

Adrian Wysocki*, Beata Olesik, Jarosław Proćków, Kamil Konowalik,
Sylwia Wierzcholska

The role of phorophyte species and interspecific interactions in co-occurrence patterns of the primeval forest relict *Dicranum viride*

Received: 3 April 2024; Accepted: 30 June 2024

Abstract: Bryophytes, particularly epiphytes, play a vital role in the nemoral forest ecosystems of the temperate climate zone, influencing microclimate, providing habitats, and contributing to biodiversity. *Dicranum viride*, a target moss species within the Natura 2000 network, is of significant conservation value. Its preservation is crucial for forest managers who strive to protect the naturalness and integrity of nemoral forest ecosystems. Understanding its habitat preferences, co-occurrence patterns, and interactions within co-created epiphytic communities is essential for effective conservation and a more comprehensive understanding of its biology. Our research examines the co-occurrence patterns of *D. viride* within epiphytic communities. Specifically, we focused on the influence of the phorophyte (host tree) species and interspecific interactions on the composition of co-occurring bryophytes. We conducted field surveys in eastern Poland to investigate the distribution of *D. viride* in several forest ecosystems located in five Natura 2000 sites. Each occurrence of the target moss was recorded along with forest type, phorophyte species, and co-occurring bryophyte taxa. The collected data were then used for network analyses, including pairwise co-occurrence interactions based on a probabilistic model of species co-occurrence. *Dicranum viride* occurred most frequently on the bark of *Fagus sylvatica* and *Carpinus betulus*, particularly in *Fagion sylvaticae* and *Carpinion betuli*. Network analyses revealed that the composition of co-occurring taxa varied depending on phorophyte species, with interspecific interactions among bryophytes significantly influencing these differences. Our study highlights the significant role of *D. viride* as an umbrella species in European woodlands, emphasizing its prevalence in *Fagion sylvaticae* and *Carpinion betuli* forest types, and its affinity for *Fagus sylvatica* and *Carpinus betulus* as phorophyte species. Implementing zonal protection for *D. viride* should be considered a progressive step in sustainable forest management, ensuring the conservation of its habitats and contributing not only to the biodiversity of woodland ecosystems, but also to the preservation of the most valuable ones. By unravelling the complex relationships within epiphytic communities, especially those involving flagship species such as *D. viride*, our research emphasises the importance of considering both the presence of co-occurring taxa and the nature of their interactions in studies of co-created community dynamics.


Keywords: bryophytes, epiphytes, nature conservation, network analyses, target species


Addresses: A. Wysocki, B. Olesik, J. Proćków, S. Wierzcholska, Department of Plant Biology, Institute of Environmental Biology, Wrocław University of Environmental and Life Sciences, Koźuchowska 7a, 51-631 Wrocław, Poland;

AW  <https://orcid.org/0000-0001-6550-1963>, e-mail: adrian.wysocki@upwr.edu.pl;

BO  <https://orcid.org/0009-0004-5002-2002>, e-mail: beataolesik1@gmail.com;

JP  <https://orcid.org/0000-0003-4100-3438>, e-mail: jaroslaw.prockow@upwr.edu.pl;

SW  <https://orcid.org/0000-0002-9868-2315>, e-mail: sylwia.wierzcholska@upwr.edu.pl;

K. Konowalik, Department of Botany and Plant Ecology, Wrocław University of Environmental and Life Sciences, Pl. Grunwaldzki 24a, PL-50-363 Wrocław, Poland;  <https://orcid.org/0000-0003-4821-0608>, e-mail: kamil.konowalik@upwr.edu.pl

* corresponding author

Introduction

Bryophytes, particularly epiphytic bryophytes, emerge as key components within the nemoral forest ecosystems of the temperate climate zone (Barkman, 1958). They modify the climate on a microscale (Stanton et al., 2014) and serve as a habitat for other organisms (Lindo & Gonzalez, 2010; Wardle et al., 2012). Furthermore, by colonising the diverse mosaic of microhabitats within the bark of trees, they contribute to the overall biodiversity of woodland ecosystems (Steel et al., 2004; Fritz & Heilmann-Clausen, 2010; Kentjens et al., 2023). Epiphytic bryophytes are considered valuable indicators of forest health and diversity, as well as key components of ecosystem resilience (Frego, 2007; Oishi & Morimoto, 2016; Shi et al., 2017; Guerra et al., 2020). This is why they are used as a tool to assess the degree of naturalness and continuity of forests (Mölder et al., 2015; Jaroszewicz et al., 2019; Wierzcholska et al., 2020).

The concept of an umbrella species, defined as one whose conservation can effectively protect a broader range of species and their habitats, has gained prominence in conservation biology (Wilcox, 1984; Roberge & Angelstam, 2004). By focusing on the habitat requirements and protection of the umbrella species, conservation efforts can indirectly safeguard numerous other species that share similar ecological niches (Wilcox, 1984; Fleishman et al., 2000; Fleishman et al., 2001; Roberge & Angelstam, 2004). Therefore, a promising umbrella species is one whose requirements for environmental resources are higher compared to co-occurring species, thereby identifying ecosystems important for the protection of highly valued areas (Roberge et al., 2008).

Investigating interactions among co-occurring species constitutes a key aspect of community ecology (D'Amen et al., 2018; Zurell et al., 2018). In this context, specialist species coexist with a limited number of other species, while generalists exhibit a broader range of co-occurring species (Fridley et al., 2007). Knowing the patterns responsible for species co-occurrence is helpful in determining their niche, as well as the environmental factors that shape their distributions (Fridley et al., 2007; Pannek et al., 2016; Li et al., 2022; Tasenkevich et al., 2022).

In the context of European forests, *Dicranum viride* (Sull. & Lesq.) Lindb., a target species *sensu* Kiehl et al. (2010), serves as a prime example of the vital

ecological and conservation role that these inconspicuous organisms play. This moss, considered a relict of European primeval forests (Cieśliński et al., 1996; Dierßen, 2001; Stebel & Żarnowiec, 2014), is subject to special protection, particularly under the Bern Convention (Annex I in Bern 19/09/1979) and the EU Habitats Directive (Annex II of the Council Directive 92/43/EEC). Its distribution, habitat preferences, and ecological interactions make it an ideal focal point for conservation efforts (Stebel, 2004; Wysocki et al., 2023). Given its international importance in the conservation of biodiversity and forest management, there is a substantial knowledge gap on the co-occurrence patterns and interspecific interactions within epiphytic communities where *D. viride* has its ecological optimum. Our aim is to investigate these complex relationships, as co-occurrence patterns are instrumental in revealing the broader ecological network centred around the presence and distribution of the umbrella species itself. Our research puts forward two hypotheses: (1) the overall composition of taxa co-occurring with *D. viride* differs regarding the phorophyte (host tree) species, and (2) the interactions among co-occurring taxa influence the overall composition of *D. viride* communities.

Methods

Study area

Our research began with an extensive examination of the distribution of *D. viride* in Poland, based on data obtained from national monitoring programmes and insights provided by experts. Subsequently, we identified particular locations within the extensive forest complexes in eastern Poland and conducted field surveys during July and August 2022. The chosen sites encompassed five Natura 2000 Special Areas of Conservation (Fig. 1): three are located in the highlands: PLH180001 'Ostoja Magurska' (Central Beskids), PLC180001 'Bieszczady' (Eastern Beskids), and PLH060017 'Roztocze Środkowe' (Roztocze) (at an average elevation per site of 634, 741, and 266 m above sea level, respectively), and two are located in the lowlands: PLC200004 'Puszcza Białowieska' (North-Podlasie Lowland) and PLB280006 'Puszcza Borecka' (Masurian Lake District) (at an average elevation of 166 and 202 m above sea level, respectively). These specific sites were chosen due to their

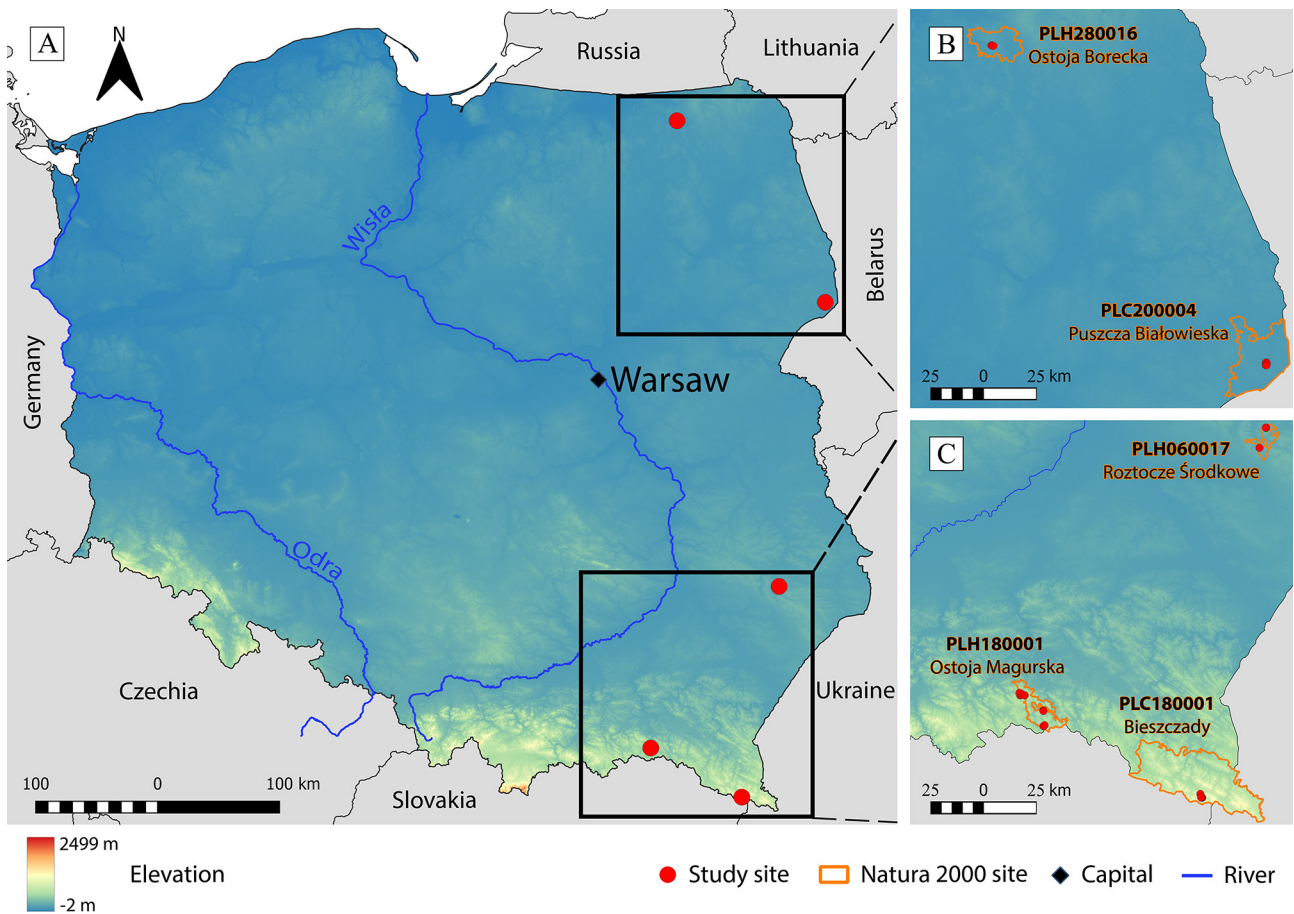


Fig. 1. Distribution of the study sites in the (A) Central-European and (B–C) regional context. The map was created using QGIS 3.22.6 (QGIS Development Team, 2021)

close resemblance to natural forests and their ability to capture varying ecological conditions, both under latitudinal and elevational gradients.

Sampling design and data collection

We actively searched for *D. viride* on the bark of living trees. Each time we successfully located this moss, we documented the co-occurring bryophyte taxa, phorophyte species on which it grew, and forest type of each study site (obtained based on coordinates from the database of the Forest Data Bank of Poland (State Forests, 2023)). To standardise and ensure repeatability of the data collection procedure, we used special linoleum frames temporarily attached to the bark of the tree (no more than once per individual tree). These frames demarcated bryophyte vegetation plots with an area of 400 cm² (a square of 20×20 cm), following the procedure described by Wysocki et al. (2023).

The nomenclature of vascular plants adheres to WFO (2023), while phytosociological names and characteristics of vegetation types follow Mucina et al. (2016). For bryophytes, we follow the nomenclature of Hodgetts et al. (2020).

Data analysis

We evaluated the affinity of each epiphyte taxon to a specific forest type and phorophyte species by quantifying the number of occurrences. In particular, this allowed us to pinpoint the forest type and phorophyte species where *D. viride* was most frequently recorded, along with the co-occurring bryophyte taxa. Subsequently, we used the *ggsankey* package (Sjoberg, 2023) to visualise these associations as a quantitative interaction network.

We constructed two networks based on the number of co-occurrences of each bryophyte taxa with *D. viride* on *Fagus sylvatica* L. and *Carpinus betulus* L., which were the two most represented phorophytes. To achieve this, we used the *cooccur::pair()* function (Griffith et al., 2016) to analyse the co-occurrence patterns of *D. viride*. The networks were built using the following packages: *ggraph* (Pedersen, 2022a), *igraph* (Csardi & Nepusz, 2006), *tidygraph* (Pedersen, 2022b) and *tidyverse* (Wickham et al., 2019).

To investigate pairwise co-occurrence interactions (whether they were positive, negative, or random) between taxa that form a composition with *D. viride* within the microhabitats of the bark of *F. sylvatica*

and *C. betulus*, we used the `cooccur::cooccur()` function (Griffith et al., 2016). This method, based on the presence-absence community data, categorises species pair's interactions using the probabilistic model of species co-occurrence by Veech (2013). The algorithm calculates observed and expected frequencies for co-occurrence between each species pair, considering the random and independent distribution of each species. We visualised the results as a matrix by plotting the object returned from the `cooccur::cooccur()` function. We performed all statistical analyses using R version 4.2.2 'Innocent and Trusting' (R Core Team, 2022).

Results

Habitat and phorophyte preferences

During field research, we documented the presence of *D. viride* in 92 bryophyte vegetation plots, located in four distinct forest types, and observed on the bark of seven phorophyte species, co-occurring with 29 other bryophyte taxa (Figs 2, 3).

In particular, *D. viride* exhibited the highest frequency in the *Fagion sylvaticae* Luquet 1926 forests (temperate European basiphilous beech and mixed fir-beech forests) and *Carpinion betuli* Issler 1931

forests (oak-hornbeam forests found on fertile soils of cool-temperate Europe), with 66 and 21 occurrences, respectively. Additionally, we identified this species in *Piceion excelsae* Pawłowski et al. 1928 (boreo-montane spruce forests and subalpine pine woods with a preference for acidic, nutrient-poor podzolic soils) and *Luzulo-Fagion sylvaticae* Lohmeyer et Tx. in Tx. 1954 (acidophilous beech and mixed fir-beech forests typical of Central Europe), but much less frequently (3 and 2 occurrences, respectively).

Regarding phorophyte species, our findings indicate that *D. viride* predominantly colonised the bark of *F. sylvatica* and *C. betulus*, with 62 and 20 occurrences, respectively. On the contrary, it occurred less frequently on *Tilia cordata* Mill., *Acer pseudoplatanus* L., *Quercus robur* L., *Betula pendula* Roth, and *Acer platanoides* L., with 4, 2, 2, 1, and 1 occurrence(s), respectively.

Co-occurring species composition depending on phorophyte species

For the two most represented phorophytes, namely *F. sylvatica* and *C. betulus*, the composition and frequency of co-occurring taxa with *D. viride* displayed significant variations, particularly when examining taxa with co-occurrence rates exceeding

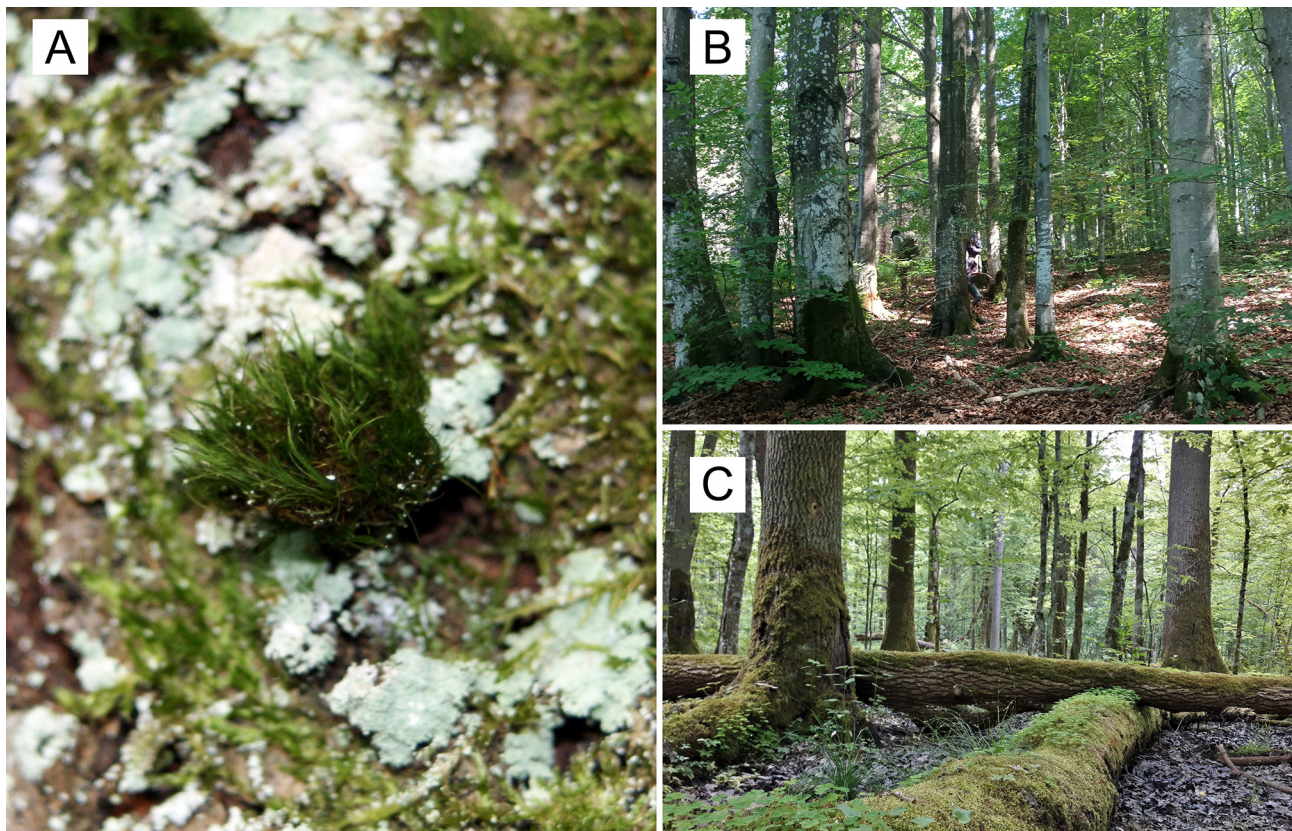


Fig. 2. (A) *Dicranum viride* on the bark of *Fagus sylvatica* and its habitats in (B) PLC180001 'Bieszczady' and (C) PLC200004 'Puszcza Białowieska' (photos: Adrian Wysocki, 23 July & 07 August 2022)

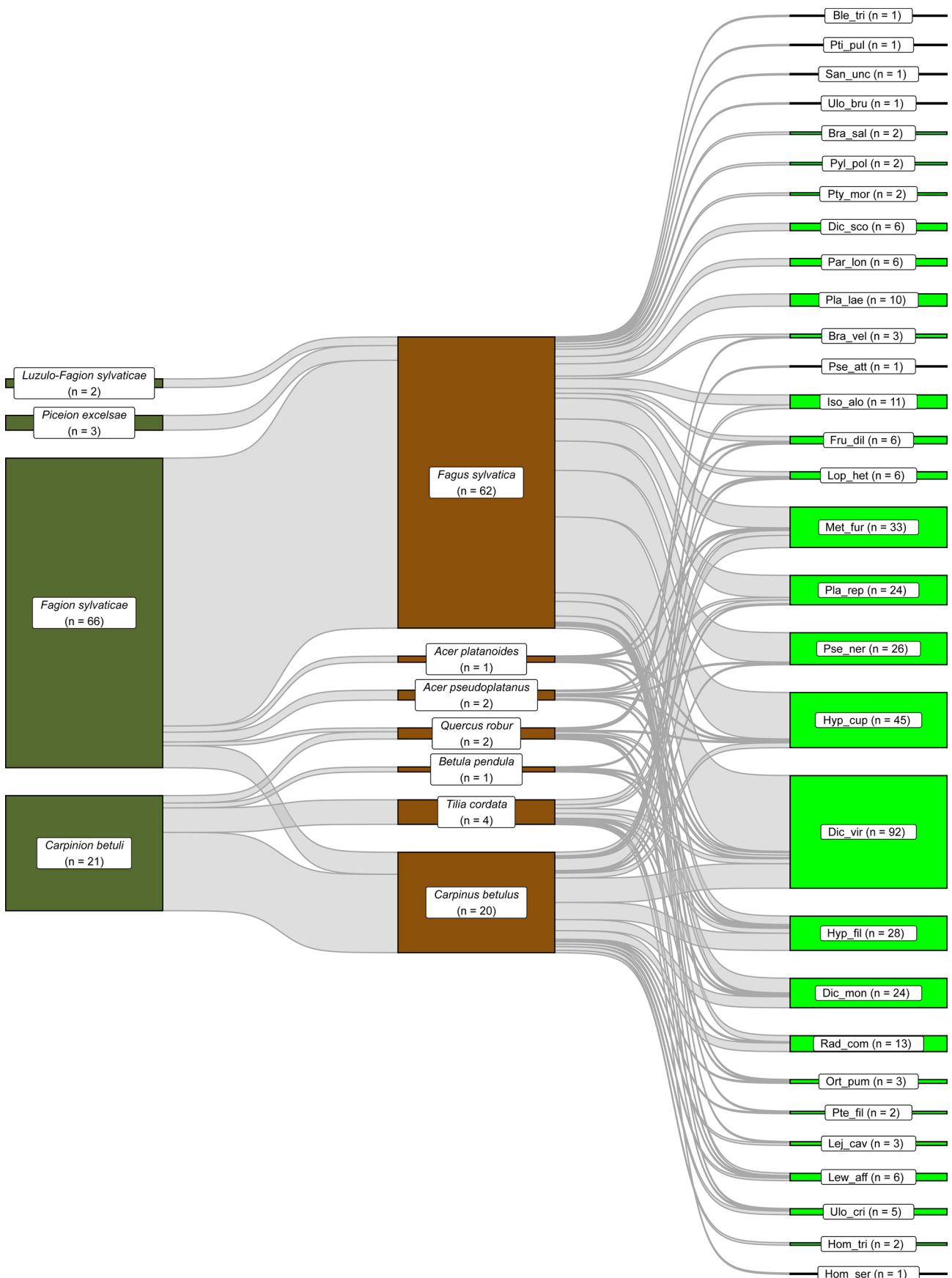
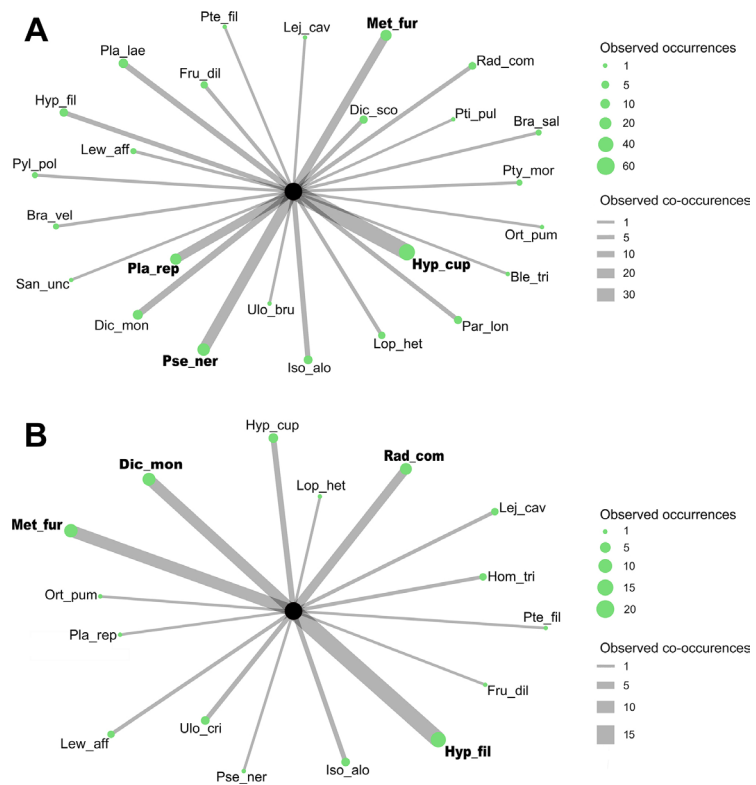


Fig. 3. Affinity of *Dicranum viride* and co-occurring bryophytes to specific forest types and phorophyte species. The bryophyte names are presented as seven-digit acronyms (explained in Table 1)

Table 1. Abbreviations of taxa names.

Acronym	Taxon full name
Ble_tri	<i>Blepharostoma trichophyllum</i> (L.) Dumort.
Bra_sal	<i>Brachythecium salebrosum</i> (Hoffm. ex F.Weber & D.Mohr) Schimp.
Bra_vel	<i>Brachytheciastrum velutinum</i> (Hedw.) Ignatov & Huttunen
Dic_mon	<i>Dicranum montanum</i> Hedw.
Dic_sco	<i>Dicranum scoparium</i> Hedw.
Dic_vir	<i>Dicranum viride</i> (Sull. & Lesq.) Lindb.
Fru_dil	<i>Frullania dilatata</i> (L.) Dumort.
Hom_ser	<i>Homalothecium sericeum</i> (Hedw.) Schimp.
Hom_tri	<i>Homalia trichomanoides</i> (Hedw.) Brid.
Hyp_cup	<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i> Hedw.
Hyp_fil	<i>Hypnum cupressiforme</i> var. <i>filiforme</i> Brid.
Iso_alo	<i>Isoetecium alopecuroides</i> (Lam. ex Dubois) Isov.
Lej_cav	<i>Lejeunea cavifolia</i> (Ehrh.) Lindb.
Lew_aff	<i>Lewinskya affinis</i> (Schrad. ex Brid.) F.Lara, Garilleti & Goffinet
Lop_het	<i>Lophocolea heterophylla</i> (Schrad.) Dumort.
Met_fur	<i>Metzgeria furcata</i> (L.) Corda
Ort_pum	<i>Orthotrichum pumilum</i> Sw. ex anon.
Par_lon	<i>Paraleucobryum longifolium</i> (Hedw.) Loeske
Pla_lae	<i>Plagiothecium laetum</i> Schimp.
Pla_rep	<i>Platygyrium repens</i> (Brid.) Schimp.
Pse_att	<i>Pseudanomodon attenuatus</i> (Hedw.) Ignatov & Fedosov
Pse_ner	<i>Pseudoleskeella nervosa</i> (Brid.) Nyholm
Pte_fil	<i>Pterigynandrum filiforme</i> Hedw.
Pti_pul	<i>Ptilidium pulcherrimum</i> (Weber) Vain.
Pty_mor	<i>Ptychostomum moravicum</i> (Podp.) Ros & Mazimpaka
Pyl_pol	<i>Pylaisia polyantha</i> (Hedw.) Schimp.
Rad_com	<i>Radula complanata</i> (L.) Dumort.
San_unc	<i>Sanionia uncinata</i> (Hedw.) Loeske
Ulo_bru	<i>Ulotia bruchii</i> Hornsch. ex Brid.
Ulo_cri	<i>Ulotia crispa</i> (Hedw.) Brid.

Fig. 4. Co-occurrence network of *Dicranum viride* with (A) *Fagus sylvatica* and (B) *Carpinus betulus* as phorophytes. The central black node symbolises *D. viride*, the size of the nodes represents the number of occurrences of each taxon, and the width of the edges defines the number of co-occurrences with *D. viride* of each taxon. The names of recorded bryophyte taxa are presented as seven-digit acronyms (explained in Table 1); taxa with at least 25% co-occurrence with *D. viride* are in bold



25%. For instance, when considering *F. sylvatica* as the host tree, the most frequently co-occurring taxa were (along with the number of co-occurrences in parentheses) *Hypnum cupressiforme* var. *cupressiforme* (38), *Pseudeskeella nervosa* (24), *Platygyrium repens* (18), and *Metzgeria furcata* (17) (Fig. 4A). However, when *C. betulus* served as a host tree, the co-occurring taxa featured *H. cupressiforme* var. *filiforme* (14), *M. furcata* (10), *Dicranum montanum* (10), and *Radula complanata* (7) (Fig. 4B).

Interactions among co-occurring species

Regarding two of the most common tree phorophytes, analysis of co-occurrence patterns revealed contrasting interactions between taxa associated

with *D. viride* (Table 2; Fig. 5). In particular, a negative interaction was observed between *H. cupressiforme* var. *filiforme* and *H. cupressiforme* var. *cupressiforme*, *Plagiothecium laetum*, and *P. nervosa*. Similarly, *D. montanum* exhibited negative interactions with *P. nervosa*, as did *M. furcata* with *P. laetum* and *P. nervosa*. Furthermore, *H. cupressiforme* var. *cupressiforme* showed negative interactions with *R. complanata*. In turn, positive interactions for *M. furcata* were demonstrated with *Frullania dilatata* and *H. cupressiforme* var. *filiforme*. Furthermore, *P. repens* demonstrated a positive interaction with *H. cupressiforme* var. *cupressiforme*, while *R. complanata* exhibited positive interactions with *M. furcata* and *H. cupressiforme* var. *filiforme*.

Discussion

Recent attention in bryophyte co-occurrence studies (Ma et al., 2020; Shen et al., 2023; Wysocki et al., 2023) highlights their potential in elucidating intricate ecological interactions within cryptogamic plant communities (Wierzcholska et al., 2024). Identifying species that frequently co-occur with protected species holds significant conservation value. However, understanding the interactions that shape their composition offers deeper insights into the occurrence patterns of protected species. Our study revealed that the taxa co-occurring with *D. viride* exhibit interactions that may affect their overall composition depending on the inhabited phorophyte species. Specifically, *D. viride* on *F. sylvatica* most often co-occurred with *H. cupressiforme* var. *cupressiforme*, whereas on *C. betulus*, it was found mainly in the presence of *H. cupressiforme* var. *filiforme*. Although *H. cupressiforme* var. *cupressiforme* is an ubiquitous taxon

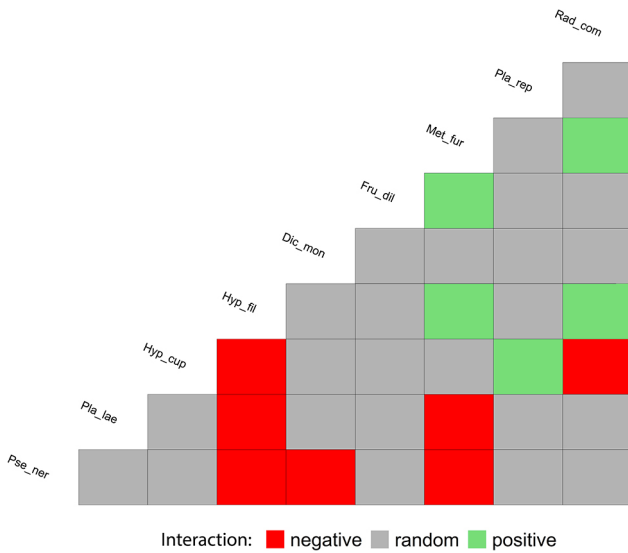


Fig. 5. Pairwise interactions of taxa co-occurring with *Dicranum viride* on *Fagus sylvatica* and *Carpinus betulus*

Table 2. Results of the analysis of interactions between taxa co-occurring with *Dicranum viride* on *Fagus sylvatica* and *Carpinus betulus*. Abbreviations: tx1_name, the name of the first compared taxon; tx2_name, the name of the second compared taxon; tx1_inc, the number of sites that have first taxon; tx2_inc, the number of sites that have second taxon; obs_coocc, observed number of sites having both taxa; p_lt, p-value for probability that the two taxa would co-occur at a frequency less than the observed number of co-occurrence sites if the two taxa were distributed randomly (independently) of one another; p_gt, p-value for probability of co-occurrence at a frequency greater than the observed number of co-occurrence sites if the two taxa were distributed randomly (independently) of one another. Statistically significant results are shown in bold

tx1_name	tx2_name	tx1_inc	tx2_inc	obs_coocc	p_lt	p_gt
<i>Frullania dilatata</i>	<i>Metzgeria furcata</i>	5	27	5	1.000	0.003
<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i>	<i>Hypnum cupressiforme</i> var. <i>filiforme</i>	42	21	0	0.000	1.000
<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i>	<i>Platygyrium repens</i>	42	19	14	0.994	0.023
<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i>	<i>Radula complanata</i>	42	12	3	0.048	0.990
<i>Hypnum cupressiforme</i> var. <i>filiforme</i>	<i>Pseudeskeella nervosa</i>	21	25	1	0.002	1.000
<i>Hypnum cupressiforme</i> var. <i>filiforme</i>	<i>Metzgeria furcata</i>	21	27	11	0.992	0.028
<i>Hypnum cupressiforme</i> var. <i>filiforme</i>	<i>Plagiothecium laetum</i>	21	10	0	0.042	1.000
<i>Hypnum cupressiforme</i> var. <i>filiforme</i>	<i>Radula complanata</i>	21	12	7	0.999	0.010
<i>Pseudeskeella nervosa</i>	<i>Metzgeria furcata</i>	25	27	4	0.026	0.994
<i>Pseudeskeella nervosa</i>	<i>Dicranum montanum</i>	25	21	1	0.002	1.000
<i>Metzgeria furcata</i>	<i>Plagiothecium laetum</i>	27	10	0	0.012	1.000
<i>Metzgeria furcata</i>	<i>Radula complanata</i>	27	12	7	0.989	0.048

with broad ecological amplitude and no specific affinities to the wood substrate (Dierßen, 2001), *H. cupressiforme* var. *filiforme* is a specialised epiphyte (Barkman, 1958; Cieśliński et al., 1996; Stebel & Żarnowiec, 2014; Skowron & Wołkowycki, 2022). Both taxa significantly influenced the co-created composition when co-occurring with *D. viride*. For instance, *P. nervosa*, the second most common co-occurring species with *D. viride* on *F. sylvatica*, was much less frequent on *C. betulus*. This decrease in frequency can be attributed to negative interactions with *H. cupressiforme* var. *filiforme*, a taxon with much longer stems (Hill et al., 2007). Given that *P. nervosa* is the most photophilic taxon in the studied group (Hill et al., 2007), its exclusion may result from the inability to gain sufficient access to light. In contrast, *P. repens*, a species that exhibits a positive interaction with *H. cupressiforme* var. *cupressiforme* was recorded much more frequently on *F. sylvatica* than on *C. betulus*. Although both taxa have similar size and form smooth, dense mats, *P. repens* is less light-demanding (Hill et al., 2007). The presence of *H. cupressiforme* var. *cupressiforme* may facilitate its presence, as they can collaboratively form a compact mat without competing for resources, thus resisting being overgrown by more competitive species such as *Dicranum scoparium* and *D. montanum*. These species are known for their robust growth and ability to form dense turfs that can dominate the substrates on which they grow on (Barkman, 1958; Dierßen, 2001). *Metzgeria furcata* is the species with the highest number of interactions: two negative (with *P. nervosa* and *P. laetum*) and two positive (with *H. cupressiforme* var. *filiforme* and *F. dilatata*). Taxa with which it exhibits negative interactions were observed more frequently on *F. sylvatica* than on *C. betulus*. In contrast, taxa that positively influence it were more prevalent on *C. betulus*, reflecting in the higher frequency of co-occurrence of *M. furcata* with *D. viride* on *C. betulus* compared to *F. sylvatica*. A similar pattern emerges with *R. complanata*, a species that co-occurred less frequently with *D. viride* on *F. sylvatica* than on *C. betulus*. This difference arises from its negative interaction with *H. cupressiforme* var. *cupressiforme* and positive interaction with *H. cupressiforme* var. *filiforme*.

Our work was carried out according to the current nomenclature for mosses by Hodgetts et al. (2020), who distinguish *H. cupressiforme* var. *cupressiforme* and *H. cupressiforme* var. *filiforme* as two separate taxa and is also supported by Terracciano et al. (2012). However, other studies (Ando, 1992; Kučera et al., 2019) suggest that they may only represent habitat specialisation. Our research, along with the studies by Bardat & Hugonnot (2002) and Gréaume et al. (2023), highlights the ecological significance of both *H. cupressiforme* var. *cupressiforme* and *H. cupressiforme* var. *filiforme* in the context of *D. viride* and co-created

communities. Nevertheless, their taxonomic status is still unclear due to limited molecular support, presenting two possible interpretations: (1) they are two different taxa with different habitat preferences or (2) they are habitat modifications within a single taxon. If we consider them as two separate taxa, this would imply distinct habitat preferences, suggesting that they exert negative interactions with each other and play different ecological roles within their respective habitats. In contrast, if these are habitat modifications of the same taxon, then the different modifications observed are the result of environmental conditions rather than intrinsic taxon differences. In this case, the apparent negative interactions between the modifications would be environmental effects, and both modifications would be responses to habitat conditions rather than true interspecific competition. Further molecular studies are needed to resolve this taxonomic ambiguity. Regardless of the chosen interpretation, our findings, derived from the application of probabilistic models (which enable systematic analysis of interspecific interactions on community structure independent of environmental variables), indicate that these interactions significantly shape the composition of *D. viride* communities.

The varying frequency of *D. viride* across different forest types, particularly its prevalence in *Fagion sylvaticae* and *Carpinion betuli*, along with its affinity for specific phorophyte species, underscores its strong association with specific host environments. This epiphytic moss implements various mechanisms to occupy the available niches, depending on the species of inhabited phorophyte (Wysocki et al., 2023). Its life strategy, which includes asexual propagation through leaf fragments, is the factor that likely impacts its phorophyte preferences (Gréaume et al., 2023; Wysocki et al., 2023) and dispersal abilities (Hallingbäck, 2002; Wierzycholska et al., 2020). Despite its specific microhabitat requirements, the history of land management also influences its presence (Baisheva et al., 2013). The limited dispersal ability of *D. viride* highlights the need to conserve of continuous forest stands to support its long-term survival (Mežaka et al., 2023). Furthermore, the importance of regional connectivity in its probability of colonisation underscores the importance of maintaining stepping-stone habitats for its persistence (Percel et al., 2024). The challenges faced by the conservation of *D. viride* emphasise the need to establish microreserves and implement long-term monitoring programmes (Mežaka et al., 2024). Discerning the habitat preferences of protected species has substantial implications for conservation practices (Weir & Collins, 2015). Therefore, by identifying and prioritising potentially valuable habitats for these species, conservation programmes can more efficiently allocate resources, focusing on preserving and restoring

crucial habitats for the survival of *D. viride* and other endangered or rare species. This targeted approach ensures a more informed and proactive conservation strategy, ultimately safeguarding ecosystems essential for the long-term survival of multiple species.

Focusing on habitat requirements and protection of an umbrella species allows conservation initiatives to indirectly protect numerous other species that share similar ecological niches. The concept of umbrella species is exemplified by another epiphytic organism, *Lobaria pulmonaria* (L.) Hoffm., a lichen that also plays a critical role in forest ecosystems (Scheidegger & Werth, 2009; Whittet & Ellis, 2013; Nadyeina et al., 2014). Similarly to *D. viride*, *L. pulmonaria* has been recognised for its ability to influence conservation strategies and forest management (Paoli et al., 2019; Bianchi et al., 2020). The strategic application of zonal protection, as for *L. pulmonaria* (see, e.g., Jüriado & Liira, 2010; Czarnota et al., 2023), can similarly benefit *D. viride*, ensuring the preservation of habitats critical not only to this moss but also to the broader biodiversity within these ecosystems. Therefore, the implementation of zonal protection for this valuable moss should be considered as an effective strategy in modern forest management practices. Studying co-occurrence patterns elucidates the broader ecological network reliant on the presence and distribution of the umbrella species. Investigating the co-occurrence patterns of *D. viride* within European woodlands is therefore crucial. It improves our understanding of its ecology and supports effective conservation strategies, providing a comprehensive understanding of the woodland ecosystem as a whole.

Conclusions

Our research sheds light on the pivotal role of *D. viride* as an umbrella species in European woodlands, demonstrating its pronounced prevalence in certain forest types and its affinity for particular phorophyte species. This emphasizes the dependence of the species on its specific host environment and underscores the importance of understanding habitat preferences for effective conservation strategies.

The co-occurrence patterns revealed in our research elucidate the complex ecological network surrounding *D. viride*. By understanding the interactions among co-occurring taxa, we gain valuable insights into the factors shaping the composition of these communities. These interactions often occur within specialised forest types, such as *Fagion sylvaticae* and *Carpinion betuli*, which are mature, climax communities providing essential ecosystem services. Our findings underscore the broader ecological impact of conserving *D. viride*, which, by promoting

the integrity of these habitats, indirectly supports the conservation of numerous associated species. Many of these, while common, rely on the continued existence and health of forest ecosystems that are increasingly threatened by human activities. Therefore, protecting *D. viride* is not only about preserving a single species of moss, but also about protecting the intricate network of life that depends on these forest ecosystems.

In practical terms, our research supports the implementation of zonal protection for *D. viride* as an effective tool in modern forest management. This approach specifically addresses the need to preserve habitats crucial to its survival and the diverse taxa with which it coexists, highlighting the need for targeted conservation initiatives. This protective measure is vital to maintaining biodiversity, ecological balance, and the resilience of forest habitats, particularly those of the highest ecological value. Zonal protection may not only help to preserve this target species, but also strengthen the ecological integrity of the entire forest system.

Author contributions

Adrian Wysocki: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. Beata Olesik: Writing – original draft, Writing – review & editing. Jarosław Proćków: Supervision, Writing – review and editing. Kamil Konowalik: Supervision, Writing – review and editing. Sylwia Wierzcholska: Methodology, Investigation, Supervision, Writing – original draft, Writing – review and editing.

Acknowledgements

This work was supported by the Wrocław University of Environmental and Life Sciences (Poland) as the Ph.D. research programme ‘Bon doktoranta SD UPWr’ N020/0002/22. The article is part of a Ph.D. dissertation titled: (PL) ‘Ekologia molekularna mszaków parasolowych (gatunków osłonowych)’; (ENG) ‘Molecular ecology of umbrella bryophyte species’, prepared during the Doctoral School at the Wrocław University of Environmental and Life Sciences.

The authors express their sincere gratitude to Damian Nowak and Jarosław Sochacki (Magura National Park), Zbigniew Kucharczyk (Bieszczady National Park), Dr Eng. Ewa Zin (Forest Research Institute (IBL), Poland), Dr Eng. Zbigniew Maciejewski (Roztocze National Park), Dr Robert Zubel (Maria Curie-Skłodowska University in Lublin), Adam Bohdan, Andrzej Sulej, and Adrian Grzegorz

(Natural Forest Foundation) for generously providing the most recent distributional data of *Dicranum viride* in Poland, and Marcin Dziejdzic for assistance during the field surveys.

References

- Ando H (1992) Studies on the genus *Hypnum* Hedw. (VIII). *Hikobia* 11: 111–123.
- Baisheva E, Mežaka A, Shirokikh P & Martynenko V (2013) Ecology and distribution of *Dicranum viride* (Sull. Lesq.) Lindb. (Bryophyta) in the Southern Ural Mts. *Arctoa* 22: 41–50. doi:10.15298/arctoa.22.07.
- Bardat J & Hugonnot V (2002) Les communautés à *Dicranum viride* (Sull. & Lesq.) Lindb. en France métropolitaine. *Cryptogamie Bryologie* 23: 123–147.
- Barkman JJ (1958) Phytosociology and ecology of cryptogamic epiphytes: including a taxonomic survey and description of their vegetation units in Europe. Van Gorcum, Assen, The Netherlands.
- Bianchi E, Benesperi R, Brunialti G, Di Nuzzo L, Fačková Z, Frati L, Giordani P, Nascimbene J, Ravera S, Vallese C & Paoli L (2020) Vitality and growth of the threatened lichen *Lobaria pulmonaria* (L.) Hoffm. in response to logging and implications for its conservation in Mediterranean oak forests. *Forests* 11: 995. doi:10.3390/f11090995.
- Cieśliński S, Czyżewska K, Faliński JB, Klama H, Mułenko W & Żarnowiec J (1996) Relicts of the primeval (virgin) forest. Relict phenomena. *Phytocenosis* 6: 197–216.
- Csardi G & Nepusz T (2006) The igraph software package for complex network research. *InterJournal, Complex Systems* 1695: 1–9.
- Czarnota P, Tuchowski M, Szymczyk R & Piegdoń A (2023) *Lobaria pulmonaria* as an umbrella species for the protection of epiphytic lichen diversity in Polish Carpathians. *Acta Mycologica* 58: 1–22. doi:10.5586/am/177130.
- D'Amen M, Mod HK, Gotelli NJ & Guisan A (2018) Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence. *Ecography* 41: 1233–1244. doi:10.1111/ecog.03148.
- Dierßen K (2001) Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophytorum Bibliotheca* 56. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Germany.
- Fleishman E, Blair RB & Murphy DD (2001) Empirical validation of a method for umbrella species selection. *Ecological Applications* 11: 1489–1501. doi:10.1890/1051-0761(2001)011[1489:EV OAMF]2.0.CO;2.
- Fleishman E, Murphy DD & Brussard PF (2000) A new method for selection of umbrella species for conservation planning. *Ecological Applications* 10: 569–579. doi:10.1890/1051-0761(2000)010[0569:ANMFSO]2.0.CO;2.
- Frego KA (2007) Bryophytes as potential indicators of forest integrity. *Forest Ecology and Management* 242: 65–75. doi:10.1016/j.foreco.2007.01.030.
- Fridley JD, Vandermaast DB, Kuppinger DM, Manthey M & Peet RK (2007) Co-occurrence based assessment of habitat generalists and specialists: a new approach for the measurement of niche width. *Journal of Ecology* 95: 707–722. doi:10.1111/j.1365-2745.2007.01236.x.
- Fritz Ö & Heilmann-Clausen J (2010) Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). *Biological Conservation* 143: 1008–1016. doi:10.1016/j.biocon.2010.01.016.
- Gréaume A, Hugonnot V, Pépin F, Blin M, Cadet S, Keller J & Chauliac C (2023) The vegetative reproduction of *Dicranum viride* (Sull. & Lesq.) Lindb. as a likely explanation for micro-habitat and stand-type relationships – implications for forest management. *Lindbergia* 2023: e01166. doi:10.25227/linbg.01166.
- Griffith DM, Veech JA & Marsh CJ (2016) *cooccur*: probabilistic species co-occurrence analysis in R. *Journal of Statistical Software* 69: 1–17. doi:10.18637/jss.v069.c02.
- Guerra G, Arrocha C, Rodríguez G, Déleg J & Benítez Á (2020) Bryophytes on tree trunks as indicators of montane forest disturbance in Panama. *Revista de Biología Tropical* 68: 492–502. doi:10.15517/rbt.v68i2.38965.
- Hallingbäck T (2002) Globally widespread bryophytes, but rare in Europe. *Portugaliae Acta Biologica* 20: 11–24.
- Hill M, Preston C, Bosanquet S & Roy D (2007) BRYOATT Attributes of British and Irish mosses, liverworts and hornworts with information on native status, size, life form, life history, geography and habitat. Centre for Ecology and Hydrology, Huntingdon, England.
- Hodgetts NG, Söderström L, Blockeel TL, Caspari S, Ignatov MS, Konstantinova NA, Lockhart N, Papp B, Schröck C, Sim-Sim M, Bell D, Bell NE, Blom HH, Bruggeman-Nannenga MA, Brugués M, Enroth J, Flatberg KI, Garilleti R, Hedenäs L, Holyoak DT, Hugonnot V, Kariyawasam I, Köckinger H, Kučera J, Lara F & Porley RD (2020) An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology* 42: 1–116. doi:10.1080/03736687.2019.1694329.
- Jaroszewicz B, Cholewińska O, Gutowski JM, Samojlik T, Zimny M & Latałowa M (2019) Białowieża

- Forest – a relic of the high naturalness of European forests. *Forests* 10: 849. doi:10.3390/f10100849.
- Jüriado I & Liira J (2010) Threatened forest lichen *Lobaria pulmonaria* – Its past, present and future in Estonia. *Forestry Studies* 53: 15–24. doi:10.2478/v10132-011-0086-6.
- Kentjens W, Glenny D, Curran TJ & Sullivan JJ (2023) Bryophyte community composition is influenced by microhabitat and cover of vascular plants and lichens in New Zealand montane forest. *New Zealand Journal of Botany*: 1–24. doi:10.1080/0028825X.2023.2284205.
- Kiehl K, Kirmer A, Donath TW, Rasran L & Hölzel N (2010) Species introduction in restoration projects – Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic and Applied Ecology* 11: 285–299. doi:10.1016/j.baae.2009.12.004.
- Kučera J, Kuznetsova OI, Manukjanová A & Ignatov MS (2019) A phylogenetic revision of the genus *Hypnum*: Towards completion. *TAXON* 68: 628–660. doi:10.1002/tax.12095.
- Li Y, Ye S, Bai W & Zhang G (2022) Species diversity patterns differ by life stages in a pine-oak mixed forest. *Dendrobiology* 88: 138–149. doi:10.12657/denbio.088.010.
- Lindo Z & Gonzalez A (2010) The bryosphere: an integral and influential component of the Earth's biosphere. *Ecosystems* 13: 612–627. doi:10.1007/s10021-010-9336-3.
- Ma J-Z, Chen X, Mallik A, Bu Z-J, Zhang M-M, Wang S-Z & Sundberg S (2020) Environmental together with interspecific interactions determine bryophyte distribution in a protected mire of northeast China. *Frontiers in Earth Science* 8. doi:10.3389/feart.2020.00032.
- Mežaka A, Irbe I, Plaksenkova I, Nitcis M, Krivmane B & Rungis D (2023) Rare epiphytic bryophyte *Dicranum viride* (Sull. & Lesq.) Lindb. (Dicranaceae, Bryophyta) spatial patterns in boreo-nemoral forest landscape. *Nova Hedwigia* 116: 283–297. doi:10.1127/nova_hedwigia/2023/0837.
- Mežaka A, Pošiva-Bunkovska A, Oļehnoviča E, Nitcis M & Bambi B (2024) EU habitat directive bryophyte species distribution and conservation in Latvia. *Biologia* 79: 1193–1207. doi:10.1007/s11756-023-01571-8.
- Mölder A, Schmidt M, Engel F, Schönfelder E & Schulz F (2015) Bryophytes as indicators of ancient woodlands in Schleswig-Holstein (Northern Germany). *Ecological Indicators* 54: 12–30. doi:10.1016/j.ecolind.2015.01.044.
- Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, García RG, Chytrý M, Hájek M, Di Pietro R, Iakushenko D, Pallas J, Daniëls FJA, Bergmeier E, Santos Guerra A, Ermakov N, Valachovič M, Schaminée JHJ, Lysenko T, Didukh YP, Pignatti S, Rodwell JS, Capelo J, Weber HE, Solomeshch A, Dimopoulos P, Aguiar C, Hennekens SM & Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science* 19: 3–264. doi:10.1111/avsc.12257.
- Nadyeina O, Dymytrova L, Naumovych A, Postoyalkin S & Scheidegger C (2014) Distribution and dispersal ecology of *Lobaria pulmonaria* in the largest primeval beech forest of Europe. *Biodiversity and Conservation* 23: 3241–3262. doi:10.1007/s10531-014-0778-3.
- Oishi Y & Morimoto Y (2016) Identifying indicator species for bryophyte conservation in fragmented forests. *Landscape and Ecological Engineering* 12: 107–114. doi:10.1007/s11355-013-0220-0.
- Pannek A, Manthey M & Diekmann M (2016) Comparing resource-based and co-occurrence-based methods for estimating species niche breadth. *Journal of Vegetation Science* 27: 596–605. doi:10.1111/jvs.12374.
- Paoli L, Benesperi R, Fackovcova Z, Nascimbene J, Ravera S, Marchetti M, Anselmi B, Landi M, Landi S, Bianchi E, Di Nuzzo L, Lackovicova A, Vannini A, Loppi S & Guttova A (2019) Impact of forest management on threatened epiphytic macrolichens: evidence from a Mediterranean mixed oak forest (Italy). *iForest – Biogeosciences and Forestry* 12: 383–388. doi:10.3832/ifer2951-012.
- Pedersen T (2022a) *ggraph*: an implementation of grammar of graphics for graphs and networks. R package version 2.1.0. <https://CRAN.R-project.org/package=ggraph>.
- Pedersen T (2022b) *tidygraph*: a tidy API for graph manipulation. R package version 1.2.2. <https://CRAN.R-project.org/package=tidygraph>.
- Percel G, Bouget C, Gosselin M, Dumas Y & Laroche F (2024) Disentangling fine- and large-scale colonization processes in metapopulation dynamics: a case study on a threatened epiphytic bryophyte. *Oikos* 2024: e10052. doi:10.1111/oik.10052.
- QGIS Development Team (2021) QGIS geographic information system (Version 3.22.6 Białowieża): Open Source Geospatial Foundation Project. <http://qgis.osgeo.org/>
- R Core Team (2022) R: a language and environment for statistical computing version 4.2.1 'Funny-Looking Kid': R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Roberge J-M & Angelstam P (2004) Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18: 76–85. doi:10.1111/j.1523-1739.2004.00450.x.

- Roberge J-M, Mikusiński G & Svensson S (2008) The white-backed woodpecker: umbrella species for forest conservation planning? *Biodiversity and Conservation* 17: 2479–2494. doi:10.1007/s10531-008-9394-4.
- Scheidegger C & Werth S (2009) Conservation strategies for lichens: insights from population biology. *Fungal Biology Reviews* 23: 55–66. doi:10.1016/j.fbr.2009.10.003.
- Shen T, Song L, Corlett RT, Guisan A, Wang J, Ma W-Z, Mouton L, Vanderpoorten A & Collart F (2023) Disentangling the roles of chance, abiotic factors and biotic interactions among epiphytic bryophyte communities in a tropical rainforest (Yunnan, China). *Plant Biology* 25: 880–891. doi:10.1111/plb.13570.
- Shi X-M, Song L, Liu W-Y, Lu H-Z, Qi J-H, Li S, Chen X, Wu J-F, Liu S & Wu C-S (2017) Epiphytic bryophytes as bio-indicators of atmospheric nitrogen deposition in a subtropical montane cloud forest: Response patterns, mechanism, and critical load. *Environmental Pollution* 229: 932–941. doi:10.1016/j.envpol.2017.07.077.
- Sjoberg D (2023) *ggsankey*: sankey, alluvial and sankey bump plots. R package version 0.0.99999. <https://github.com/davidsjoberg/ggsankey>.
- Skowron D & Wołkowycki D (2022) Uwarunkowania ochrony mchów i wątrobowców w lasach: Lasy przyszłości, wyzwania współczesnego leśnictwa (ed. by M Aleh & W Dan) Oficyna Wydawnicza Politechniki Białostockiej, Białystok, Poland, pp. 41–60. doi:10.24427/978-83-67185-47-9_4.
- Stanton DE, Huallpa Chávez J, Villegas L, Villasante F, Armesto J, Hedin LO & Horn H (2014) Epiphytes improve host plant water use by microenvironment modification. *Functional Ecology* 28: 1274–1283. doi:10.1111/1365-2435.12249.
- State Forests (2023) Forest Data Bank. Available: www.bdl.lasy.gov.pl.
- Stebel A (2004) *Dicranum viride* (Sull. & Lesq.) Lindb. Gatunki roślin. Poradniki ochrony siedlisk i gatunków Natura 2000 – podręcznik metodyczny (ed. by B Sudnik-Wójcikowska & H Werblan-Jakubiec) Ministerstwo Środowiska, Warsaw, Poland, pp. 36–38.
- Stebel A & Żarnowiec J (2014) Gatunki puszczańskie we florze mchów Bieszczadzkiego Parku Narodowego (Karpaty Wschodnie). *Roczniki Bieszczadzkie* 22: 259–277.
- Steel JB, Wilson JB, Anderson BJ, Lodge RHE & Tangney RS (2004) Are bryophyte communities different from higher-plant communities? Abundance relations. *Oikos* 104: 479–486. doi:10.1111/j.0030-1299.2004.12840.x.
- Tasenkevich L, Boratyński A, Skrypec K, Seniv M, Khmil T & Walas Ł (2022) Biodiversity of high-mountain woody plants in the East Carpathians in Ukraine. *Dendrobiology* 89: 1–19. doi:10.12657/denbio.089.001.
- Terracciano S, Giordano S & Spagnuolo V (2012) A further tessera in the two-centuries-old debate on the *Hypnum cupressiforme* complex (Hypnaceae, Bryopsida). *Plant Systematics and Evolution* 298: 229–238. doi:10.1007/s00606-011-0540-1.
- Veech JA (2013) A probabilistic model for analysing species co-occurrence. *Global Ecology and Biogeography* 22: 252–260. doi:10.1111/j.1466-8238.2012.00789.x.
- Wardle DA, Jonsson M, Bansal S, Bardgett RD, Gundale MJ & Metcalfe DB (2012) Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. *Journal of Ecology* 100: 16–30. doi:10.1111/j.1365-2745.2011.01907.x.
- Weir CR & Collins T (2015) A review of the geographical distribution and habitat of the atlantic humpback dolphin (*Sousa teuszii*): *Advances in marine biology* (ed. by TA Jefferson & BE Curry) Academic Press, Cambridge, Massachusetts, USA, pp. 79–117. doi:10.1016/bs.amb.2015.08.001.
- WFO (2023) World Flora Online. Available: <http://www.worldfloraonline.org/>.
- Whittet R & Ellis CJ (2013) Critical tests for lichen indicators of woodland ecological continuity. *Biological Conservation* 168: 19–23. doi:10.1016/j.biocon.2013.09.011.
- Wickham H, Averick M, Bryan J, Chang W, McGowan L, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen T, Miller E, Bache S, Müller K, Ooms J, Robinson D, Seidel D, Spinu V & Yutani H (2019) Welcome to the Tidyverse. *Journal of Open Source Software* 4: 1686. doi:10.21105/joss.01686.
- Wierzcholska S, Dyderski MK & Jagodziński AM (2020) Potential distribution of an epiphytic bryophyte depends on climate and forest continuity. *Global and Planetary Change* 193: 103270. doi:10.1016/j.gloplacha.2020.103270.
- Wierzcholska S, Łubek A, Dyderski MK, Horodecki P, Rawlik M & Jagodziński AM (2024) Light availability and phorophyte identity drive epiphyte species richness and composition in mountain temperate forests. *Ecological Informatics* 80: 102475. doi:10.1016/j.ecoinf.2024.102475.
- Wilcox BA (1984) In situ conservation of genetic resources: determinants of minimum area requirements: National parks, conservation, and development: proceedings of the world congress on national parks (ed. by JA McNeely & KR Miller KR) Smithsonian Institution Press, Washington, USA, pp. 639–647.
- Wysocki A, Czortek P, Konowalik K, Proćków J & Wierzcholska S (2023) Opposite effects of host tree species on the realised niche of *Dicranum*

viride – A model species belonging to the group of endangered epiphytes. *Forest Ecology and Management* 545: e121303. doi:10.1016/j.foreco.2023.121303.

Zurell D, Pollock LJ & Thuiller W (2018) Do joint species distribution models reliably detect interspecific interactions from co-occurrence data in homogenous environments? *Ecography* 41: 1812–1819. doi:10.1111/ecog.03315.