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Contrasting ecological and biological characteristics of high-altitude populations of *Drepanocladus turgescens* in the Vanoise national park

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Drepanocladus turgescens is a calciphilic arctic-alpine moss species that is highly endangered in central Europe. Lowland populations are at risk of extinction, while high alpine populations have a favourable conservation status. We studied ten high-altitude populations of *D. turgescens* in Vanoise national park, French Alps, at the south-western margin of its range. The microtopography, substrate depth, vascular plant and bryophyte species cover, and water physico-chemical properties were sampled in the field. Sexuality and branching were studied in the laboratory. In the high alpine area, the moss either thrives on a sparsely vegetated, mineral percolating substrate where female gametangia are regularly produced on mostly unbranched stems or on peaty substrate, where individuals are sterile and tend to branch out. Competition is suggested as the main driver of the species' occurrences. We found neither male gametangia nor any sporophytes, a situation typical for most of the Alps. The high-altitude populations of *D. turgescens* likely episodically recruit following exceptional sporophyte production in the Alps, and by vegetative fragmentation. Management actions removing competitors may benefit the persistence of the moss in sites where the peat layer exceeds 20 cm deep.

Keywords: Alps, Amblystegiaceae, arctic-alpine, bryophyte, conservation, *Drepanocladus turgescens*, France, habitat, Vanoise

Introduction

Although wetlands are increasingly recognised as playing a fundamental role in our environment by the scientific community, they have been reduced by more than 50% since industrialisation (Davidson 2014). The functioning and dynamics of these wetlands are increasingly well understood (Eller et al. 2021), but there is a lack of knowledge on one of their most iconic taxonomic groups, bryophytes, in comparison with vascular plants (Becker Scarpitta et al. 2017).

Accounting for 70% of these wetlands, peatlands are largely populated by bryophytes (Chapman et al. 2003, Moor et al. 2017, Vitt and House 2021). Within the bryophyte taxa, which are dependent on wetlands and therefore water-dependent, we find brown mosses (Moore 1989, Kuhry and Turunen 2006, Vitt and House 2021). Brown mosses are an informal name for species belonging to the Calliergonaceae, Amblystegiaceae or Scorpidiaceae families, whose taxonomy was – and still is – being actively studied (Hedenäs et al. 2005, Kučera and Hedenäs 2020, Ignatova et al. 2021). Brown mosses frequently dominate temperate, boreal and arctic wetlands in what is known as rich fens (McBride and Scottish Natural Heritage 2011, Vitt and House 2021). These mosses have a critical ecological function because they initiate the process of terrestrialisation of aquatic environments by initiating turfigenesis (Tveit et al. 2020). They are often dioecious (Hedenäs 1993) and, as such, often do not have structures dedicated to vegetative reproduction (Bisang and Hedenäs 2005). The biology of these species is not well known and is still rarely studied for many aspects such as reproduction, ecological needs and competition (Bisang et al. 2008, Campbell et al. 2019, Hedenäs and Bisang 2019, Hedenäs et al. 2021). This is notably the case for *Drepanocladus turgescens* (T.Jensen) Broth., which is an arctic-alpine species (Karczmarz 1971) widely distributed in the circumpolar region, with disjunct occurrences in Asia, Africa and South America (Karczmarz 1971, Hedenäs 2002, 2003). *Drepanocladus turgescens* is an amphibious species that is dioecious and rarely develops sporophytes, which are produced cyclically and show dependence on environmental and climatic variables (Hedenäs 2002, Hedenäs et al. 2016, Hedenäs and Bisang 2019).

Drepanocladus turgescens is red-listed in many European countries. While *D. turgescens* is assessed as of least concern (LC) in Europe (Hodgetts et al. 2019), its status ranges from Extinct to LC in different countries (Table 1). Although human activities may also generate favourable habitats for this species (Holler 1877, Schäfer-Verwimp 1985, Krajewski 2017), such activities seem to be at the root of its decline (Holler 1877, Köckinger and Schröck 2017). In France, at the southwestern limit of its range, it has a very restricted distribution, being recorded only in the Jura and the Alps. The species has suffered a sharp reduction in its range in the French Jura, where it is now in danger of extinction (Magnin 1904, CBNFC ORI 2023). In the French Alps, it is confined to the Vanoise massif. Recent observations of healthy and densely populated high-alpine populations in France (Vanoise) or Switzerland (Bergamini et al. 2019) oppose with relict populations known in the lowlands of western and central Europe (Schröck 2013, Zechmeister et al. 2013, Bergamini et al. 2019).

The present study aims to determine the ecological requirements of *D. turgescens* in the French Alps and to better understand the ecology of the species in general to eventually suggest conservation measures. What is the habitat used by this species in its alpine zone? Are all alpine populations found in the same ecological context? If not, how do we explain such differences and what are their impacts on *D. turgescens* reproductive capacity and morphological plasticity?

Material and methods

Study sites

The fieldwork took place in the Vanoise massif in July 2018 and we focused on ten populations where the species was recently found, or that correspond to historical records of its occurrence (Fig. 1, Table 2).The Vanoise massif is characterized by large surfaces of limestone and a calc-schist geological substrate surrounded by crystalline rocks (Gensac 1990). All populations were found within the core park area of the Vanoise national park (codes: A1, A2, A3 + 4, B1 + 2, BP2, LR1, CV1, ML1, PN1) except for the Fournache location (code: F1).

Sampling design and data collection

To sample a population, a representative part of it was subjectively delineated, accounting for border effects, with a tape measure and poles (Fig. 2). Each population was sampled with a minimum of 30 contiguous quadrats of 70 × 70 cm (0.49 m^2) for a total of 451 quadrats.

To describe vascular plant and bryophyte communities as well as their habitat, we determined visually the percentage of cover of every bryophyte and vascular plant species at the 0.49 m^2 quadrat scale. Since we noticed a variation in the water table proximity at small scales, the percentage of cover for three micro-topographical elements (channels permanently water-filled; banks; elevated and drier mounds) was also determined visually. We then collected a handful of *D. turgescens* (if present) that was stored in a mailing envelope, dehydrated, and carried to the lab. Finally, soil depth from apices of living mosses to the bedrock was measured using a metallic rod.

To describe water chemistry at the population level, water samples were taken from among each of the ten studied populations. Precautions were taken not to collect the water after

Table 1. IUNC status of *D. turgescens* of the European countries where it is or was found. ○ meaning LC or the absence of status.

	Austria	Estonia	Finland	France	Germany	Great Britain	Iceland	Italy	Kaliningrad
IUCN status	2 (Highly endangered)	○	CR	○	1 (CR)	VU	○	○	○
	Macedonia	Norway	Arctic Russia	NW Russia	Poland	Slovenia	Svalbard	Sweden	Switzerland
IUCN status	VU	○	○	○	Ex	EN	○	○	CR

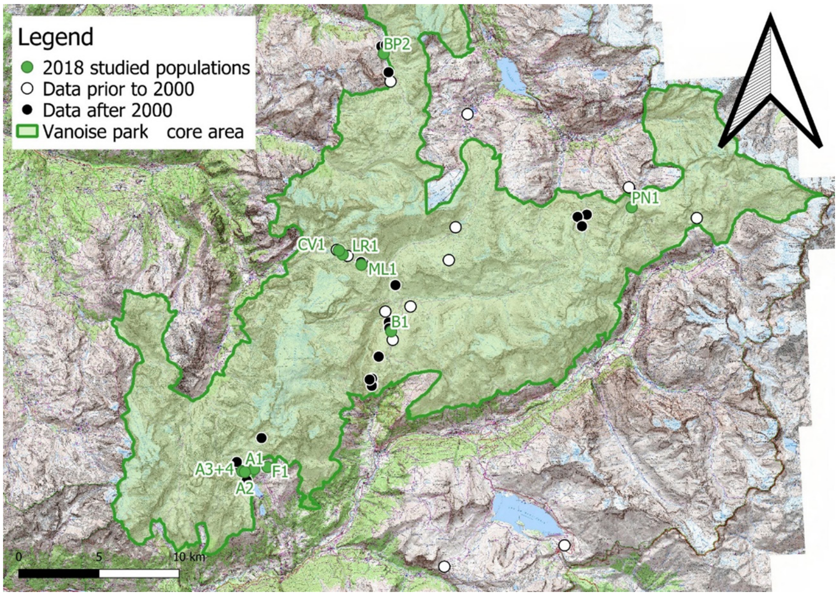

Figure 1. *Drepanocladus turgescens* populations found in Vanoise national park before and after 2000 plus the studied populations and their code names. The green area is the park's most protected one: core area.

rain, to store it in a cooler with icepacks and deliver it to a nationally certified laboratory (accreditation COFRAC number 1-5822 (Comité Français d'Accréditation 2023)). The laboratory then analysed contents of total nitrogen (Ntot), phosphorus (P), bicarbonate (HCO_3) and calcium (Ca) as well as the electric conductivity (Conduc), and the pH following standard protocols.

To better understand bryophyte succession in our study area, peat core samples were extracted with the help of a Russian peat borer wherever possible in each population (there was a frequent absence of underlying substrate). The peat cores were cut into 10 cm long pieces then sifted through decreasing diameter meshes down to 800 µm. Bryophyte fragments were then identified to the specific level when possible and quantified (1: sparse; 2: moderate; 3: abundant) under the stereomicroscope.

In the laboratory, we determined the sexuality of our specimens as well as their branching along the stem, a characteristic that varied greatly between populations but not within the same population. From each *D. turgescens* sample coming from one quadrat, five stems were rehydrated to count for sexual structures (archegonia, antheridia, sporophytes) and the total number of stem branches with indices ranging from 0 to 4 (0: 0 branches; 1: < 5 branches; 2: 5 branches; 3: > 5–10 branches; 4: > 10 branches).

Herbarium samples

We studied 130 herbarium sheets from Herbier National Muséum National d'Histoire Naturelle (PC), Conservatoire et Jardin Botanique de la Ville de Genève (G), Conservatoire Botanique National Alpin, Conservatoire Botanique National de Franche-Comté and the private herbaria of Vincent Hugonnot and Thierry Delahaye. Taxonomic identification and sexual structures were checked.

Statistical analysis

The data as well as figures were processed using R ver. 4.0.3 (www.r-project.com). All georeferenced data was computed with QGIS 3.10.13 (QGIS Development Team 2022).

To represent how the percentage of cover of *D. turgescens* varied among the sampled quadrats, we produced a density curve using package ggplot2 ver. 3.4.0 (Wickham 2016).

Table 2. Code, localisation, altitude, mention's origin, and population density of the ten studied ones

Code	Localisation	Altitude (m)	Mention's origin	Population density
A1	Aussois, St-Benoît's brook, left bank	2307	> 2000	low
A2	Aussois, guard's chalet	2529	> 2000	medium
A3 + 4	Aussois, St-Benoît's brook, right bank	2314	new	low
B1 + 2	Termignon, Plan du Lac's shelter	2368	new	medium
BP2	Peisey-Nancroix, Ponturin's bank	2098	new	low
F1	Aussois, Fournache's brook	2552	> 2000	medium
LR1	Termignon, Rond lake	2498	< 1950	high
CV1	Termignon, Vanoise's pass	2518		high
ML1	Termignon, Mollard de la Loza	2446	> 2000	high
PN1	Bonneval-sur-Arc, Pont de la Neige	2527	> 2000	medium

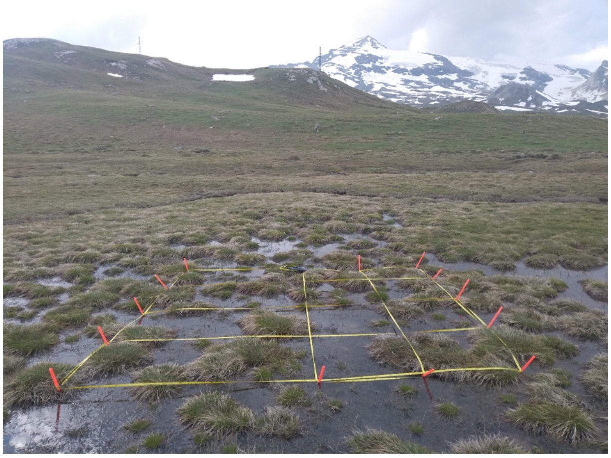

Figure 2. Example of the sampling design on one of the study sites.

To describe the range of water chemistry within populations we produced boxplots using package 'ggplot2' ver. 3.4.0 (Wickham 2016).

Linear mixed-effects model analysis without interactions was performed to define the impact of the fixed variables channels, banks, mounds, and vascular plant covers as well as soil depth, sexuality, branching and water chemistry variables (Ntot, Ca, conductivity, HCO_3, pH and P as chemically determined) on our response variable: the percentage of cover of *D. turgescens* (scaled from 0.05 to 1). The population ID was added as a random variable since we have a nested sampling design with numerous quadrats in our ten different populations. We removed rows without the presence of *D. turgescens* as it gave NA values for sexuality for example. The numeric explanatory variables were standardized using the function scale in R (www.r-project.org). The model was built using the package 'lme4' (Bates et al. 2015). The effects of explanatory variables on the percentage of cover of *D. turgescens* were plotted using the package 'sjPlot' (Lüdecke 2018) with p-values over the 95% confidence interval.

A cluster analysis was made to represent the differences between plant assemblages in each studied population (n = 10). The cluster analysis was based on the grouping of bryophyte and vascular plant species data, on the understanding that these plant communities form an ecologically coherent whole. Plots were classified with the function *pvclust* in the 'pvclust' package using a distance based on correlation, a technique also known as 'centered Pearson' (Suzuki and Shimodaira 2006). Significant clusters are produced with p-values over a 95% confidence interval and 1000 bootstrap replications.

Results

Habitat

All populations of *D. turgescens* were at high altitudes (> 2000 m) in sites fed by fluxes of flush water. The water in the sites was mostly alkaline, but pH values were widely variable, ranging from 6.6 (F1) to 8.1 (CV1). Ca, HCO_3, and accordingly, conductivity, also varied over a wide range of values. Ntot values were mostly low, at highest 24 mg l^{-1} (F1). P content varied from < 10 µg l^{-1} (A2, A3 + 4, B1 + 2) to 160 µg l^{-1} (PN1) (Fig. 3). Despite these large amplitudes of variation, the water chemistry had no significant influence on the cover of *D. turgescens* (Fig. 4).

Even if it was not significant, *D. turgescens* cover was higher on banks, while channels or mounds were associated with low cover of *D. turgescens* (Table 3, Fig. 4). At the quadrat scale, the cover of *D. turgescens* was either low or high (Fig. 5), with few intermediate percentages of cover (40–70%).

The soil of *D. turgescens*' growing sites was largely of mineral origin, with no or minimal accumulation of peat (Table 3), the peat being often less than 20 cm deep, taking into consideration that the living stems of *D. turgescens* can measure up to 10–15 cm long. Only on one occasion (A3 + 4) was the soil thicker. Soil depth to bedrock was negatively correlated with the species cover (Fig. 4).

Plant communities

A total of 34 vascular plant and 23 bryophyte species were recorded in association with *D. turgescens* (Table 3). The most frequently associated vascular plant species were *Carex nigra*, *Trichophorum cespitosum*, *Equisetum variegatum* and *Eriophorum angustifolium*, whereas the most frequent bryophyte species were *Scorpidium cossonii, Campylium stellatum* and *Ptychostomum pseudotriquetrum*. Additionally, *D. turgescens* was observed once at the base of a dripping limestone cliff at Vallon des Fours, Val-d'Isère, where it has been previously reported. The species covered less than 200 cm^2 together with *Hygrohypnum luridum* and *Amphidium lapponicum*.

Two significantly different communities appeared among the ten studied populations. In one grouping was a cluster including stations CV1, LR1 and ML1, and in the other grouping, a cluster including all other populations except A3 + 4, which was not included in any cluster (Fig. 6). Notably, CV1, LR1 and ML1 were also the populations with a high cover of *D. turgescens* (> 67%), and low cover by vascular plants (< 24%), which are negatively correlated to the cover of *D. turgescens* (Fig. 4), and little or no peat (< 17 cm) which, as mentioned above, was also negatively correlated to cover by the species. In addition, CV1, LR1 and ML1 were also the only stations with individuals bearing archegonia in 2018.

Fertility

In 2018, archegonia were found in three of the studied populations (ML1, LR1 and CV1) and in Vallon des Fours. In 2017, female gametangia were also spotted in PN1 but not subsequently at the same place in 2018. Female gametangia were also observed in herbarium samples (12 out of 136 samples). Neither male gametangia nor sporophytes were found in any of the studied populations out of 1710 stems checked for sexual structures, nor were they found in herbarium samples except for one sporophyte in Pike Bay, lake Huron, Ontario, Canada. The presence of sexual structures

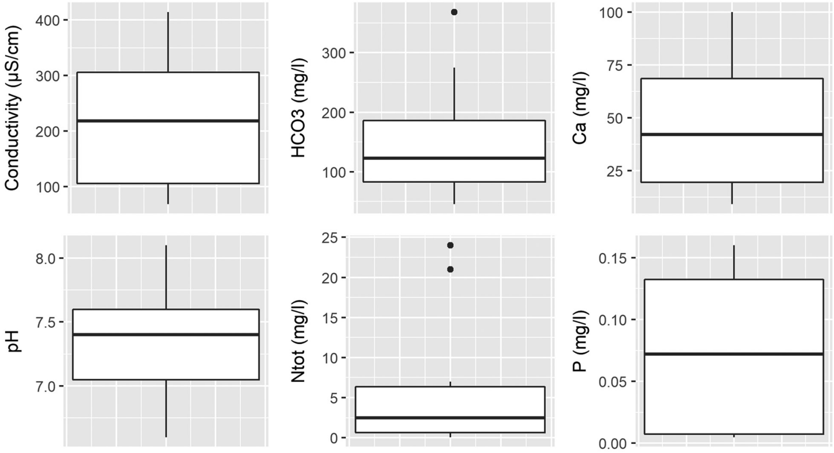

Figure 3. Boxplots showing the variations of the studied water chemistry variables in the ten studied populations.

in *D. turgescens* was positively correlated with its percentage of cover (Fig. 4).

Macrorests

Only station A3 + 4, at Aussois, allowed macro plant remains to be studied. *D. turgescens*, and *Scorpidium cossonii* were recorded throughout the peat core; below 40 cm, no bryophyte fragments were detected. *Calliergon richardsonii* decreased from 40 to 20 cm and was replaced by *Campylium stellatum*, which is also found in present above-ground vegetation (Fig. 7).

Discussion

At the western margin of its Alpine range, *D. turgescens* has similar ecological requirements to those reported in previous studies (Bisang and Hedenäs 2017, Bergamini et al. 2019). Above 2000 m, it grows mainly in soligenous, mineral and peat-free fens fed by hard or less calcium-rich water. The other chemical elements showed similar variability. This is consistent with previously available data, where electrical conductivity vary from 145 to over 500 µS cm^{-1} (Hedenäs 2002, Johnson and Steingraeber 2003), calcium from 15.4 mg l^{-1} to over 100 mg l^{-1} (Hedenäs 2002, Johnson and Steingraeber 2003) and pH from < 7 to > 8 (Schäfer-Verwimp 1985, Hedenäs 2002, Johnson and Steingraeber 2003, Krajewski 2017).

We found *D. turgescens* in species-rich communities, which is also the case in Scandinavia (Hedenäs 2002). Apart from a few characteristic species frequently associated with each other (*Equisetum variegatum*, *Trichophorum cespitosum*, *Scorpidium cossonii* and *Campylium stellatum*), the floristic assemblages show significant variability in Vanoise and are not really comparable to those observed in Switzerland (Bisang and Hedenäs 2017), Italy (Buffa et al. 1998), Germany (Holler 1877, Schäfer-Verwimp 1985), Scandinavia (Hedenäs 2002) or Scotland (Birks and Dransfield 1970).

From our results, in high-altitude populations, two contrasting ecological conditions can be distinguished:

1. high cover of bryophytes (> 50%), fertile (only female gametangia), unbranched *D. turgescens*, growing directly on mineral substrates, invading banks, with low vascular plant cover (< 25%) [PN1, ML1, CV1, LR1];
2. low cover of bryophytes (< 30%), sterile (no gametangia), profusely branched *D. turgescens*, growing on shallow peat layers, with a significant vascular plant cover (> 40%), located mostly on banks [A1, A2, A3 + 4, B1, BP2, F1].

In Vanoise, *D. turgescens* appears to be confined to competition-free ecological microsites in banks, apparently being unable to invade channels that are permanently water-filled or drier mounds. This high sensitivity to competition (Schröck 2013) and its pioneering behaviour (Krajewski 2017) have been previously discussed and may explain its presence on bare, dry cliffs (Schröck 2013). To some extent, the presence of the species on bare, dry cliffs is reminiscent of that described in the alvars of southern Scandinavia and the

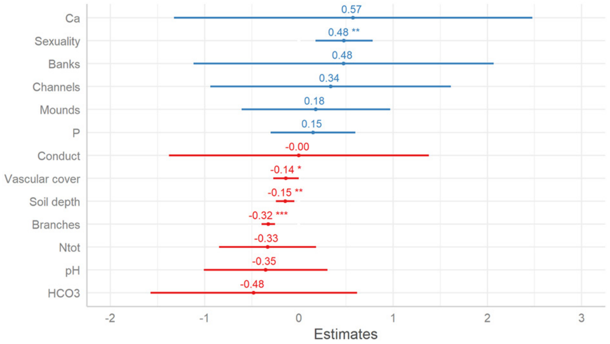

Figure 4. Plot showing the estimates of the linear mixed effects model for each fixed variable where the response variable is the percentage of cover of *Drepanocladus turgescens* and the random variable is the site. Estimates are sorted in a decreasing order while the significance level at a 95% confidence interval is shown with the stars (*marginally significant, **significant, ***highly significant). Estimates represented in blue mean a positive influence of the variable on the percentage of cover of *Drepanocladus turgescens* while red mean a negative influence of the variable.

Table 3. Table showing, for each studied station the presence or absence of sexual structures (archegonia only), the mean soil depth (cm), the percentage of cover of microtopographic elements, of each vascular plant and of each bryophyte species as well as the total percentage of cover of vascular plants and bryophytes

Station ID		A1	A2	A3 + 4	B1	BP2	F1	PN1	ML1	CV1	LR1
Sexuality		sterile	sterile	sterile	sterile	sterile	sterile	sterile (♀ 2017)	fertile	fertile	fertile
Soil depth (cm)		24.19	19.63	38.85	20.00	20.00	27.00	20.77	17.19	15.03	13.69
Microtopography (%)											
	Depressions	28	35	51	59		18	25	22	34	6
	Banks	65	58	40		97	82	75	78	62	94
	Mounds	7	7	9	40	3				4	
Vascular plants cover (%)											
	Equisetum variegatum	4	6	3	5	13	3	1	3	3	4
	Trichophorum cespitosum	22	22	23	14	13	13		2	1	1
	Carex nigra	15	6	11	0	20	10	5	10	1	1
	Eriophorum angustifolium	7	6	6	2	7	2		6	3	2
	Sesleria caerula		22		14			5			
	Bistorta vivipara	4	1				2	3		1	4
	Salix herbacea	4						5		1	2
	Carex foetida									3	
	Juncus triglumis										6
	Salix foetida	4	3	3	3		2				
	Ranunculus glacialis							2		1	1
	Carex davalliana	4		3	3						
	Pinguicula alpina		3	6							
	Selaginella selaginoides		3		2		2				
	Viola palustris	4			2		2				
	Saxifraga aizoides			1				2			
	Bartsia alpina		3	3							
	Carex dioica								3		
	Carex rostrata					7					
	Eriophorum sp							2			
	Eriophorum vaginatum			6							
	Primula farinosa					7					
	Salix reticulata					3		1			
	Alchemilla cf_demissa						2				
	Arabis_soyeri subsp. *subcoriacea*							1			
	Caltha palustris					3					
	Gentiana bavarica						2				
	Juniperus communis subsp. *nana*			3							
	Micranthes stellaris									1	
	Poa alpina						2				
	Salix repens					3					
	Silene acaulis		3								
	Soldanella alpina		3								
	Triglochin palustre										1
	Total vascular plant cover (%)	67	79	67	45	76	40	24	24	13	20
Bryophytes cover (%)											
	Drepanocladus turgescens	5	26	4	9	24	32	51	91	68	91
	Scorpidium cossonii	35	25	19	29	37	42	36	6	10	2
	Campylium stellatum	18	19	58	4	4	10	10			2
	Bryum pseudotriquetrum	1	6	2	1	2	9	2	1	2	2
	Cinclidium stygium	16		4							
	Palustriella decipiens				2	9	1			1	

(Continued)

Table 3. Continued.

Station ID	A1	A2	A3+4	B1	BP2	F1	PN1	ML1	CV1	LR1
Sexuality	sterile	sterile	sterile	sterile	sterile	sterile	sterile (♀ 2017)	fertile	fertile	fertile
Soil depth (cm)	24.19	19.63	38.85	20.00	20.00	27.00	20.77	17.19	15.03	13.69
Tomentypnum nitens	6	4								
Calliergon richardsonii					7					
Brachythecium turgidum		2			2					
Fissidens osmundoides		1	2							
Aneura pinguis	1		1				1			
Aulacomnium palustre		2								
Cratoneuron filicinum					1					
Ditrichum flexicaule		1								
Blindia acuta		1								
Drepanocladus aduncus					1					
Straminergon stramineum			1							
Tortella fragilis		1								
Meesia uliginosa										
Hymenostylium recurvirostrum										
Sarmentypnum exannulatum										
Timmia norvegica										
Meesia triquetra										
Sarmentypnum sarmentosum										
Total bryophyte cover (%)	83	87	91	47	87	92	98	98	81	96

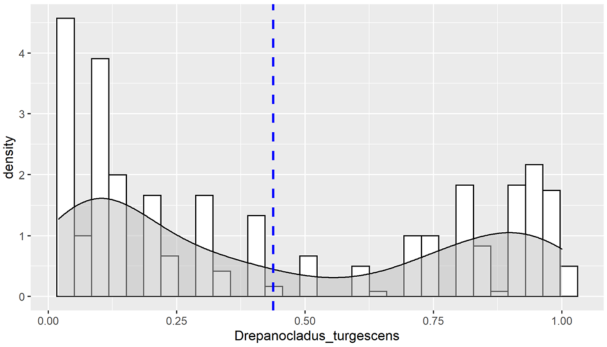

Figure 5. Density curve showing the percent of covers (scaled from 0 to 1) of *D. turgescens* found in all quadrat unit where it was detected.

Great Lakes region or in the limestone pavements of the UK (Hedenäs 2002, Porley 2013, Catling 2016) where the species grows massively directly on sparsely vegetated limestone outcrops. However, the alvar basins dry up completely in summer, in stark contrast to the meltwater from the glaciers that constantly percolates in Vanoise.

In addition to competition-free ecological conditions in banks, *D. turgescens* also occurs in sites with a peat layer and is apparently more constrained by competing vascular plants and bryophytes. Our single peat core indicates that an obviously wetter and sparsely vegetated environment (earlier dominance of *Calliergon richardsonii*) prevailed prior to the present ecological conditions. In this case, the more abundant branching system could be a consequence of competition. *Hamatocaulis vernicosus*, another Amblystegiaceae, has been shown to change its growth pattern when exposed to volatile organic compounds produced by *Sphagnum flexuosum*, a frequent competitor (Vicherová et al. 2020), and this may provide an analogue for this pattern of growth behaviour.

Hedenäs et al. (2021) observed that sexual expression was higher in late successional stages than in early successional stages in *Scorpidium cossonii* and *Campylium stellatum*. In contrast, for *D. turgescens*, gametangia production was recorded in pioneer ecological conditions only. Although gametangia

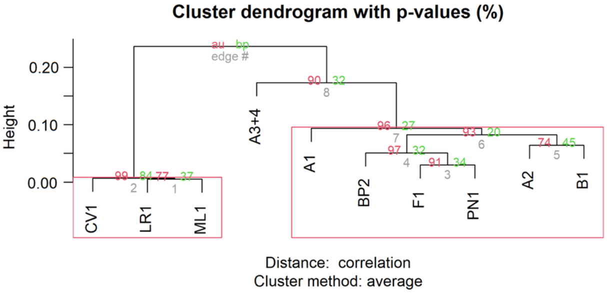

Figure 6. Grouping of the ten study populations according to the correlation between their vascular plant and bryophyte communities. The categorisation also takes into account the percentage cover of each species. The red boxes group communities that are statistically identical at the 95% confidence interval.

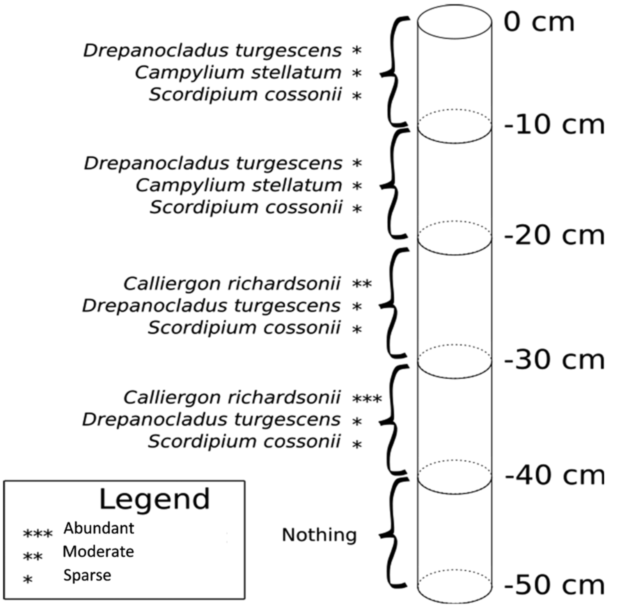

Figure 7. Synthesis of the sampled peatcore's bryophytes macrorests ranked from very abundant to not abundant every −10 cm under the surface.

formation is clearly dependent on a complex physico-chemical sequence of interacting parameters, this question certainly deserves to be explored.

On the western margin of its alpine range, sexual reproduction of *D. turgescens* is constrained by the apparent total absence of male partners. Studies in Scandinavia found male buds and sporophytes in only ~ 4% of 224 specimens studied (Bisang et al. 2014). The absence of males is a classic condition explaining the frequent sterility of dioecious bryophytes (Hedenäs et al. 2010, Bisang et al. 2014), among which are many wetland species, including *D. turgescens* (Hedenäs 2002, Porley 2013, Hedenäs et al. 2016, Campbell et al. 2019, Krajewski et al. 2020). However, even if we could not detect males, it is still possible that they are present as sterile colonies, so called "shy males", not expressing their sexual parts (Stark et al. 2010). Then, sexual identification of non-sterile individuals by molecular methods (Hedenäs et al. 2016) would be desirable. Hedenäs and Bisang (2019) also showed that the production of archegonia and antheridia can vary interannually, suggesting that currently non-expressing individuals could potentially produce gametangia, but irregularly.

The only sporophytes of the moss in the Alps were found in the Austrian lowlands at altitudes of 165 and 300 m during the 19th century (Austrian Museum of Natural History, Hedenäs 2002, Hedenäs and Bisang 2019), once in a short-grass marshy meadow with a calcareous subsoil and once in a ditch. The occurrence of sexual reproduction events in the Alps can therefore not be completely excluded. Vegetative propagation by deciduous apical buds (Holler 1877, Limpricht 1904, Hedenäs 2002) could also contribute to the more local spread and maintenance of alpine haplotypes.

In the central European lowlands, *D. turgescens* is seriously threatened by unfavourable habitat change (Holler 1877, Schröck 2013, Zechmeister et al. 2013, Bergamini et al. 2019). Intensive agriculture and forestry have contributed to a lowering of the water table, leading to a natural proliferation of grasses, shrubs and trees (Schröck 2013, Zechmeister et al. 2013), which in turn can influence competitive relationships, to which *D. turgescens* is very sensitive. In addition, the afforestation of damp pastures and encroachment may be less favourable for successful establishment from spores (Sundberg and Rydin 2002, Miles and Longton 1990).

Widespread historical maintenance of hydrologically pristine bogs and fens by extensive mowing and grazing (especially trampling pressure) has contributed significantly to small-scale disturbance of the superficial peat substrate that can favour pioneer bryophyte species (Groeneveld et al. 2007, Ingerpuu and Sarv 2015, Guêné-Nanchen 2018) such as brown mosses (Udd et al. 2016). The presence of the species in anthropogenic ponds (Holler 1877, Schäfer-Verwimp 1985, Krajewski 2017), may be explained by the dynamic behaviour of the species in a newly formed competition-free environment.

Finally, from a practical point of view, we suggest that lowland or less healthy alpine populations alone should be subject to management, which should be low intensity, while alpine populations expressing sex should be preserved from disturbance. The main objective would be to reduce the cover of competitive plants. Low-pressure grazing or artificial stripping of the substrate could favour pioneer bryophytes (McBride and Scottish Natural Heritage 2011, Takala et al. 2014, Liebig 2016, Boch et al. 2018).

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Author contributions

NA, VH and TD conceived and designed the experiments. NA performed the experiments and produced the data. NA analysed the data. NA wrote the initial manuscript. VH and TD edited and commented the manuscript..

Data availability statement

There are no additional data for this paper

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