Bryophyte species richness and functional traits in the managed temperate forests are also driven by bedrock and tree species composition

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Abstract

Questions

Bryophytes represent an important component of forest biodiversity and vegetation, responding to a variety of environmental factors. These include geological conditions with upper soil horizons and tree species composition, which is the result of both natural and anthropogenic factors. The bryophyte species and functional diversity and composition were studied in different temperate forests.

Location

Representative managed forests from lowlands to high mountain areas in Slovenia, Europe.

Methods

Bryophytes growing on a variety of substrates, including terricolous, lignicolous, corticolous and saxicolous species, were identified in 57 ICP-Forests monitoring plots in a wide range of managed forests. Considering data on tree layer composition (broadleaves vs. coniferous), bedrock and soil type (carbonate vs. silicate), all study plots were classified into five groups representing different forest types, including stands dominated by: i) broadleaves on calcareous bedrocks, ii) broadleaves on intermediate bedrocks/soils, iii) broadleaves on siliceous bedrocks, iv) conifers on calcareous bedrocks, and v) conifers on siliceous bedrocks. The species composition and diversity of bryophytes and their functional traits were studied.

Results

Among broadleaves, European beech (*Fagus sylvatica*) was the dominant tree species in the studied forests, while Norway spruce (*Picea abies*) was the most common tree species among conifers. The most frequent bryophyte species were *Hypnum cupressiforme* (present in 91.2% of all plots), *Brachytheciastrum velutinum* (63.2%) and *Polytrichum formosum* (61.4%). The mean species richness per plot was 19.4 (minimum: 5, maximum: 36). In the studied plots, tree species composition and bedrock were important drivers in bryophyte species richness and composition. Considerable changes in bryophyte species composition were observed along the tree species composition and edaphic gradient. The bryophyte species richness was significantly higher on calcareous bedrock with very different microhabitats than on siliceous bedrock. The functional diversity and composition of bryophytes were significantly influenced by bedrock and soil, but less by tree species composition.

Conclusions

This study shows that bedrock and tree species composition have a significant effect on bryophyte species, functional traits, and diversity patterns. Tree species composition was also related to past forest management, which could lead to a higher proportion of spruce or other commercial conifers in the small portion of plots. However, the studied forests are mainly managed according to close-to-nature and sustainable principles.

1. Introduction

Bryophytes are an integral part of forest ecosystems and account for a significant proportion of plant species diversity. Bryophytes are considered good ecological indicators because their specific characteristics make them sensitive to the environmental changes (Gignac, 2001), and they are also reliable ecological indicators of forest condition and naturalness (Sabovljevic et al. 2010; Czerepko et al., 2021). Bryophytes respond to management intensities and disturbances in the temperate forests and therefore have important implications for forest management and conservation (Horvat et al., 2017).

Bryophyte assemblages in forest ecosystems is influenced by climatic factors such as air temperature and precipitation (Sun et al., 2013), historical factors (Fritz and Brunet, 2010), forest integrity, which includes natural biodiversity, stand structure, and continuity (Frego, 2007), and silvicultural treatments combing tree felling and burning (Kantvilas et al., 2015) and disturbance from logging (Nelson and Halpern, 2005). Elevation gradient, which is closely related to climatic conditions, is an important driver of bryophyte diversity (Grau et al., 2007; Horvat et al., 2017). Moreover, significant turnover in bryophyte species composition might be expected along a longitudinal gradient (Heilmann-Clausen et al., 2014) and along latitudinal gradient as well. In addition to latitudinal, longitudinal and altitudinal gradients, topography in terms of microrelief diversity is also an important factor in bryophyte diversity (Bruun et al., 2006). On a small scale, forest management can determine bryophyte diversity and composition through its effects on tree species diversity, vertical structure, canopy closure, microclimate, and deadwood availability (Bengtsson et al., 2000; Paillet et al., 2010; Czerepko et al., 2021). Forest structure determines the light conditions, which strongly affect the bryophyte diversity (Márialigeti et al., 2009; Tinya et al., 2009, 2021; Tinya and Ódor, 2016), and microclimatic conditions and substrate availability are of high importance for composition, cover and diversity of bryophytes (Márialigeti et al., 2009; Király and Ódor, 2010).

Certain bryophyte species are able to grow ubiquitously i.e. on different substrates (soil, rocks, bark and deadwood) (Stokland et al., 2012), whilst some of them grow exclusively as epixylic (wood dwelling) or epiphytic (living on the surface of plants, like bark) and thus strongly depend on the quantity of available substrate. Epixylic and epiphytic bryophytes are more abundant and diverse in unmanaged forests than managed ones (Lesica et al., 1991), and natural silvicultural regeneration practices increase ground bryophyte diversity after clearcutting (Yan et al., 2013). Because of forest management effects, cryptogamic epiphytes are considered a threatened group in temperate forests (Paillet et al., 2010) and useful for the evaluation of the forest management impact.

However, comparison of bryophyte species richness in unmanaged beech, selection beech, and age class forests in Germany showed that beech selection forests were the most species rich management type, whereas unmanaged beech forests revealed even lower species numbers than age-class forests. Therefore, managed forests may even exceed unmanaged forests in bryophyte species richness due to higher substrate availability and therefore represent important habitats for bryophytes (Müller et al., 2019). This is mainly due to the creation of new microhabitats following forestry interventions and disturbances in forest stands and soils, as well as changes in resource availability, such as light quality, nutrient status, soil and air moisture variability.

Diversity and quality of different growing substrates for bryophytes is significantly affected by forest management, therefore bryophytes, especially typical woodland bryophytes are suitable indicators of the forest management (Nordén et al., 2007; Kriebitzsch et al., 2013, Mölder et al., 2015; Müller et al., 2019), and are valuable indicator organisms to estimate the naturalness and integrity of forest stands (Frego, 2007). Species richness of typical woodland indicator bryophytes, which are strictly depending on forest conditions are negatively affected by management intensity and therefore better indicate forest integrity than the species richness of all bryophytes (Müller et al., 2019). Consequently, nature conservation efforts should focus on the reduction of management intensity.

In forests, different ecological guilds of bryophytes can be distinguished by the substrate on which they are growing, including terricolous (occur on soil), lignicolous (deadwood), corticolous (bark of living trees and shrubs) and saxicolous (rocks) species. The permanent availability of suitable substrates is most important for bryophyte species richness in forests (Müller et al., 2019).

Although the species composition and diversity of bryophytes in Central Europe are quite well recognized, the patterns associated with their plant life traits are still relatively unknown (Żarnowiec et al., 2021). The concept of bryophyte life-forms has been discussed in several studies (Schofield and Hébant, 1984; Düll, 1991; During, 1992; Longton, 1997; Bates, 1998). Under different ecological conditions, the potential of bryophyte life-forms as ecological indicators has been tested (Żarnowiec, 1995, 1996; Vittoz et al., 2010; Pardow et al., 2012; Vieira et al., 2012; Spitale et al., 2020). In addition to life-forms, the type of substrate inhabited is another key element for the classification of bryophytes into plant functional groups (Andersson and Hytteborn, 1991; Kürschner, 1999; Jagodziński et al., 2018; Fojcik et al., 2019; Staniaszek-Kik et al., 2019). Bryophytes functional traits explaining the colonization of coarse woody debris (CWD) and their properties, such as decomposition rate, moisture, the length of a log, tree species (Żarnowiec et al., 2021).

There are few databases with bryophytes-traits available (Düll, 1991; Hill et al., 2007; Schmidt et al., 2011; Bernhardt-Römermann et al., 2018). Contemporary bryophyte trait databases include not only different life forms but also their habitat requirements expressed by Ellenberg indicator values associated with regeneration, plant size, and some regional characteristics related to the phytogeographic conservation status of a species.

In Slovenia, species diversity of bryophytes has been studied in various forests and within forest ecosystems such as forest reserves (Hočevar et al., 1980a, 1980b, 1980c, 1985; Ódor et al., 2005, 2006), selected managed forests (Kutnar and Martinčič, 2008), and mires and surrounding forests (Piskernik and Martinčič, 1970, 1985; Kutnar and Martinčič, 2001, 2002, 2003).

However, till present, there has been no systematic approach to the species diversity and composition of bryophytes and their functional traits in different managed forests in Slovenia. Therefore, the aim of this study was to i) explore the species composition and diversity of bryophytes in managed forests, ii) explore the functional trait composition and diversity of bryophytes in managed forests, iii) analyse the response of bryophyte species and functional trait diversity to variation in tree species composition and bedrock-soil characteristics in different managed forests.

2. Materials And Methods

2. 1. Study area and sampling of bryophytes

The studied plots were located in very different Slovenian forest vegetation types (Kutnar et al., 2012), which are mainly managed according to close-to-nature, sustainable and multifunctional principles. In lowland areas that are periodically flooded, forest stands occur in narrow strips along rivers and streams, dominated mainly by willows (*Salix* sp.), alders (*Alnus glutinosa* (L.) Gaertn., *A. incana* (L.) Moench), ashes (*Fraxinus excelsior* L., *F. angustifolia* Vahl) and Pedunculate oak (*Quercus robur* L.) with admixtures of European hornbeam (*Carpinus betulus* L.). In the hilly areas above the floodplains, mixed forests of Sessile oak (*Quercus petraea* (Matt.) Liebl.) and European hornbeam are the predominant forest type. Most of the mid-altitude mountain areas are covered by forests formed by European beech (*Fagus sylvatica* L.), with admixtures of other broadleaves (e.g., *Acer pseudoplatanus* L., *Fraxinus excelsior*, *Ulmus glabra* Huds.) and conifers (*Abies alba* Mill., *Picea abies* (L.) Karst.). In the Alpine region, various European beech forests mixed with Norway spruce (*Picea abies*), European silver fir (*Abies alba*) and European larch (*Larix decidua* Mill.) reach the timberline up to the belt of the Dwarf mountain pine (*Pinus mugo* Turra). The forests of Scots pine

(*Pinus sylvestris* L.) can be found throughout the country on shallow soils on dolomite and also on acidic, nutrient-poor soils. Minor areas of Austrian pine (*Pinus nigra* Arnold) forests grow on extreme sites with warmer microclimate. Sub-mediterranean region is covered with forest and shrubby vegetation of thermophilous broadleaf species (e.g., *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Sorbus aria* (L.) Crantz, *Quercus cerris* L., *Q. pubescens* Willd.). Similar type of forest is also present all over the country on sun-exposed, south-facing slopes with predominant limestone and dolomite bedrock. Described natural forest types are intersected by numerous forms of secondary forest communities (often characterized by even-aged stands with homogeneous structure), which are a consequence of management-moderated tree species composition and related abiotic (edaphic) conditions. These secondary forest communities mainly dominated by Norway spruce are significantly exposed to climate change and various disturbances during the latest period (Kutnar et al., 2021).

Bryophytes (including mosses and liverworts) were sampled in different managed forest in Slovenia between 2004 and 2010. The study area encompasses 47 monitoring plots of ICP Forests Level I and 10 monitoring plots belonging to ICP Forests Level II (Intensive Monitoring programme; (Kutnar and Martinčič, 2008), i.e., 57 plots in total. ICP Forests is a transnational European network for monitoring the forest status in Europe (de Vries et al. 2003). Level I plots are systematically distributed in a 16 km × 16 km (Urbančič et al., 2009; Kutnar, 2011) and in 16 km × 8 km grid across Slovenia. Level II plots were established in 10 different locations, representative for the heterogeneity of Slovenian forest types (Urbančič et al., 2016). Detailed information on these study plots can be found in different recent studies (Kutnar et al., 2019; Kermavnar and Kutnar, 2020; Kermavnar et al., 2021a, 2021b). Jointly, Level I and Level II plots were in forest sites with a wide variety of climatic, geological, edaphic and topographical conditions as well as a broad range of forest vegetation composition. Altitude of study plots ranged from 160 to 1490 m, mean annual temperature varied from 3.2 to 11.7°C and mean annual precipitation from 791 to 2499 mm. The climatic parameters were taken from WorldClim database (WorldClim, 2021).

Contemplating data on forest tree layer composition, geology and soil type, all study plots were classified into five groups representing different forest types. Study plots were assembled in following five groups (Fig. 1): i) stands dominated by broadleaves on calcareous bedrocks (21 plots; Fig. 2), ii) stands dominated by broadleaves on intermediate bedrocks/soils (12 plots; Fig. 3), iii) stands dominated by broadleaves on siliceous bedrocks (10 plots; Fig. 4), iv) stands dominated by conifers on calcareous bedrocks (6 plots; Fig. 5), and v) stands dominated by conifers on siliceous bedrocks (8 plots; Fig. 6).

Among broadleaves, European beech most frequently dominated the forest stands, while Norway spruce was the dominant coniferous species. Among the calcareous bedrocks (groups (i) and (iv)), limestone and dolomite were predominant. In the plots of these groups, the most common soils were Eutric Cambisols, Rendzic Leptosols and Chromic Cambisols (Urbančič et al., 2005, 2009, 2016). In the group with intermediate bedrocks (ii), pleistocene sediments, alluvium and various mixed rock types were more common, on which Eutric Cambisols, Luvisols, Gleysols, Fluvisols or even Dystric Cambisols were formed. In the group with siliceous bedrocks (groups (iii) and (v)), various non-carbonate rocks predominated, such as different siliceous metamorphic and igneous rocks, moraines, fluvioglacial gravels and sands, and also siliceous flysch. Among them were very diverse bedrock types such as sandstones, mica schists, dioritoid, tonalite, gneiss, amphibolite and others. Dystric Cambisols, Dystric Leptosols and Eutric Cambisols were the predominant soil types in groups with siliceous bedrocks (Urbančič et al., 2005, 2009, 2016).

Bryophytes were sampled in all plots in area of 400 m^2. All different bryophyte types were systematically sampled, including epixylic bryophytes (occurring on deadwood), epiphytic (occurring on bark of living trees), epilithic (occurring

on rock and stones), terricolous (occurring on open soils). Determination of species identity was finalized in the laboratory using microscope. The nomenclature followed Hodgetts et al. (2020).

2.2. Bryophyte functional traits

We obtained data on different autecological, morphological and reproductive traits of bryophyte species selected for this study from Bernhardt-Römermann et al., 2018 (Table 1).

The following autecological traits were selected:

- indicator values for light, temperature, continentality, moisture, soil reaction and nutrient availability,
- boundness to forest habitats and
- hemeroby.

In case of morphological traits of the whole plant, we selected three traits:

- life form,
- life strategy and
- shoot length.

Two traits associated with sexual reproduction were also included in the analysis:

- mean size of spores and
- fruiting frequency.

All data were compiled from BryForTrait database (Bernhardt-Römermann et al., 2018). Indicator values for nutrients were additionally complemented with information provided by Simmel et al. (2021). The selection of traits was done based on our expert-based decision, previous studies, data completeness and preliminary analysis of response to predictor variable. Mean data completeness across all selected traits was 94.6%.

Table 1
List of selected traits (8 autecological, 3 morphological and 2 regeneration traits). For details regarding trait attributes of categorical traits, see Bernhardt-Römermann et al. (2018).

Functional trait	Variable type	Description
Autecological traits		
Indicator value for light (L)	Ordinal	Occurrence in relation to the relative irradiance intensity at the time when the deciduous plants are full in leaf
Indicator value for temperature (T)	Ordinal	Occurrence in the temperature gradients from the Artic and the Mediterranean and from the alpine levels to lowlands
Indicator value for continentality (K)	Ordinal	Occurrence in the gradient from the Atlantic coast to the inner parts of Eurasia, especially with regards to temperature ranges
Indicator value for moisture (F)	Ordinal	Occurrence in the gradient from dry, shallow-soil rocky slopes to swampy ground
Indicator value for soil reaction (R)	Ordinal	Occurrence in the gradient of soil acidity and lime content
Indicator value for nutrient availability (N)	Ordinal	Occurrence in the gradient of nutrient availability, eutrophication
Boundness to forest habitat	Categorical	Information how strong species are bound to forest habitats; 4 trait attributes (M1.1, M1.2, M2.1, M2.2)
Hemeroby	Ordinal	Occurrence in the gradient of background human impact on the ecosystem, ranging from absent (1) to very strong (9)
Morphological traits		
Life form	Categorical	Life forms based on Mägdefrau (1969); 5 trait attributes (cushion, dendroid, mat, turf, weft)
Life strategy	Categorical	Life strategies according to During (1979); 4 trait attributes (colonists, perennial shuttle, perennial stayers, short-lived shuttle)
Shoot length	Numeric	Mean shoot length expressed in cm
Regeneration traits		
Size of spores	Numeric	Mean size of spores expressed in µm
Fruiting frequency	Categorical	Frequency of fruiting; 5 trait attributes (common, frequent, occasional, rare, very rare)

2.3. Data analyses

All statistical analyses were performed in R version 4.1.1 (R Core Team, 2021). The compositional gradient in the presence-absence species × plot matrix was explored by multivariate analyses. Non-metric multidimensional scaling (NMDS) ordination with Bray-Curtis dissimilarity coefficients was used to depict differences in species composition data (function *metaMDS* in vegan package; Oksanen et al., 2020). For this analysis, we used two dimensions ($k = 2$), resulting in stress level of 0.175, which is below the stress < 0.2 criterion sensu Clarke (1993). We used the *ordiellipse* function (Oksanen et al., 2020) to plot the 95% confidence intervals of group scores onto the NMDS ordination diagram. To test whether groups (forest types) differed significantly in terms of species composition, we first

employed permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017) with 9999 permutations (vegan package, function *adonis2*). We then extracted NMDS axis 1 and axis 2 scores of plots and compared them between groups (forest types) with non-parametric Kruskal-Wallis test on ranks with Bonferroni correction for multiple comparisons (agricolae R package; de Mandiburu, 2021). Differences in species richness (defined as the number of species per plot) between groups were tested using a Generalized linear model (GLM) with Poisson error distribution for count data and visualized with boxplots. Significantly different means among groups (forest types) were separated using post-hoc Tukey's test.

For functional characterization of bryophyte assemblages, we first calculated community mean values for each of the 13 traits (Table 1) using the function *funtcomp* in the FD package (Laliberté et al., 2015). The mean values of traits and trait states (27 in total), expressing functional composition of assemblages, were then used as an input data for Principal component analysis (PCA) to explore distribution of plots and plot groups in the ordination space using *PCA* function with automatic data standardization in FactoMineR package (Husson et al., 2020). Visualizations were done with factoextra R package (Kassambara and Mundt, 2020) to plot the 95% confidence intervals of group scores onto the two-dimensional PCA ordination diagram. Differences between five groups in PCA1 and PCA2 scores were tested with non-parametric Kruskal-Wallis test on ranks with Bonferroni correction for multiple comparisons. Plot-level functional diversity was calculated with *dbFD* function in the FD package. Functional dispersion was used as an index of functional diversity. and visualized with boxplots. For each species trait, differences in functional dispersion were tested using GLM with Gamma error distribution. Significantly different means among groups (forest types) were separated using post-hoc Tukey's test.

Statistical significance was declared at $\alpha = 0.05$ for all tests.

3. Results

3.1 Species composition and diversity

Among 200 bryophyte species identified on 57 plots, *Hypnum cupressiforme* Hedw. (present on 91.2% of all plots), *Brachytheciastrum velutinum* (Hedw.) Ignatov & Huttunen (63.2%), and *Polytrichum formosum* L. (61.4%) were the most frequent species. Among more common species are also *Ctenidium molluscum* (Hedw.) Mitt. and *Isothecium alopecuroides* (Lam. Ex Dubois) Isov.. Bryophyte species composition differed significantly between the five groups (PERMANOVA: $p < 0.001$, $R^2 = 0.189$; Fig. 7). Forest plots dominated by broadleaves and conifers on calcareous bedrocks had significantly higher NMDS axis 1 scores than plots dominated by broadleaves on siliceous bedrocks. With respect to the NMDS axis 2 scores, plots dominated by broadleaves on intermediate and calcareous bedrocks exhibited significantly higher values compared to plots dominated by conifers on siliceous bedrocks (Fig. 7).

Forest types differed with respect to forest stand and vegetation characteristics (Table 2).

Table 2
Stand and vegetation characteristics of five forest types. Values are means, with ranges (min – max) in parentheses.

	Broadleaves on calcareous b. (n = 21)	Broadleaves on intermediate b. (n = 12)	Broadleaves on siliceous b. (n = 10)	Conifers on calcareous b. (n = 6)	Conifers on siliceous b. (n = 8)
Dominant tree species	*Fagus sylvatica, Acer pseudoplatanus*	*Quercus robur, Q. petraea, Carpinus betulus, Fagus sylvatica*	*Fagus sylvatica, Castanea sativa*	*Picea abies, Pinus nigra*	*Abies alba, Picea abies, Pinus sylvestris*
Bryophyte species richness	23.8 (7–36)	18.8 (9–33)	13.8 (5–25)	22.8 (14–34)	14.1 (5–32)
Bryophyte layer cover (%)	6.3 (0.5–33.1)	5.8 (0.5–37.1)	4.8 (0.3–20.0)	12.1 (1.9–38.0)	15.1 (0.6–56.8)
Most frequent bryophyte species	*Ctenidium molluscum*, *Hypnum cupressiforme*, *Brachytheciastrum velutinum*, *Polytrichum formosum*, *Tortella tortuosa* (Hedw.) Limpr.	*Hypnum cupressiforme*, *Brachythecium rutabulum*, *Isothecium alopecuroides*, *Metzgeria furcata* (L.) Dumort., *Atrichum undulatum* (Hedw.) P. Beauv.	*Hypnum cupressiforme*, *Polytrichum formosum*, *Leucobryum glaucum* (Hedw.) Angst., *Lejeunea cavifolia* (Ehrh.) Lindb., *Atrichum undulatum*	*Ctenidium molluscum*, *Fissidens dubius* P. Beauv., *Hypnum cupressiforme*, *Brachytheciastrum velutinum*, *Dicranum scoparium* Hedw.	*Hypnum cupressiforme*, *Brachytheciastrum velutinum*, *Dicranum scoparium*, *Lophocolea heterophylla* (Dumort.) Dumort., *Polytrichum formosum*
Cover of stones and rocks (%)	15.0 (0.1–50.0)	6.7 (0.0–50.0)	3.2 (0.0–30.0)	24.2 (0.0–50.0)	2.5 (0.0–9.8)
Deadwood cover (%)	6.4 (1.0–25.0)	6.4 (1.5–15.0)	6.7 (1.0–40.0)	5.0 (1.5–15.0)	7.9 (1.8–15.0)
Tree layer cover (%)	92.7 (60.0–100.0)	91.1 (50.0–100.0)	97.1 (85–100.0)	64.0 (45.0–89.0)	60.9 (46.0–97.0)
Shrub layer cover (%)	19.8 (1.0–60.0)	22.9 (1.0–60.0)	26.4 (4–70.0)	34.7 (8.3–75)	14.2 (0.1–60.0)
Herb layer cover (%)	41.4 (5.0–85.0)	45.4 (1.0–90.0)	27.2 (0.3–50.0)	56.6 (25.0–75.0)	69.2 (20.0–99.8)

Overall, mean species richness per plot was 19.4. The highest plot-level richness amounted to 36 species whereas the most species-poor plot contained only 5 bryophyte species. Forest types differed significantly in bryophyte species richness (Fig. 8; Table 2), with the groups of plots dominated by broadleaves (mean richness: 23.3) and conifers (22.8) on calcareous bedrocks exhibiting significantly higher species richness than the broadleaves (13.8) and

conifers (14.1) on siliceous. Forest type broadleaves on intermediate bedrocks (18.8) significantly differed from the group of plots dominated by broadleaves on siliceous bedrocks (Fig. 8).

3.2 Functional trait composition and diversity

In the two-dimensional PCA space, the first axis explained 18.9% of trait variation and the second axis explained 12.7% of variance (Fig. 9). Forest types did not differ significantly in terms of axis 1 scores. However, we found significant differences when PCA axis 2 were tested. Plots dominated by broadleaves on intermediate and calcareous bedrocks had significantly higher axis 2 scores than plots dominated by broadleaves and conifers on siliceous bedrocks (Fig. 9). Overall, functional traits (trait states) with highest contribution were hemeroby (9.1%), indicator value for soil reaction (7.5%), common fruiting frequency (7.4%), mat as a life form (6.5%) and shoot length (5.8%). On the contrary, traits with lowest explanatory power were indicator value for temperature (1.3%), dendroid as a life form (0.8%) and the category expressing species boundness to forest habitats - species preferring forest edges and in clearings (0.7%). Traits most strongly positively correlated with the first PCA dimension were hemeroby (0.88), species occurring in forests as well as in open land (0.69) and common fruiting frequency (0.63), whereas the following traits showed strong negative correlation with PCA1: species largely restricted to closed forests (-0.64), mat as a life form (-0.61) and indicator value for soil reaction (-0.52). Traits most strongly positively correlated with the second PCA dimension were indicator value for soil reaction (0.61), common fruiting frequency (0.48) and perennial shuttle as a life strategy (0.47), whereas the following traits showed strong negative correlation with PCA2: shoot length (-0.68), indicator value for soil moisture (-0.52) and perennial stayer as a life strategy (-0.42) (Fig. 9).

In case of functional diversity, statistically significant differences among forest types were detected for five traits: indicator value for light, indicator value for continentality, indicator value for moisture, shoot length and life form (Fig. 10). Plots dominated by broadleaves on intermediated bedrocks had significantly higher functional dispersion for light indicator values compared to broadleaves on siliceous bedrocks. Plots dominated by broadleaves on calcareous bedrocks were characterized by significantly lower dispersion for continentality values than conifers of siliceous bedrocks. The latter group also exhibited significantly higher dispersion for moisture indicator values compared to the plots dominated by broadleaves on intermediate bedrocks. Largest differences in functional diversity were identified for shoot length. The highest dispersion for this trait was in the group of broadleaves on siliceous bedrocks, which was significantly higher than for broadleaves on calcareous and intermediate bedrocks. Plots dominated by conifers on siliceous bedrocks also differed significantly from the group of broadleaves on calcareous bedrocks. Lastly, diversity of life forms was highest in the group of conifers on calcareous bedrocks but lowest in the group of conifers on siliceous bedrocks (Fig. 10).

4. Discussion

4.1 Species composition and diversity

A large number of bryophyte species were identified during this study in various Slovenian temperate forests. A total of 200 bryophyte species were recorded in all plots, and the average species richness per plot was 19.4. The number of bryophyte species per plot varied from 5 to 36, and the estimated bryophyte cover ranged from 0.3 to 56.8% of the plot surface. Overall, the most common species were *Hypnum cupressiforme*, *Brachytheciastrum velutinum*, *Polytrichum formosum*, *Ctenidium molluscum*, and *Isothecium alopecuroides*. These species occurred in more than half of the plots studied.

Bryophyte diversity was studied in five different forest types that differed in stand characteristics, tree species composition, and bedrocks. Bryophyte species composition and diversity differed significantly among groups of similar temperate forests. The highest bryophyte species richness was observed in stands dominated by broadleaves on calcareous bedrocks (23.8 species per plot), and the lowest species richness was observed in stands dominated by broadleaves on siliceous bedrocks (13.8 species per plot). In both groups, *Fagus sylvatica* was the dominant tree species, while *Acer pseudoplatanus* in the first group and *Castanea sativa* Mill. in the second group were among the most abundant co-dominant tree species.

Mean species richness per plot was 19.9 in broadleaved and 17.9 in coniferous forests, and 23.2 in forests on calcareous bedrock, and 13.9 in forests on siliceous bedrock. The mean percentage of rocks and stones per plot area was 17.1% in forests on calcareous bedrock, and 2.9% in forests on siliceous bedrock.

Among the most important factors influencing bryophyte species diversity are stand structure and tree species composition (Tinya et al., 2021), which are also significantly influenced by forest management. Forest management is an important influencing factor causing changes in tree species composition and canopy closure, stand structure, and also the amount of deadwood (Paillet et al., 2010; Czerepko et al., 2021). Heterogeneous stand structure and tree species composition support in different ways various groups of organisms, including bryophytes. In the studied plots in Slovenian temperate forests, tree species composition and bedrock were also important factors for bryophyte species diversity and composition. The species diversity and composition of bryophytes respond to tree species composition (e.g., broadleaves versus coniferous). However, it appears that bedrock has an even more significant influence on bryophyte species richness, as significant changes in bryophyte species richness were observed along geologic and edaphic gradients. Bryophyte species richness was significantly higher on calcareous bedrock than on siliceous bedrock. A higher proportion of rocks and stones was observed on the plot surface in broadleaved and coniferous forests on calcareous bedrock. This may also imply variability in the different microsites on rocks/stones and between them. The presence of rocks and stones on the ground surface may significantly increase the availability of different growth substrates for bryophytes, possibly affecting their composition, cover, and diversity (Márialigeti et al., 2009; Király and Ódor, 2010).

As in some other temperate forests in Central Europe (e.g., Tinya et al., 2021), we observed a richer ground-floor bryophyte community with a specific species composition in some secondary *Pinus sylvestris* forests on former sites of beech forests on silicious bedrock that had been significantly modified in the past for historical land use reasons. In these *Pinus sylvestris* forests in Slovenia, dense layer of dwarf shrubs such as *Vaccinium myrtillus* L. and *V. vitis-idaea* L. grew in relatively open stands. In such relatively open stands with pines dominating the overstory layer, it is mainly light that determines the species composition of ground-dwelling bryophytes (Tinya et al., 2009, 2021; Jagodziński et al. 2018). It has been demonstrated that epiphytic bryophytes (e.g., bryophytes growing on roots and lying deadwood) are much less dependent on light conditions than bryophytes growing on soils. There are similar numbers of bryophytes in the ground layer of shaded stands, but the composition of bryophytes species varied (Tinya et al., 2021). In addition, deciduous broadleaved tree species may restrict the growth of some ground-dwelling bryophytes through their leaf litter, thereby affecting the humus forms, nutrient cycling, and understory composition of these forests (Startsev et al., 2008).

Epiphytic bryophytes are much more sensitive to humidity and temperature changes, requiring shadier conditions and constant humidity. Therefore, they may suffer from abrupt exposure to sunlight and lower humidity following intensive logging (Friedel et al., 2006). The high number of epiphytic bryophytes in Slovenian temperate forests can possibly be attributed to the high tree layer cover, especially in broadleaved forest in which ranged from 91.1 to 97.1%.

Much lower tree layer cover was observed in *Pinus sylvestris* and *P. nigra* forests and also in *Picea abies* stands at higher altitudes.

In contrast to Müller et al. (2019), increasing conifer proportion did not increase bryophyte species richness in temperate Slovenian forests (19.9 species per plot in broadleaved vs. 17.9 in coniferous forests). In some studies (e.g., Goia and Gafta, 2019), no consistent relationship between the preference of bryophytes on beech or spruce deadwood was revealed. Therefore, species richness of all bryophytes and also of threatened bryophytes did not differ between deadwood of beech and spruce (Goia and Gafta, 2019), which are also the two dominant tree species in the studied forests in Slovenia. Substrate pH is an important factor, as the probability of occurrence of epiphytic bryophytes growing on bark (considered as early successional) increased with the pH of the deadwood substrate, and the probability of occurrence of epixylic bryophytes growing on deadwood (considered as mid to late successional) decreased with the pH of the deadwood substrate (Goia and Gafta, 2019).

Less intensive forest management and silviculture in Slovenian temperate forests, implementing close-to-nature, sustainable and multifunctional principles (ZGS, 2022), can thus also contribute to the diversity of bryophyte species. Such management practises, including selective cutting and small-scale shelterwood logging, promote bryophyte diversity by maintaining and increasing variability of substrates and habitats, including coarse woody debris, increasing stand structural heterogeneity, and maintaining favourable microclimatic conditions by retaining clusters of old, mature to over-mature trees in managed forests. Also in managed forests, deadwood is a key habitat and determines not only the number of epixylic species, but also the whole richness of bryophyte species (Fojcik et al., 2019). The availability of suitable substrates in forests is an important factor for bryophyte species richness (Müller et al., 2019).

The bryophyte richness decreases with more intensive forest management. Loss of suitable microhabitats, such as large trees, decreases bryophytes richness, especially in highly disturbed forests (Horvat et al., 2017). With aim to conserve bryophytes, it has been recommended to avoid intensive forest management and minimize silvicultural practices on steep slopes that are prone to soil erosion (Horvat et al., 2017). Therefore, most Slovenian forests on steep slopes are declared as protection forests or even forest reserves, including unmanaged or less intensively managed forests (ZGS, 2022).

4.2 Functional trait composition and diversity

The specific composition and diversity of bryophyte functional traits and their ecological indicator values (Bernhardt-Römermann et al., 2018; Simmel et al., 2021) were observed in five forest types in Slovenia across gradients of tree species composition and stand characteristics as well bedrocks and soils.

Functional composition of bryophytes was significantly influenced by bedrock and soil, but much less by tree species composition. However, when examining the functional characteristics of the bryophytes on the fallen logs, it was found that the differences in plant traits were related to the host tree. The bryophyte species that preferred a more nutrient-rich substrate and alkaline environment were found to correlate with beech logs, while the species that preferred higher moisture content correlated with spruce logs (Żarnowiec et al., 2021). The main host trees in this study were *Fagus sylvatica* and *Picea abies*, which are also the dominant tree species in the studied forests in Slovenia.

In terms of functional trait composition of bryophytes, forests on intermediate and calcareous bedrocks differed from forests on siliceous bedrocks. High values of the bryophyte indicator value for soil reaction were associated with forests on calcareous and intermediate bedrocks, and low values were associated with forests on siliceous bedrocks.

Longer shoot lengths of bryophytes were associated with forests on siliceous bedrocks where tall grasses *Calamagrostis arundinacea* (L.) Roth and *C. villosa* (Chaix) J.F. Gmel., *Molinia caerulea* (l.) Moench subsp. *arundinacea* (Schrank) K. Richt, ferns *Pteridium aquilinum* (L.) Kuhn, *Blechnum spicant* (L.) Roth, and berries *Vaccinium myrtillus* and *V. vitis-idaea* were common. In some plots studied, the forest floor was almost completely overgrown by these species. This may be consistent with experimental study of traits in which the bryophyte specific shoot length increased with increasing vegetation height and litter cover, indicating stronger competition from vascular plants (Van Zuijlen et al., 2021). However, significantly higher functional dispersion of bryophyte shoot length was attributed to plots dominated by broadleaves on intermediate bedrock, where various *Quercus* species, *Carpinus betulus*, and *Fagus sylvatica* predominated. Studied trait of common fruiting frequency was also the highest in these forests.

On average, it appears that hemeroby, indicating the intensity of human impact on the ecosystem through the bryophytes, is scored higher in plots dominated by conifers on siliceous bedrocks than in plots dominated by broadleaves on calcareous bedrocks. In contrast, the frequency of bryophyte species which are largely restricted to closed forests is higher in plots dominated by broadleaves on calcareous bedrocks. In the group of plots dominated by conifers on siliceous bedrocks there are also some secondary stands of *Picea abies* and *Pinus sylvestris*, which developed on the primary sites of broadleaved forests.

In the Slovenian forests studied, bryophytes in plots dominated by broadleaves on intermediate bedrocks had significantly higher functional dispersion for light indicator values than plots with broadleaves on siliceous bedrocks. For the moisture indicator, functional dispersion was the highest in plots dominated by conifers of siliceous bedrocks, and the lowest in plots dominated by broadleaves on intermediate bedrocks.

Diversity of bryophyte life forms was found to be lower on siliceous bedrocks. Interestingly, the highest functional dispersion for this trait was found in coniferous forests on calcareous bedrock whereas lowest diversity characterized conifers on siliceous bedrock. Turf (upright shoots with little or no branching, standing close together; Bernhardt-Römermann et al., 2018) was by far the most common life form in the studied dataset. In addition, we observed that turf life form strongly determined functional trait dispersion of bryophyte assemblages. Plots with high representativeness of turfs were characterized by lower diversity of life forms and vice versa (linear regression between life form community mean value and FD: $R^2 = 0.95$).

Measuring community-level traits for different groups, it was found that bryophytes may be more affected by future global warming trends than vascular plants and lichens (Van Zuijlen et al., 2021). To a large extent, this could also apply to the Slovenian forests studied, especially those occurring on calcareous bedrock. Among them, forests on limestone bedrock are particularly sensitive to warming because of the development of shallow soils with low water storage capacity. In forests with broadleaves on limestone, containing various available substrates, a high bryophyte species richness and also functional trait diversity were found.

5. Conclusions

In managed forests in Slovenia, the bryophyte species diversity and composition, as well as their functional diversity and composition, were observed along tree species composition and edaphic gradients. Tree species composition and bedrock were important drivers of bryophyte species diversity and composition. Functional diversity and composition of bryophytes were also significantly affected by bedrock and soil, but somewhat less by tree species composition. This also supports the assumptions of the study of herb layer vegetation in Slovenian forests that the taxonomic and functional facets of vegetation are mainly influenced by a similar set of ecological determinants, but their relative

importance varies among individual taxonomic and functional diversity measures (Kermavnar et al. 2021a). However, different groups of primary producers may respond differently to the same environmental changes, such as climate warming (Van Zuijlen et al., 2021).

Declarations

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Conflict of interest

The authors of this manuscript have no conflict of interest to declare.

Author Contributions

The conceptualization of study was done by L.K., J.K., M.S.S.; preparation of methodology by L.K., J.K., M.S.S.; formal analysis by L.K. and J.K.; data curation by L.K. and J.K.; writing - original draft preparation by L.K., J.K., M.S.S.; funding acquisition by L.K.

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Figures

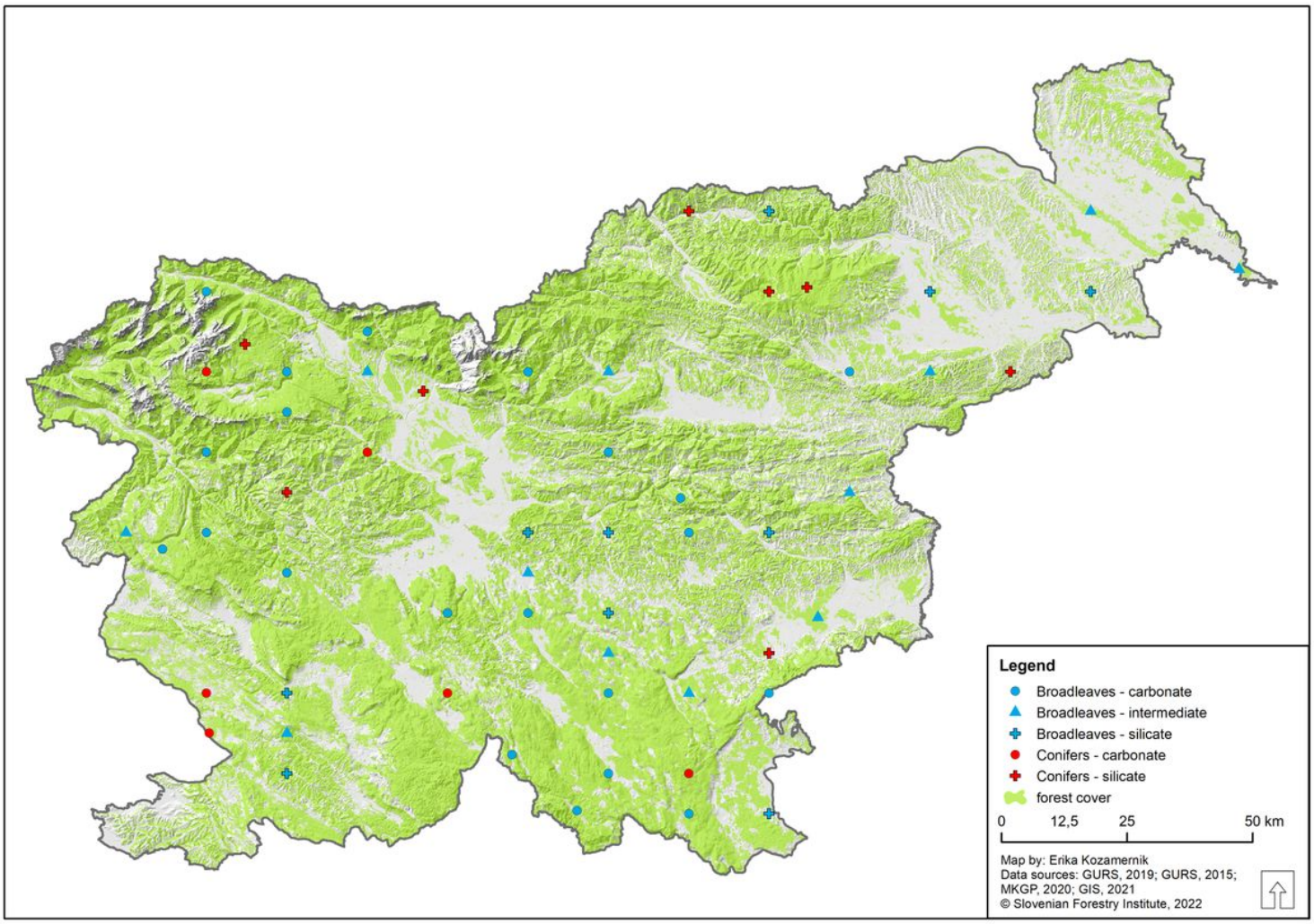

Figure 1

Distribution of 57 study plots across Slovenia, belonging to five groups indicating forest types with similar tree layer composition, bedrock, and soil characteristics.

Figure 2

Selected representative sites dominated by broadleaves on calcareous bedrocks (Photo: L. Kutnar)

Figure 3

Selected representative sites dominated by broadleaves on intermediate bedrocks/soils (Photo: L. Kutnar)

Figure 4

Selected representative sites dominated by broadleaves on siliceous bedrocks (Photo: L. Kutnar)

Figure 5

Selected representative sites dominated by conifers on calcareous bedrocks (Photo: L. Kutnar)

Figure 6

Selected representative sites dominated by conifers on siliceous bedrocks (Photo: L. Kutnar)

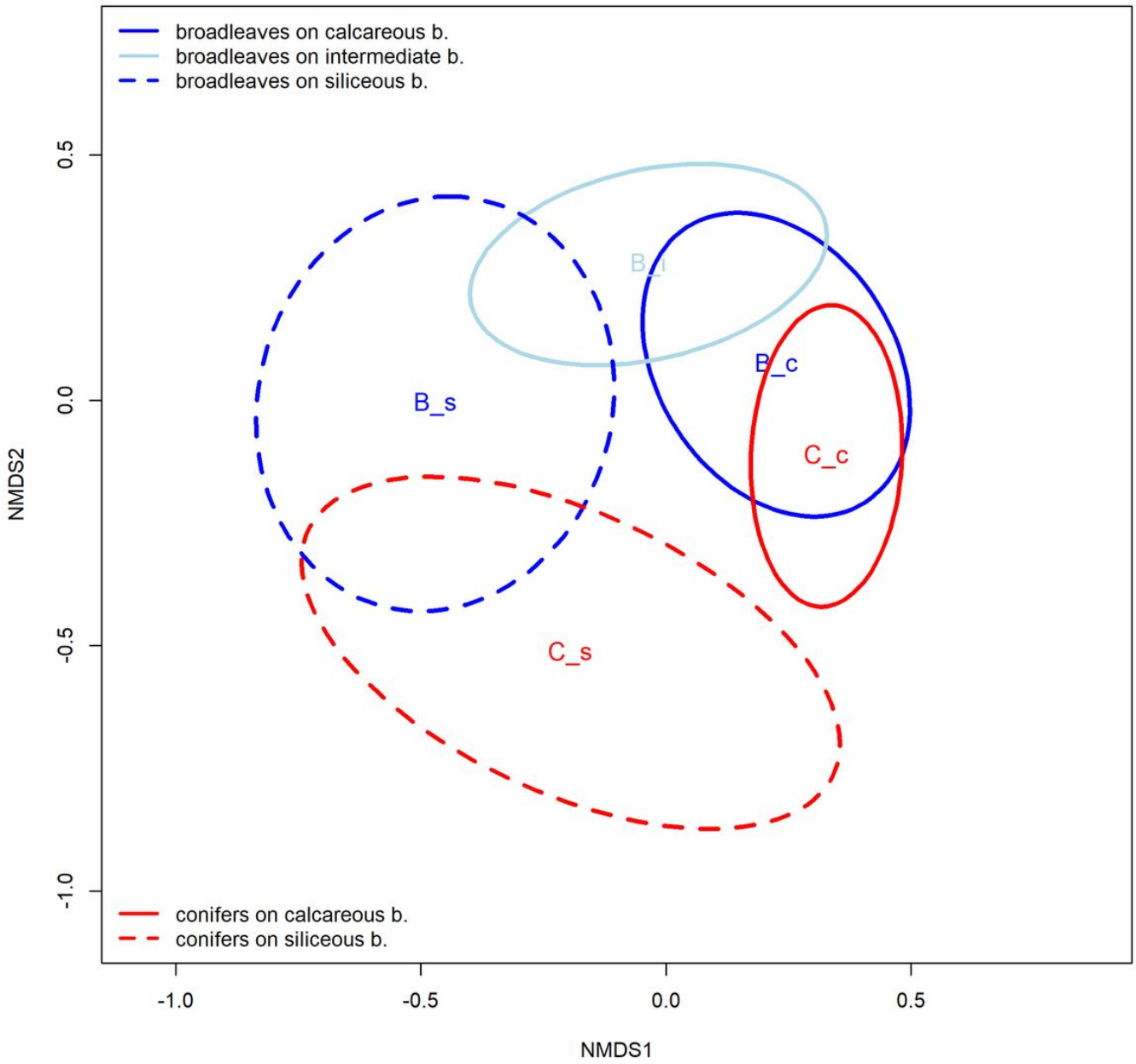

Figure 7

Non-metric multidimensional scaling (NMDS) ordination according to bryophyte species composition. Ellipsoid hulls represent 95% confidence constructed around each of the five forest types: B_c - broadleaves on calcareous bedrocks, B_i - broadleaves on intermediate bedrocks/soils, B_s - broadleaves on siliceous bedrocks, C_c - conifers on calcareous bedrocks, and C_s - conifers on siliceous bedrocks.

Figure 8

Comparison of plot-level bryophyte species richness among five forest types: B_c - broadleaves on calcareous bedrocks, B_i - broadleaves on intermediate bedrocks/soils, B_s - broadleaves on siliceous bedrocks, C_c - conifers on calcareous bedrocks, and C_s - conifers on siliceous bedrocks. Bold lines indicate medians and whiskers above and below the box mark the 10th and 90th percentiles. Groups not sharing the same letter (beside boxplot) significantly differ at $p < 0.05$ (Tukey's test).

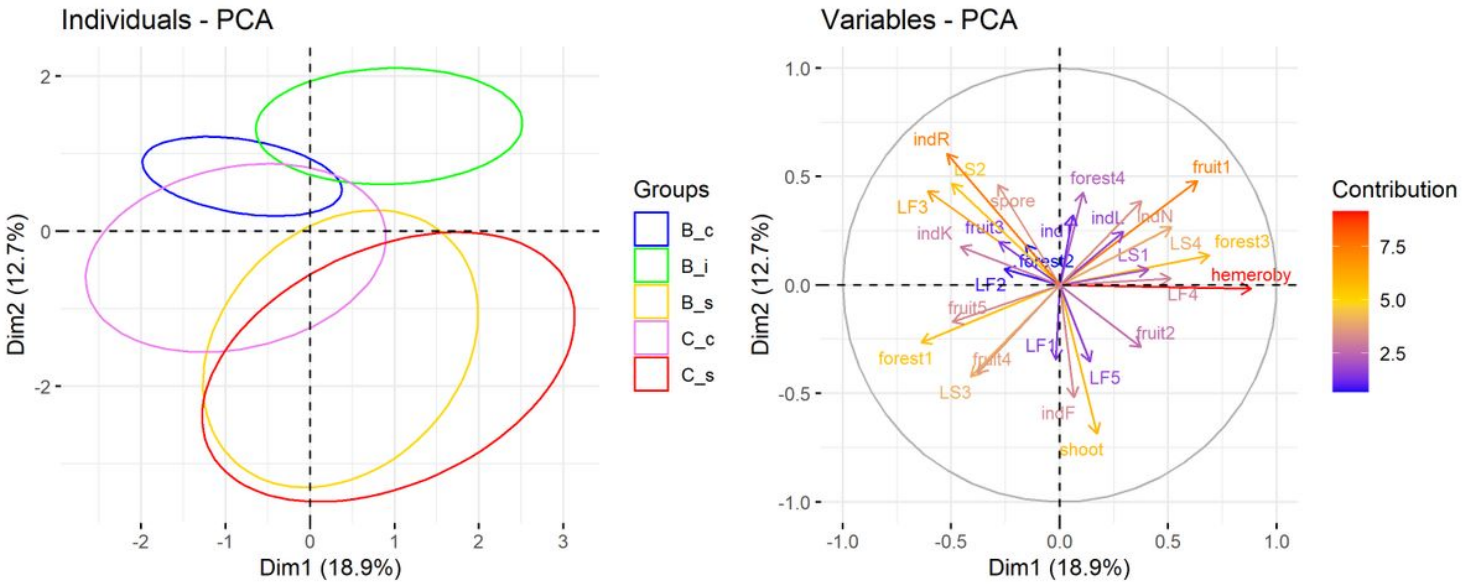

Figure 9

Principial component analysis (PCA) ordination diagrams based on bryophyte functional traits. On the left panel, 95% confidence ellipses indicate five forest types: B_c - broadleaves on calcareous bedrocks, B_i - broadleaves on intermediate bedrocks/soils, B_s - broadleaves on siliceous bedrocks, C_c - conifers on calcareous bedrocks, and C_s - conifers on siliceous bedrocks. On the right panel, traits and trait states are coloured according to their contribution (relative importance) and are labelled as follows: indL = indicator value for light, indT = indicator value for temperature, indK = indicator value for continentality, indF = indicator value for moisture, indR = indicator value for soil reaction, indN = indicator value for nutrients; forest1 = species largely restricted to closed forests, forest2 = species preferring forest edges and in clearings, forest3 = species occurring in forests as well as in open land, forest4 = species that may occur in forests, but prefer open land; hemeroby = refer to human impact; LF1 = cushion as a life form, LF2 = dendroid as a l. f., LF3 = mat as a l. f., LF4 = turf as a l. f., LF5 = weft as a l. f.; LS1 = colonist as a life strategy, LS2 = perennial shuttle as a l. s., LS3 = perennial stayer as a l. s., LS4 = short-lived shuttle as a l. s.; shoot = shoot length; spore = size of spores; fruit1 = common fruiting frequency , fruit2 = frequent fruiting, fruit3 = occasional fruiting, fruit4 = rare fruiting, fruit5 = very rare fruiting.

Figure 10

Comparison of functional dispersion among five forest types for indicator value for light, indicator value for continentality, indicator value for moisture, shoot length and life form. Groups are abbreviated as: B_c - broadleaves on calcareous bedrocks, B_i - broadleaves on intermediate bedrocks/soils, B_s - broadleaves on siliceous bedrocks, C_c - conifers on calcareous bedrocks, and C_s - conifers on siliceous bedrocks. Bold lines indicate medians and

whiskers above and below the box mark the 10th and 90th percentiles. Groups not sharing the same letter (beside boxplot) significantly differ at $p < 0.05$ (Tukey's test).