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The vegetative reproduction of *Dicranum viride* (Sull. & Lesq.) Lindb. as a likely explanation for micro-habitat and stand-type relationships – implications for forest management

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Dicranum viride is a bark-dwelling and woodland species listed in Annex II of the ‘EU Habitat Directive’. It occurs mainly in heavily managed forests. The effects of stand age, tree diameter and host tree species on the occurrence of *D. viride* have been studied at two distinct scales. We suggest that the effects of tree diameter and tree species are mainly related to bark roughness. The occurrence of *D. viride* on trees with a smooth bark is strongly related to the abundance of *Hypnum cupressiforme* var. *filiforme*, which may facilitate establishment of large leaf fragments on smooth bark. Vegetative dispersal and establishment of *D. viride* are inferred from the current occurrence pattern and biological traits of the species and are hypothesized as having been critical for its survival within managed forests. A straightforward and widely applicable new method of compartment prioritization is provided to facilitate the implementation of modified interventions.

Keywords: bark structure, connectivity, *Dicranum viride*, facilitation, *Hypnum cupressiforme* var. *filiforme*, leaf fragment, phorophytes, stand age

Introduction

Dicranum viride is a well-known moss species of the family Dicranaceae, and grows in large lowland forests under moderately shaded and humid conditions (Dierßen 2001, Nebel and Philippi 2001, Bardat and Hugonnot 2002). It supposedly prefers the moderately acidic and smooth bark of trees such as *Fagus sylvatica* and *Carpinus*

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betulus (Stebel et al. 2011, 2015) and more exceptionally, rough bark such as that of *Quercus* sp. (Mežaka et al. 2008, Wierzcholska et al. 2020).

The global range of *D. viride* was long considered to span the circumboreal belt, from East Asia to North America and to Europe (Nebel and Philippi 2001). Recently a combined morpho-molecular taxonomic study of fragile-leaved *Dicranum* taxa provided evidence for the reinstatement of the Asiatic *D. viride* var. *hakkodense* (Cardot) Takaki (as *D. hakkodense* Cardot), resulting in a significant reduction of the geographic range of *D. viride* s.str. (Ignatova and Fedosov 2008). In Europe, it is recorded from isolated localities in the Basque country (in Spain and France), central and eastern France (Bardat and Hugonnot 2002), south-west Germany (Stebel et al. 2011, Meinunger and Schröder 2007), south Scandinavia (Baisheva et al. 2013), and Poland (Stebel et al. 2011). French populations define the western limit of its European range.

Sporophytes of the species have rarely been observed in Europe, and apparently never in France (Pichonet 2006). They have exceptionally been found in Poland (Stebel et al. 2011). Thus, *D. viride* relies mainly (even presumably exclusively) on the caducous fragile leaf apices of the gametophyte for its dissemination (Ignatova and Fedosov 2008, Donskov 2011).

Dicranum viride is listed in Annex II of the 'EU Habitat Directive', and it has consequently been the subject of many recent studies, mainly in the field of bryosociology (Bardat and Hugonnot 2002, Perdrizet and McKnight 2012). It grows in closed bryophytic communities, being associated with a diverse assemblage of common woodland bryophyte species (Mežaka et al. 2008, Baisheva et al. 2013). It is generally considered to be a moss of old-growth forest, and its occurrence is often associated with veteran trees and large trunks (Bardat and Hugonnot 2002, Infante et al. 2012, Stebel et al. 2012, Fudali and Wolski 2015). This association with mature forests was confirmed by SDM (species distribution modelling) studies at European (Wierzcholska et al. 2020) and regional

scales (Schmidt et al. 2018). Consequently, these authors recommend the conservation of old-growth, mature or primary forest ecosystems. However, in Europe, the vast majority of forests are managed more or less intensively (Bauhus and Pyttel 2015, Mikoláš et al. 2018), while natural forests currently represent less than 1% of the total (Paillet et al. 2010). While we agree with Wierzcholska et al. (2020) and Schmidt et al. (2018) that it is of the utmost importance to conserve natural and ancient forests, the question arises as what to do with the remaining 99% of heavily managed woodlands.

In this paper, we explore the importance of compartment age and inter-compartment connectivity at a small scale consistent with forest management. In addition, to our knowledge, the significance of associated bryophytes at an even finer scale has never previously been studied. Here, we investigate the effects of small-scale aggregation, compartment age and co-occurrence of bryophytes on populations of *D. viride*. Management and conservation measures are discussed in detail since this species is mostly recorded in managed forests.

Material and methods

Study site

The study sites are located in the Bourgogne-Franche-Comté region, in three departments: Haute-Saône, Doubs and Territoire de Belfort (Fig. 1).

The climate of Haute-Saône is continental-montane with Mediterranean influence while the climate of Doubs and Territoire de Belfort are respectively more markedly Continental or Semi-continental (Table 1). The native forests of Bourgogne-Franche-Comté are mainly composed of *F. sylvatica*, *C. betulus* and *Quercus petraea*. Non-indigenous species widely used for forestry are *Picea abies* and *Pseudotsuga menziesii*. The forest vegetation is therefore generally considered to

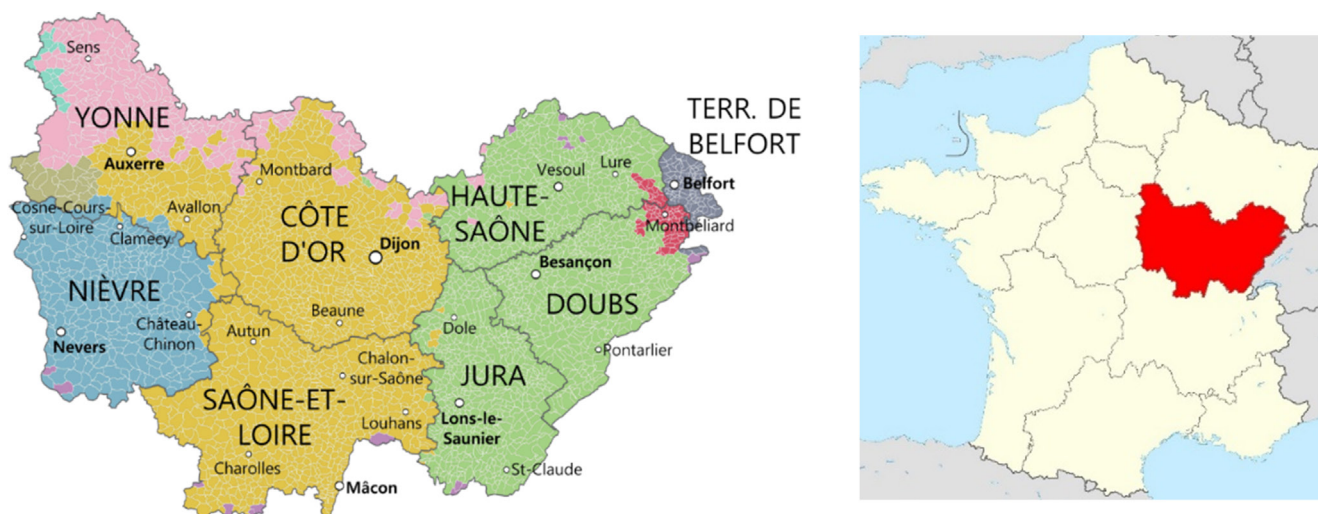


Figure 1. Maps of the Bourgogne-Franche-Comté and of departments of the region. (www.actualitix.com/carte-bourgogne-franche-comte.html).

Table 1. Climatic characterization of the three areas surveyed.

Department	Climate	Annual precipitation (mm)	Mean temperature (°C)
Haute-Saône	Continental-montane-mediterranean	1137.6	10.2
Territoire de Belfort	Semi-continental	1050.0	9
Doubs	Continental	1121.2	8

belong to the alliance *Carpino betuli-Fagion sylvaticae* Bœuf, Renaux and Royer in Bœuf 2011. Forests are mainly developed on limestone formations often covered with a thin layer of silt. *Dicranum viride* is relatively frequent and at times even abundant in woodlands with this type of ecosystem.

Survey protocol

A total of nine forests were selected and surveyed for this study (Table 2). The selection of forests was based on two criteria: occurrence of *D. viride* in the forest area and presence of compartments of at least 2 ha. Each forest was composed of a variable number of compartments, each corresponding to an operational management unit, varying from 2 to 7 ha. We established one sampling plot within each selected compartment. Survey methods are described below.

Forest compartment

For each compartment, information on stand age was extracted from Forest Management documents (ONF – www1.onf.fr/lire_voir_ecouter/sommaire/amenagements/@@index.html). The following categories were used:

- 1) Submature compartment (>90 years)
- 2) Intermediate compartment (70–90 years)
- 3) Young compartment (50–70 years)
- 4) Very young compartment (<50 years)

Seven out of the nine forests were selected, while two were rejected as being too small with an insufficient number of adequate compartments. A sampling effort of 20 min was allocated to the search for *D. viride* on phorophytes within each compartment. During this time, the compartment was crossed along the full length of its longer axis, by moving randomly from one extremity to the other. The presence or absence of *D. viride* was noted on each tree encountered. A total of 317 compartments were surveyed in the seven selected forests.

Sampling plots

Within the nine forests, 45 compartments were selected to establish sampling plots. These plots were randomly selected from those where *D. viride* had been identified during previous surveys. One sampling plot was defined and randomly placed within each compartment. Each sampling plot was a square with 33 m sides which was delineated in the field using a 10 m tape. Sampling plots were classified in three categories for stand age (submature, intermediate and young). Very young compartments were not present in sufficient numbers to be included. Each sampling plot was located in compartments where *D. viride* had already been observed. Various ecological parameters were systematically recorded (Table 3).

A total of 1548 phorophytes within the 45 sampling plots were surveyed.

After completing the first phase of field work in Haute-Saône, it was decided to add the percentage cover of *Hypnum cupressiforme* var. *filiforme* to the survey protocol for the forests located in Doubs and Territoire de Belfort. The rationale for this addition was to obtain a better understanding of the interaction of *D. viride* with this species as it was apparent that the occurrence of the two species could be linked.

Cultivation experiments

The regeneration capabilities of leaf fragments of *D. viride* were tested. Clumps of *D. viride* were collected in Chauv forest (Doubs department). During the spring-summer in 2021, freshly collected specimens were gently scraped with a knife over an Erlenmeyer flask to generate leaf fragments. The flask was then filled with tap water and shaken to put the fragments into suspension. Afterwards the liquid was dispersed over two culture pots filled with peat (each pot has a diameter of 40 cm). The pots were placed in a cold glasshouse, kept constantly moist, with natural length of day and night, under moderate shade, for six months. The regenerating leaf fragments were observed with a microscope and a binocular magnifier.

Mapping and data analysis

In order to provide guidelines for the management of forests that host *D. viride*, maps of conservation interest for the species in the forests of Étupes, Montbéliard, Chatenois-les-forges and Exincourt were generated using QGIS software ver. 3.18.2.










For data management purposes, data on the abundance of *D. viride* on phorophytes in compartments and on compartment aggregation were transformed into analytical categories (four categories: 0, 1, 2 and 3). The categories for the abundance of *D. viride* were:

- 1) Absence of *D. viride* (0)
- 2) >0–20% of frequency of *D. viride* (1)
- 3) >20–40% of frequency of *D. viride* (2)
- 4) > 40% of frequency of *D. viride* (3)

The categories for aggregation were:

- 1) No adjacent compartments with *D. viride* (0)
- 2) 1–2 adjacent compartment(s) with *D. viride* (1)
- 3) 3–4 adjacent compartments with *D. viride* (2)
- 4) >4 adjacent compartments with *D. viride* (3)

Table 2. Main characteristics of the nine surveyed forest massifs.

Forest massif	Department	Surface (ha)	Mean altitude (m)	Sampling plots	Geology	Forests selected
Hauts-Bois	Haute-Saône	774	205–245	9	Sandy-silty formations of the Pleistocene	
Bellevaivre	Haute-Saône	770	206–251	5	Sandy-silty formations of the Pleistocene	
La Chapelle-Saint-Quillain	Haute-Saône	126	240–255	6	Sandy-silty formations of the Pliocene	
Montbéliard	Doubs	263	340–455	4	Upper Jurassic limestone formations	
Chatenois-Les-Forges	Territoire de Belfort	341	340–405	4	Upper Jurassic limestone formations	
Bethoncourt	Doubs	198	320–400	4	Upper/Middle Jurassic limestone formations	
Grand Charmont	Doubs	166	360–420	3	Upper/Middle Jurassic limestone formations	
Exincourt	Doubs	76	360–402	6	Loess plateau of the Pleistocene	
Etupes	Doubs	314	335–406	4	Loess plateau of the Pleistocene	

For each compartment, the analytical categories for abundance and aggregation were summed and averaged to produce a graduated value of conservation interest (Table 4).

The establishment of these gradients of conservation interest makes it possible to propose an accessible solution for forest managers to properly manage the species.

All the statistical analyses carried out are detailed and explained in the sections below (Table 5). The statistical analyses were conducted on R ver. 3.6.1 (www.r-project.org).

Occurrence pattern

The degree of association between the binary dependent variable (presence/absence of *D. viride* in a compartment) and the independent variable (number of adjacent compartments that host *D. viride*) was tested with a generalized linear model (GLM) with a binomial error distribution and a logit-link function.

Compartment age

Occurrences of *D. viride* in submature, intermediate, young and very young compartments were compared using a χ^2 test of independence. χ^2 analyses were used due to the wide

potential errors associated with compartment ages. In addition, the number of old, intermediate, young and very young compartments is variable. It was therefore decided to compare the occurrence of *D. viride* according to these four age classes of forest compartments. 83 very young, 44 young, 25 intermediate and 165 submature compartments were identified constituting a total of 317 compartments.

Biological relationships at the tree level

Occurrences of *D. viride* on phorophytes according to trunk diameter only, and according to trunk diameter and tree species, were tested using χ^2 tests, while surfaces occupied by *D. viride* were tested using parametric Student tests (for small diameter [SD] and very large diameter [VLD]) and non-parametric Kruskal–Wallis tests (for medium diameter [MD] and large diameter [LD]). Tests of the surface area occupied by *D. viride* were applied using the sums of surface areas at the different classes of height. The cover of *H. cupressiforme* var. *fili-forme* by trunk diameter for each tree species was tested with non-parametric Kruskal–Wallis tests. The cover of *H. cupressiforme* var. *fili-forme* between tree species by trunk diameter was tested with a non-parametric Mann–Whitney U test (for SD), non-parametric Kruskal–Wallis tests (for MD and LD) and

Table 3. Survey protocol of sampling plots. SD: small diameter; MD: medium diameter; LD: large diameter; VLD: very large diameter.

Scale recording	Recorded parameters	Tool/method	Unit/classes
Sampling plot	GPS point (on the centroid of the sampling plot)	GPS Garmin Etrex GPSMAP 64	Degrees / minutes / seconds
	Type of forest	Direct observation in the field	Irregular forest / regular forest
	Canopy openness (tree stratum)	Evaluation of canopy cover	Percentage
Phorophyte	Basal area	Relascope	m ²
	Height of the forest stand	Telemeter	m
	GPS point	GPS Garmin eltrex GPSMAP 64	Degrees / minutes / seconds
	Tree species	Direct observation in the field	
	Phorophyte diameter at 1.30 m height	Tape measure	Four categories; SD: 17.5–27.5 cm/MD: 27.5–47.5 cm/LD: 47.5–67.5 cm/VLD: >67.5 cm) in circumference
	Phorophyte inclination	Estimation in the field	
	Presence or absence of <i>Dicranum viride</i>	Direct observation in the field	2 min search on each phorophyte
	Presence or absence of <i>Dicranum scoparium</i>	Direct observation in the field	2 min search on each phorophyte
	Surface occupied by <i>D. viride</i>	Estimation in the field	cm ² , three height classes surveyed: 0–1, 1–2 and > 2 m
	Cover of accompanying bryophytes	Estimation in the field with the flora	Three height classes surveyed: 0–1, 1–2 and > 2 m
	Dominant species	Direct observation in the field with the flora 'Mousses et hépatiques de France'	Three height classes surveyed: 0–1, 1–2 and > 2 m
Cover of <i>Hypnum cupressiforme</i> var. <i>filiforme</i>	Estimation in the field		

with a parametric Student test (for VLD). The dataset used was the cover of *H. cupressiforme* var. *filiforme* on each phorophyte calculated from the average cover at the three height classes. Occurrences of *D. viride* on phorophytes according to the dominant species for each height class were tested with χ^2 tests. A GLM evaluation was performed to test the relationship between the binary dependent variable (presence/absence of *D. viride*) and the independent variable (percentage of

cover of *H. cupressiforme* var. *filiforme*) (Table 5). The dataset used consisted of the combined datasets for the cover of *H. cupressiforme* var. *filiforme* in the three height classes.

Results

Occurrence pattern

The occurrence of *Dicranum viride* was found to increase according to the number of occupied adjacent compartments. The probability of finding *D. viride* increases by a factor of three (from 25 to 75% probability) when it is surrounded by five adjacent compartments containing *D. viride*. The probability rises to 90% when seven adjacent compartments containing *D. viride* surround a compartment (Fig. 2).

















Compartment age

The probability of finding *D. viride* is multiplied by a factor of 9–10 when very young compartments are compared with intermediate or young compartments (4.8% for very young compartments, rising to 43 and 50% for young and intermediate compartments), while this probability increases by a factor of 18 when compared to submature compartments (87% for submature compartments) (Fig. 3).

Biological relationships

The phorophyte diameter has a very significant effect on the presence of *D. viride* (χ^2 test, p-value < 0.0001). The frequency of *D. viride* increases with trunk diameter (SD: 10%,

Table 4. Ranking of the conservation interest of forest compartments for *D. viride*.

Abundance of <i>Dicranum viride</i> (0–3)	Aggregation categories (0–3)	Ranking of conservation interest (0–3)	Colour gradient of conservation interest
0	0	0	
0	1	0.5	
0	2	1	
0	3	1.5	
1	0	0.5	
1	1	1	
1	2	1.5	
1	3	2	
2	0	1	
2	1	1.5	
2	2	2	
2	3	2.5	
3	0	1.5	
3	1	2	
3	2	2.5	
3	3	3	

MD: 18%, LD: 37%, VLD: 73%). By adding the variable relating to tree species, *D. viride* is significantly more present on *F. sylvatica* at VLD (93% on *F. sylvatica* compared to only 34% on *Q. petraea*) and significantly less present on *F. sylvatica* at MD (31% on *Q. petraea*; 25% on *C. betulus*; 12% on *F. sylvatica*). The frequency of *D. viride* increases systematically between the different age categories for smooth bark while it remains almost constant for rough bark (average for *Q. petraea*: 31% at MD; 36% at LD; 49% at VLD) (Fig. 4).

Additionally the surface occupied by *D. viride* on trunks is significantly higher on *F. sylvatica* at VLD (with a mean of 128 cm² for *F. sylvatica* against only 61 cm² for *Q. petraea*) (Fig. 5).

The cover of *H. cupressiforme* var. *filiforme* increases significantly between each age category for smooth barks, while for rough bark the cover of *H. cupressiforme* var. *filiforme* remains fairly constant. At VLD, *H. cupressiforme* var. *filiforme* cover is significantly greater on *F. sylvatica*. At LD, *H. cupressiforme* var. *filiforme* cover is significantly lower on *Q. petraea* and significantly higher on *C. betulus*. At MD, *H. cupressiforme* var. *filiforme* cover is significantly greater on *C. betulus*. Finally, at SD, *H. cupressiforme* var. *filiforme* cover is higher on *C. betulus*, but without reaching significance (Fig. 6).

Dicranum viride is very rarely found alone on a bark (12% of occurrence) and it is mainly found when the dominant species on the phorophyte is *H. cupressiforme* var. *filiforme* (Fig. 7). It is more frequent at the base of trees compared with the higher sectors (20% frequency at 0–1 m, 14% frequency at 1–2 m and 7% frequency above 2 m). The association with other species is low especially at medium and higher levels.

In addition, the occurrence of *D. viride* is positively correlated with the percentage of cover of *H. cupressiforme* var. *filiforme*: whereas the probability of finding *D. viride* is almost nil when no *H. cupressiforme* var. *filiforme* is present, and is multiplied by about eight when the cover of *H. cupressiforme* var. *filiforme* is between 20–80% (Fig. 8).

Cultivation experiment

After 29 days of culture, filaments with oblique walls are observed on the proximal end of leaf fragments (Fig. 9). Filaments with transverse walls are observed on the distal end

of leaf fragments after 90 days of culture. Gametophytic buds are later observed growing directly on the filaments emerging from the distal end (Fig. 10).

Compartment prioritization

Compartments with the highest conservation interest for *D. viride* are almost exclusively submature. Of the four forests analysed, 95.24% of compartments with a conservation interest gradient greater than two are considered submature (100% for Montbéliard, 92.85% for Etupes, 100% for Béthoncourt and 100% for Exincourt). Of compartments with no conservation interest for *D. viride*, 26.67% are submature, 13.33% intermediate, 13.33% young and 33.33% very young (the remaining 13.34% are attributed to resinous woods and empty compartments).

Discussion

Dicranum viride is widely considered to be a species preferentially colonizing smooth bark (Bardat and Hugonnot 2002, Stebel et al. 2011, 2015). We are able to confirm a strong relationship between *D. viride* and smooth-barked trees, especially *F. sylvatica*, at VLD. However, we also show that at MD, *Q. petraea*, a species with rough and fissured bark from a very early age (Eaton et al. 2016), is the most frequent host of *D. viride* and is still a frequent phorophyte at both LD and VLD. Note that the absence of data on *Q. petraea* SD and *C. betulus* VLD is attributed to a silvicultural artefact due to management practices (small *Quercus* are rare because of silvicultural extirpation). *D. viride* spreads only by vegetative means (Pichonet 2006, Ignatova and Fedosov 2008). Given the considerable size of the leaf units (1135 ± 16 µm according to the study of Donskov 2011), it is reasonable to assume that these fragments attach more easily on rough barks than onto smooth ones so that the apparent affinity for phorophytes like *F. sylvatica* is somewhat contradictory. In summary, the distinct relationships between trunk diameter and frequency of *D. viride* as regards bark structure (the frequency of *D. viride* rises constantly from SD to VLD for smooth barks whereas it is relatively constant across diameter in *Q. petraea*) clearly suggests the intervention of an external cause.

Table 5. Summary of the statistical tests performed in the 'Biological relationships at the tree level' section. Student, Mann–Whitney U and Kruskal–Wallis tests were used after checking for normality and homoscedasticity with R software (www.r-project.org).

Tested data	Tests
Occurrences of <i>Dicranum viride</i> on phorophytes (according to trunk diameter, tree species and other epiphytic bryophytes)	– χ^2 tests
Total surface (cm ²) occupied by <i>D. viride</i> on phorophytes (according to trunk diameter and tree species)	– Student tests (for small diameter [SD] and very large diameter [LD]) – Kruskal–Wallis tests (for medium diameter [MD] and LD)
Cover of <i>Hypnum cupressiforme</i> var. <i>filliforme</i> (according to the trunk diameter and tree species)	– Kruskal–Wallis tests – Mann–Whitney U tests – Student tests
Occurrence of <i>D. viride</i> according to cover of <i>Hypnum cupressiforme</i> var. <i>filliforme</i>	– Generalized linear model (GLM – binomial error distribution – logit link function)

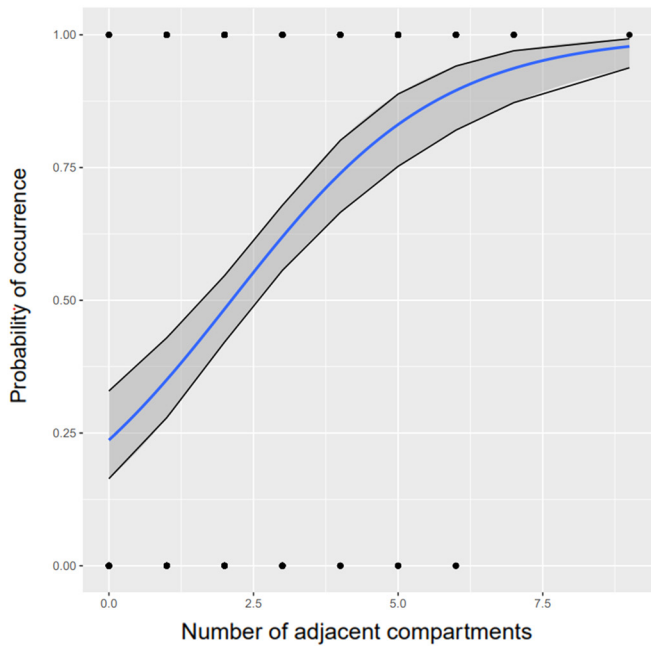


Figure 2. Generalized linear model (GLM) representation of the occurrence of *Dicranum viride* in a compartment as a function of the number of adjacent compartments where the species is present ([GLM], p-value < 0.0001).

On *Q. petraea*, the cover of *H. cupressiforme* var. *filiforme* and the frequency of *D. viride* remain constant between the different diameter categories. For smooth barks, these two variables increase in relation to diameter. From diameter category LD, the cover of *H. cupressiforme* var. *filiforme* becomes higher on *F. sylvatica* than on *Q. petraea*. It is also at this diameter that the frequency of *D. viride* becomes higher on *F. sylvatica*. This suggests a relationship between *D. viride* and *H. cupressiforme* var. *filiforme*, a relationship highlighted by

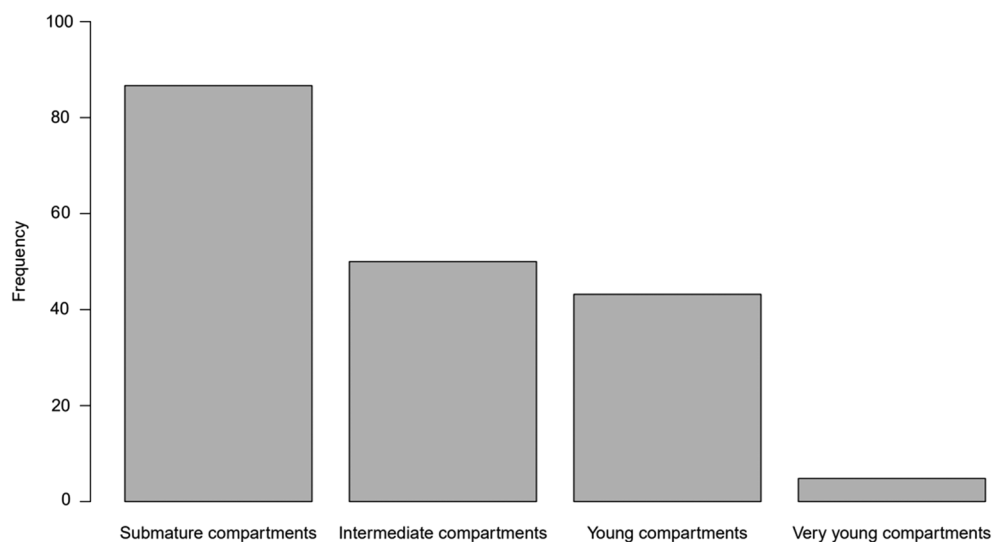


Figure 3. Frequency of *D. viride* in relation to the age of compartments. The age of compartments has a significant effect on the occurrence of *D. viride* (χ^2 test, p-value < 0.0001).

the direct analysis of the probability of the occurrence of *D. viride* based on the cover of *H. cupressiforme* var. *filiforme*.

A strong association between *D. viride* and *H. cupressiforme* var. *filiforme* is also widely highlighted in the bryo-sociological literature (Bardat and Hugonnot 2002, Mežaka et al. 2008, Baisheva et al. 2013). We suggest then that *H. cupressiforme* var. *filiforme* could facilitate the initial establishment of *D. viride* by means of a ‘nesting’ effect, although to our knowledge no previous study alludes to such a facilitating relationship between these species. *H. cupressiforme* var. *filiforme* grows tightly appressed to the substrate, forming thin, flat mats of densely interwoven and pendant shoots on phorophytes (Guillaumot 1949, Frahm 2009). This growth form probably constitutes an efficient, moisture-retentive network that is liable to trap vagrant propagules. Thus, under this hypothesis, mats of *H. cupressiforme* var. *filiforme* would counteract the unfavourable smoothness of the bark surface of the most common woodland trees. The sequential development (1: growth of rhizoids; 2: growth of chloronema) of filaments originating from leaf fragments could easily be viewed as an adaptive device promoting 1) anchoring by rhizoids; 2) growth of gametophytic structures. The rhizoid system of *Dicranum* is one of the most robust and ramified (Odu 1978) of all acrocarp mosses, which is certainly an advantage for active attachment to peripheral layers of bark. Owing to a more robust and erect architecture, *D. viride*, once settled, would be able to competitively exclude *H. cupressiforme* var. *filiforme* by overtopping prostrate mats of this species. This possibility should be studied in greater depth by establishing permanent monitoring devices or performing field experiments.

An alternative interpretation of our results would be that *Dicranum viride* is a genuine pioneer species that is able to colonize bare bark and whose young colonies would be secondarily invaded by an aggressive *H. cupressiforme* var. *filiforme*. This would be in contradiction to our results, which show

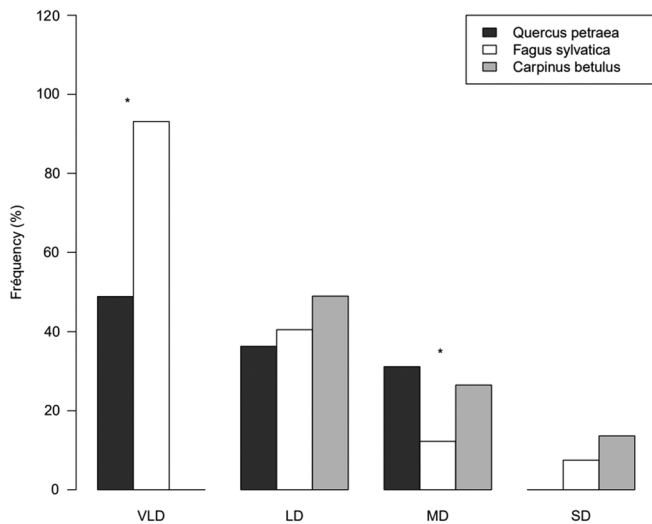


Figure 4. Occurrence of *D. viride* in relation to trunk diameter and tree species. Two tests are significant (For VLD, χ^2 test, p-value < 0.0001; for MD, χ^2 test, p-value < 0.0001).

that *D. viride* is rarely found without *H. cupressiforme* var. *filiforme*, and that they are significantly associated. Moreover, we very frequently observed juvenile individuals of *D. viride* growing epiphytically on *H. cupressiforme* var. *filiforme* (Fig. 12), suggesting that they are later arrivals.

Vegetative fragmentation of large leaf units is likely to be key to understanding the role of connectivity between forest compartments. In our study, young and very young compartments in which *D. viride* is observed were often located near compartments where the species is abundant. Occupied compartments most probably act as source populations, permanently or intermittently dispersing leaf fragments, which potentially settle in unoccupied stands. Large vegetative dispersal units are known to spread less readily than the lighter and smaller spores (Van Zanten 1984, Laaka-Lindberg et al.

2003, Muñoz et al. 2004), which reach a size of less than 20 μm in *D. viride* (Bellolio-Trucco and Ireland 1990). Epiphytic bryophytes are affected by connectivity between different forest units, but especially so when dispersal is achieved by asexual diaspores. (Snäll et al. 2003, Löbel et al. 2006). On the basis of our results, we can roughly estimate that source compartments allow the colonisation of unoccupied compartments at a distance of a few dozen metres within a few decades (Fig. 11). It can be concluded that the colonization efficiency of *D. viride* is low and that unoccupied areas are invaded very slowly. This ultimately emphasizes the role of time in colonization.

The dispersal of vegetative fragments of *D. viride* may also explain stand-age relationships. We have shown that compartment age plays a significant role in the occurrence of *D. viride* at the compartment scale. Our results also demonstrate that *D. viride* is not randomly distributed, but is more frequent on large trees. These links between large trees (Stebel et al. 2011, Infante et al. 2012, Fudali and Wolski 2015) and old-forest stands have been suggested many times for *D. viride* at larger scales (Schmidt et al. 2018, Wierzcholska et al. 2020). On the other hand, many bryophytes are considered bio-indicator species for old-growth forests (Lesica et al. 1991, Brunialti et al. 2010, Löbel et al. 2012), including *D. viride* (Mežaka et al. 2008, Schmidt et al. 2018, Wierzcholska et al. 2020). Since a covariation occurs between tree age and trunk diameter (Matsushita et al. 2015) and between tree age and forest antiquity, it is difficult to determine which is the key driver. In addition, one central point in the vigorous debate concerning old-growth forests concerns the impossibility of disentangling maturity from antiquity (Honnay et al. 1999, Spies 2004). It is difficult to determine whether it is continuity per se or the peculiar ecological conditions generated by an ancient forest that is responsible for the occurrence of specialized species (Nordén and Appelqvist 2001, Nordén et al. 2014). According to the study of Fenton and

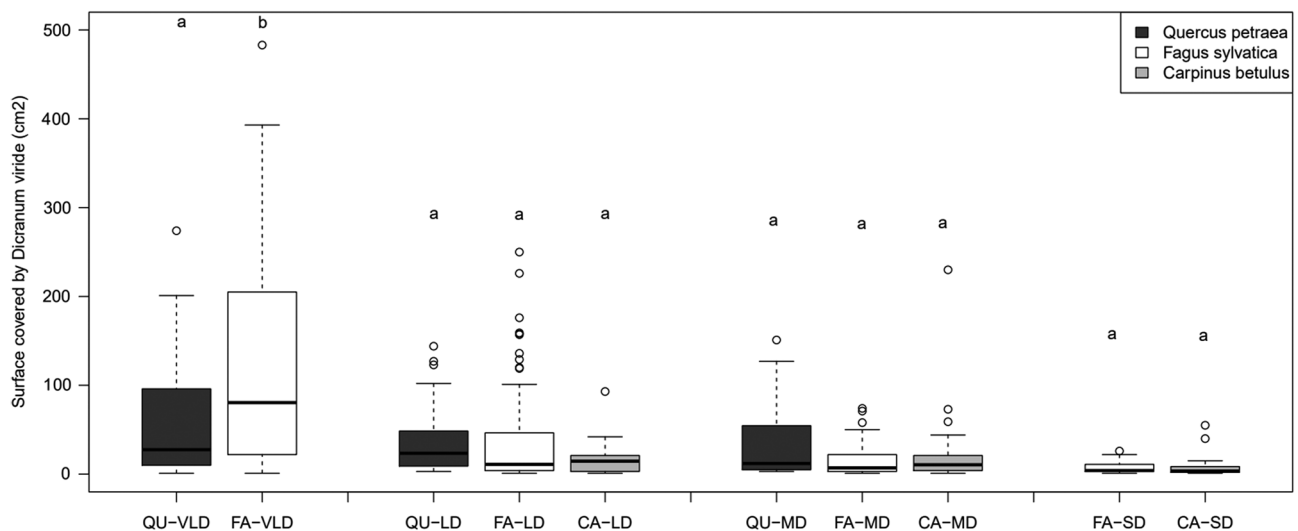


Figure 5. Surface occupied by *D. viride* in relation to trunk diameter and tree species. QU: *Quercus petraea*; FA: *Fagus sylvatica*; CA: *Carpinus betulus*. One test is significant (for VLD: Student test, p-value = 0.0190).

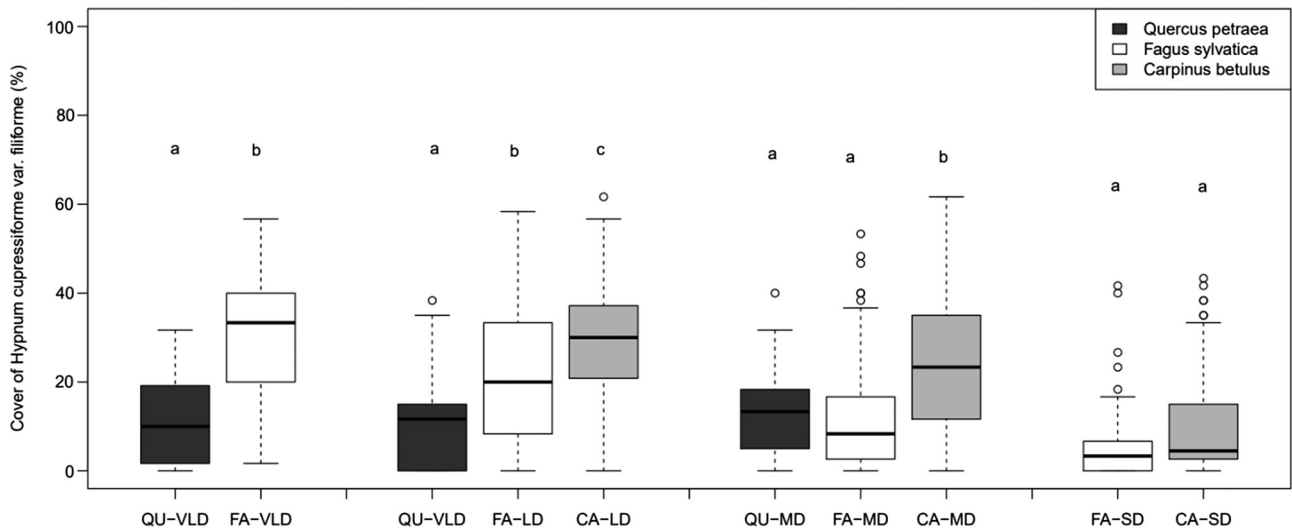


Figure 6. Cover of *Hypnum cupressiforme* var. *filiforme* according to trunk diameter and tree species. QU: *Q. petraea*; FA: *F. sylvatica*; CA: *C. betulus*. For the comparison of the cover between tree species for each diameter class, all tests are significant: at VLD (Student test, p-value < 0.0001) at LD (Kruskal–Wallis test: for QU-FA, p-value = 0.0027; for QU-CA, p-value < 0.0001; for FA-CA, p-value = 0.0062), at MD (Kruskal–Wallis test; for QU-FA, p-value = 0.1580; for QU-CA, p-value = 0.0130; for FA-CA, p-value < 0.0001), and at SD (Student test, p-value = 0.0017). For the comparison of the cover between diameters for each tree species, two tests are significant: For *C. betulus* (Kruskal–Wallis test, for SD-MD, p-value < 0.0001; for SD-GB, p-value < 0.0001; for MD-LD, p-value = 0.0470) and for *F. sylvatica* (Kruskal–Wallis test, for SD-MD, p-value < 0.0001; for SD-LD, p-value < 0.0001; for SD-VLD, p-value < 0.0001; for MD-LD, p-value < 0.0001; for MD-VLD, p-value < 0.0001; for LD-VLD, p-value = 0.0023).

Bergeron (2008), time is a much more important factor for the occurrence of some bryophytes independent of habitat, and vice versa for other species. It seems that bryophyte species whose distribution is mainly influenced by time often have a low dispersal capacity (Öckinger et al. 2005, Fenton and Bergeron 2008). Thus, in accordance with the literature and with our results, we suggest that it is not the peculiar ecological conditions of the mature stands but the relative inefficiency or slowness of dispersal that is one of the critical factors explaining the higher frequency and abundance of *D.*

viride in aged stands. Despite this, one should not underestimate the impact of certain other factors such as local humidity conditions on the presence and abundance of *D. viride*.

Particularly interesting is the case of *Dicranum tauricum* Sapjegin which is a European temperate species that is widespread throughout Europe. The sporophytes of this species were formerly reported to be very rare, but seem to be more frequently mentioned recently (Blockeel et al. 2014, Gréaume et al. unpubl. in France). Similar to *D. viride*, it spreads by means of large leaf fragments. *D. tauricum*

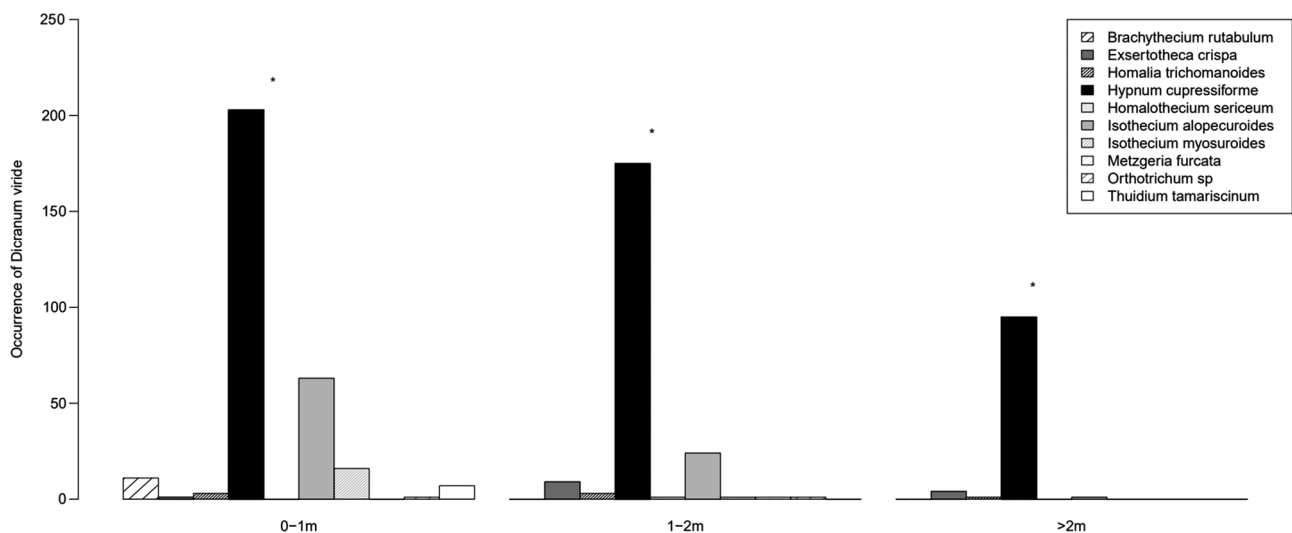


Figure 7. Occurrence of *D. viride* according to the dominant species on the phorophyte at different trunk heights. All tests are significant (χ^2 tests, p-value < 0.0001 for 0–1 m; p-value < 0.0001 for 1–2 m; p-value < 0.0001 for > 2 m).

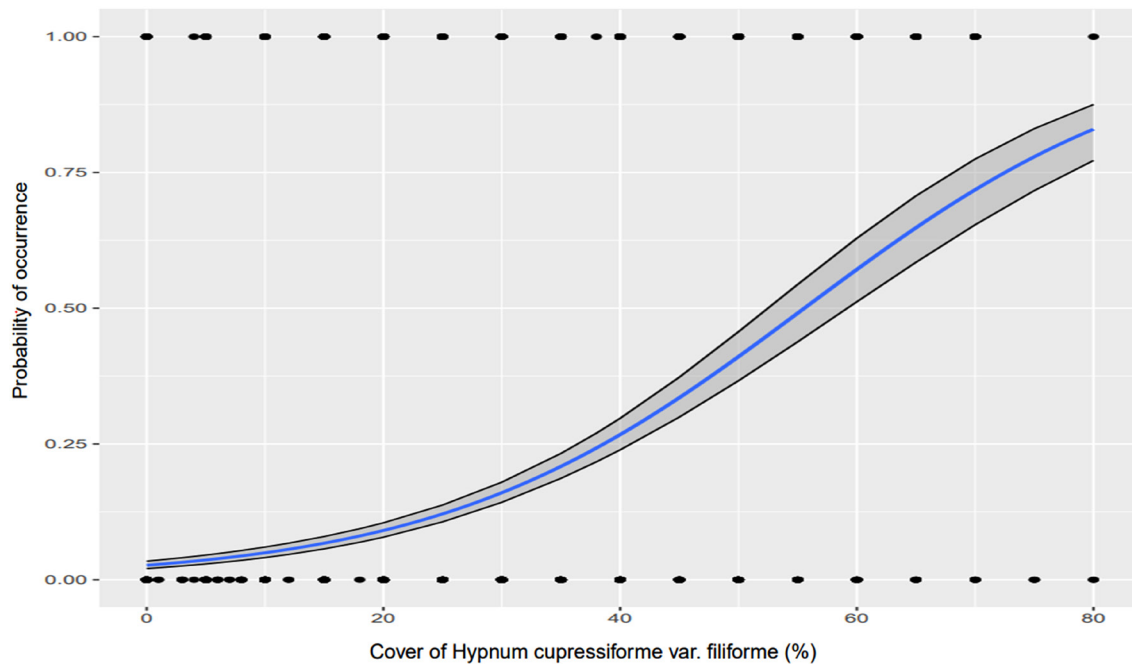


Figure 8. GLM representation of the occurrence of *D. viride* as a function of the cover of *H. cupressiforme* var. *filiforme* on phorophytes. The representation and the test were achieved using the three combined data sets for cover of *Hypnum cupressiforme* var. *filiforme* (0–1, 1–2, >2 m). The two variables are significantly correlated (GLM, p-value < 0.0001).

frequently produces two other types of uniseriate much smaller gemmae, which have never been mentioned (nor observed during our study) in *D. viride* (on leaf tips or on leaf axils and on protonema) (Price and Lang 2011). Since the 1980s the species has become very common in many European regions (Hegewald 1991, Meinunger and Schröder 2007, Németh 2009, Stebel et al. 2012) and has evidently been able to spread between unconnected blocks of woodland over quite large distances. The combination of occasional spore production with massive production of small gemmae could explain the success of *D. tauricum* in Europe and its apparent insensitivity to connectivity.

Although it is a well-known and protected species, the occurrence of *D. viride* is only exceptionally taken

into consideration during routine management activities. Schmidt et al. (2018) and Wierzcholska et al. (2020) recommend the maintenance of forest continuity and the conservation of mature and virgin forests. These general statements are mostly applicable from European to regional scales, but may prove irrelevant for conservation of the species at local scale.

From a practical perspective, it is necessary to reconcile the spatio-temporal aspects linked to the biology of *D. viride* with the requirements of forest management. The age of a compartment seems to be an essential prerequisite for the abundance of *D. viride*, but the management history and

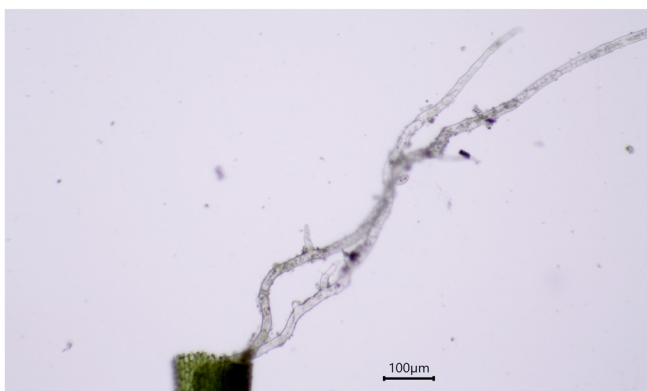


Figure 9. Photograph of the proximal part of a leaf fragment of *D. viride* on which rhizoids are developing (29 days after cultivation).

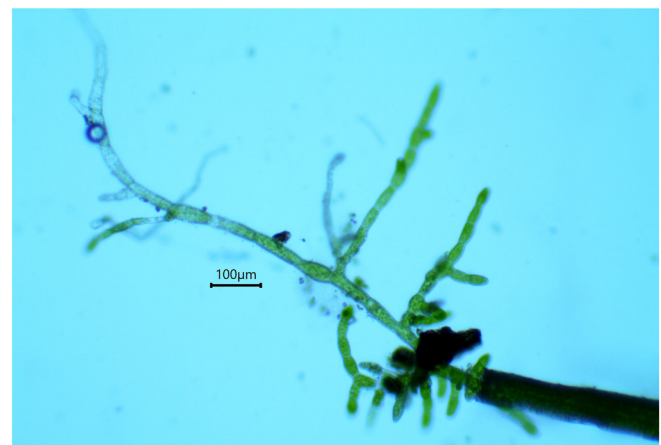


Figure 10. Photograph of the chloronema present on the distal pole of a leaf fragment of *D. viride*.

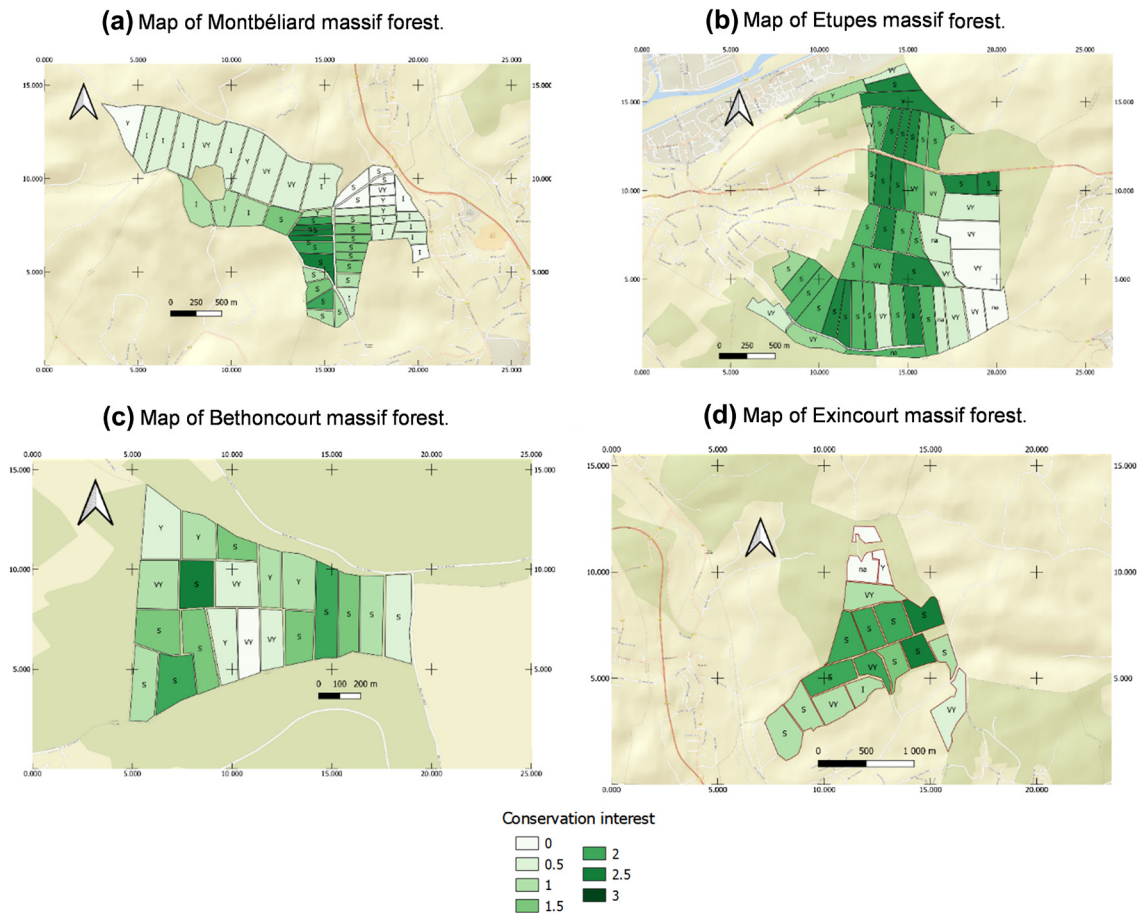


Figure 11. Conservation interest maps of *D. viride* in forest massifs. S: Submature compartment; I: intermediate compartment; Y: young compartment; VY: very young compartment; na: resinous wood or empty compartments.

environment of the compartment must also be taken into account. A conservation strategy specially aimed at promoting *D. viride* must be developed from the outset of the management plan. The first step in this direction should be to create a hierarchy of forest stands hosting *D. viride* populations at

forest scale (Fig. 12). Our sampling method (method section) requires only one or two days of surveying depending on the extent of the compartments. The detection of *D. viride* in the field is relatively straightforward and feasible for non-bryologists. Management maps can then be generated on the basis of Table 4. Priority compartments, from a conservation point of view, are those that contain a certain abundance of *D. viride* and are surrounded by a maximum of compartments occupied by the species.

It is important that any hierarchical system adopted must allow for flexibility of practice, whether the silvicultural interventions are regular or irregular. Priority stands are obviously source areas where the maintenance of ecological and structural conditions is desirable. Some of the stands could be simply left intact (creation of 'old-growth wood islands'). This is optional within the framework of an irregular management system, aimed at maintaining a sustainable stand structure, favouring existing phorophytes and short-distance dispersal of the species. By contrast, old-growth wood islands are essential within the framework of a regular management system since it makes it possible to delay the destruction of *D. viride* caused by regeneration cuts (by lengthening the duration of exploitation periods) or to avoid it altogether (by voluntarily foregoing exploitation of the stand).

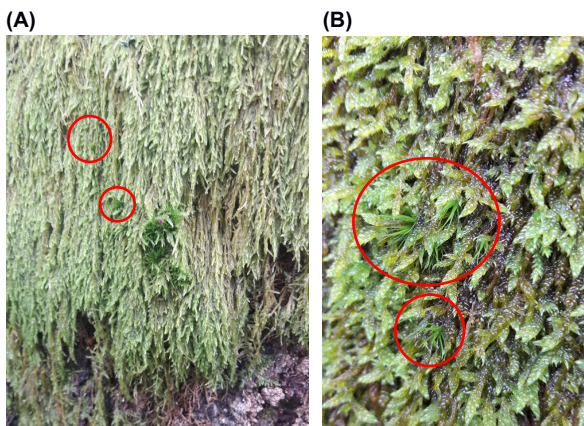


Figure 12. *Hypnum cupressiforme* mats with juvenile epiphytic individuals of *Dicranum viride*.

Certain recommendations can be implemented without necessarily causing additional costs or reduced profitability. A selection of old trees and directly adjacent trees may enable the survival of *D. viride* populations in regenerating stands. This approach is recommended in regular woodlands, in regenerating stands and in compartments assessed as low priority (and especially those adjacent to priority compartments). In view of the dispersal capacities of *D. viride* and the constraints linked to forestry, it is recommended that trees are preserved on the periphery of harvested compartments (i.e. not in the core) to facilitate functional corridors and to ensure the conservation of structured edges. The size of regeneration compartments should not exceed a maximum of 5.5 ha (Blin and Cadet 2019) to mitigate edge effects potentially detrimental to *D. viride*.

At the phorophyte scale, the recruitment of greater numbers of rough-barked trees (mostly *Q. petraea*) in young compartments should be encouraged. This would compensate to a certain extent for the absence of older stands as the most quantitatively important reservoirs of diaspores, since it is apparent (above) that *D. viride* is also able to colonise young trees provided that adequate substrates are available. This is not an argument to challenge the relevance of old stands for biodiversity conservation in general. Within a global warming context, it is expected that there will be regression of *F. sylvatica* (Geßler et al. 2007) and *C. betulus* (Gülçin et al. 2021) and that significant change will happen in the future.

The establishment of corridors that favour the connectivity and dissemination of the species usefully complements the conservation strategy. They are to be positioned in the most advantageous sectors for *D. viride* with regard to humidity, soil acidity, climatic stability, and the presence of autochthonous species favourable to its vegetative recruitment. These parameters are all the more important in the context of climate change.

Other silvicultural techniques may be of interest. The vertical structuring of the edges and the understory guarantees climatic stability within the stands, essential to the forest bryoflora in general. The maintenance of tall stumps (50–130 cm) promotes prolonged dissemination of the species or can be used to protect the trees carrying *D. viride* from impacts generated by the skidding and circulation of forestry machines, in particular in steep terrain.

Fine-scale silvicultural actions will benefit from renewed studies of relevant thresholds. For example, what are the dendrological thresholds to be respected? Preliminary data obtained in lowland beech-oak forests have established that a favourable threshold for *D. viride* is reached when stands have a minimum basal area of 20 m² ha⁻¹ and a canopy closure rate greater than or equal to 70% (Blin et al. 2019). Further studies are clearly desirable in beech-fir forests, continental oak forests etc.

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Data availability statement

There are no additional data for this paper.

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