indicate the sampling points.

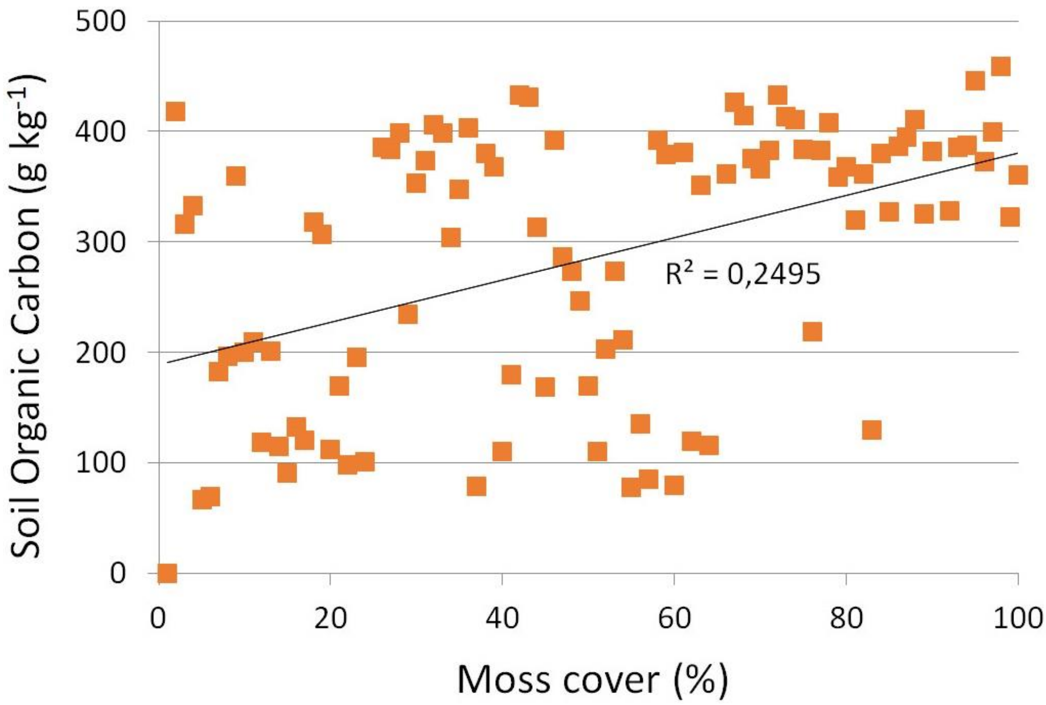

Figure A8. Relationship between total moss cover and C concentration in the 0 to -15 cm soil layer according to the points sampled (squares).

Table A1. Distribution of C stock within the four mire sites studied, each one split into areas corresponding to distinct categories of C stock.

Location	C stock categories ($kg.m^{-2}$)	Partial area (m^2)	C content (kg)	Mire area (m^2)	Total C stock (kg)	Average C stock ($kg.m^{-2}$)
Pallerols	4.67–5	162	784	10,888	152,863	14.04
	5–10	4,742	35,564			
	10–15	1,914	23,930			
	15–20	1,508	26,387			
	20–25	1,382	31,091			
	25–30	663	18,237			
	30–35	481	15,627			
	35–35.21	35	1,242			
Rubió	5.32–10	2,182	16,715	18,005	286,911	15.94
	10–15	6,276	78,451			
	15–20	5,983	104,711			
	20–25	2,691	60,546			
	25–30	405	11,132			
	30–35	421	13,685			
	35–37.09	46	1,671			
Estanyeres	4.92–5	127	630	12,248	238,868	19.50
	5–10	1,428	10,707			
	10–15	1,376	17,195			
	15–20	3,891	68,096			
	20–25	2,769	62,301			
	25–30	1,391	38,258			
	30–35	1,083	35,187			
	35–35.49	184	6,494			
Sotllo	10.8–15	379	4,888	25,906	550,856	21.26
	15–20	9,222	161,382			
	20–25	13,148	295,826			
	25–30	2,869	78,896			
	30–35	191	6,203			
	35–39.75	98	3,662			

Table A2. Correlation matrix of the Pearson test indices of the variables considered for the soil samples: SOC at distinct soil depths (a: 0 to -5 cm; b: -5 to -10 cm; c: -10 to -15 cm; d: -20 to -30 cm), total C in the entire profile, peat thickness, and terrain slope. Coloured cells indicate correlation values over ± 0.8 (dark green) or between ± 0.8 and ± 0.6 (pale green).

	SOC_a	SOC_b	SOC_c	SOC_d	Total C	Peat
SOC_a						
SOC_b	0.848					
SOC_c	0.720	0.910				
SOC_d	0.597	0.676	0.801			
Total C	0.342	0.425	0.468	0.492		
Peat	0.540	0.678	0.730	0.707	0.780	
Slope	-0.318	-0.380	-0.328	-0.263	-0.238	-0.361