

Article

Restoring High Mountain *Sphagnum* Communities in the Central Pyrenees

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Abstract

A handful of *Sphagnum* species and their ecosystems find their southernmost occurrence in the Pyrenees, and these small, relict units are endangered through anthropic activities and climatic change. A number of hydropower reservoirs covered former mire systems with water or let them ashore. These infrastructures will eventually become useless and abandoned, and the mires could possibly be restored, but there have been no known experiments in the Pyrenees in this field. The removal of the dam of a small reservoir in the Central Pyrenees in 2012 uncovered bare ground that was appropriate for testing mire restoration. In 2017, we started the restoration of two Habitats of Community Interest (HCIs), i.e., transition mires and quaking bogs (HCI 7140) and active raised bogs (HCI 7110*). To restore HCI 7140, we set a *Carex rostrata* population by planting cuttings and then small tufts of two *Sphagnum* species within the sedge sward. In parallel, we set small clumps of two other *Sphagnum* species intended to grow into hummocks (HCI 7110*). After seven growing seasons, HCI 7140 reached a good progression level, with a prosperous *C. rostrata* sward and progressive expansion of the *Sphagnum* populations. HCI 7110* turfs had varying performance, exhibiting moderate survivorship and positive expansion of the remaining turfs. The varying performance of the restored populations illustrates the possibilities of restoring mire communities in suboptimal environments. Interestingly, such restorative actions are appropriate for enhancing populations of species under threat, such as *Sphagnum divinum*.

Keywords: wetlands; transition mires; hummocks; alpine; Habitats of Community Interest; transplantation; monitoring



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1. Introduction

The transformations made to nature by humankind are so generalized and ancient that natural protected areas are also affected in a wide variety of ways. Some such transformations are even operative in protected areas [1–3]. In the Central Pyrenees, as in other Alpine mountains, there are many hydropower infrastructures (i.e., dams, power engines and canals) in protected natural areas and elsewhere; in fact, most of these infrastructures were built prior to the implementation of the protection rules [2,4].

The generalized need for restoring ecosystems is particularly appropriate in protected areas, since one of the goals of these areas is to strengthen the knowledge of the contents and functions of ecosystems [5]. Therefore, such areas are appropriate for field research

activity or regular monitoring. This is noteworthy because to improve restoring procedures, it is necessary to conduct sound monitoring and to accurately evaluate the actions performed [6].

Indeed, the National Park Aigüestortes i Estany de Sant Maurici and other Pyrenean protected areas include a number of hydropower infrastructures which, in the future, will need restoration [4]. This process will include the removal of the dams to recover the hydrology and sediment flow of the natural basins, and ecology-based interventions to promote vegetation succession and habitat recovery. In many cases within the Alpine mountains, the natural habitats to restore will correspond to mires (peat-forming wetlands, i.e., fens and bogs). Many dams have already been removed all over Europe to restore ecological functions [7], but the procedures of mire restoration in high mountains are far from known. Concretely, to our knowledge no experiments of mire restoration have been carried out in the Pyrenees, and not much more is known from similar Alpine mountain systems [8]. The particular biogeographic and ecological situation of mountain mires in the Pyrenees [9,10] reinforces the need to create local, sound knowledge on their restoration.

Project LIFE+ LimnoPirineus gave us the opportunity of planning and performing the restoration of two Habitats of Community Interest (HCIs) in a recently created wasteland after removing a small dam, named Font Grossa: transition mires and quaking bogs (7140) and active raised bogs (7110*) [11]. These habitats have particular significance within the National Park Aigüestortes i Estany de Sant Maurici due to their relative abundance in this space and their rarity in the Catalan Pyrenees [12,13]. The two types of mire are well represented in the Trescuro lakes, located just above the Font Grossa and within the same basin, making them particularly appropriate for restoration trials under full natural conditions.

Under a broader view, the local opportunity of learning to restore vulnerable ecosystems (i.e., raised bogs and transition mires) should contribute to the focus on the restoration of habitats at the edge of their distribution area. In our case, the National Park includes a number of vulnerable species and sensitive ecosystems—even more under climate change [12]—which must be managed or restored from ancient anthropic activities (i.e., water use). Restoring ecosystems that are so scarce within the landscape poses a particular strength in enhancing the appropriate plant succession, i.e., in improving the appropriate abiotic conditions to initiate ecosystem development, and in facilitating the targeted species of these ecosystems to build promising populations and communities [14,15]. Such species are very rare within the landscape, mainly in water-related environments; thus, immigration from other populations seems less likely.

Referring to the scientific knowledge of vegetation, we must face the difficulties in initiating ecological succession from scratch over degraded land, under suboptimal environment conditions and with the lack of applied knowledge under alpine conditions. Moreover, restoration must focus on the mid- and long-term to ensure that, beyond the first step (i.e., setting reasonable populations of engineer species), spontaneously immigrating species assemble into appropriate plant communities, or that further hampering factors (i.e., meteorological events, competition from unpredicted species, geochemical dynamics) do not divert the ecological succession [15,16].

At present, there is wide expertise in sphagnum mire restoration, mainly covering situations where ancient peatland had been deeply degraded [16–19]. Most of the acquired knowledge refers to new plant communities developing on ancient bare peat, sometimes being rewetted [20]. However, to our knowledge, no experiments have been reported on the treatment of ancient reservoirs, i.e., previously inundated peaty substrata, which are now greatly mineral, and very few case studies refer to Alpine mountains [8,21].

The main objectives of this study are to (i) assess the better way of restoring mire ecosystems in alpine landscapes, on the basis of required analysis of the response of appropriate species to the local conditions, their adequate transplantation, and detailed monitoring of the new populations and communities, and (ii) evaluate the weight of operating hampering forces and disturbance events that shape the progress of succession progress and their phases—in our case, the growing frequency of dry spells or high temperature events in summer, or hydrological irregularities related to alpine landscapes. We therefore aim to gain knowledge on alpine mires and on how to shape their restoration. This becomes necessary for providing nature managers with science-based solutions to restore sensitive ecosystems that are scarce within fragmented landscapes.

2. Materials and Methods

2.1. The Restoring Site

The area studied, Font Grossa, lays in the Peguera water course (2007 m a.s.l., 42°33'19" N 1°03'46" E), in the National Park Aigüestortes i Estany de Sant Maurici, in the Catalan Central Pyrenees, NE Spain. The main environmental conditions come from the local high mountain climate, with mean annual temperature of 5.7 °C and annual precipitation of 1150 mm, with spring and autumn peaks (data from the last 15 years [22]). The annual growth period lasts less than five months [23], roughly from mid-May to the beginning of October (more information can be found in Appendix A). The surrounding landscape is dominated by mesophilous mountain pine (*Pinus uncinata* Ram. ex DC.) and alpenrose (*Rhododendron ferrugineum* L.) forest, which, given the rough physiography and the ancient land use of the area, is spotted by mat grassland, rocky areas and water related vegetation units (Figure 1).



Figure 1. General view of the Font Grossa site. The pond is bordered by the restored transition mire—*Carex rostrata* population—and lies in the rough subalpine landscape dominated by *Pinus uncinata* forests and rocky areas (September 2021).

Along the main Peguera water course and surrounding springs and rivulets, these vegetation units include small pieces of mire, in the form of tiny spots of *Trichophorum cespitosum* (L.) Hartm. fens (Tofieldio-Scirpetum cespitosi), *Carex rostrata* Stokes transition mires (Sphagno-Caricetum rostratae) and sphagnum hummocks (Vaccinio-Sphagnetum capillifolii; [24]. The two latter associations correspond to two Habitats of Community

Interest [25]: HCI 7140 transition mires and quaking bogs, in the form of open swards of *C. rostrata* with hydrophilic sphagnum carpets bordering still waters, and HCI 7110* active raised bogs (a priority Habitat), in the form of small (<5 m²) sphagnum hummocks protruding from fens. Both habitats find their southernmost European locations in the National Park and nearby mountains, a biogeographic particularity shared with the handful of *Sphagnum* species found in them. One of these species, *S. divinum* Flatberg & K. Hassel (formerly included in the *S. magellanicum* agg.) is classified as Vulnerable in the Iberian Peninsula [26,27].

While several reservoirs upstream remain in use for hydropower production, there was a small reservoir (area ~1500 m²) at Font Grossa which became useless at the turn of the century. In 2012 the dam and the associated infrastructure were mostly removed to re-naturalize the area, according to an initiative from the National Park that aimed to provide the first experiment of passive restoration. This led to a decrease in the water level of the reservoir to about 80 cm and a decrease in its area to about 620 m². Thus, it transformed into an almost-natural pond with the Peguera ravine course running through the bottom and the remaining base of the old dam retaining water downstream. In addition, over the right shore of the pond, there is a significant water surge and some diffuse sources that maintained a small mire spot prior to construction of the reservoir, of which the part above the flood level remained in a good condition.

The ground strip uncovered by water following the elimination of the dam was quite uneven, containing numerous granite blocks. Between these, there was a set of slightly sloping (~3°) relatively soft surfaces, formed by a sandy and silty substrate coming from granite and slate bedrock. Here, the water table remains relatively superficial, determined by slope runoff and a small seasonal oscillation of the pond surface, and subjected to sporadic highs and lows caused by the hydroelectric use of the upstream waters (shifts in the water level up to 13 cm during the growing seasons of 2014 and 2015). The lower part of the shore was potentially appropriate for targeted transition mire development. The ground water (measured in summer 2014) was slightly acidic and poorly mineralized (pH from 5 to 5.5, electric conductivity from 17 to 31 µS/cm, and Ca content from 3.8 to 7 ppm), whereas the water in the pond gave slightly higher values (pH = 5.5, EC = 48 µS/cm, and Ca = 16 ppm).

After the lowering of the water and until 2017, the most favourable parts of the newly exposed ground had been irregularly colonized by opportunistic mire or meadow plants, whereas substantial parts of the ground remained bare.

2.2. Prior Experiments with Plant Material

Before beginning with the restoration experiment, from autumn 2014 to spring 2017, we experimented with distinct plant propagules of appropriate species to improve the success of the restorative action. The tests were mainly performed under controlled conditions at the University of Barcelona facilities, and eventually in small (~1 m²) plots at the restoring site, Font Grossa. Thus, we studied which are the best environmental conditions and sizes of plant propagules during transplantation. The plant material was collected in nearby locations. This chiefly included cuttings of *Carex rostrata* and small swards of three *Sphagnum* species. In all cases, they were species that have a structural role in one habitat or another, covering a certain range of the ecological gradient prevailing in acid mires, mainly that of flooding [12,13,24]. In addition, they were clonal species, i.e., capable of forming large populations from the lateral expansion of one or few individuals [28]. In the case of vascular plants, *C. rostrata* uses to be dominant in periodically flooded mires and on lake shorelines [24]. Regarding mosses, we chose *Sphagnum teres* (Schimp.) Ångström as typical of substantially flooded environments, particularly HCI 7140; *S. capillifolium* (Ehrh.)

Hedw., typical of the upper part of the sphagnum hummocks in relatively dry conditions (HCI 7110*); and *S. divinum*, which is found in an intermediate spectrum of hydrological conditions, but which frequently forms low hummocks (HCI 7110*) [24,29,30].

We tested these species under controlled conditions at two water levels and in distinct competition regimes, as well as in field plots at the restoring site at distinct water levels and, in the case of vascular plants, also in distinct competition regimes. Under controlled conditions, *C. rostrata* survived and established at a very high proportion from small cuttings. After three months of culture, growth (leaves, rhizomes) was optimal in young plants in pure culture, regardless of the two water levels tested. Under field conditions from summer 2015 to autumn 2016, young plants of *C. rostrata* were established better under flooding conditions than ashore, regardless of whether they faced competition. Therefore, this sedge showed good capacity for implantation and establishment from cuttings into the transition mire to be restored, both in and out of the water [31].

Regarding mosses, we assembled small ($\sim 1 \text{ cm}^2$) culture pots in the first experiment, where we arranged caulidium segments of *Sphagnum* including the capitula. The trials under controlled conditions included distinct water levels and substrata (such as peat, dead wood or sand). For all three species, almost all of the fragments survived, and growth was significantly affected by the level of flooding and the type of substrata, with more growth using peat and with the water being at the same level as the substrate [32]. Afterwards, we run some field experimental trials from midsummer 2016 to autumn 2017. We used commercial peat and entire shoots of *Sphagnum*, since larger fragments proved to grow more vigorously and seemed less sensitive to occasional dry conditions. Moreover, we added a fourth species, *S. subsecundum* Nees, typical of permanently wet sphagnum carpets, to have a second species for the flooded habitat (HCI 7140). The trials were based on small pots of pressed peat ($4.5 \times 4.5 \times 5 \text{ cm}$) with just four shoots of *Sphagnum* on each, covered with a wide mesh of natural fibre. The results highlighted that the reintroduction of *Sphagnum* populations would be sensitive to summer droughts, and that it would improve by creating particular protective microhabitats [16,20] since some experimental pots become disturbed, or disappeared, due to episodes of greater intensity in the water flow.

2.3. Setting and Monitoring the Restoration of Habitats

Restoration of the transition mire (HCI 7140) started in summer 2017, when the appropriate areas were slightly reshaped and protected from violent flowing episodes with wood stakes sunk into the bottom of the pond (Figure A4). Then, the lower part of the gentle shores and the slightly flooded margins of the pond—a patchy area amounting to about 135 m^2 —were planted with *C. rostrata*, to form the basis for HCI 7140 (Figure A5). The transplanting units were short (2–4 cm) segments of rhizome with one rosette of leaves each, collected from the margins of a nearby reservoir. These cuttings were directly planted in the restoring area, in a density of about 45 units per square metre. We expected that such a light population could shortly grow into a more tied and structured population, similar to those found in natural environments. As monitoring system, we fixed five plots of about $1 \times 2 \text{ m}$ evenly distributed within the restoring area, where we evaluated the cover and development of *C. rostrata*. This evaluation was based on photographic images taken periodically from the same point for each plot, which could be later analyzed. In this way, we assigned foliage density values to each image after overlying them with a virtual grid, standardized as percentage quartiles.

In June and July 2018, we transplanted the four *Sphagnum* species treated so far into the restoring places. Thus, we prepared 44 plots (each composed of four peat pots of $4.5 \times 4.5 \times 5 \text{ cm}$) of *S. subsecundum* and 30 plots of *S. teres* to restore the transition mire (HCI 7140, Figure A6). The plots of these two species were set at three distinct water levels

along the shore gradient. In the just-inundated location, namely 1–2 cm below the water level under regular midsummer conditions, we placed 20 and 13 plots of the two species, respectively. Just ashore, namely at 3–4 cm over this water level, we set the same number of plots (20 and 13, respectively). In addition, at about 8–9 cm over the water level we placed four plots for each species. This setting was distributed within the area already settled by *C. rostrata*. There, we expected that the light sward of this sedge would exert some protection from wind and sun on the young sphagnum turfs [14]. To restore the sphagnum hummocks (HCI 7110*) we set 20 plots of *S. capillifolium* and five plots of *S. divinum*, as the starting point of the hummocks. They were set framed by some protective elements such as pieces of dead wood.

Once the plots with *Sphagnum* propagules were set, we sowed a few specialist plant species onto them through seeds collected in nearby natural populations. In the transition mire (HCI 7140) we sowed *Carex canescens* L. (a few more than 10 seeds in each pot within 33 plots of *S. teres* and *S. subsecundum*) and *Viola palustris* L. (more than 10 seeds in each pot within 10 plots of *S. teres*). In the restoring sphagnum hummocks (HCI 7110*) we sowed *Drosera rotundifolia* L. (more than 20 seeds in each pot within 15 plots of *S. capillifolium*) and *Potentilla erecta* (L.) Rauschel (more than 20 seeds in each pot within 10 plots of *S. capillifolium*).

During the first summer most of the *Sphagnum* propagules remained in place. The protective mesh proved to be a key element in preventing the small sphagnum turfs moving through water flows (Figure A1) and in giving some protection against high radiation and temperatures. The plots reached autumn 2018 in good condition, with most *Sphagnum* shoots grown through the protective mesh (Figure A6).

To monitor the progression of the new *Sphagnum* populations, we assessed the survival and the size of the transplants at the start and end of summer in 2018, 2019 and 2020, and at the end of summer in 2021, 2022, 2023 and 2024. The size was assessed through the height achieved by the sphagnum turf at each container in mm, and their canopy projected area in cm². To record these canopy areas we took one digital image with a camera set over each group of four pots (i.e., one plot) and we digitized each image to contour the *Sphagnum* canopy (Figure A7) and to calculate its projected area through the software ImageJ 1.54k [33]. In 2021, the estimation of the area occupancy of the sphagnum swards in the transition mire became inaccurate in some cases, since the lateral expansion of the swards had led a number of them to coalesce. Then, we set a different design for further monitoring intended to more generally cover the area restored, although not differentiating the two *Sphagnum* species. This was based on 21 transects beginning in the external drier parts of the mire and heading to the flooded parts, distributed in the whole area of the restored transition mire and crossing a high proportion of the original sphagnum plots. Along these transects, we recorded the frequency of the sphagnum swards from 2021 to 2024, as well as that of other plant species or relevant elements (water, rocks) through the intercept method at each 10 cm. Moreover, in the monitoring of sphagnum plots of both habitats, we recorded the occurrence of plant species, including the ones sown in the restoration and those that arrived spontaneously.

2.4. Data Analysis

Statistical analyses included the survivorship of pots in every sampling campaign (in percentage of pots alive per plot) from 2018 to 2024 and the canopy area of the sphagnum swards with time (in cm²). We tested the differences between the three distinct water levels in HCI 7140. Moreover, we analyzed the differences on survivorship and canopy area among the different species for each HCI (*S. teres* and *S. subsecundum* in HCI 7140; *S. capillifolium* and *S. divinum* in HCI 7110*). Since the variables showed strong non-

normal distributions, we analyzed them with the Kruskal–Wallis test. For multiple group comparisons, we used the Bonferroni p -value correction. Analyses were performed with R [34], using the package “vegan 2.6-4” [35].

3. Results

The overall *C. rostrata* population was established very well. By late summer 2017, the plants had barely produced new leaves, but they had rooted and formed new rhizomes, and mortality was very scarce (Figures 2 and A4). In 2018, there was noticeable densification and high survivorship, even after two very strong floods, one coming from the massive snow thaw at the end of spring and the other from an extraordinary rain event in August (Figure A1). The sedges remained all in place, although they were partly buried by flood debris in some sectors. In 2019, both snow melting and summer rainfall were poor, and temperatures were high in the first half of summer. Although these conditions strongly limited the development of the outermost fringe of the *C. rostrata* population, at the end of summer, overall densification proceeded overall—achieving similar cover to that of natural mires—and the population spontaneously expanded from the area planted through neighbouring shallow water (Figure A5). Moreover, the established shoots produced massive blossoms and fruiting.

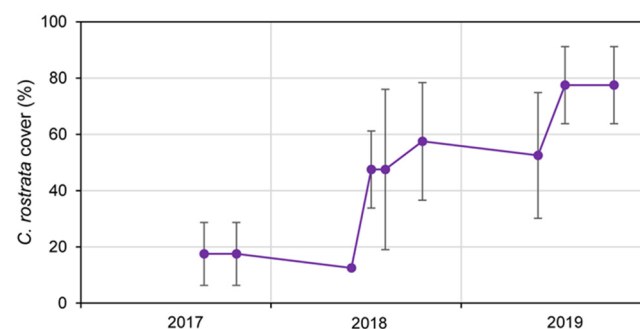


Figure 2. Progression in the *Carex rostrata* population from midsummer 2017 to autumn 2019, assessed as leaf cover percentages. The purple line represents average values, while vertical bars indicate the standard deviation in each monitoring record.

The survival pattern in the newly established *Sphagnum* populations was contrasting between the two habitats, once established in 2018. Both *S. teres* and *S. subsecundum* turfs that were transplanted in the transition mire—within the *C. rostrata* population—kept very high survivorship from 2019 onwards at the mid and low water levels (Figure 3). In fact, some of the turfs that were first recorded as dead in early summer 2019 because of signs of decline of most *Sphagnum* shoots, proved to be alive (and growing) along the same summer, which gives some positive slopes in the survivorship graphs. From 2021 onwards, survivorship was presumably very high, and anywhere the very active lateral expansion of most sphagnum turfs made the survival assessment of each plot impractical. The response in the two *Sphagnum* species was clearly poorer at the high water level (flooded condition), where the turfs survived only moderately until late summer 2019, and dropped to low rates through 2020, particularly in *S. teres*. According to non-parametrical tests, the survivorship of both species was significantly lower under the high water table in late summer 2021 (Figure 3). Moreover, we found no differences on the survivorship between the two species in the transition mire.

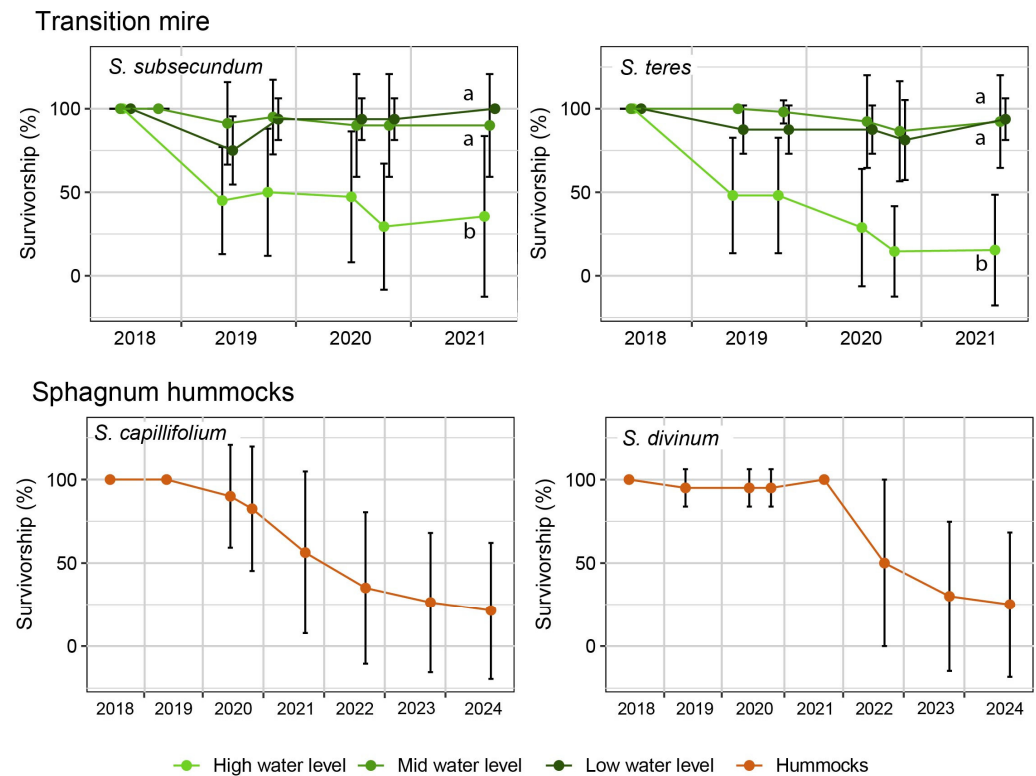


Figure 3. Survivorship of *Sphagnum subsecundum* and *S. teres* in the restoring transition mire from summer 2018 to the end of summer 2021, and *S. capillifolium* and *S. divinum* in the restoring sphagnum hummocks from summer 2018 to the end of summer 2024. Coloured lines depict average values, while vertical bars indicate the standard deviation in each monitoring record. Different letters in *S. subsecundum* and *S. teres* mean significant survivorship differences between distinct water levels at the end of 2021.

In the sphagnum hummocks, *S. capillifolium* survivorship decreased from 2019 to the end of summer 2024, when barely one quarter of the plants remained alive (Figures 3 and A8). In the same habitat, *S. divinum* maintained very high survivorship until the end of summer 2021, while dropping to about one half of the plants alive after summer 2022 (Figure 3), and decreasing to one quarter in 2024. Nonetheless, the final values were not significantly different between the two species. Interestingly, survivorship was almost 100% from 2023 onwards. Then, after some mortality recorded at short-term monitoring, living sphagnum turfs would have already successfully established in the area. Thus, the survival pattern of the *Sphagnum* species after the mid-term monitoring depended primarily on the water table level in the transition mire, and secondly on the habitat, since the sphagnums in the hummocks showed lower survivorship than those in the non-inundated area of the transition mire.

The lateral expansion of each *Sphagnum* species, measured through the projection area of the living samples, produced swards significantly larger in 2021 than at the beginning of the experiment in all cases (Figure 4). In the transition mire, both *S. teres* and *S. subsecundum* expanded through the same pattern, which was different according to the water level. At the low and mid water levels, both *Sphagnum* species behaved similarly, expanding regularly from 2019 to the end of 2021—with sharper expansion in the middle of the growing periods. At the intermediate level, the living swards of each species occupied at the end of 2021 roughly four times the area set in early 2018. Growth was slightly poorer at the low water level, especially in *S. teres*, where summer drought events were more influential and where the *C. rostrata* population maintained a lower density during the monitoring. At the high water level, the area of the living samples already decreased

from early to late summer 2018, and did not expand from there to 2021, when it showed noticeable growth. In addition, the flowing dynamics may have affected these sphagnum plots during the whole experiment, via sediment arriving on the swards (field observations). In terms of general cover in the area restored (Figure 5), the *Sphagnum* in the transition mire extended broadly along the mid water level, while faint expansions took place at lower and higher levels. Measured through transects, the two *Sphagnum* species covered together about 25% of the area in 2021 and reached over 51% in 2024 (Figures 6 and 7) and showed good vitality. The high cover variability found between transects reflected the noticeable patchiness of the sphagnum lawn in the restored mire, which is usual in natural transition mires.

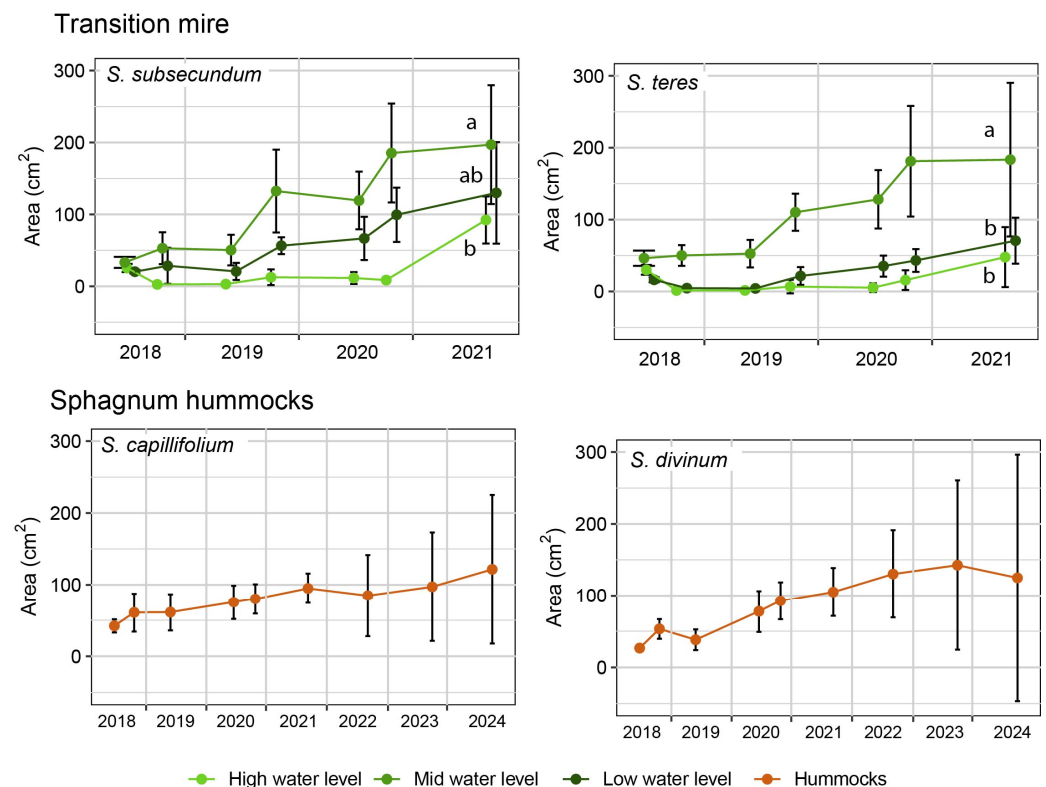


Figure 4. Progression of the area covered by the turfs alive of *Sphagnum subsecundum* and *S. teres* in the restoring transition mire from summer 2018 to the end of summer 2021, and *S. capillifolium* and *S. divinum* in the restoring sphagnum hummocks from summer 2018 to the end of summer 2024. Coloured lines depict average values, while vertical bars indicate the standard deviation in each monitoring record. Different letters in *S. subsecundum* and *S. teres* mean significant differences in expansion at the end of 2021 between distinct water levels.

In the sphagnum hummocks (Figure A8), the expanding growth of the two species used was moderate and not lineal until 2019 (Figure 4). However, from then until 2024 the area of living swards increased in both species. While the swards of *S. divinum* expanded regularly at a good rate and slightly decreased in the last year, those of *S. capillifolium* grew moderately most years. At the end of 2024, the living swards of *S. divinum* occupied five times the area set in early 2018. Ultimately, the loss of vanishing turfs might be compensated by the growth of the remaining ones (Figure 5).

A general trend arising in the lateral expansion of *Sphagnum* through habitats, species and water levels is the increasing variability in response within each case. Namely, the expansion by lateral growth became increasingly variable with time between replicate swards (Figure 4).

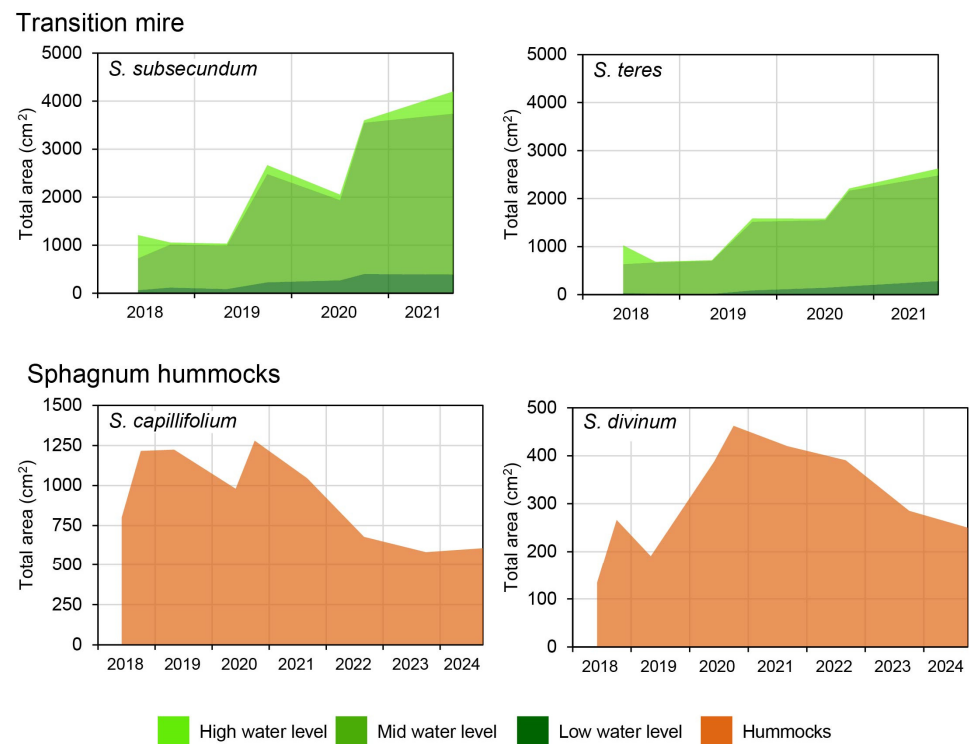


Figure 5. Progression of the total area covered by *Sphagnum subsecundum* and *S. teres* in the restoring transition mire from summer 2018 to the end of summer 2021 in the three water levels considered, and by *S. capillifolium* and *S. divinum* in the restoring sphagnum hummocks from summer 2018 to the end of summer 2024.

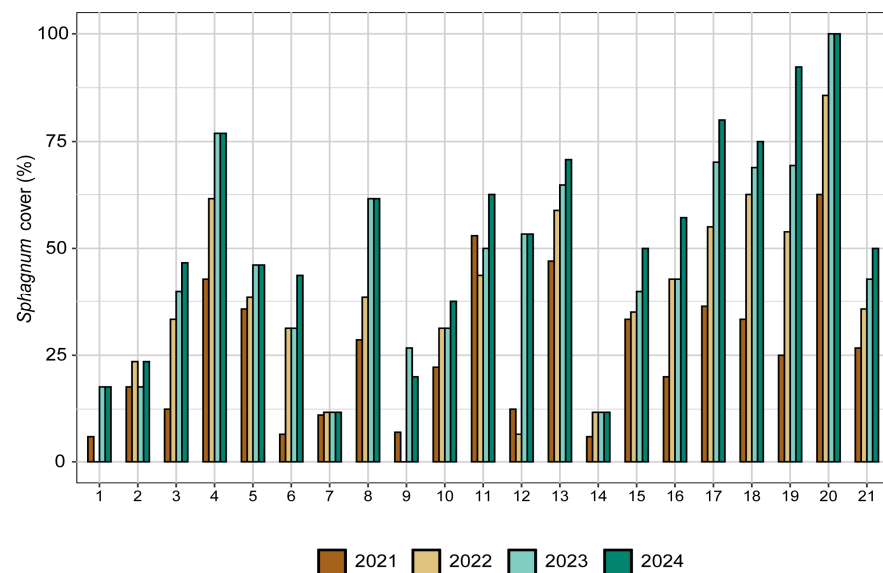


Figure 6. Progression of the percentage cover of the two *Sphagnum* species together (*Sphagnum subsecundum* and *S. teres*) from late summer 2021 to late summer 2024, found along 21 transects set in the transition mire of *Carex rostrata* (HCI 7140) at Font Grossa. The global cover increased from 25% to over 51%.

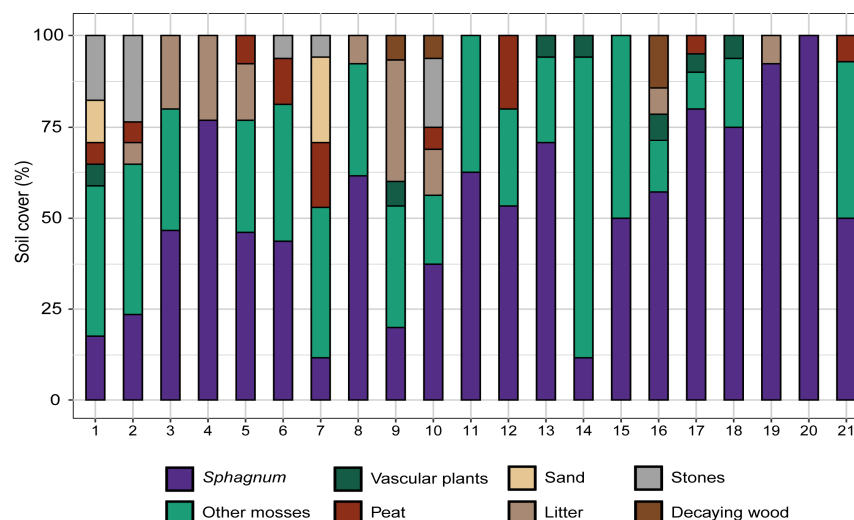


Figure 7. Percentage cover of different elements (colours) found along 21 transects (vertical bars) monitored in the restored transition mire of *Carex rostrata* (HCI 7140) in Font Grossa, in late summer 2024. The dark purple colour represents together the two *Sphagnum* species transplanted (*S. subsecundum* and *S. teres*). Note that all transects have remaining area suitable for sphagnum colonization (peat, sand, litter or wood).

Referring to the vascular species sown on the sphagnum swards, *Potentilla erecta* and *Drosera rotundifolia* emerged and established in most experimental sphagnum plots of HCI 7110* before 2021, whereas *Carex canescens* and *Viola palustris* settled on just one third of the transition mire plots, HCI 7140 (Figure A3).

From the installation of the sphagnum plots onwards, a number of species established spontaneously in them in both habitats, mostly due to seeds—or spores—immigrated and in some cases through rhizome expansion (Table A1). In the case of the transition mire, in the 2021 monitoring only one plot remained not settled by any of the 23 species recorded as spontaneously arrived. Here, *C. rostrata* had invaded 83% of plots from the surroundings—where it had been planted—by means of its active rhizomes. Other frequent species were *Potentilla erecta* (20%), *Juncus articulatus* L. (18%), *Epilobium* sp. (16%) and *Prunella vulgaris* L. (13%) (Figure A11). A few moss species—apart from *Sphagnum*—established with lower frequency in the plots of both habitats. In the sphagnum hummocks, none of the plots remained free from being spontaneously settled by at least one vascular plant species. In 2024 these were 17 in the whole, the most frequent being *Pinus uncinata* as small seedlings (found in 66% of the plots), *Carex rostrata* (44%), *Potentilla erecta* (33%) and *Eleocharis quinqueflora* (Hartmann) O. Schwarz (33%) (Figure A12).

4. Discussion

Our aim of restoring bare ground fostering plant succession towards target mire habitats has yielded promising results, albeit including some pitfalls. On the one hand, *C. rostrata* grew and became denser into few years, and the living turfs of *Sphagnum* expanded steadily in the two restored habitats. Moreover, in the transition mire the structure and the species richness of the habitat progressed significantly over the seven monitored years. On the other hand, *Sphagnum* survival was uneven between distinct microhabitat positions within each habitat.

Climatic variability worsened the challenge of restoring habitats and species so dependent on even water availability during the growing season, as shown by previous studies in southern Europe [36]. Due to climate variability and the clear trend towards warming temperatures [37], it is foreseeable that these effects will make restoration projects

more unpredictable [38]. Moreover, the relative success in building plant populations and communities, as demonstrated through our short-term monitoring, could develop to varying degrees in the mid-term, when indicators other than plant growth and new species occurrence would be considered [15,16,21,39].

4.1. Plants Response to the Restoration Procedure

The restoration of the transition mire has been reasonably successful, from various aspects. The main structural species, the sedge *C. rostrata*, proceeded even faster than predicted, since in barely two years it formed a uniform, dense sward, despite the short growth periods and some sudden flood events (Figure A9). Transplanting the sphagnum plots one year later than the *C. rostrata* cuttings would have enhanced facilitation from the sedge to the mosses, given the very high survivorship and the expanding trend of the sphagnum swards—at least, in those set at mid or low water levels. Other restoration studies have emphasized the role played by sedges or grasses in facilitating *Sphagnum* establishment, in the form of the partial interception of light and wind, and in amelioration of the soil structure and water ascent [14,16,40,41].

The *Sphagnum* populations in the transition mire performed positively in any case. Both species responded similarly with time and through distinct ecological positions, with *S. subsecundum* being slightly more expansive than *S. teres*, seemingly through less sensitivity to drought. Setting and monitoring the plots according to an elevation gradient on the shore gave us good information on the limiting factors for sphagnum restoration. On the one hand, these hygrophilous mosses need the proximity of the water level; the plots at the upper position on the slope survived but grew less than those set at the intermediate level did. On the other hand, the semi-flooded position was detrimental mainly due to hydrodynamic disturbance—causing early mortality or loss of turfs—and to microhabitat unsuitability, through growth limitation. Thus, the intermediate position enhanced the very satisfactory *Sphagnum* implantation and would be a good place for a whole—though small—example of transition mire, from which expansion to the neighbouring water levels may proceed [16]. The carpet of these *Sphagnum* species showed cumulative growth even after the unfavourable 2021 and 2022 summers (Figures 5–7).

Hummock sphagnums performed less positively and more diversely among plots. Their swards survived the first years well, but progressively disappeared through 2021 and 2022 summers. At the same time, however, most of the remaining swards continued exhibiting expanding trends. Between the two species used, *S. divinum* responded better in the short-term than *S. capillifolium* did, both in survivorship and in lateral expansion. This may be connected to the higher affinity of *S. divinum* for settling on open new habitats, where its development would initiate hummocks, whereas *S. capillifolium* would perform better on hummocks already developed [42,43]. This should be an expression of the more ombrophilous characteristic for *S. capillifolium* than for *S. divinum* [13,24]. In our case study, poor rainfall occurred some summers which would make the initial hummocks more influenced by ground water than by rainfall. This shift to less ombrotrophic conditions would have worsened the poor conditions that the restored hummocks—barely elevated from the ground—offered to *S. capillifolium* (Figure A10). However, during the two last growing seasons, the different response of the two hummock *Sphagnum* species tended to equalize their success. In any case, the restored hummocks became good opportunities to reinforce the most threatened *Sphagnum* species in the area, *S. divinum* [25,26].

The response in both hummock *Sphagnum* species became more variable during the monitoring period. This reflects the fact that small differences between plots in terms of microtopography or proximity to protective elements grew into larger differences in plant response, which was emphasized by the fact that Font Grossa is a suboptimal location

for sphagnum hummocks [10,13]. Under adverse conditions, subtle differences in micro-habitats likely determined the survival of hummock-forming *Sphagnum*. However, after the first seven years we observe that the surviving individuals progressively expand their cover and appear to be on a trajectory towards long-term persistence. Given that initiating sphagnum hummocks from scratch is a challenging task—since optimal conditions are rarely met within the core of a minerotrophic mire [19]—we consider the method employed to be successful enough, replicable, and scalable across the Pyrenean region.

4.2. Ecological Succession in the Newly Restored Habitats

While *C. rostrata* and *Sphagnum* formed noticeable populations in the restored transition mire, the structure and complexity of this new ecosystem increased noticeably from 2018 to 2024. Several vascular wetland plants were progressively settled on, and some hydrophilic mosses apart from the *Sphagnum* species joined at the moss level. Therefore, the structure and the species richness of the mire community approached to those of natural sites of this habitat [24]. Similarly to more natural situations, the habitat showed some patchiness, partly due to the roughness of the area restored. Apart from granite blocks, other bare spots corresponding to sand or peat ground or to dead wood would become appropriate substrata for the mire species in the medium term. The ecosystem is therefore still in a young successional phase.

As expected in the succession of the sphagnum hummocks in an earlier stage, the accumulation of organic litter is still very poor. The occurrence of dry summers sharply reduces the productivity of these *Sphagnum* species [42]. In our case, this throws some uncertainty on the fate of this restoring habitat in Font Grossa. The mature hummocks found in areas next to this site may have developed through long periods (Figure A10). Thus, the formation of new hummocks might only occur under periods of regularly rainy summers. In any case, the initial hummocks set in the most favourable microenvironments have persisted and grown after several unfavourable summers. Meanwhile, they become place for some immigrated vascular plants—mainly sedges and grasses—that would enhance their stability and performance if remaining at low to medium densities [14]. Therefore, the restored habitat is prone to positive—though slow—progression when sphagnum turfs are transplanted in favourable microhabitats. In both restored habitats, the proximity of natural spots of the same habitats should help immigrating new species and maintaining the populations of the extant ones.

4.3. Learning Points

It is crucial to gain precise knowledge on the system and species to restore through direct experiments, prior to addressing any restorative action. Even with the availability of quality information on the species and ecosystems, the precise environment conditions may cause unpredicted responses. In our case study, previous experiments with different species under distinct conditions were essential to design and rule the mire restoration.

Restoration planning should evaluate the actual possibility of jumping to further successional stages by artificial means in each case. Transplantation should proceed after physical–chemical improvement of the site where abiotic conditions do not meet some minimum conditions needed for plant communities [15]. Restoring hummocks would probably improve if the sphagnum turfs were set on domes of peat or other appropriate substrata disposed of previously (Figure A13).

Restoring habitats give the opportunity to reintroduce or enhance populations of threatened species. Contrasting with their biogeographic vulnerability or local rarity, they may develop good colonizing capacity in a restoration context, as with *S. divinum* in our

study. The use of propagules of these species should not compromise the persisting capacity of the populations sampled in any case.

We particularly emphasize the importance of monitoring the ecosystems and populations restored. This is key not only to reliably assessing the progress made, but also to describing the plant succession in reasonable detail. This is particularly useful in poorly known systems, as is the case of peatlands in southern European mountains. Thus, restorative actions and ecological knowledge of natural systems must coexist and strengthen each other [44]. While restorative actions need some knowledge of the structure and function of ecosystems, such knowledge stems from management and restorative actions—including proper monitoring of the ecosystems restored.

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

Appendix A. Summer Meteorology and Flooding Dynamics

The study area, Font Grossa, exhibits a typical subalpine bioclimate. To detail this statement, we use the records of the nearest meteorological station, Espot (2519 m a.s.l., 42°32'2.79" N, 1°3'17.08" E). Since it is located about 2.5 km in distance and is 500 m higher in elevation from the study area, we may predict there a similar meteorology in Font Grossa, although translated to this lower site. In the case of temperatures, the mean annual temperature at the Espot station (2.72 °C in the last 15 years [22]) would be 3 °C higher in Font Grossa (about 5.7 °C), and the annual regime would also run similarly higher. Thus, in this site the growing period (with regular daily mean temperatures higher than 5 °C [23]) would extend on average from mid-May to the beginning of October, with average daily temperatures of 12.2 °C (Figure A1).

The high amount of annual precipitation at the Espot station (1560 mm, mean of the last 14 years [22]) should correspond to about 1150 mm in the study area, with maxima in spring and autumn. In any case, rainfall is high during the growing season, although the rain events may vary substantially in magnitude (Figure A1). More in detail, contrasting with events of high rainfall, rainless episodes (e.g., ten or more days) occur in most years. Such episodes coincide normally with sunny periods, and sometimes also with high temperatures. These coincidences turned into the most influential climatic phenomena regarding *Sphagnum* development, such as that occurred in June and July 2019; in August 2021; and in May, June, and July 2022 (Figure A1).

In the case of the transition mire, the flowing dynamics of the pond may turn into disturbance events for the establishment and growth of the sphagnum swards. According to our records of the water level in Font Grossa, there was relative uniformity during most of the growing season during the monitoring years, which contrasted with sudden

raising events in spring and autumn. Depending on the year, they consisted of one or a few peaks in late May or in June reaching 3–4 cm over the regular level, and of one or two similar peaks in September or October. The main cause for these increases is heavy rain events, which in spring may coincide with massive snowmelt and, at other times, may respond to hydropower activities. Although these level increases seem moderate, they reflect strong flowing dynamics in the small pond in practice, which strongly affect the *Sphagnum* populations in the transition mire and even disturb the *C. rostrata* swards (Figure A9).

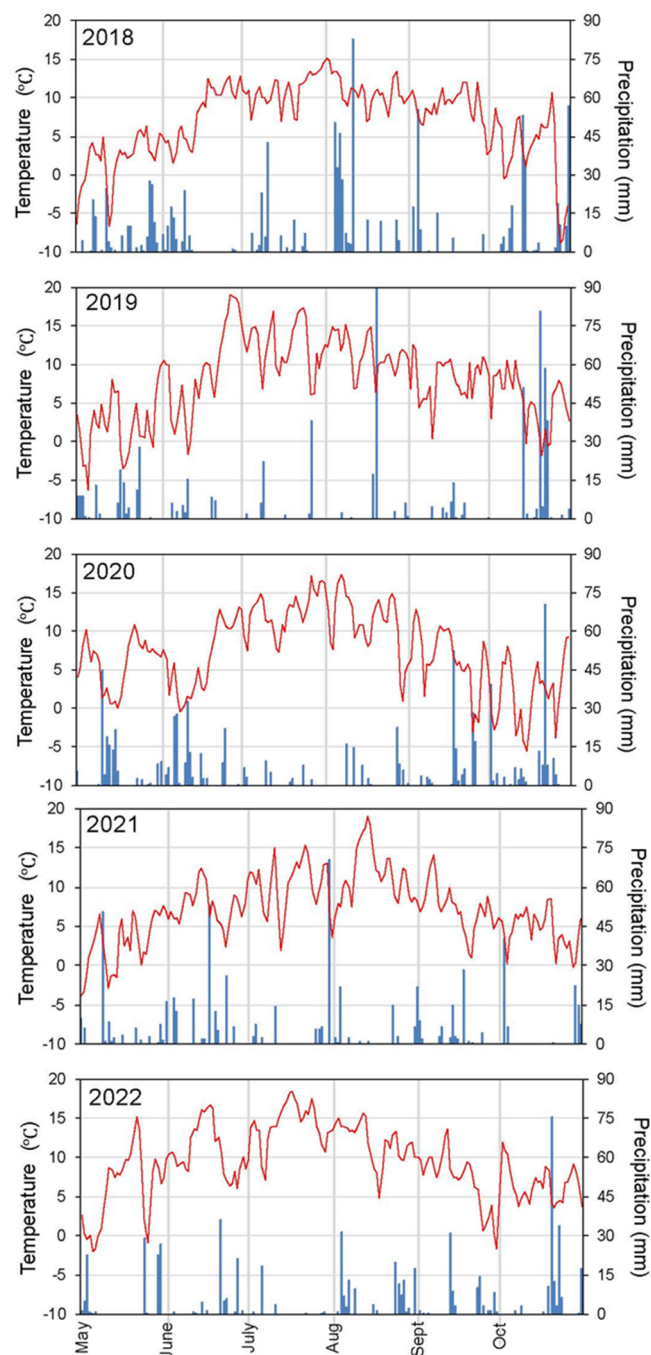


Figure A1. Progression of the mean daily temperature (red line) and daily rainfall (blue bars) from the beginning of May to the ending of October through the first five years monitored.

Appendix B. Complementary Results on *Sphagnum* Restoration

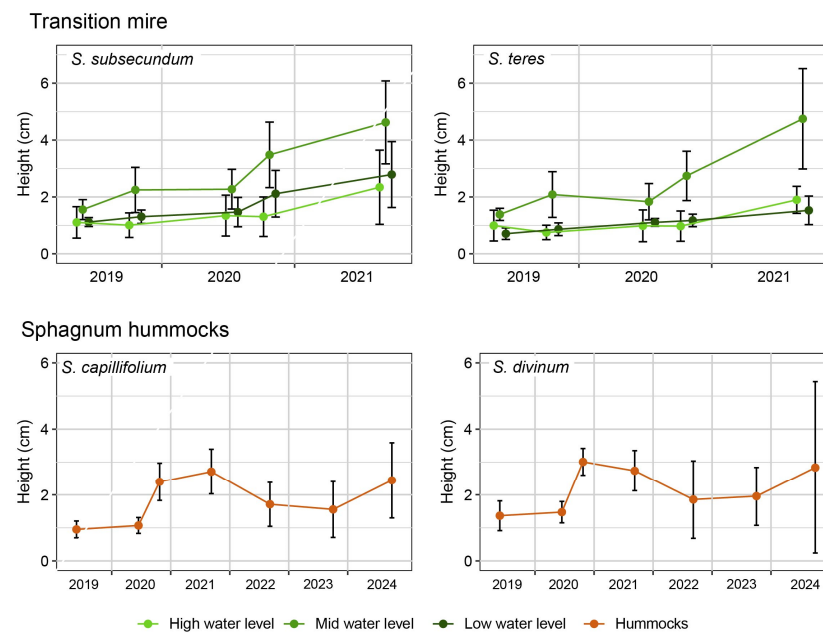


Figure A2. Height achieved by the swards of *Sphagnum subsecundum* and *S. teres* in the restored transition mire from early summer 2019 to late summer 2021 at the three water levels considered, and of *S. capillifolium* and *S. divinum* in the restored sphagnum hummocks from early summer 2019 to late summer 2024. Lines give average values and vertical segments represent the standard deviation. In the case of the transition mire, both species responded similarly as they did in terms of lateral expansion (see Figure 4 from the paper), with optimal growth in the intermediate water level; indeed the height increase was sharper since late summer 2020. By contrast, the species of the sphagnum hummocks decreased in 2022, which may be due to higher mortality in the swards that had grown higher (see Figure 3).

Appendix C. Other Plant Species in the Experimental *Sphagnum* Plots

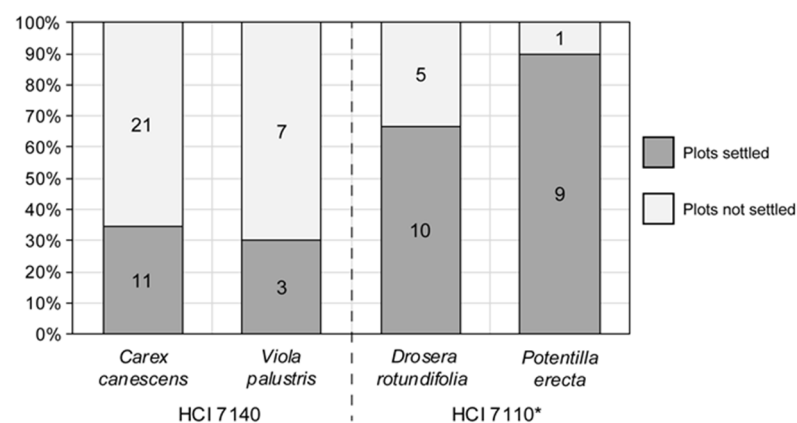


Figure A3. Success in the emergence and establishment of four plant species sown in the small plots of *Sphagnum*, corresponding to the transition mire (HCI 7140) and the sphagnum hummocks (HCI 7110*). Numbers and percentages refer to plots (groups of four pots), according to records in late summer 2021.

Table A1. Occurrence of plant species that spontaneously immigrated in the *Sphagnum* plots, expressed as a percentage of plots settled in the two habitats restored (data from summer 2021). The small area of the plots (roughly 10 × 10 cm) explains the invasion by rhizomatous species abundant in the surroundings (e.g., *Carex rostrata*) whereas that of species that arrived as seeds (*Potentilla erecta*, *Juncus articulatus* or *Pinus uncinata*) should reflect a more generalized process in mires.

Species	Transition Mire (7140)	Sphagnum Hummocks (7110*)
<i>Carex rostrata</i> Stokes	93	28
<i>Potentilla erecta</i> (L.) Raeusch.	20	8
<i>P. erecta</i> (seedlings)	4	4
<i>Juncus articulatus</i> L.	18	4
<i>J. articulatus</i> (seedlings)	4	
<i>Pinus uncinata</i> Ram. ex DC. (seedlings)	2	24
<i>Carex flava</i> L. agg.	2	
<i>C. flava</i> agg. (seedlings)		20
<i>Eleocharis quinqueflora</i> (Hartmann) O. Schwarz		20
<i>E. quinqueflora</i> (seedlings)		4
<i>Carex flacca</i> Schreb.		16
<i>Epilobium</i> sp.	16	
<i>Prunella vulgaris</i> L.	13	
<i>Carex</i> sp. (seedlings)	5	4
<i>Succisa pratensis</i> Moench.	5	4
Pleurocarpous mosses	9	4
<i>Pedicularis pyrenaica</i> Gay agg.	5	
<i>P. pyrenaica</i> agg. (seedlings)		8
<i>Sagina</i> cf. <i>saginoides</i> H. Karst.	9	
<i>Polytrichum</i> sp.		8
<i>Trifolium</i> sp.	7	
<i>Viola palustris</i> L.	5	
<i>Lotus corniculatus</i> L.	5	

Appendix D. Supplementary Images



Figure A4. General view of the transition mire at an early phase of restoration (late summer 2017), with the *Carex rostrata* population just established between the sloping shore and wooden poles and boards set in shallow waters to give some protection against occasional strong water flow.



Figure A5. Detail of the population of *C. rostrata* in summer 2019, showing noticeable densification of the sward and expansion through the wooden boards into shallow waters.

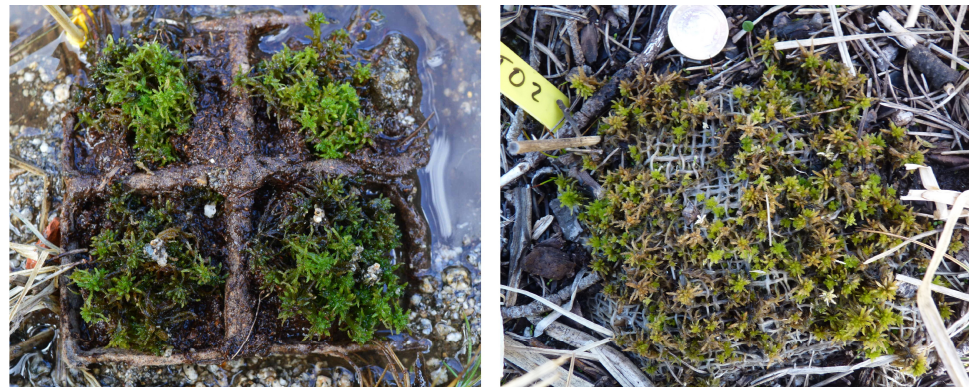


Figure A6. Overhead views of one group of four pots with small *Sphagnum teres* swards. On the left, just set into the substrate at the beginning of the restoration, still not covered by the protecting mesh (June 2018). On the right, after one year (May 2019) with the *Sphagnum* shoots already grown through the mesh and expanding laterally.

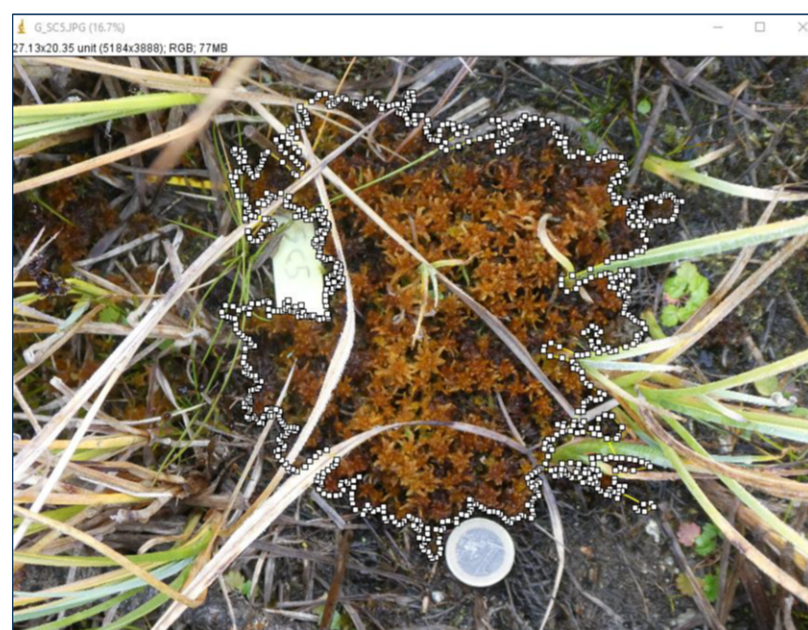


Figure A7. Overhead image of one sward of *Sphagnum subsecundum* after being digitally contoured (white dashed line) to calculate its canopy area through the software ImageJ 1.52r (October 2019).

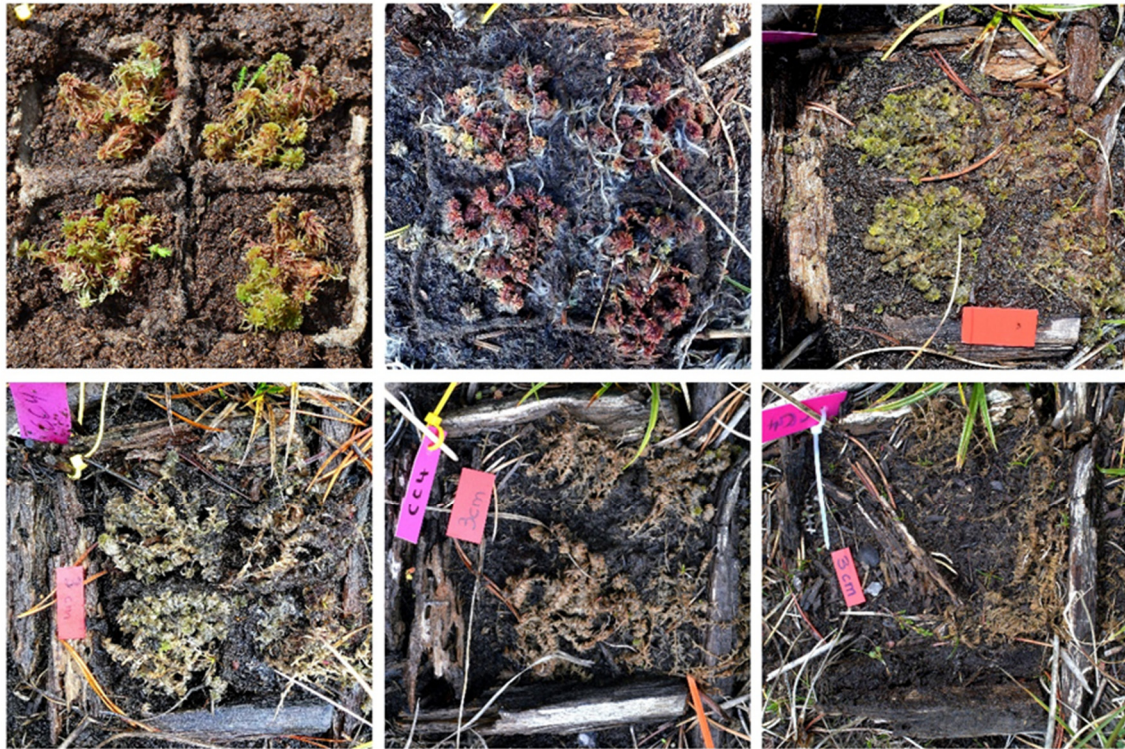


Figure A8. Progression of one plot of *Sphagnum capillifolium* from transplanting (upper left: still not covered by the protecting mesh, in June 2018) along the monitoring (from left to right, and from up to bottom: May 2019, July 2020, October 2020, September 2021, September 2022). After a fair establishment and growth until July 2020, it became severely damaged after summer dry spells and vanished at ending summer 2022.



Figure A9. View of the restoring transition mire under an exceptional water rising due to hydroelectric use (15 June 2020).



Figure A10. View of sphagnum hummocks neighbouring the restoration area, occurring over the water level before the dam removal. On the foreground, *Sphagnum capillifolium* hummocks colonized by *Rhododendron ferrugineum* and *Pinus uncinata*. On the background, restoration area (HCI 7110*) protected with a fence.



Figure A11. Overhead image of one sward of *Sphagnum subsecundum* established in the transition mire, between the open *Carex rostrata* turfs (October 2020).

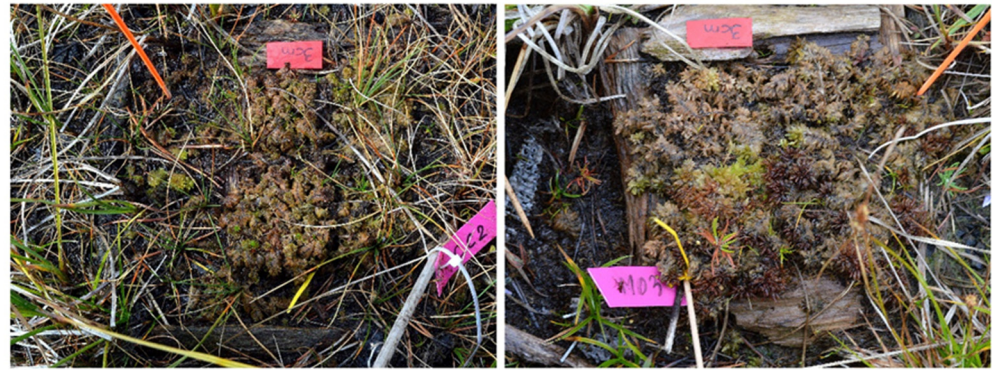


Figure A12. Two young sphagnum hummocks (*Sphagnum capillifolium*, left, and *S. divinum*, right) set within a frame of dead wood. They grew reasonably well from transplants, while a few vascular plants are settling on them: *Eleocharis quinqueflora* and *Carex flava* agg. (**left**), and *Pinus uncinata* and *Carex flava* agg. (**right**) (September 2022).



Figure A13. A young hummock grown from sphagnum transplanted on decaying wood (not included in this study). The dominant *S. capillifolium* sward shows healthy growth and hosts vascular plants (*Calluna vulgaris*, *Potentilla erecta*) (September 2022).

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