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Congruence between vascular plants and bryophytes in response to ecological conditions in sustainably managed temperate forests (taxonomic- and trait-based levels)

Lado Kutnar[1] · **Janez Kermavnar**[1] · **Marko S. Sabovljević**[2,3]

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Abstract

Vascular plant species (VP) and bryophytes (B) constitute a significant portion of forest biodiversity and respond to both management intensity and natural disturbances within forests. In this study, we investigated the cross-taxa congruence between understorey VP and B at both diversity and composition levels across a wide range of sustainably managed forests in Slovenia. The taxonomic and functional characteristics of the selected plant groups were studied, with a particular emphasis on ground-dwelling species. We employed a trait-based approach to examine the functional characteristics. On average, the species richness of B in sustainably managed temperate forests increased with the corresponding number of VP. Furthermore, a moderate positive correlation in species composition between the studied groups of ground-dwelling organisms was also observed. The ground-dwelling VP and B were congruent in terms of trait-based composition, which was influenced by soil reaction and nutrients and light availability, while trait-based diversity was only slightly similar in response to moisture. A negative correlation between the composition of stress-tolerant VP and B hemeroby was found, indicating forest environments with a low level of disturbance. This is likely due to the sustainable management of Slovenian forests, where climate change and natural disturbances have intensified in recent years. A cross-taxon comparison of the two groups at four different levels, namely taxonomic-based diversity and composition and trait-based diversity and composition, revealed varying degrees of congruence. It is therefore important to monitor the status and temporal trends of both groups from different aspects to draw reliable conclusions.

Keywords Understory · Mosses · Terricolous species · Diversity · Composition · Taxonomy · Life-history traits · Environmental gradients · Managed forest · ICP Forests program · Slovenia

Introduction

Vascular plants and bryophytes are integral components of forest ecosystems and constitute a significant portion of forest biodiversity (Kriebitzsch et al. 2013). Both groups respond to management intensity and disturbances in temperate forests and therefore have important implications for forest management and conservation (de Groot et al. 2016; Kutnar et al. 2016; Horvat et al. 2017; Lombardi et al. 2018; Tinya et al. 2021). While studies on the effects of forest management on biodiversity often focus on limited groups of organisms, such as vascular plants, cryptogams, which contribute significantly to forest biota, are less frequently investigated (Nascimbene et al. 2007; Paillet et al. 2010; Boch et al. 2013; Király et al. 2013; Kaufmann et al. 2017). Among cryptogams, bryophytes constitute an important and permanent component of forest flora and diversity.

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✉ Lado Kutnar
lado.kutnar@gozdis.si

[1] Department of Forest Ecology, Slovenian Forestry Institute, Večna Pot 2, 1000 Ljubljana, Slovenia

[2] Institute for Botany and Botanical Garden, Faculty of Biology, University of Belgrade, Takovska 43, 11 000, Belgrade, Serbia

[3] Department of Botany, Institute of Biology and Ecology, Faculty of Science, Pavol Jozef Šafárik University in Košice, Mánesova 23, 040 01 Košice, Slovakia

They colonize various substrates less suitable for vascular plants because of low light intensity or low nutrient levels, such as deadwood, bark, rocks, and open soil. They provide shelter, food, and nest material for many animals (Müller et al. 2019). The diversity and quality of different growing substrates for bryophytes are significantly affected by forest management practices. Therefore, bryophytes, especially typical woodland species, exhibit a sensitive response to forest management (Frego 2007; Nordén et al. 2007; Mölder et al. 2015; Müller et al. 2019).

Forest management systems and intensities significantly affect stand structure and tree species composition, both of which are key drivers of biodiversity because they support different groups of organisms in different ways. The effects of the overstory layer are also evident in microclimatic conditions. Management has the potential to create favorable conditions for biodiversity. For example, in a study by Tinya et al. (2021), stand structure, tree species diversity and composition, and microclimate conditions (influenced by the forest stand) were the most important determinants of forest organisms. The study revealed that variables related to stand tree species diversity and composition were drivers for most of the organisms studied, including herbs, woody seedlings, ground floor, and epiphytic bryophytes, and that stands containing more tree species sustained a higher species richness of many taxa (Tinya et al. 2021).

To identify the main biodiversity indicators in forests, a multi-taxa approach is useful (Tinya et al. 2021), analyzing in particular the relationships between the species richness of different taxa and the relationship between these data and forest structural parameters. This approach examines the co-occurrence of species at different forest sites and identifies the taxonomic groups that are most indicative of overall forest composition (Blasi et al. 2010). Vascular plants and bryophytes can be considered as appropriate ecological indicators because their specific characteristics make them sensitive to environmental changes (Gignac 2001; Kermavnar et al. 2020), and they are also reliable ecological indicators of forest condition and naturalness (Blasi et al. 2010; Sabovljević et al. 2010; Czerepko et al. 2021).

To assess biodiversity responses to climate warming and future global change, a multi-taxa approach that includes monitoring of different taxonomic groups and diverse communities has also been proposed (Di Nuzzo et al. 2021; Becker-Scarpitta et al. 2022). Some studies have emphasized the importance of studying different groups of primary producers simultaneously, as they may respond differently to the same environmental changes (Roos et al. 2019; Van Zuijlen et al. 2022). In a recent study conducted by Becker-Scarpitta et al. (2022) in an area with a strong warming trend, significant increases in local diversity and dissimilarity (β-diversity) were found for vascular plants, but not for bryophytes, whose local diversity remained unchanged despite strong compositional changes. In the study, the authors quantified the magnitude of changes in species' distributions along an elevation gradient, species richness, and community composition, and they found that presence–absence data did not provide sufficient power to detect elevational shifts in species distributions. In contrast, Van Zuijlen et al. (2022) showed that bryophytes in *Dryas octopetala* heath in Norway may be more affected by future warming than vascular plants and lichens. In addition, Di Nuzzo et al. (2021) indicated that cryptogams in Mediterranean mountains might be more affected by climate change than vascular plants.

The simultaneous response of vascular plants and cryptogams to altitudinal gradients, which can also serve as a spatial–temporal proxy for predicting the effects of future climate warming (Sundqvist et al. 2013; Elmendorf et al. 2015), has emerged as an important driver of species turnover, intraspecific variation, and covariation in their communities (Bruun et al. 2006; Vittoz et al. 2010; Staniaszek-Kik et al. 2019; Roos et al. 2019; Di Nuzzo et al. 2021).

It can therefore be assumed that very different drivers, such as geological and soil characteristics, climate, biological interactions, forest stand structure, substrate availability, disturbances, and forest management practices, govern the diversity and composition of vascular plants and bryophytes at both taxonomic and functional levels. This raises several research questions: (i) Are the responses of vascular plants and bryophytes to current ecological factors in forests congruent? (ii) Do vascular plants indicate ecological conditions differently from bryophytes in sustainably managed forests?

The aim of our study is to compare the diversity and composition of vascular plants and bryophytes in various close-to-nature and sustainably managed forests in Slovenia, ranging from lowland floodplains to the upper timberline. Both community parameters were studied at taxonomic- and trait-based levels. Based on previous studies, we hypothesized a relatively high correspondence between vascular plants and bryophytes, but the degree of correlation is expected to differ among the four levels analyzed: taxonomic-based diversity and composition and trait-based diversity and composition.

Materials and methods

Study area and plots

The study plots were located in very different Slovenian forest vegetation types (Kutnar et al. 2012), most of which are managed according to the principles of close-to-nature, sustainable, and multifunctional forest management. In the forests studied, a continuous cover forestry approach is practised to maintain a permanently irregular stand structure, created and maintained by the selection and harvesting of individual trees or small groups of trees, resulting in uneven-aged forest stands. Such management practices, including selective logging, group selection, and small-scale irregular shelterwood, promote biodiversity by increasing the structural heterogeneity of stands, maintaining favorable microclimatic conditions via the preservation of clusters of old, mature to over-mature trees, and increasing the variability of substrates and small-scale habitats, including coarse woody debris. All study plots predominately featured mature trees with a relatively closed canopy layer (mean tree-layer cover was 86.0 ± 17.6%) and had a diverse tree species composition (mean number of tree species was 4.7 ± 2.4). On average, forest stands across the study plots were well structured with a developed shrub layer (mean cover 22.4 ± 20.5%) and herb layer (mean cover 45.7 ± 27.4%) (Fig. 1, Table 1).

In lowland forest plots periodically subjected to flooding, forest stands occur in narrow strips along rivers and streams, primarily characterized 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-elevation forests are dominated by European beech (*Fagus sylvatica* L.), with admixtures of other deciduous trees (e.g., *Castanea sativa* Mill., *Acer pseudoplatanus* L., *Fraxinus excelsior*, *Ulmus glabra* Huds.) and conifers (*Abies alba* Mill., *Picea abies* (L.) Karst., *Pinus sylvestris* L.). 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 and the belt of dwarf mountain pine (*Pinus mugo* Turra). Forests of Scots pine (*Pinus sylvestris* L.) are found throughout the country on shallow soils on dolomite and also on acidic, nutrient-poor soils. Smaller areas of Austrian pine (*Pinus nigra* Arnold) grow on extreme steep sites with warmer microclimates. The Sub-Mediterranean region is covered with forest and shrub vegetation of thermophilous broadleaf species (e.g., *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Sorbus aria* (L.) Crantz, *Quercus cerris* L., *Q. pubescens* Willd.). Similar forest types with an admixture of beech are also found throughout the country on sun-exposed, south-facing slopes with predominant limestone and dolomite. The natural forest types described are intersected by numerous forms of secondary forest communities, primarily dominated by Norway spruce and are exposed to a significant degree to climate change and various recent disturbances (Kutnar et al. 2021).

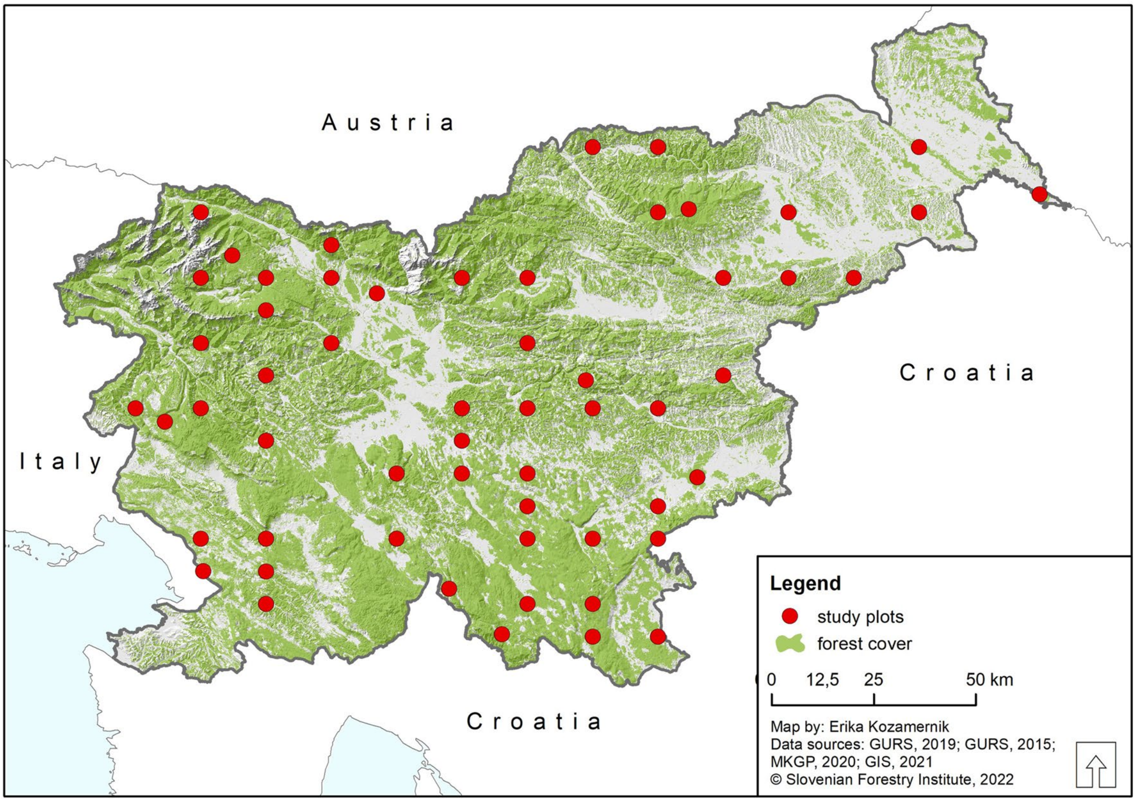

Fig. 1 Distribution of 57 study plots within the ICP Forests Level I and Level II network across Slovenia

Table 1 Topographic and site characteristics and vegetation-based characteristics of the studied forests in Slovenia

	Min	Max	Mean ± SD
Elevation (m a.s.l.)	160.0	1490.0	625.1 ± 342.2
Slope (%)	0.0	90.0	33.8 ± 23.8
Rockiness (%)	0.0	60.0	11.2 ± 17.9
Deadwood (%)	1.0	40.0	6.4 ± 6.8
Sum vegetation cover (%)	75.0	100	97.6 ± 4.8
Tree-layer cover (%)	45.0	100	86.0 ± 17.6
Shrub-layer cover (%)	0.1	75	22.4 ± 20.5
Herb-layer cover (%)	0.3	99	45.7 ± 27.4
Moss-layer cover (%)	0.3	56.8	7.8 ± 12.7
N of tree-layer species	1.0	10.0	4.7 ± 2.4
N of shrub-layer species	1.0	25.0	8.8 ± 5.8

The variables include minimum (Min), maximum (Max), and mean (± standard deviation) values. N of tree-layer species indicates the number of different woody species whose individuals are more than 5 m high (including trees, taller shrubs, and woody climbers). N of shrub-layer species indicates the number of different woody species whose individuals are between 0.5 and 5 m high

Between 2004 and 2010, data on vascular plant species and bryophytes were recorded in different managed forests in Slovenia. A total of 57 study plots were selected (Fig. 1). Of these, 47 plots belonging to Level I of the European ICP Forests network were systematically selected in a 16 km × 16 km and 16 km × 8 km grid across Slovenia (Urbančič et al. 2009; Kutnar 2011). In addition, 10 plots belonging to Level II of the European ICP Forests network (Intensive Monitoring Program) were selected in order to reflect the diversity of Slovenian forests as comprehensively as possible (Urbančič et al. 2016). ICP Forests is a transnational European network for monitoring forest condition in Europe (de Vries et al. 2003). Detailed information on these study plots can be found in several recent studies (Kutnar et al. 2019, 2023; Kermavnar and Kutnar 2020; Kermavnar et al. 2021a, b).

Level I and Level II plots were located at forest sites with a wide variety of climatic, geologic, edaphic, and topographic conditions, resulting in a wide vegetation gradient. The elevation of the study sites ranged from 160 to 1490 m (Table 1, Supplementary Information). The mean annual temperature ranged from 3.2 to 11.7 °C and mean annual precipitation ranged from 791 to 2499 mm. Climate parameters were taken from the WorldClim database (WorldClim 2021). The study sites were located on different parent materials and edaphic conditions. Among the calcareous bedrocks, limestone and dolomite were predominant. The most common soils on these bedrocks were *eutric cambisols*, *rendzic leptosols,* and *chromic cambisols* (Urbančič et al. 2005, 2009, 2016). On intermediate bedrocks, including Pleistocene sediments, alluvium, and various mixed rock types, led to the formation of *eutric cambisols*, *luvisols*, *gleysols*, *fluvisols,* and occasionally *dystric cambisols*. In the group of siliceous bedrocks, various non-carbonate rocks predominate, including sandstones, mica-schists, dioritoid, tonalite, gneiss, and amphibolite. *Dystric cambisols*, *dystric leptosols*, and *eutric cambisols* were the predominant soil types on siliceous bedrocks (Urbančič et al. 2005, 2009, 2016).

In the deciduous forest stands of the study plots, European beech was the most dominant species, while Norway spruce predominated among coniferous species.

Vascular plants and bryophyte sampling

Vascular plants and bryophytes (including mosses and liverworts) were sampled and recorded in an area of 400 m^2 in all study plots. Vascular plants were surveyed according to harmonized ICP Forests protocols (Canullo et al. 2011). Surveys were conducted during the summer months (June, July) when all forest vegetation layers were fully developed. All vascular plant species in the tree layer (woody individuals taller than 5 m), shrub layer (woody individuals from 0.5 to 5 m tall), and herb layer (all herbaceous species and woody individuals less than 0.5 m tall) were recorded. Species nomenclature followed Tutin et al. (1993, 1964–1980) and Martinčič et al. (2007).

All bryophyte species were systematically sampled, including epixylic bryophytes (on deadwood), epiphytic bryophytes (on the bark of living trees; from the base of the tree to a height of 2 m), epilithic bryophytes (on rocks and stones), and terricolous bryophytes (on open soils). Species identification was completed in the laboratory. Nomenclature followed Hodgetts et al. (2020). In the plots studied, only data on the presence of bryophytes (without estimates of cover or abundance) were collected.

More detailed information on plant species composition can be found in several recent studies: for vascular plant species, see Kutnar et al. (2019), Kermavnar and Kutnar (2020), Kermavnar et al. (2021a, b) and for bryophytes, see Kutnar et al. (2023).

During the vegetation survey, the following parameters were also estimated: total (sum) cover of all vegetation layers (%) and cover of each vegetation layer (tree, shrub, herb, and moss layers) separately (%), cover of outcropping rock and rock fragments (%), and cover of woody debris (deadwood) (%). The main topographic and site characteristics, such as elevation (m) and slope (vertical degrees), were recorded for each plot. Descriptive statistics for these parameters are summarized in Table 1.

Plant traits

Plant functional traits are defined as any morpho-, physio-, and phenological characteristics of plants affecting overall plant fitness through their influence on survival, growth, and reproduction (Violle et al. 2007). We selected a set of ecological and life-history traits of vascular plants (VP) and bryophytes (B) (Table 2). Ecological indicator values for all the main factors (light, temperature, continentality, soil moisture, reaction, and nutrients) were sourced from Ellenberg et al. (1992) for vascular plants (VP) and from Bernhardt-Römermann et al. (2018) for bryophytes (B). Data on species' affinity to forests was taken from Heinken et al. (2022) for VP and from Bernhardt-Römermann et al. (2018) for B. While the latter database defines one category per each species, Heinken et al. (2022) have created a list of vascular plant species for 24 geographical regions across 13 countries in Western, Central, and Northern Europe to classify forest specialist and generalist species. The classification of VP species is thus region specific. We summed the number of times each species was counted in each category across all countries. The most frequent category was used as a final criterion to classify the species into one of the four categories (1.1, 1.2, 2.1, and 2.2). In instances of equal tallies (but these were rare), species were classified using our expert-based knowledge. Lastly, ecological strategies of vascular plants were estimated by the means of the C-S-R model (C-Competitors, S-Stress tolerators, R-Ruderals; Grime 1977). Data were taken from the Pladias open-source database (Chytry et al. 2021). Grime classified species into seven different categories (C, S, R, CS, CR, SR, CSR). From this classification, we converted the categories into three variables (GrimeC, GrimeS, GrimeR) for each species using fuzzy logic. The fuzzy coding procedure indicates the extent to which a taxon exhibits each trait category (Chevenet et al. 1994). For example, species with the CSR strategy were coded as 0.33 for GrimeC, 0.33 for GrimeS and 0.33 for GrimeR. Species with the CS strategy were coded as 0.5 for GrimeC, 0.5 for GrimeS and 0.0 for GrimeR. The analogy with CSR data for VP was the hemeroby index of B species (Bernhardt-Römermann et al. 2018). It is expected that in plots experiencing greater human impact and disturbance, the functional composition would have a higher hemeroby index based on B data and VP composition and would tend to favor the ruderal component (GrimeR), while the opposite was assumed for stress-tolerant taxa (GrimeS) (Table 2).

Statistical analysis

Within each plot, vascular plant (VP) and bryophyte (B) assemblages were compared for species richness (number of species per plot) and trait diversity, as well as for species composition and trait composition.

The congruence of responses between ground-dwelling VP and B to ecological conditions at taxonomic- and trait-based levels was studied in detail. For these in-depth analyses, only terricolous VP and B found on the ground/soil at least once in all plots were selected. This data subset resulted in 405 VP species (N of all VP species was 413) and 104 B species (N of all B species was 199). Only presence–absence data on VP and B were used for the statistical analyses.

We tested the correlation in species richness between VP and B with the Spearman's rank correlation method and visualized the data using a scatterplot with a linear regression line.

For trait diversity, we first calculated plot-level functional dispersion values for each ecological and life-history trait listed in Table 2. This was done using the function *dbFD* in the *FD* package (Laliberté et al. 2015). Functional dispersion (Laliberté and Legendre 2010) is estimated as the mean distance of all species to the centroid of the community in the trait space, which is equivalent to multivariate dispersion (Anderson et al. 2006). A higher functional dispersion value for a community indicates greater ecological trait dissimilarity among species compared to a community with a lower dispersion value. For example, in the case of phytoindication for soil reaction, a plant community composed of both more acidophilous and more calciphilous species would result in a wide range of EIV-R values and high level of dispersion for this trait. Relationships between VP and B for each plant trait were tested with the Spearman's rank correlation method and visualized with a correlation matrix.

In the case of species composition, both community data matrices (one for VP and one for B) were subjected to calculation of the Jaccard dissimilarity index based on presence-absence data. This was done using the *vegdist* function in the *vegan* package (Oksanen et al. 2020). The dissimilarity values were transformed to similarity values using the following formula: similarity = 1 − dissimilarity. For all pairwise comparisons ($n = 1596$), we tested the correlation in compositional similarity between VP and B with the Spearman's rank correlation method and a scatterplot with a linear regression line was used for data visualization.

For trait composition, we calculated unweighted community mean values for each of the traits (Table 2) using the function *functcomp* in the *FD* package (Laliberté et al. 2015). The mean values of traits and trait states (13 for VP and 11 for B, 27 in total), expressing the functional composition of assemblages, were subsequently used as input data for testing the strength of the correlation between VP and B (Spearman's rank correlation method).

The R language and environment for statistical computing was employed for all analyses (R Core Team 2021).

Results

Species and trait diversity

The study plots were systematically distributed within an elevation range of more than 1300 m in sustainably managed

Table 2 Explanation of ecological and life-history traits of vascular plant species (VP) and bryophyte species (B)

Variable (abbreviation)	Definition/notes
VP_eivL	Indicator value for light (L) for vascular plant (VP) (Ellenberg et al. 1992). Scale: 1—Indicator of deep shade, … 9—Indicator of full light, Ind—Indifferent
VP_eivT	Indicator value for temperature (T) for vascular plant (VP) (Ellenberg et al. 1992) Scale: 1—Indicator of cold conditions, … 9—Indicator of extremely warm conditions, Ind—Indifferent
VP_eivK	Indicator value for continentality (K) for vascular plant (VP) (Ellenberg et al. 1992) Scale: 1—Extreme oceanic plant, … 9—Extreme continental plant, Ind—Indifferent
VP_eivF	Indicator value for moisture (F) for vascular plant (VP) (Ellenberg et al. 1992) Scale: 1—Indicator of extreme dryness, … 9—Indicator of wet sites, 10—Indicator of shallow-water sites, 11—Plant rooting under water, but at least for a time exposed above, 12—Submerged plant, permanently or almost constantly under water, Ind—Indifferent
VP_eivR	Indicator value for soil reaction (R) for vascular plant (VP) (Ellenberg et al. 1992) Scale: 1—Indicator of extreme acidity, … 9—Indicator of basic reaction, Ind—Indifferent
VP_eivN	Indicator value for soil nutrients (N) for vascular plant (VP) (Ellenberg et al. 1992) Scale: 1—Indicator of extremely infertile sites, … 9—Indicator of extremely nutrient rich situations, Ind—Indifferent
VP_forest1.1	Vascular plant (VP) that can be found mainly in closed forests (Heinken et al. 2022)
VP_forest1.2	Vascular plant (VP) occurs predominantly along forest edges and in forest openings (Heinken et al. 2022)
VP_forest2.1	Vascular plant (VP) that is part of at least one near-natural (late-successional) forest type. The majority of these species probably occur primarily in forests, surviving and regenerating in open (cultural) landscape habitats, but also in remnant forests (Heinken et al. 2022)
VP_forest2.2	Vascular plant (VP) that only inhabit open forests created by afforestation or during succession of open vegetation (dwarf-shrub heaths, calcareous and sand grasslands, wet meadows) (Heinken et al. 2022)
VP_GrimeC	Competitive (C) vascular plant (VP) that predominate in habitats with low disturbance and low stress (Grime 1977)
VP_GrimeS	Stress-tolerant (S) vascular plant (VP) that predominate in habitats with low disturbance and high stress (Grime 1977)
VP_GrimeR	Ruderal (R) vascular plant (VP) that predominate in habitats with high disturbance and low stress (Grime 1977)
B_eivL	Indicator value for light (L) for bryophyte (B) (Düll 1991); occurrence in relation to the relative irradiance intensity at the time when the deciduous plants are full in leaf (Bernhardt-Römermann et al. 2018) Scale: 1—Plant in deep shade, … 9—Plant in full light, found mostly in full sun, Ind—Indifferent
B_eivT	Indicator value for temperature (T) for bryophyte (B) (Düll 1991); occurrence in the temperature gradients from the Artic and the Mediterranean and from alpine levels to lowlands (Bernhardt-Römermann et al. 2018) Scale: 1—Cold-indicator plant, found only in high mountains, mostly in alpine and nival levels, … 9—Indicator of extremely warm conditions, Ind—Indifferent
B_eivK	Indicator value for continentality (K) for bryophyte (B) (Düll 1991); occurrence in the gradient from the Atlantic coast to the inner parts of Eurasia, especially with regard to temperature ranges (Bernhardt-Römermann et al. 2018) Scale: 1—Extreme oceanic, in Central Europe only in a few outposts, …9—Extreme continental, virtually absent from Western Europe, Ind—Indifferent
B_eivF	Indicator value for moisture (F) for bryophyte (B) (Düll 1991); occurrence in the gradient from dry, shallow-soil rocky slopes to swampy ground (Bernhardt-Römermann et al. 2018) Scale: 1—Indicator of extreme dryness, restricted to soils that often dry out for some time, … 9—Wet-site indicator, often on water-saturated, badly aerated soils, Ind—Indifferent
B_eivR	Indicator value for soil reaction (R) for bryophyte (B) (Düll 1991); occurrence in the gradient of soil acidity and lime content (Bernhardt-Römermann et al. 2018) Scale: 1—Indicator of extreme acidity, never found on weakly acid or basic soils, … 9—Indicator of basic reaction, always found on calcareous or other high-pH soils, Ind—Indifferent
B_eivN	Indicator value for soil nutrients (N) for bryophyte (B) (Düll 1991); occurrence in the gradient of nutrient availability, eutrophication (Bernhardt-Römermann et al. 2018) Scale: 1—Plants on sites with very low nutrient content, … 9—No bryophytes occur (outcompeted by vascular plants)
B_forest1.1	Bryophyte species (B) that is largely restricted to closed forest (Bernhardt-Römermann et al. 2018)
B_forest1.2	Bryophyte species (B) that prefers forest edges and clearings (Bernhardt-Römermann et al. 2018)
B_forest2.1	Bryophyte species (B) that occurs in forests as well as in open land (Bernhardt-Römermann et al. 2018)
B_forest2.2	Bryophyte species (B) that may occur in forests, but prefers open land (Bernhardt-Römermann et al. 2018)
B_hemeroby	Indicates occurrence of bryophyte species (B) in the gradient of background human impact on the ecosystem (Bernhardt-Römermann et al. 2018). Scale: 1—Absence of human impact, … 9—Very strong human impact

forests in Slovenia. Both herb-layer species and bryophytes across Slovenian-managed forests exhibited a wide range of taxonomic- and trait-based diversity metrics.

A total of 413 vascular plant (VP) species in the herb layer (terricolous, epilithic, epixylic, and epiphytic species of ferns, forbs, graminoids, woody climbers, young trees, and shrubs, all less than 0.5 m tall) and 199 bryophyte (B) species (terricolous, epilithic, epixylic, and epiphytic bryophytes) were recorded in all 57 study plots. The total number of recorded species (VP and B together) per plot ranged between 17 and 111 (mean ± standard deviation was 63.0 ± 24.1). Across all plots, the five most frequent VP in herb layer were *Acer pseudoplatanus*, *Fagus sylvatica*, *Picea abies*, *Mycelis muralis* (L.) Gaertn., and *Carex digitata* L. Seventy-nine VP were present in at least 10 plots. The five most frequent B were *Hypnum cupressiforme* Hedw., *Brachytheciastrum velutinum* (Hedw.) Ignatov & Huttunen, *Polytrichum formosum* Hedw., *Ctenidium molluscum* Mitten, and *Isothecium alopecuroides* (Lam. ex Dubois). Isov. Among the 199 B, 40 taxa were present in at least 10 study plots.

In our dataset, the number of all B exhibited a significant positive correlation with vascular species richness (Spearman's correlation coefficient $r_s = 0.48$, $p < 0.001$).

The mean species richness (± standard deviation) of all VP in the herb layer at the plot level was 43.6 ± 19.3, and the mean species richness (± standard deviation) of all B (including all species on different substrates) at the plot level was 19.4 ± 7.9. On average, the number of all VP was 2.3 times higher than the number of B. However, in a few plots (6), the number of all B exceeded the number of VP in the herb layer.

For a detailed analysis of the congruence between VP and B in their responses to ecological conditions on both taxonomic- and trait-based levels, we focused solely on ground-dwelling species from both groups. In total, 405 ground-dwelling VP in the herb layer and 104 ground-dwelling B were identified in all 57 surveyed plots. In this subset comprising only species growing on the ground/soil, the total number of bryophytes exhibited a significant positive correlation with vascular species richness (Spearman's correlation coefficient $r_s = 0.51$, $p < 0.001$; Fig. 2).

The mean species richness (± standard deviation) of ground-dwelling VP in the herb layer at the plot level was 42.7 ± 18.7, and the mean species richness (± standard deviation) of ground-dwelling B at the plot level was 14.5 ± 6.0.

The correspondence of diversity based on ecological and life-history traits between ground-dwelling VP and B was examined. In our analysis, we focused only on traits that were analogous or similarly described for both groups concurrently (Table 3). The diversity of these groups of organisms, as determined by ecological and life-history traits, indicates key factors that determine ecological conditions in temperate forests. The correlation between trait-based diversity indicating moisture for vascular plant species (V_eivF) and for bryophytes

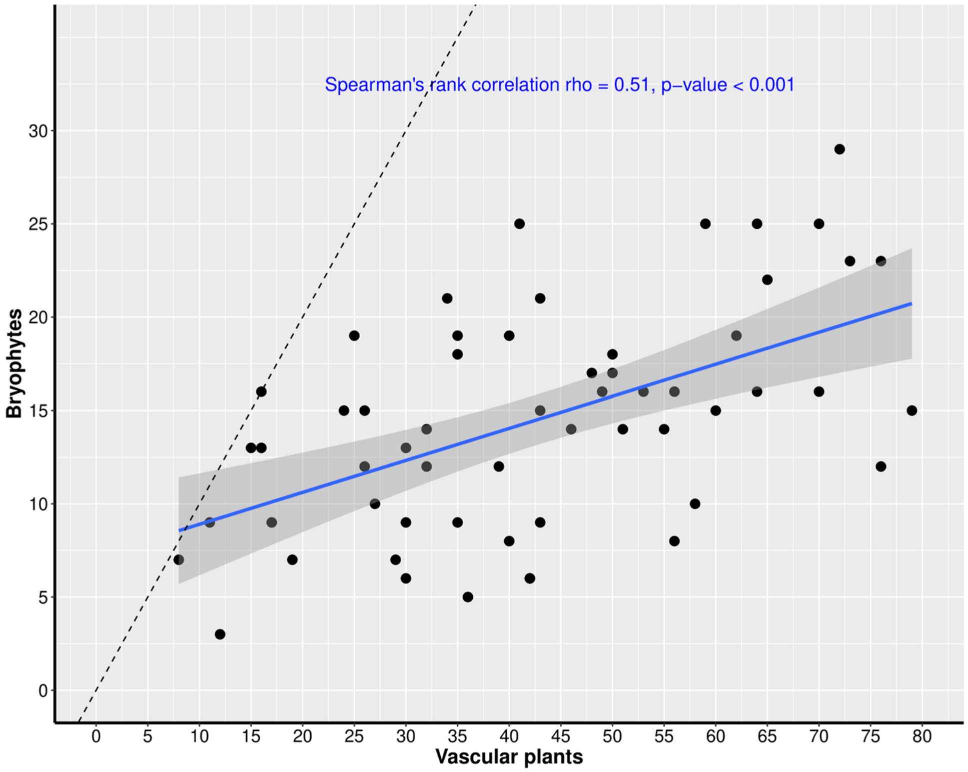

Fig. 2 Linear regression analysis of plot-level species richness between ground-dwelling vascular plants (VP) in the herb layer and bryophytes (B). The gray ribbon surrounding the blue regression line represents the 95% confidence interval. The dashed line indicates equal numbers of VP and B

Table 3 Spearman rank correlation coefficients for ecological and life-history trait diversity between ground-dwelling vascular plants (VP) in herb layer and bryophytes (B)

Trait	Correlation coefficient	*p* value
EIV-L	0.206	> 0.05
EIV-T	0.144	> 0.05
EIV-K	0.135	> 0.05
EIV-F	*0.257*	< 0.1
EIV-R	0.099	> 0.05
EIV-N	0.140	> 0.05
Forest	− 0.098	> 0.05
VP_Grime vs. B_hemeroby	0.085	> 0.05

Marginally significant correlations are in italics

(B_eivF) was positive ($r_s = 0.26$, $p < 0.1$). However, the correlations between the diversity of all other comparable ecological traits (eivL, eivT, eivK, eivN) and life-history traits (forest, VP_Grime/B_hemeroby) were not significant (Table 3).

Species and trait composition

The comparison regarding pairwise compositional similarity in the studied plots across managed temperate forests showed a moderate correlation between ground-dwelling VP and B (Fig. 3). When evaluating composition of vascular species and bryophytes with a large number of individual pairwise comparisons ($n = 1596$), a positive correlation was calculated ($r_s = 0.41$, $p < 0.001$) (Fig. 3), although the data were quite scattered.

When comparing trait-based composition by ground-dwelling vascular plant (VP) species and bryophytes (B) indicative of ecological conditions, only a few significant correlations were found (Table 4).

A relatively strong positive correlation was found between trait composition indicating soil reaction for vascular plant species (VP_eivR) and for bryophytes (B_eivR) ($r_s = 0.70$, $p < 0.001$) (Table 4). Trait composition for soil nutrients (VP_eivN and B_eivN) also showed a strong positive correlation ($r_s = 0.61$, $p < 0.001$). The correlation of trait composition for light (VP_eivL and B_eivL) was weaker ($r_s = 0.31$, $p < 0.05$). When comparing trait composition in terms of stress-tolerant vascular plants (VP_GrimeS) and

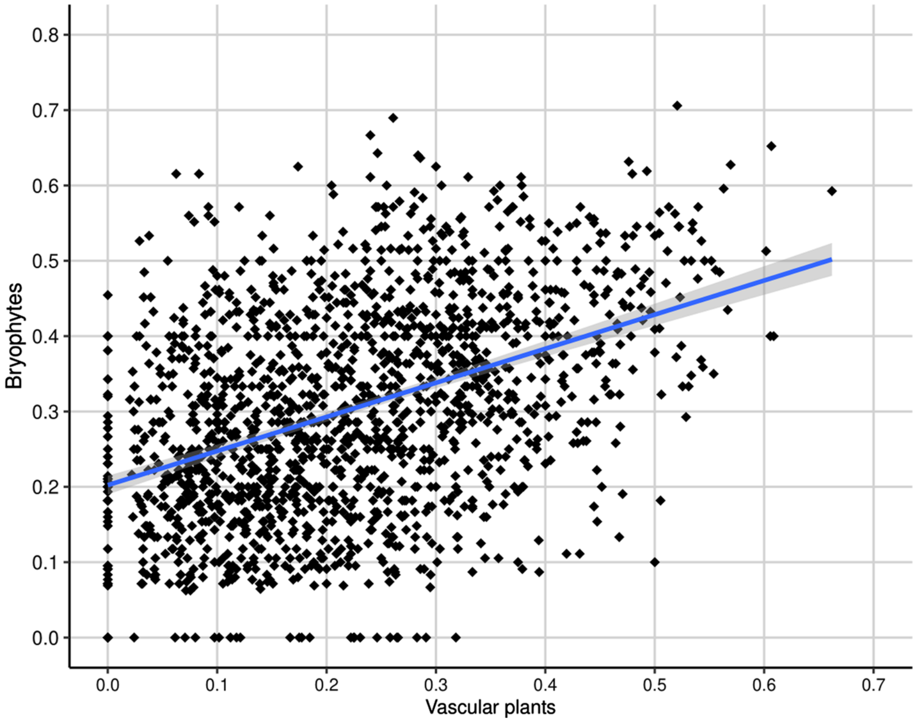

Fig. 3 Comparison of compositional similarity between ground-dwelling vascular plants (VP) in the herb layer and bryophytes (B). The panel indicates the similarity based on all pairwise comparisons ($n = 1596$) of the study plots ($n = 57$). For example, the dot in the position for Vascular plants—VP (axis x) is equal to 0.0 and Bryophytes—B (axis *y*) is equal to 0.0 (position: $x = 0.0$; $y = 0.0$) indicates a pair of two study plots (out of 1.596 pairs) that did not share a single common species from the group VP and also none from group B. The dots in the VP line equal to 0.0 and > 0.0 for B (positions: $x = 0.0$; $y > 0.0$) indicate pairs of plots that have no common VP species but some common B species. The dots in the line VP is > 0.0 and B is equal to 0.0 (positions: $x > 0.0$; $y = 0.0$) indicate pairs of plots that share some common VP species and no common B species

Table 4 Spearman rank correlation coefficients for ecological and life-history trait composition between ground-dwelling vascular plants (VP) in the herb layer and bryophytes (B)

Trait	Correlation coefficient	*p* value
EIV-L	**0.314**	< 0.05
EIV-T	− 0.024	> 0.05
EIV-K	− 0.083	> 0.05
EIV-F	0.175	> 0.05
EIV-R	**0.698**	< 0.001
EIV-N	**0.607**	< 0.001
Forest1.1	0.190	> 0.05
Forest1.2	− 0.078	> 0.05
Forest2.1	− 0.010	> 0.05
Forest2.2	− 0.095	> 0.05
VP_GrimeC vs. B_hemeroby	*0.247*	< 0.1
VP_GrimeS vs. B_hemeroby	**− 0.317**	< 0.05
VP_GrimeR vs. B_hemeroby	− 0.067	> 0.05

Significant correlations are in bold, and marginally significant correlations are in italics

hemeroby, which indicates the extent of human impact on bryophyte communities (B_hemeroby), a significant negative correlation was found ($r_s = -0.32$, $p < 0.05$). However, correlations between other relevant traits indicating the same ecological conditions (e.g., eivF, eivT, eivK) and other trait states (forest1.2, forest2.1, forest 2.2) were not significant (Table 4).

Discussion

The multi-taxa approach enables the comparison of the diversity patterns of different groups of organisms and their responses to different environmental conditions (Tinya et al. 2021). While some studies have attempted to explain overall forest biodiversity using just one or a few taxa (Lewandowski et al. 2010), this approach is considered an approximation and is subject to controversy. Several studies have demonstrated that the diversity of various forest taxa is more strongly associated with stand structural variables than with the diversity of other groups of organisms (Blasi et al. 2010; Sabatini et al. 2016). Therefore, it is necessary to study numerous taxa simultaneously to assess overall forest biodiversity (de Groot et al. 2016; Sabatini et al. 2016; Jokela et al. 2018; Burrascano et al. 2018). Furthermore, changes in vascular plant diversity and composition cannot be directly extrapolated to predict the response of bryophytes to global change (Becker-Scarpitta et al. 2022) and vice versa. Therefore, to understand the response of plant communities to environmental factors in sustainably managed forests in Slovenia, we used a multi-taxa approach combined with functional trait analysis (Roos et al. 2019; Di Nuzzo et al. 2021). This approach allowed us to investigate the concurrent response of vascular plants and bryophytes, particularly ground-dwelling species, to environmental factors and human impacts in temperate forests at taxonomic- and trait-based levels.

Species and trait diversity

In our datasets collected in the various managed forests in Slovenia, we identified an overall positive correlation between bryophyte and vascular plant species richness. This correlation likely reflects similar requirements for light, moisture, and nutrients within forest stands (Tinya et al. 2009). Furthermore, the resemblance in patterns of bryophyte species richness to those of vascular plants with respect to management suggests a probable similar response to management activities (Ingerpuu et al. 2003; Boch et al. 2013). Müller et al. (2019) observed similar findings, which indicated a positive relationship between the richness of terricolous bryophyte and herbaceous vascular plant species both across and within regions in Germany.

The results obtained in our study also showed that bryophytes, often considered as weak competitors, were not outcompeted by stronger vascular plant competitors, but are in a dynamic equilibrium enabled by close-to-nature and sustainable forest management in Slovenia. In diverse forest ecosystems in Slovenia, spanning from the lowlands to high mountain areas, the average number of all vascular plants in the herb layer per plot was 2.3 times higher than that of bryophytes. In a more detailed analysis of ground-dwelling species, the number of vascular plants in the herb layer was almost three times higher than that of bryophytes.

Although in most surveyed plots, the number of all vascular plant species exceeded that of bryophytes, there were exceptions where the opposite situation was observed. These instances were mainly characterized by dystric cambisols and dystric leptosols on different siliceous bedrocks, dominated by beech or spruce. The majority of these plots belong to different acidophilous beech forests, including *Blechno-Fagetum*, *Castaneo-Fagetum,* and *Luzulo-Fagetum* communities. The higher number of bryophytes in more acidic soils is also in line with the findings of Müller et al. (2019), who demonstrated that the richness of terricolous bryophyte species increased with decreasing soil pH. As soil pH declines, it becomes more difficult for many vascular plants to take up minerals, thus providing more potential microhabitats for bryophytes. Bryophytes are also favored by their ability to obtain most of their minerals from atmospheric precipitates.

On the other hand, there was no clear pattern in plots with much higher numbers of vascular plant species compared to bryophytes. Plots with low numbers of bryophytes (less than 25% of that of vascular plants) were dominated by conifers or broadleaf trees. They were located on very different bedrock, from carbonate rock to mixed and also siliceous rock at different elevations.

The species richness of bryophytes studied in different managed temperate forests in Slovenia (199 bryophytes on all substrates and 19.4 species per plot; 104 ground-dwelling bryophytes and 14.5 species per plot) was higher than that found in German forests (186 bryophytes, 13.0 species per plot; Müller et al. 2019) for the same plot size (400 m^2) in both countries. The higher number in Slovenia compared to Germany could be party explained by an increasing trend in the species richness of bryophytes from north to south, which was observed in Germany by Müller et al. (2019). However, the high species richness of vascular plant and bryophyte species found in Slovenian temperate forests can also be partly explained by less intensive forest management and silviculture based on close-to-nature, sustainable, and multifunctional principles, which is practised in these forests (ZGS 2022). In addition to the large number of common bryophyte species in these forests, close-to-nature and sustainable management also support the occurrence of some rare, threatened, and protected bryophyte species (Kutnar et al. 2023). The availability of suitable substrates, including deadwood, is an important factor contributing to high species richness and diverse composition, especially of bryophytes (Fojcik et al. 2019; Müller et al. 2019). However, even in sustainably managed forests, the amount of deadwood is considerably lower than in unmanaged forests (Nagel et al. 2017).

The most influential drivers of forest biodiversity are under the direct control of current forest management. Heterogeneous stand structure and tree species composition promote different groups of organisms. Therefore, the long-term maintenance of structural and compositional heterogeneity at stand and landscape levels is an important aspect of ecologically sustainable forest management (Tinya et al. 2021).

In addition to the high number of bryophytes, a high number of all vascular plants (413) and ground-dwelling species (405) in the understory of Slovenian forests were identified. Higher species richness of both studied groups in Slovenia compared to neighboring forests in western Hungary (Tinya et al. 2021) is expected since the elevation gradient of plots in Slovenia is much larger (more than 1300 m) than in Hungary (plots are located between 250 and 350 m a.s.l.). Given the differences in the elevation gradients, methodological approaches, and size of plots in both countries, the mean number of species seems quite comparable between the two neighboring areas.

Tinya et al. (2021) examined the congruence among different organisms and found correlations between the species richness and species composition of the groups of organisms studied, with significant correlations mainly between photosynthetic organisms (herbs, seedlings, ground-dwelling and epiphytic bryophytes, and lichens). In terms of species richness and composition, the congruence between understorey herbs and ground-dwelling bryophytes is somewhat lower in Slovenia than in western Hungary (Tinya et al. 2021), where the forests studies were more similar forests and restricted to a rather narrow altitudinal belt. The correlation between species richness of ground-dwelling vascular plant species in the herb layer and bryophytes in Slovenia was 0.51, while the correlation between understory herbs and woody seedlings and bryophytes on the ground in Hungary was 0.67 and 0.61, respectively (Tinya et al. 2021).

Since the functional traits are influenced by different factors in each taxonomic group (Di Nuzzo et al. 2021), we attempted to reveal the common influencing factors in vascular plants and bryophyte communities in managed forests in Slovenia and to observe the congruence of ecological and life-history traits of both groups at diversity and composition levels. We detected a few correlations between ground-dwelling vascular plants and bryophytes for trait-based diversity and composition. Our two datasets were slightly congruent in terms of trait-based diversity influenced by moisture, to which both groups appear to respond similarly. In a previous study by Kermavnar et al. (2021a), soil properties and the local stand characteristics (which might also be a proxy for moisture in forest stands, e.g., on average, more closed, vertical structured forest stands are characterized by higher air moisture) also proved to be the main controlling factors for both species- and trait-based diversity in herb-layer communities across temperate forests. The effects of the overstory tree layer on forest biodiversity are manifested in many cases by diverse microclimatic conditions. Such different stand structures and tree species diversity and composition, as well as microclimate, studied in sustainably managed forests in Slovenia, also proved to be highly influential drivers even at the multi-taxon level (Tinya et al. 2021).

Species and trait composition

The correlation between the species composition of ground-dwelling vascular plant species and bryophytes in Slovenia was 0.41, while the correlations in Hungary were 0.55 (woody seedlings vs. ground bryophytes bryophytes) and 0.54 (understory herbs vs. ground bryophytes) (Tinya et al. 2021). This difference might be explained by Burrascano et al. (2018), who found that the cross-taxa congruence in species composition is more scale dependent. The lower inter-plot congruence in the species composition (and also species richness) of vascular plants and bryophytes in Slovenia could be attributed to the wide range of forest ecosystems studied. Evaluating the composition of ground-dwelling vascular plant species and bryophytes on 57 plots with a large number of individual pairwise comparisons (1596) revealed instances where some plot pairs shared neither a single vascular plant species nor a bryophyte species in common. Furthermore, some of the compared plot pairs did not have a single vascular plant species in common in their species composition (with some common bryophyte species), while others did not have a single bryophyte species in common (with some common vascular plant species).

At the trait-based composition level (Ellenberg et al. 1992; Bernhardt-Römermann et al. 2018; Heinken et al. 2022), the correlations between ground-dwelling vascular plants and bryophytes were observed for soil reaction and soil nutrients, with somewhat weaker correlations for light. A weak-negative correlation in trait composition was observed between stress-tolerant vascular plants (VP_GrimeS) and B_hemeroby. VP_GrimeS indicates environments with low disturbance and high stress (Grime 1977), while higher values of B_hemeroby indicate stronger human impacts on bryophyte communities (Bernhardt-Römermann et al. 2018). The low level of disturbance in the habitats studied can largely be attributed to the close-to-nature and sustainable management of Slovenian forests. However, in recent decades, the combined effects of climate change, natural disturbances, and human interventions have increased in Slovenian forests (Kutnar et al. 2019; 2021), potentially leading to significant changes in the assemblages of vascular plant species and bryophytes and their responses to these drivers at different levels.

The trait composition of the studied herb-layer vegetation of temperate forests in the transition zone between Central and SE Europe exhibited significant links to soil conditions and tree-layer characteristics, both directly influenced by forest management interventions (Kermavnar et al. 2021b). Moreover, Kermavnar et al. (2021a) suggested that the taxonomic and functional facets of herb-layer vegetation are primarily influenced by a similar set of ecological determinants, but their relative importance varies across individual taxonomy- and functional trait-based diversity measures.

In our study, a relatively small number of common drivers controlling the trait-based diversity and composition of vascular plant species and bryophytes in managed temperate forests in Slovenia were observed simultaneously, as the consistency of responses between these two groups could be influenced and offset by the different set of drivers controlling the diversity and composition of the two groups studied. Therefore, the trait variation of bryophytes may exhibit very different responses to the same environmental factors compared to vascular plants, particularly at higher elevations and latitudes (Roos et al. 2019).

However, the response of different taxonomic groups of organisms may change in the near future, as cryptogams, i.e., bryophytes, could be more impacted by climate change than vascular plants. Cryptogams are more sensitive to changes in climate due to their narrower ecological niches (microhabitat specialists), which suggests their comparatively lower eco-genetic plasticity. Moreover, contrasting species–climate and trait–climate relationships were also found between lichens and bryophytes, suggesting that each group may be sensitive to different components of climate change (Di Nuzzo et al. 2021). These findings underscore the need to use a multi-taxa approach at both taxonomic- and trait-based levels to better understand the response of terrestrial communities to climate and other environmental changes.

In addition, a simultaneous multi-taxa approach is also valuable for unraveling the relationships between the species richness data of different taxa and structural indicators that are useful for monitoring and conservation purposes in close-to-nature and sustainable managed forests in Slovenia. A comprehensive perspective provided by different taxonomic groups is needed to identify reliable structure-based indicators of highly complex ecosystems, such as old-growth forests, encompassing different components closely related to structure, function, and composition (Blasi et al. 2010). Given that herb-layer plants and stand structural factors have been shown to be limited surrogates for overall biodiversity in well-preserved European beech forests, it is suggested that a larger number of target taxa should be included in biodiversity studies (Sabatini et al. 2016). In addition to different organisms, it is proposed to study and monitor different levels of biodiversity, including taxonomic and functional aspects.

Conclusion

The multi-taxa approach remains relatively uncommon in studies of forest biodiversity. Our study revealed cross-taxa congruence in the responses of vascular plant species in the herb layer and bryophytes to various ecological factors across a wide spectrum of managed temperate forests in Slovenia, ranging from lowland floodplains to the upper timberline. However, the majority of multi-taxa studies (e.g., Blasi et al. 2010; de Groot et al. 2016; Sabatini et al. 2016; Jokela et al. 2018; Burrascano et al. 2018; Tinya et al. 2021) have considered only taxonomic-based diversity and composition in different groups of organisms. In contrast, our study adopted a comprehensive cross-taxa approach, comparing ground-dwelling vascular plants and bryophytes across four different levels: taxonomic-based diversity and composition and trait-based diversity and composition. The study revealed both congruences and discrepancies in the drivers controlling the diversity and composition of the two groups of organisms at taxonomic and functional trait levels in close-to-nature and sustainable managed temperate forests of Slovenia. This type of forest management aims at heterogeneous stand structure and tree species composition in forest stands that facilitate the coexistence of various organism groups, including vascular plants and bryophytes.

Therefore, the long-term maintenance of the structural and compositional heterogeneity of stands, including diverse tree species composition and various growth substrates, is an important goal of close-to-nature and sustainable forest management in the studied temperate forests.

Supplementary information

Figures 1–6 show different study plots located within Level I and Level II of the ICP Forests network in Slovenia. These images show some representative Slovenian forest types situated at different altitudes.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11258-023-01357-7.

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Author contributions The conceptualization of study was done by LK, JK, and MSS; preparation of methodology was done by LK, JK, and MSS; formal analysis by LK and JK; data curation by LK and JK; writing and preparation of original draft was done by LK, JK, and MSS; funding acquisition was done by L.K and J.K.

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Data availability Species datasets, including vascular plants and bryophytes used for this study, are available from the authors. More detailed information on plant species composition can also be found in several recent studies: for vascular plant species, see Kutnar et al. (2019), Kermavnar and Kutnar (2020), Kermavnar et al. (2021a, b) and for bryophytes, see Kutnar et al. (2023).

Declarations

Conflict of interest The authors of this manuscript have no conflicts of interest to declare.

References

Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. Ecol Lett 9:683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Becker-Scarpitta A, Auberson-Lavoie D, Aussenac R, Vellend M (2022) Different temporal trends in vascular plant and bryophyte communities along elevational gradients over four decades of warming. Ecol Evol 12:e9102. https://doi.org/10.1002/ece3.9102

Bernhardt-Römermann M, Poschlod P, Hentschel J, Chytrý M (2018) BryForTrait—a life-history trait database of forest bryophytes. J Veg Sci 29(4):798–800. https://doi.org/10.1111/jvs.2018.29.issue-410.1111/jvs.1264

Blasi C, Marchetti M, Chiavetta U, Aleffi M, Audisio P, Azzella MM, Brunialti G, Capotorti G, Del Vico E, Lattanzi E et al (2010) Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. Plant Biosyst 144(1):160–170. https://doi.org/10.1080/11263500903560538

Boch S, Müller J, Prati D, Blaser S, Fischer M (2013) Up in the tree—the overlooked richness of bryophytes and lichens in tree crowns. PlosOne 8(12):e84913. https://doi.org/10.1371/journal.pone.0084913

Bruun HH, Moen J, Virtanen R, Grytnes JA, Oksanen L, Angerbjörn A (2006) Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. J Veg Sci 17:37–46. https://doi.org/10.1111/j.1654-1103.2006.tb02421.x

Burrascano S, de Andrade RB, Paillet Y, Ódor P, Antonini G, Bouget C, Campagnaro T, Gosselin F, Janssen P, Persiani AM et al (2018) Congruence across taxa and spatial scales: are we asking too much of species data? Global Ecol Biogeogr 27:980–990. https://doi.org/10.1111/geb.12766

Canullo R, Starlinger F, Granke O, Fischer R, Aamlid D, Neville P (2011) ICP forests manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests; part VII.1: Assessment of ground vegetation; UNECE ICP Forests Programme Coordinating Centre: Hamburg, Germany, p 19. https://www.icp-forests.org/pdf/manual/2016/ICP_Manual_2016_01_part07-1.pdf

Chevenet F, Dolédec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. Freshw Biol 31:295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x

Chytrý M, Danihelka J, Kaplan Z, Wild J, Holubová D, Novotný P, Řezníčková M, Rohn M, Dřevojan P, Grulich V et al (2021) Pladias database of the Czech Flora and vegetation. Preslia 93:1–87. https://doi.org/10.23855/preslia.2021.001

Czerepko J, Gawryś R, Szymczyk R, Pisarek W, Janek M, Haidt A, Kowalewska A, Piegdoń A, Stebel A, Kukwa M, Cacciatori C (2021) How sensitive are epiphytic and epixylic cryptogams as indicators of forest naturalness? Testing bryophyte and lichen predictive power in stands under different management regimes in the Białowieża forest. Ecol Indic 125:107532. https://doi.org/10.1016/j.ecolind.2021.107532

de Vries W, Vel EM, Reinds GJ, Deelstra H, Klap JM, Leeters EEJM, Hendriks CMA, Kerkvoorden M, Landmann G, Herkendell J et al (2003) Intensive monitoring of forest ecosystems in Europe.

1. Objectives, set-up and evaluation strategy. For Ecol Manag 174:77–95. https://doi.org/10.1016/S0378-1127(02)00029-4

de Groot M, Eler K, Flajsman K, Grebenc T, Marinsek A, Kutnar L (2016) Differential short-term response of functional groups to a change in forest management in a temperate forest. For Ecol Manag 376:256–264. https://doi.org/10.1016/j.foreco.2016.06.025

Di Nuzzo L, Vallese C, Benesperi R, Giordani P, Chiarucci A, Di Cecco V, Di Martino L, Di Musciano M, Gheza G, Lelli C et al (2021) Contrasting multitaxon responses to climate change in Mediterranean mountains. Sci Rep 11:4438. https://doi.org/10.1038/s41598-021-83866-x

Düll R (1991) Zeigerwerte von Laub- und Lebermossen. In: Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (eds) Zeigerwerte von Pflanzen in Mitteleuropa, vol 18. Scr. Geobot, pp 175–214

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1992) Zeigerwerte von Pflanzen in Mitteleuropa. Scr Geobot 18:1–248

Elmendorf SC, Henry GHR, Hollister RD, Fosaa AM, Gould WA, Hermanutz L, Hofgaard A, Jónsdóttir IS, Jorgenson JC, Lévesque E et al (2015) Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proc Natl Acad Sci 112:448–452. https://doi.org/10.1073/pnas.1410088112

Fojcik B, Wierzgoń M, Chmura D (2019) Response of bryophytes to disturbances in managed forests. A case study from a Polish forest. Cryptogam Bryol 40(10):105–118. https://doi.org/10.5252/cryptogamie-bryologie2019v40a10

Frego KA (2007) Bryophytes as potential indicators of forest integrity. Forest Ecol Manag 242:65–75. https://doi.org/10.1016/j.foreco.2007.01.030

Gignac LD (2001) Bryophytes as indicators of climate change. Bryologist 104:410–420

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194. https://doi.org/10.1086/283244

Heinken T, Diekmann M, Liira J, Orczewska A, Schmidt M, Brunet J, Chytrý M, Chabrerie O, Decocq G, De Frenne P et al (2022) The European forest plant species list (EuForPlant): concept and applications. J Veg Sci. https://doi.org/10.1111/jvs.13132

Hodgetts NG, Söderström L, Blockeel L, Caspari S, Ignatov MS, Konstantinova NA, Lockhart N, Papp B, Schröck C, Sim-Sim M et al (2020) An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. J Bryol 42(1):1–116. https://doi.org/10.1080/03736687.2019.1694329

Horvat V, Heras P, García-Mijangos I, Biurrun I (2017) Intensive forest management affects bryophyte diversity in the western Pyrenean silver fir-beech forests. Biol Conserv 215:81–91. https://doi.org/10.1016/j.biocon.2017.09.007

Ingerpuu N, Vellak K, Liira J, Pärtel M (2003) Relationships between species richness patterns in deciduous forests at the north Estonian limestone escarpment. J Veg Sci 14:773–780. https://doi.org/10.1111/j.1654-1103.2003.tb02209.x

Jokela J, Juutilainen K, Korpela L, Kouki J, Kuntsi S, Koivula M, Siitonen J (2018) Cross-taxon congruence and relationships to stand characteristics of vascular plants, bryophytes, polyporous fungi and beetles in mature managed boreal forests. Ecol Indic 85:137–145. https://doi.org/10.1016/j.ecolind.2017.10.036

Kaufmann S, Hauck M, Leuschner C (2017) Comparing the plant diversity of paired beech primeval and production forests: management reduces cryptogam, but not vascular plant species richness. For Ecol Manag 400:58–67. https://doi.org/10.1016/j.foreco.2017.05.043

Kermavnar J, Kutnar L (2020) Patterns of understory community assembly and plant trait-environment relationships in temperate SE European Forests. Diversity 12:91. https://doi.org/10.3390/d12030091

Kermavnar J, Kutnar L, Marinšek A (2021a) Disentangling the ecological determinants of species and functional trait diversity in herb-layer plant communities in European temperate forests. Forests 12(5):552. https://doi.org/10.3390/f12050552

Kermavnar J, Kutnar L, Marinšek A (2021b) Variation in floristic and trait composition along environmental gradients in the herb layer of temperate forests in the transition zone between Central and SE Europe. Plant Ecol 223:229–242. https://doi.org/10.1007/s11258-021-01203-8

Kermavnar J, Ferlan M, Marinšek A, Eler K, Kobler A, Kutnar L (2020) Effects of various cutting treatments and topographic factors on microclimatic conditions in Dinaric fir-beech forests. Agric for Meteorol 295:1–12. https://doi.org/10.1016/j.agrformet.2020.108186

Király I, Nascimbene J, Tinya F, Ódor P (2013) Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. Biodivers Conserv 22(1):209–223. https://doi.org/10.1007/s10531-012-0415-y

Kriebitzsch W-U, Bültmann H, Oheimb G, Schmidt M, Thiel H, Ewald J (2013) Forest-specific diversity of vascular plants, bryophytes, and lichens. In: Kraus D, Krumm F (eds) Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Joensuu, pp 158–169

Kutnar L (2011) Diversity of woody species on forest monitoring plots in Slovenia. GozdVestn 69:271–278 (**in Slovenian with English Summary**)

Kutnar L, Veselič Ž, Dakskobler I, Robič D (2012) Typology of Slovenian forest sites according to ecological and vegetation conditions for the purpose of forest management. GozdVestn 70:195–214 (**in Slovenian with English Summary**)

Kutnar L, Eler K, Marinšek A (2016) Effects of different silvicultural measures on plant diversity—the case of the Illyrian Fagus sylvatica habitat type (Natura 2000). iForest 9:318–324. https://doi.org/10.3832/ifor1587-008

Kutnar L, Nagel TA, Kermavnar J (2019) Effects of disturbance on understory vegetation across Slovenian forest ecosystems. Forests 10:1048. https://doi.org/10.3390/f10111048

Kutnar L, Kermavnar J, Pintar AM (2021) Climate change and disturbances will shape future temperate forests in the transition zone between Central and SE Europe. Ann For Res 54(2):67–86. https://doi.org/10.15287/afr.2021.2111

Kutnar L, Kermavnar J, Sabovljević MS (2023) Bryophyte diversity, composition and functional traits in relation to bedrock and tree species composition in close-to-nature managed forests. Eur J For Res. https://doi.org/10.1007/s10342-023-01560-1

Laliberté E, Legendre P, Shipley B (2015) Package "FD"—measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Available on CRAN: https://cran.r-project.org/web/packages/FD/FD.pdf

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. https://doi.org/10.1890/08-2244.1

Lewandowski AS, Noss RF, Parsons DR (2010) The effectiveness of surrogate taxa for the representation of biodiversity. Conserv Biol 24:1367–1377. https://doi.org/10.1111/j.1523-1739.2010.01513.x

Lombardi F, Di Lella S, Altieri V, Di Benedetto S, Giancola C, Lasserre B, Kutnar L, Tognetti R, Marchetti M (2018) Early responses of biodiversity indicators to various thinning treatments in mountain beech forests. iForest 11:609–618. https://doi.org/10.3832/ifor2733-011

Martinčič A, Wraber T, Jogan N, Podobnik A, Turk B, Vreš B, Ravnik V, Frajman B, Strgulc Krajšek S, Trčak B et al (2007) Mala Flora Slovenije: Ključ za določanje praprotnic in semenk; Tehniška založba Slovenije: Ljubljana, Slovenia, p 967

Mölder A, Schmidt M, Schönfelder E, Engel F, Schulz F (2015) Bryophytes as indicators of ancient woodlands in Schleswig-Holstein (Northern Germany). Ecol Indic 54:12–30. https://doi.org/10.1016/j.ecolind.2015.01.044

Müller J, Boch S, Prati D, Socher SA, Pommer U, Hessenmöller D, Schall P, Schulz ED, Fischer M (2019) Effects of forest management on bryophyte species richness in Central European forests. For Ecol Manag 432:850–859. https://doi.org/10.1016/j.foreco.2018.10.019

Nagel TA, Firm D, Pisek R, Mihelic T, Hladnik D, de Groot M, Rozenbergar D (2017) Evaluating the influence of integrative forest management on old-growth habitat structures in a temperate forest region. Biol Conserv 216:101–107. https://doi.org/10.1016/j.biocon.2017.10.008

Nascimbene J, Marini L, Nimis PL (2007) Influence of forest management on epiphytic lichens in a temperate beech forest of northern Italy. For Ecol Manag 247(1–3):43–47. https://doi.org/10.1016/j.foreco.2007.04.011

Nordén B, Paltto H, Götmark F, Wallin K (2007) Indicators of biodiversity, what do they indicate? Lessons for conservation of cryptogams in oak-rich forest. Biol Conserv 135:369–379. https://doi.org/10.1016/j.biocon.2006.10.007

Oksanen J, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P et al (2020) Package "vegan" - Community Ecology Package v. 2.5-7. Available on CRAN. https://cran.r-project.org/web/packages/vegan/vegan.pdf

Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma R-J, De Bruyn L, Fuhr M, Grandin U et al (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv Biol 24:101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Roos RE, van Zuijlen K, Birkemoe T, Klanderud K, Lang SI, Bokhorst S, Wardle DA, Asplund J (2019) Contrasting drivers of community-level trait variation for vascular plants, lichens and bryophytes across an elevational gradient. Funct Ecol 33:2430–2446. https://doi.org/10.1111/1365-2435.13454

Sabatini FM, Burrascano S, Azzella MM, Barbati A, De Paulis S, Di Santo D, Facioni L, Giuliarelli D, Lombardi F, Maggi O et al (2016) One taxon does not fit all: herb-layer diversity and stand structural complexity are weak predictors of biodiversity in Fagus sylvatica forests. Ecol Indic 69:126–137. https://doi.org/10.1016/j.ecolind.2016.04.012

Sabovljević M, Vujičić M, Sabovljević A (2010) Diversity of saproxylic bryophytes in old-growth and managed beech forests in the Central Balkans. Plant Biosyst 144:234–240. https://doi.org/10.1080/11263500903561015

Staniaszek-Kik M, Chmura D, Żarnowiec J (2019) What factors influence colonization of lichens, liverworts, mosses and vascular plants on snags? Biologia 74(4):375–384. https://doi.org/10.2478/s11756-019-00191-5

Sundqvist MK, Sanders NJ, Wardle DA (2013) Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Annu Rev Ecol Evol Syst 44:261–280. https://doi.org/10.1146/annurev-ecolsys-110512-135750

Tinya F, Márialigeti S, Király I, Németh B, Ódor P (2009) The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Őrség, Western Hungary. Plant Ecol 204:69–81. https://doi.org/10.1007/s11258-008-9566-z

Tinya F, Kovács B, Bidló A, Dima B, Király I, Kutszegi G, Lakatos F, Mag Z, Márialigeti S, Nascimbene J et al (2021) Environmental drivers of forest biodiversity in temperate mixed forests—a multi-taxon approach. Sci Total Environ 795:148720. https://doi.org/10.1016/j.scitotenv.2021.148720

Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (1964–1980) Flora Europaea, vol 1–5. Cambridge University Press, Cambridge

Tutin TG, Burges NA, Chater AO, Edmondson JR, Heywood VH, Moore DM, Valentine DH, Walters SM, Webb DA (1993) Flora Europaea, 2nd edn. Cambridge University Press, Cambridge

Urbančič M, Kutnar L, Kralj T, Kobal M, Simončič P (2009) Site characteristics of permanent plots on the Slovenian 16 km × 16 km net. GozdVestn 2009(67):17–48 (**in Slovenian with English Summary**)

Urbančič M, Kutnar L, Kobal M, Žlindra D, Marinšek A, Simončič P (2016) Soil and vegetation characteristics on intensive monitoring plots of forest ecosystems. GozdVestn 74:3–27 (**in Slovenian with English Summary**)

Urbančič M, Simončič P, Prus T, Kutnar L (2005) Forest soil atlas of Slovenia. Ljubljana: Zveza gozdarskih društev Slovenije: Gozdarski vestnik: Gozdarski inštitut Slovenije, 100 p (**in Slovenian with English Summary**)

Van Zuijlen K, Klanderud K, Dahle OS, Hasvik Å, Knutsen MS, Olsen SL et al (2022) Community-level functional traits of alpine vascular plants, bryophytes, and lichens after long-term experimental warming. Arct Sci 8:843–857. https://doi.org/10.1139/as-2020-0007

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116:882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Vittoz P, Camenisch M, Mayor R, Miserere L, Vust M, Theurillat J-P (2010) Subalpine-nival gradient of species richness for vascular plants, bryophytes and lichens in the Swiss Inner Alps. Bot Helv 120(2):139–149. https://doi.org/10.1007/s00035-010-0079-8

WorldClim (2021) Global climate and weather data. https://www.worldclim.org/

ZGS (2022) Zavod za gozdove Slovenije (Slovenia Forest Service). http://www.zgs.si/