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Plant communities and their relations to habitat and microhabitat features along a management gradient in beech forests in Denmark

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ABSTRACT

Aims: Many empirical studies have found neutral or positive effects of forestry on plant alpha diversity in temperate deciduous forests, reflecting a positive effect of soil and canopy disturbances caused by forestry operations. The level to which this positive response to artificial disturbances mimics processes in natural forest ecosystems is less clear; hence, the systemic effects of forest management on ground floral communities remain obscure.

Location: Temperate Europe, Denmark.

Methods: We studied communities of ground-dwelling bryophytes and vascular plants in 400 plots distributed across 40 beech stands across four classes of forest management intensity – long unmanaged, recently unmanaged, near-to-nature managed, and shelterwood managed – while recording the incidence of a diverse array of microhabitats related to hydrology, canopy closure and soil disturbance.

Results: Microhabitat availability differed considerably among forest management classes as a response to management. Overall, forest management had a significant positive effect on the plot-level alpha diversity of both vascular plants and bryophytes. In contrast, beta diversity and total ecospace decreased with forest management intensity. Litter accumulation simultaneously decreased alpha diversity in both groups, while light availability, soil exposure and presence of wetlands respectively, were crucial for vascular plant and bryophyte richness. Forestry-created canopy gaps had a similar effect on alpha diversity as natural tree-fall gaps but supported a different set of species, mainly ubiquitous generalists.

Conclusions: Even if plant alpha diversity was lower in unmanaged forest stands, this did not significantly affect gamma diversity across the sampled stands, suggesting that plant richness needs to be considered at a relevant scale when evaluating forest management impact on biodiversity. These scaling issues seem to reflect fundamental differences in disturbance dynamics in managed and unmanaged forest ecosystems, which are typically not well accounted for in monitoring and research. A better understanding of disturbance dynamics in forest ecosystems and their spatial impact on biodiversity is needed to guide ecological restoration and management for biodiversity in production forest.

1. Introduction

Forest plant communities are shaped by a suite of factors working on scales from continental to local. While the regional species pool is mainly shaped by climate and the overall biogeographic history of the region in focus, local community composition is filtered mainly by edaphic conditions and the microclimate in interplay with natural and human disturbance dynamics. More specifically, soil pH and humidity,

humus and litter thickness, and light availability are key drivers determining forest understory plant community composition (Márialigeti et al., 2009; Schmidt, 2005) mediated by successful dispersal and establishment (Ehrlén and Eriksson, 2000; Gilbert and Lechowicz, 2004).

Many studies have shown that species diversity is lower in managed than in old-growth forests due to changed disturbance dynamics, reduced structural complexity and lack of suitable habitats for old-growth forest specialists (e.g. Chaudhary et al., 2016; Müller et al., 2019; Paillet et al., 2010). However, several studies have indicated that understory herbaceous plants are differently affected by management than most other organism groups. Indeed, the fact that managed forest stands often have higher light levels than undisturbed stands may benefit vascular plant species richness (e.g. Christensen et al., 2007; Schmidt, 2005). In addition, various forestry artefacts, such as roads, pathways, skid trails and ditches, may provide increased niche space for plants (Graae and Heskjær, 1997; Boch et al., 2013). Based on these observations, some authors have even argued that active management may be needed to sustain rich plant communities in forests (Mölder et al., 2014; Schmidt, 2005).

However, other studies indicate that the reduced local plant richness recorded in unmanaged or old-growth forests may be compensated by higher beta diversity reflecting differences in disturbance regimes (e.g. Kaufmann et al., 2017, 2018) and that forest management changes the composition of plant communities compared to unmanaged or pristine forests. Lelli et al. (2019), working with a subset of the data analysed in this paper, found that several plant traits changed with increasing human impact, indicating a substantial turnover, with functionally simplified but species-rich communities prevailing in managed forest stands. Hence, we find it premature to recommend active forest management to maintain high plant diversity in European forests. Rather, we identify a strong need to better disentangle the drivers of plant richness in these ecosystems.

The importance of light availability as a driver of plant diversity is not least relevant in forest types dominated by shade-tolerant tree species, such as European beech (*Fagus sylvatica* L.), a dominant tree species in major parts of temperate Europe (Packham et al., 2012; Peters and Poulson, 1994). This species naturally inhibits the growth of many vascular plants and bryophytes due to the strong shade cast by its dense canopy (Aude and Lawesson, 1998; Wulf and Naaf, 2009). Further, high levels of slowly degraded litter in *F. sylvatica* stands limits plants and bryophytes as it acts as a barrier, preventing propagules from reaching the mineral soil and hampering germination and establishment due to the deep shade under the litter layer (Aude and Lawesson, 1998; Loydi et al., 2014; Márialigeti et al., 2009; Wulf and Naaf, 2009). European beech forests have been altered by management activities over several centuries (Giesecke et al., 2007), resulting in habitat loss with only small remnants of unmanaged, old-growth fragments remaining (Christensen et al., 2005). Management systems show considerable variation in time and space (Bergès et al., 2013; Bergès and Dupouey, 2021; Márialigeti et al., 2016), but they have overall shifted natural patch dynamics to dynamics and disturbances governed by logging activities, thus disrupting, simplifying and shortening the forest cycles and affecting microclimatic conditions as well as habitat availability (Brunet et al., 2010; Wulf and Naaf, 2009; Zielińska, 2017). Partly to counteract these negative effects on forest biodiversity, new near-to-nature forestry principles are increasingly advocated and implemented to balance production with biodiversity conservation (Brunet et al., 2010). However, recent studies (Gossner et al., 2013; Schall et al., 2018) indicate that such approaches may not benefit biodiversity unless great care is taken to understand how management actions affect habitat abundance and quality.

Several recent studies have investigated how tree-associated microhabitats relate to forest management and, in turn, affect epiphytic lichens and bryophytes, saproxylic arthropods, birds and bats (e.g. Basile et al., 2020; Fritz and Heilmann-Clausen, 2010). Similar studies on forest floor plants and bryophytes have mostly investigated the effects of canopy gaps and, to some extent, soil exposure or the presence of wetlands (Gálhidy et al., 2006; Jonsson and Esseen, 1990; Zielińska, 2017). To our knowledge, few studies have investigated the effect of several soil microhabitats simultaneously, and even fewer have compared the effects of natural and anthropogenic microhabitats on species diversity and community structure (Baltzinger et al., 2011; Burton and Eggleton, 2016; Kermavnar et al., 2019).

Here, we apply a microhabitat approach to explore how local conditions shape plant communities on beech forest floors along a gradient in management intensity. Apart from analysing simple species richness as affected by microhabitat features and overall environmental conditions, we also investigated species composition and indicator species associated with natural versus management-induced microhabitats. Further, we adapted an ecospace approach (Brunbjerg et al., 2017, 2020) to investigate the total diversity of plant habitats available across the full study in relation to a management gradient spanning from long unmanaged to intensively managed shelterwood stands.

It is important to note that none of the included stands are in close to pristine condition. All stands were subject to livestock grazing, pig pannage and varied types of utility forestry from medieval times to the early 19th century, and with a few exceptions also to more intensive timber-oriented forestry since 1805, when a forest protection act prioritised timber production by making it the only legal management goal in Danish forests (Fritzbøger, 1999).

Our overall aim in undertaking this study is to explore how forest management affects understory vegetation in Danish beech-dominated forests by examining the alterations of niche availability and ecological conditions across a gradient of management intensity and abandonment. Rather than taking a hypothesis-testing approach, we took a curious approach to investigate the effects of microhabitat conditions and environmental drivers by quantifying species richness and diversity (alpha, beta and gamma), identifying indicator species associated with natural versus management-induced microhabitats and compare the effects of these microhabitats on species diversity and community structure. Additionally, we apply an ecospace approach to explore plant habitat diversity across a management gradient, from long unmanaged to intensively managed shelterwood stands, to determine how management intensity correlates with ecological conditions and niche availability. By addressing these aims, the study will provide a nuanced understanding of how varying degrees of forest management influence the ecological conditions and understory vegetation diversity in beech forests.

2. Material and methods

2.1. Study sites

The study was conducted in 40 stands of European beech-dominated (*Fagus sylvatica* L.) forests across six forest areas (clusters) in Denmark (Fig. 1). The forest clusters were selected based on the following criteria: (1) presence of unmanaged old growth and protected remnants of at least 10 ha, (2) large overall forests with remaining substantial areas of semi-natural forest types, and (3) complementarity in coverage of climatic and geographical variation in Denmark. Following the terminology suggested by Trentanovi et al. (2023), the stands can be described as single- to multi-storeyed stands affected by ongoing or past shelterwood forestry. The stands ranged between 3.01 and 6.5 ha in size and were delimited to avoid larger wetland areas and external forest edges. European beech comprised > 60 % of the basal area in all stands where overstory trees were at least 70 years old (for a full site description, see Appendix A, Tables A1 and A2). The stands were chosen to represent a gradient in forest management intensity organised in four broad classes: a) structurally simple conventionally managed shelter wood stands with a single tree layer, dominant trees 70–100 years old, no or little coarse woody debris (CWD), b) more structurally complex managed stands
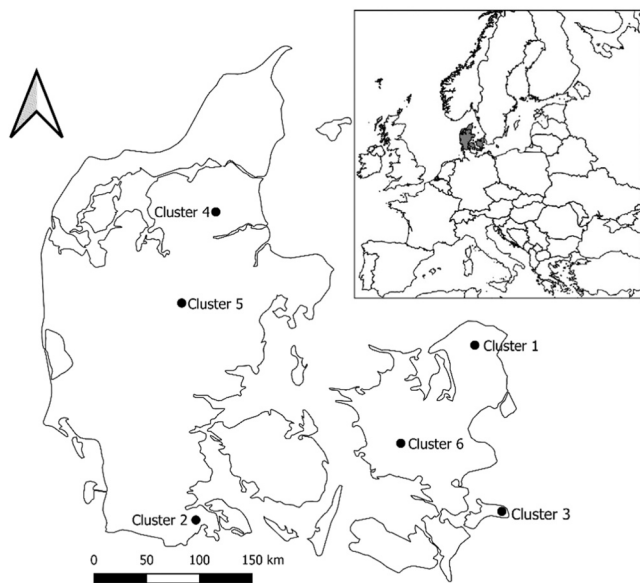
Fig. 1. The locations of different forest clusters in Denmark. Cluster 1 – Gribskov, cluster 2 – Gråsten, cluster 3 – Møn, cluster 4 – Rold, cluster 5 – Silkeborg, cluster 6 – Sorø.

with multiple tree layers, dominant trees 80–150 years old, some CWD present – often subject to near-to-nature management, c) stands with recent abandonment of management (< 30 years) with dominant trees being 100 years or older, d) long unmanaged stands (in principle > 50 years but often with slight management more recently) with dominant trees older than 200 years. All four management classes were represented by one stand in each cluster, except for the Gribskov cluster, which comprised 20 stands equally distributed across the four management classes. Part of the dataset was previously analysed by Lelli et al. (2019) using a different analytical approach, with a focus on multi-taxa diversity, and by Atrena et al. (2020) focusing on saproxylic fungi, and these two studies provides additional overview of the structural differences between the management classes.

2.2. Data collection

In 2015 (Gribskov) and 2017 (other clusters), we conducted surveys of vascular plants and bryophytes in 10 circular plots (5-metre radius) per stand. Our plot selection employed a semi-strategic approach: first, 10 plots were placed randomly within each stand using GIS, with a minimum distance of 30 m between plots. Second, the field survey botanist could choose to replace up to five random plots strategically. This adjustment aimed to maximise the capture of gamma diversity of vegetation within each stand, without compromising representativity. Thus, strategic plots where typically placed in parts of the stands characterized by rich or somewhat divergent vegetation reflecting gap conditions, soil disturbance or humid soil conditions, but still representing the overall forest type. This approach was selected based on the observation that as plant alpha and beta diversity patterns were often very different between managed and unmanaged stands, using randomly placed plots might lead to a serious underestimation of stand-level gamma diversity in unmanaged stands, as also observed by Kaufmann et al. (2017).

The age of the forest stands was recorded from forest maps provided by the forest owners (mainly the Danish state), while management types were determined based on personal communications with local forest managers and data in Graae and Buchwald (1997). Further, the years since last management intervention (typically logging) was recorded based on the same sources. Where reliable data were lacking, the decay stage of cut stumps was used to infer the approximate years since the last

intervention. We expected the forest floor and soil conditions to have an impact on plant communities; hence, at plot level we measured soil pH, light availability, thickness of litter and presence of a well-defined humus layer. Apart from these mainly continuous variables, the impact of natural and artificial disturbance and hydrology was assessed by recording the presence of more overall forest floor microhabitats divided into three main groups, namely, canopy openings, wetlands, and soil exposure, comprising a total of eight microhabitat types (Appendix A, Table A3). The classification of ditches in the soil exposure group was based on the observation that these were mainly dry, except during periods with excess precipitation, and were therefore expected to influence plant communities by exposing mineral soil rather than providing wetland habitats. All parameters considered in subsequent analyses are described in detail in Table 1.

2.3. Statistical analysis

2.3.1. Ecospace and species richness

In total, 400 plots from forty stands were investigated. To assess the impact of forest floor disturbances and environmental factors on the species richness and community composition of the target taxa, we conducted the analyses at plot level.

One-way ANOVAs were applied to evaluate the distribution of microhabitat types across management classes. As the microhabitat count per stand is a proportion of the total number of plots, arcsine transformation was applied to normalise the data distribution. One-way ANOVAs and Tukey's tests (and their non-parametric alternatives, where ANOVAs assumptions where not met) were applied to examine differences in continuous environmental variables across the management classes.

To test for differences in species richness in plots with, without and across microhabitats, we summarised the species count across plots and ran a permutational analysis of variance (ANOVA) (R 'permuco' package, Frossard and Renaud, 2021). To investigate differences in cumulative species richness across different forest management classes, we created rarefaction curves (R 'vegan' package, Oksanen et al., 2024). Rarefaction curves allow for a standardized comparison of species richness, thus providing a robust method to compare the gamma diversity of the four management classes.

Generalised linear mixed effect models (GLMM) were run to test for differences and the relative contributions of different microhabitats and management classes to explain species richness while accounting for variation in environmental gradients and pseudo-replicated sampling design (R 'glmmTMB' package, Brooks et al., 2017). Two models were fitted, namely, 1) log-linear regression with Poisson error distribution for bryophyte and 2) negative binomial for vascular plant richness, both using Laplace approximation and maximum likelihood (Bolker et al., 2009).

The relationships between variables were checked by Spearman-rank correlation (R 'corrplot' package, Wei and Simko, 2017). Further, we tested the predictor variables for multicollinearity by applying variance inflation factor before (VIF; R 'usdm' package, Naimi et al., 2014) and after (R 'performance' package, Lüdecke et al., 2024) adding them to the starting model and removed variables if the value exceeded four. For both models, the 'Management' variable exceeded the value of four and was hence not used in further models. To account for the pseudo-replicated sampling design, a nested random effect structure was chosen with 'Clusters' and 'Stands' as random factors. The goodness-of-fit and assumptions of the models were assessed with quantile residual plots, Q-Q plots and dispersion plots (R 'DHARMa' package, Hartig and Lohse, 2022). Both models had a larger number of observed zeros than predicted; therefore, the zero-inflation formula was applied. To simplify the presentation of predictor variable effects, model estimates were presented using incidence rate ratios (IRR) (Rita and Komonen, 2008).

Table 1

Summary of the variables used in the study. Levels: C – cluster, S – stand, P – plot. Application - usage of variables as fixed versus random effects in generalized mixed effect models (GLMM).

Variable as used in analyses	Description	Level	Range/Category	Application
Cluster	Aggregates of forest stands in geographical clusters	C	1–6	Random
Stand no.	Forest stand number	S	1–40	Random
Stand age (yrs)	Stand age in 2019	S	77–350	Fixed
Years since last logging	Years since last logging or thinning	S	1–70	Fixed
Management	Forest management types in investigated stands	S	Long unmanaged; recently unmanaged; near to nature managed; conventionally managed	Fixed
Soil disturbances	Plots with some level of open soil	P	Ditch; wheel track; soil exposed by fallen tree	Fixed
Canopy openings	Plots with evident gaps in canopy cover	P	Natural gaps; forestry gaps	Fixed
Wetlands	Plots with presence of wetland habitat	P	Ditched depression; natural depression; spring	Fixed
Plot placement	Plots with strategic or random placement	P	Random plots (total = 231); strategic plots (total = 169)	Fixed
Humus	Presence/absence of a well-defined humus soil layer	P	Present (244); absent (156)	Fixed
Densitometer	Degree of light precipitation through canopy as measured by convex densitometer at four points, placed in cardinal directions five metres from the plot centre	P	Min – 0; max – 99.5, average – 11.26	Fixed
Litter thickness	Thickness of litter layer (cm)	P	Min – 0.17 cm; max – 9 cm; average – 3.3 cm	Fixed
pH	Soil pH measured with a pH-meter after mixing soil with distilled water (2:1) and leaving it to settle for one hour	P	Min – 3.74; max – 7.69; average – 4.89	Fixed

2.3.2. The effect of microhabitats and management classes and geography on species composition

To identify species-specific associations with the investigated microhabitats, we tested whether any of the plant or bryophyte species had a significant preference for any given microhabitat group (i.e. soil disturbances, canopy openings and wetlands, or within-group combinations) by using indicator species analyses (R 'indicspecies' package; De Cáceres and Legendre, 2009). We used Pearson's phi coefficient of association to measure the strength of the association. The analysis was run separately for the three sets of microhabitats allowing within-group combinations.

To assess if the ecological range of indicator plant and bryophyte species differed among microhabitats, the Ellenberg indicator values of light (L), moisture (F), reaction (R) and nutrients (N) (the latter only to the vascular plants) was applied. We used one-way ANOVA tests and Tukey's post-hoc tests to determine if the differences in Ellenberg values between the different microhabitat types were significant. Where ANOVA assumptions of normal distribution and homogeneity of variance were not met, we used permutational ANOVAs. However, only microhabitats with minimum of five indicator species were included in the analysis.

Non-metric multidimensional scaling (NMDS) with the Bray–Curtis distance matrix calculated for species occurrence data was used to analyse the overall dimensions of ecospace as present within the four management classes. The ordinations were set to 999 iterations, and the minimal number of axes was chosen with stress value < 0.2. We then calculated correlations between community composition and environmental data to identify variables related to turnover in community structures. We evaluated the statistical significance ($p < 0.05$) of these differences in community structures by applying a permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations, and when significant, we used pairwise permutational tests. We applied dispersion tests to account for possible Type 1 and 2 errors due to unbalanced design, as the number of microhabitats was not equal across the sites (Anderson and Walsh, 2013). As proposed by Anderson et al. (2006), multivariate dispersion can also be used as a measure of beta diversity; hence, we compared the beta dispersion across different management classes. All tests were carried out using the R 'vegan' package by Oksanen et al. (2024).

To assess the extent to which the community structure was affected by geographic location, we used the same NMDS procedure as described above. As one of our geographical clusters (Gribskov) represented 50 % of the data, we selected only one sub-cluster of four sites from this area

to make the design for the PERMANOVA balanced, resulting in 24 study sites (240 plots). We included clusters as a factor variable in correlations made between community structure and environmental data, as described above.

3. Results

In total, 299 species, of which 209 were vascular plants and 90 were bryophytes, were recorded. At least one microhabitat type was recorded in 281 of 400 plots, with a maximum of three microhabitat types being present in the same plot. The most frequent microhabitats were natural gaps (111 plots), followed by wheel tracks (59 plots) and forestry gaps (49 plots) (Appendix A). Gamma diversity (i.e. species richness across all plots and stands) showed no consistent trend in relation to management intensity, neither based on raw species numbers (Table 2) or rarefaction (Appendix C)

Several environmental factors showed large differences between the management classes (Table 3). Stand age (F =148, p > 0.001) and years since last logging (F = 193.4, p > 0.001) decreased with management intensity, but data for years since last logging showed that the rough classification of unmanaged stands in two classes did not reflect the actual conditions. In addition, some managed stands had not been thinned for up to 30 years. Canopy openness was slightly higher in unmanaged stands, although this difference was not statistically significant. Furhter, unmanaged stands demonstrated the greatest variability in canopy openness. Soil pH was on average higher and more varied in unmanaged than managed stands (F =3.51, p = 0.014).

3.1. Microhabitat presence in relation to management

Microhabitat presence was strongly related to management intensity (Fig. 2). Among soil microhabitats (Fig. 2.1), both classes of managed forest stands had significantly higher numbers of wheel tracks (F = 11.26, p > 0.001), while both classes of unmanaged forest stands had

Table 2

Total species richness across different management classes; Management: LU – long unmanaged, RU – recently unmanaged, NN – near-to-nature managed, MA – conventionally managed.

Species richness	LU	RU	NN	MA
Vascular plants	135	152	140	132
Bryophytes	78	81	77	81

Table 3

Summary statistics of the main environmental variables used in the study divided across the four management intensity classes. Asterisks (ns: p > 0.05, *: p < 0.01, *****: p < 0.001) under P value reflect the results from ANOVAs and non-parametric ANOVAs, where parametric ANOVA's assumptions were not met.

| Environmental variable	Long unmanaged		Recently unmanaged		Near-to-nature managed		Conventionally managed		P
	Mean ± SD	*Range*	*Mean ± SD*	*Range*	*Mean ± SD*	*Range*	*Mean ± SD*	*Range*	
Canopy openness (%)	12.3 ± 14.8	2.75 – 95.5	12.7 ± 14	2.75 – 67.25	11.1 ± 10.5	2.5 – 57.25	8.9 ± 6.3	2.75 – 36.5	ns
Litter thickness (cm)	3.6 ± 1.5	0.33 – 7.33	3.2 ± 1.5	0.33 – 8.33	3.1 ± 1.7	0.33 – 9.0	3.3. ± 1.2	0.17 – 6.33	ns
Soil pH	4.9 ± 1.1	3.81 – 7.67	5.1 ± 1.1	3.94 – 7.94	4.8 ± 0.9	4.01 – 7.64	4.7 ± 0.6	3.74 – 6.96	*
Stand age (yrs)	229 ± 67	125 – 350	175.6 ± 42.4	124 – 251	133.4 ± 26.4	100 – 189	111.8 ± 18	77 – 140	***
Years since logging	44.5 ± 19.4	15 – 70	23 ± 9.3	5 – 40	8.6 ± 6.2	1–25	10.1 ± 8.3	1 – 30	***
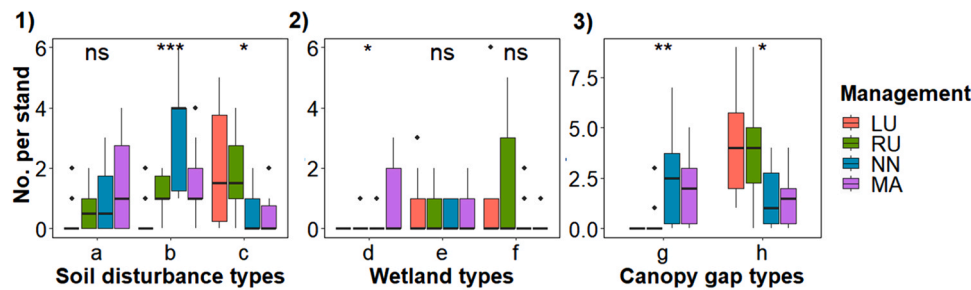
Fig. 2. Distribution of microhabitats across management classes. Asterisks (ns: p > 0.05, *: p < 0.01, ***: p < 0.001) above the boxplots indicate the results from ANOVA tests of each microhabitat versus management classes. Soil disturbances: a) ditch, b) wheel track, c) soil exposed by a fallen tree; wetland types: d) ditched depression, e) natural depression, f) spring; canopy gaps: g) from forestry, h) natural. Management: LU – long unmanaged, RU – recently unmanaged, NN – near-to-nature managed, MA – conventionally managed.

higher amounts of soil exposed by fallen trees (F = 3.32, p = 0.035). Among wetlands (Fig. 2.2), only ditched depressions showed significant differences among management classes (F = 3.17, p = 0.035), with conventionally managed forest stands having the highest values (Fig. 4b). Both canopy gap types showed different distributions across management classes (Fig. 2.3), with gaps caused by felling (F = 7.52, p > 0.001) being almost absent in both unmanaged stand classes, while natural gaps (F = 4.30, p = 0.014) were present in significantly higher numbers in unmanaged stands.

### 3.2. Plant alpha diversity across microhabitats and management classes

Long unmanaged stands had slightly lower alpha diversity than near-to-nature and conventionally managed stands for both organism groups (Fig. 3.1, 3.2) (vascular plants: *p = 0.01*, F = 3.78; bryophytes: *p = 0.003*, F = 4.52). Similarly, plots where microhabitats were present (Fig. 3.3, 3.4) supported significantly more species (vascular plants: mean = 12.9; SD = 6.1; bryophytes: mean = 4.9; SD = 3.4) than plots without microhabitats (vascular plants: mean = 7.4; SD = 4.61; bryophytes: mean = 3.3; SD = 3.03) for both organism groups (vascular plants: *p < 0.001*; F = 97.44; bryophytes; *p < 0.001*; F = 20.74). Zooming in on individual microhabitats (Fig. 3.5–3.10), patterns were slightly more complex. Canopy openings supported significantly higher species richness than plots with closed canopy (vascular plants: *p < 0.001*; F = 26.95; bryophytes; *p < 0.001*, F = 19.74). However, only natural gaps had higher richness for bryophytes than plots in closed canopy or forestry-caused gaps, and for vascular plants both canopy opening types had higher richness than plots in closed canopy, but there was no significant difference between the two canopy opening types. Ditches had the highest alpha diversity across all soil disturbance types for both vascular plants and bryophytes (vascular plants: *p < 0.001*; F = 6.84; bryophytes: *< 0.001*, F = 13.88), and soil exposed by fallen trees supported more bryophyte species (*p = 0.015*) than plots without soil disturbances, while other soil disturbance types did not support more species than plots without soil disturbances. Among wetland microhabitats, only ditched depressions for vascular plants (*p < 0.001*, F = 5.89) supported more species than plots without wetland microhabitats.

3.3. Effect of total ecospace on alpha diversity

The multiple regression models, including environmental variables and disturbance types, explained 57 % of the variation in vascular plant species richness and 47 % of the bryophyte species richness at the plot level (Table 4 & 5). Incorporating geographical clusters and stands as random effects significantly contributed to model performance, explaining approximately 20 % of the variation in species richness for both groups. Notably, increasing litter thickness had a strong negative effect on vascular plant richness, while decreasing canopy cover had a positive effect. For bryophyte richness, years since last logging, increasing litter thickness and soil pH had strong negative effects. Additionally, various microhabitat types exhibited strong positive effects on both vascular plants and bryophytes. Ditches positively impacted species richness, especially bryophytes, while soil exposure by wheel tracks increased richness for vascular plants, and soil exposed by fallen trees did the same for bryophytes. Among wetland microhabitats, the presence of both natural and ditched depressions contributed to vascular plant richness. Both natural and forestry gaps had a strong positive effect on vascular plant richness, while the effect was not present for bryophytes.

3.4. Effects of management on species composition and beta-diversity

NMDS ordinations showed that geographical location (i.e. cluster) had a strong effect on species composition, with distinct geographical clustering in both organism groups across Denmark, explaining 29 % of the variations in vascular plant and 20 % in bryophyte community structures (Fig. 4.3 and 4.4). This geographical segregation was strongly related to turnover in soil pH and, to a smaller extent, canopy cover, litter and humus accumulation (Fig. 4.5 and 4.6). A much smaller yet significant effect on species composition was detected for management class (Fig. 4.1 and 4.2), explaining 2 % of the differences in the bryophyte (PERMANOVA: *p = 0.001*; F = 2.87) and 4 % in the vascular plant (PERMANOVA: *p = 0.001*; F = 3.34) community structures. Communities in unmanaged stands had significantly larger expansion in the ordination space than managed stands measured by pairwise PERMANOVAs, while no differences were observed between long versus
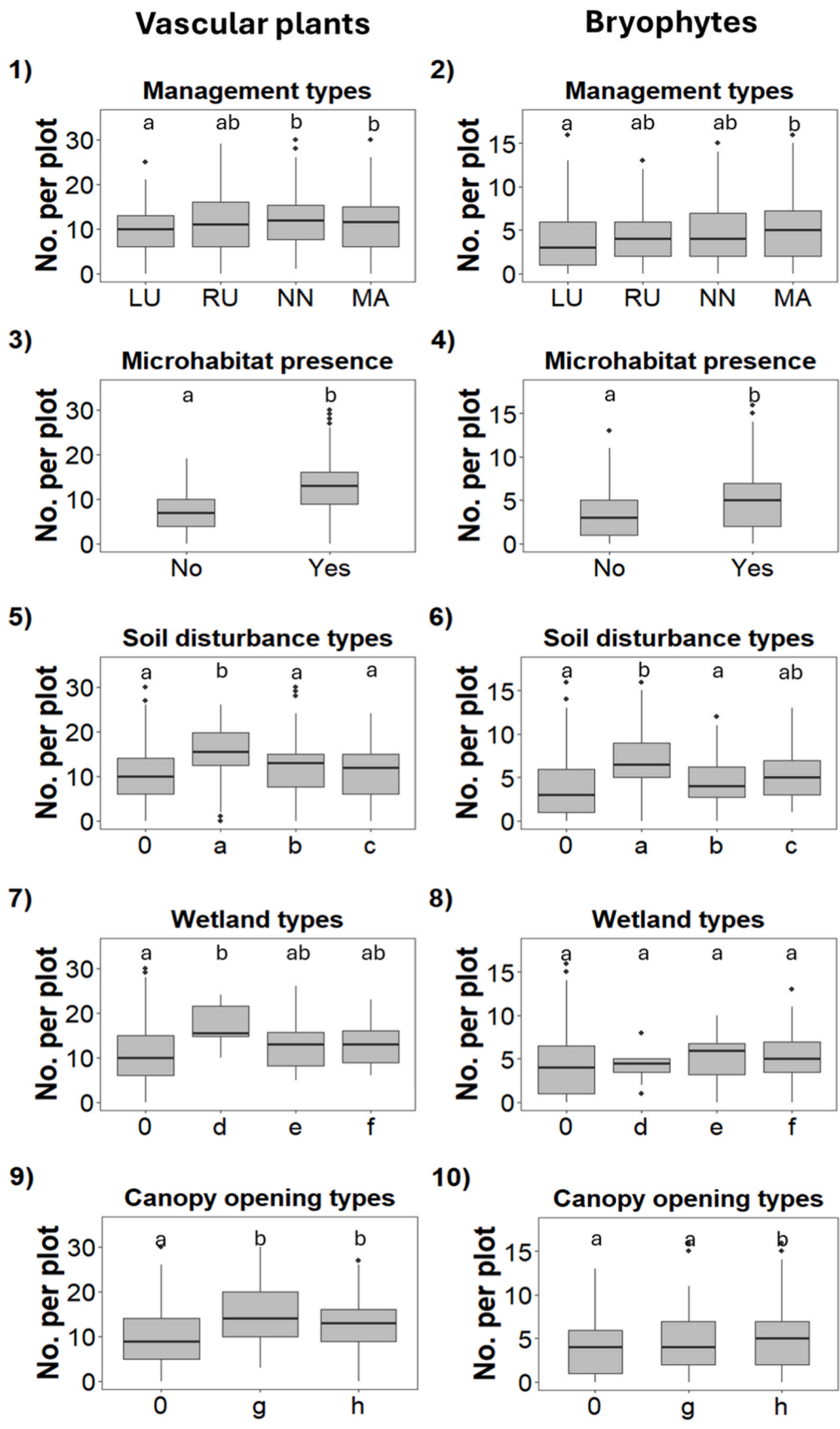
(caption on next page)

Fig. 3. Species richness of vascular plants (1,3,5,7,9) and bryophytes (2,4,6,8,10) across microhabitats and different management classes. Letters above each boxplot figure indicate the results from pairwise comparisons from a Tukey test and ANOVA and their non-parametric alternatives, where parametric ANOVAs' assumptions were not met. The abbreviations below the boxplots indicate management: LU – long unmanaged, RU – recently unmanaged, NN – near-to-nature managed, MA – conventionally managed. The letters below each boxplot indicate microhabitats: soil disturbances a) ditch, b) wheel track, c) soil exposed by a fallen tree; wetland types d) ditched depression, e) natural depression, f) spring; canopy gaps g) from forestry, h) natural. In all microhabitat boxplots "0" represents plots without any microhabitat.

Table 4

GLMM variable effects on vascular plant species richness. The results are expressed in IRR values, where the reference point is one, indicating no effect on species richness, and values above one indicate a positive effect, while values below one indicate a negative effect on species richness. For categorical variables, a 'reference' category was selected to allow comparisons with the other categories within the variable. Random effects: σ2 – residual or unexplained variability; τ00 – variance explained by different combinations of random factors; ICC – intra-class correlation between individuals within groups; N – number of individual groups within each random effect; Marginal R2 – explained variance without accounting for random effects (as in GLM); Conditional R2 – explained variance with accounting for random effects, as calculated by Nakagawa and Schielzeth, (2013).

GLMM for vascular plant species richness				
Predictors	Incidence Rate Ratios	Std. Error	Z stat	p value
(Intercept)	**8.962**	**0.656**	**29.946**	**<0.001**
Years since last logging	0.934	0.043	−1.475	0.14
Stand age	0.942	0.035	−1.594	0.111
Canopy openness	**1.078**	**0.021**	**3.825**	**<0.001**
Litter thickness (cm)	**0.915**	**0.019**	**−4.333**	**<0.001**
Increasing pH	1.053	0.028	1.911	0.056
Humus layer – not present	*Reference*			
Humus layer – present	**0.909**	**0.043**	**−2.009**	**0.044**
Soil exposure: no exposure	*Reference*			
Soil exposure by ditch	**1.174**	**0.066**	**2.841**	**0.004**
Soil exposure by wheel track	**1.166**	**0.056**	**3.175**	**0.001**
Soil exposure by fallen tree	1.054	0.058	0.96	0.337
Wetlands: dry plots	*Reference*			
Wetland: ditched depression	**1.296**	**0.116**	**2.887**	**0.004**
Wetland: natural depression	**1.17**	**0.08**	**2.28**	**0.023**
Wetland: spring	1.138	0.085	1.738	0.082
Canopy openings: no gap	*Reference*			
Forestry gaps	**1.312**	**0.073**	**4.902**	**<0.001**
Natural gaps	**1.226**	**0.062**	**4.043**	**<0.001**
Sample plot placement: random	*Reference*			
Sample plot placement: strategic	**1.215**	**0.042**	**5.58**	**<0.001**
Zero-Inflated Model				
(Intercept)	**0.028**	**0.009**	**−10.917**	**<0.001**
Random Effects				
σ²	0.11			
τ00 stand:cluster	0.04			
τ00 cluster	0.01			
ICC	0.31			
N stand	40			
N cluster	6			
Observations	400			
Marginal R² / Conditional R²	0.376 / 0.572			

recently unmanaged stands and near-to-nature versus conventionally managed stands. For bryophytes, a more systematic response to years since last logging was also evident along NMDS2 (Fig. 4.6) Table 5.

Both bryophytes (*p = 0.027*; F = 3.19) and vascular plants (*p < 0.001*; F = 6.34) showed significantly higher beta diversity in unmanaged than in managed stands at plot level. However, the significance of the differences disappeared when aggregating data at stand level (vascular plants *p = 0.168*; F = 1.84; bryophytes: *p = 0.234*; F = 1.49), even if the trend remained the same (Table 6).

3.5. Microhabitat effects on species composition and single species presence

Based on PERMANOVA (vascular plants: p > 0.001; F = 6.9; bryophytes: p > 0.001; F = 4.34), small but significant differences in community structure were evident when comparing plots without and with microhabitats. Across both organism groups, the strongest response to microhabitat presence compared to control was found for ditches, natural gaps and springs (Table 7). Among the soil disturbance microhabitats, plots with ditches differed significantly in species composition from plots with other types of soil disturbance, while plots with natural depressions differed significantly from plots where springs were present. Natural and forestry caused canopy gaps hosted different bryophyte communities, while this effect was not present for vascular plants.

Zooming in on individual species preferences, 135 (41 bryophyte and 94 vascular plant species) out of 333 species showed significant indicator values for one or more microhabitats, of which 86 showed strong associations (association coefficient higher than 0.2) (summary Table 8, full tables Appendix B). For vascular plant indicator species, Ellenberg values more commonly indicated moderate to high values for moisture and nitrogen, and moderate to high light and moisture values for bryophyte indicator species (full tables Appendix B). As several of the microhabitat groups had very few associated species, statistical comparison of Ellenberg values between different microhabitats were not possible.

Canopy gaps had the highest number of indicator species (62 in total) within both organism groups, but only 14 of these had an association coefficient higher than 0.2. Wetlands had 56 associated indicator species, but all with a coefficient of association > 0.2. Soil disturbances had 51 indicator species, 30 of which had a coefficient of association > 0.2. Among bryophytes, 19 species were associated with soil disturbances and 11 with a strong association, while vascular plants had 32 species with 19 strong associations.

4. Discussion

We studied vascular plant and bryophyte diversity across a forest management gradient in Danish beech forests as related to management intensity and abandonment. The plot-scale alpha diversity of both plant groups was higher in managed stands, while beta diversity showed the opposite trend. We interpret these differences to reflect principal differences in disturbance regimes, influencing light availability in the field layer. In long unmanaged beech forests, biostatic phases characterised by strong competition for light cause strong shade dominance in the field layer. However, high light availability occurs patchily in canopy gaps due to natural tree death in the degradation and innovation phases (e.g. Emborg et al., 2000). This implies that such orthodox unmanaged beech forests tend to be spatially dominated by plant communities drawn from a rather small regional species pool of shade-tolerant herbs, with canopy gaps acting as hot-spots supporting shade-intolerant herbaceous communities, drawn from a much larger species pool (Brunet et al., 2010; Naaf and Wulf, 2007). In Denmark and many other European countries, beech forests are generally managed as shelterwood systems with regular thinning, as described by Brunet et al. (2010). This practice creates even-aged stands with modest, but uniform light availability during most of the rotational cycle after a period of almost full light extinction on the forest floor during the regenerative phase.
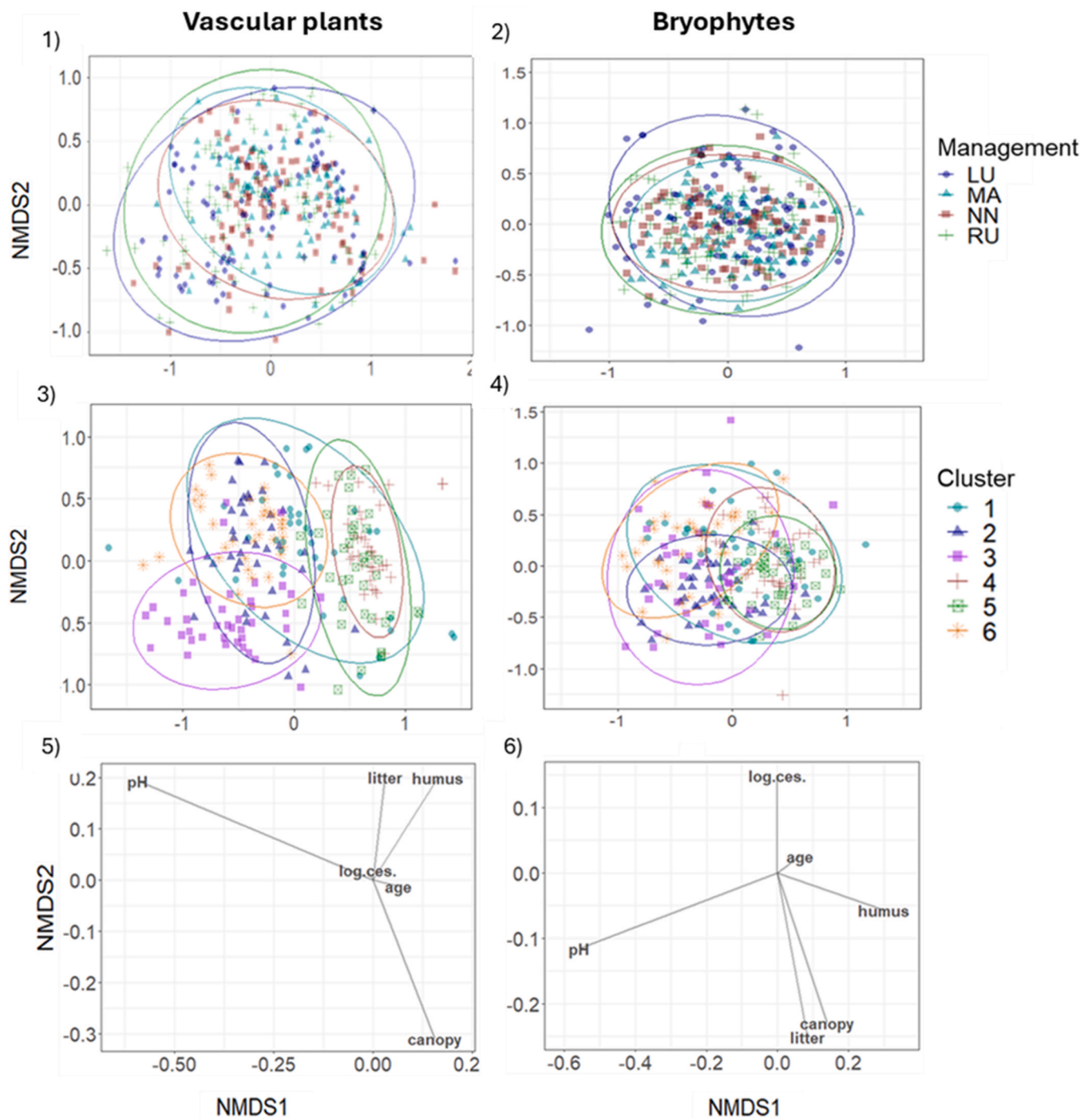
Fig. 4. NMDS results for vascular plants in different (1) management and (3) cluster classes, and bryophytes in different (2) management and (4) cluster classes. Different management classes: LU – long unmanaged; RU – recently unmanaged; NN – near-to-nature managed; MA – conventionally managed. Further, the main environmental gradients for (5) vascular plants and (6) bryophytes from the envfit analysis are: pH – soil pH value, canopy – light intensity, humus – presence of humus layer, litter – litter thickness, log.ces. – years since last management activities in the stand, age – stand age; stress for bryophyte ordination – 0.18: stress for vascular plant ordination – 0.16.

4.1. Drivers of plot-level richness

Vascular plant richness at the plot level was strongly related to canopy openness, measured both as relative canopy cover and by the presence of manmade and natural canopy gaps, reflecting the well-known effect of diminishing vascular plant diversity with increasing canopy shading (e.g. Cornwell and Grubb, 2003). The weak and statistically insignificant response of bryophyte richness to canopy openness

is more surprising, as other studies have found bryophytes to be very sensitive to forest light conditions (e.g. Tinya et al., 2009). In our study system bryophyte growth is generally limited to small, favourable microsites rather than occurring as wide mats or carpets as seen in, for example, coniferous forests (cf. Müller et al., 2019). This restricted and patchy occurrence is probably the main reason that we did not find light availability to matter much. Litter accumulation constrained diversity in both groups as previously reported for both vascular plants (Eriksson,

Table 5
GLMM variable effects on bryophyte species richness. For a full description of the abbreviations, see Table 4.

GLMM for bryophyte species richness				
Predictors	Incidence Rate Ratios	Std. Error	Z stat	p value
(Intercept)	**3.045**	**0.33**	**10.288**	**<0.001**
Years since last logging	**0.844**	**0.061**	**−2.335**	**0.02**
Stand age	1.04	0.073	0.555	0.579
Canopy openness	1.049	0.034	1.495	0.135
Litter thickness (cm)	**0.78**	**0.026**	**−7.348**	**<0.001**
Increasing pH	**0.881**	**0.04**	**−2.812**	**0.005**
Humus layer – not present	Reference			
Humus layer – present	**1.283**	**0.101**	**3.17**	**0.002**
Soil exposure: no exposure	Reference			
Soil exposure by ditch	**1.849**	**0.163**	**6.949**	**<0.001**
Soil exposure by wheel track	1.125	0.094	1.398	0.162
Soil exposure by fallen tree	**1.468**	**0.127**	**4.432**	**<0.001**
Wetlands: dry plots	Reference			
Wetland: ditched depression	0.773	0.128	−1.548	0.122
Wetland: natural depression	1.158	0.131	1.305	0.192
Wetland: spring	1.063	0.121	0.532	0.595
Canopy openings: no gap	Reference			
Forestry gaps	0.958	0.088	−0.462	0.644
Natural gaps	1.091	0.093	1.021	0.307
Sample plot placement: random	Reference			
Sample plot placement: strategic	**1.12**	**0.065**	**1.948**	**0.049**
Zero-Inflated Model				
(Intercept)	**0.09**	**0.022**	**−9.863**	**<0.001**
Random Effects				
σ^2	0.25			
$\tau_{00\ stand:cluster}$	0.07			
$\tau_{00\ cluster}$	0.01			
ICC	0.27			
N_{stand}	40			
$N_{cluster}$	6			
Observations	400			
Marginal R^2 / Conditional R^2	0.302 / 0.473			

Table 6
Beta diversity of different management classes as measured by beta dispersion on a community data matrix. Different management classes: LU – long unmanaged; RU – recently unmanaged; NN – near-to-nature managed; MA – conventionally managed.

Organism group	Management classes			
	LU	RU	NN	MA
Bryophytes – plot level	0.54	0.53	0.49	0.49
Bryophytes – stand level	0.39	0.38	0.38	0.32
Vascular plant – plot level	0.57	0.57	0.52	0.52
Vascular plants – stand level	0.47	0.44	0.41	0.4

1995; Sydes and Grime, 1981a, 1981b) and bryophytes (Müller et al., 2019; Startsev et al., 2008). This effect is easy to understand ecologically, as leaf litter suppresses plant establishment and growth by several mechanisms (e.g. Loydi et al., 2014; Xiong and Nilsson, 1999). The presence of exposed soil favoured species richness in both groups, but most strongly in bryophytes. Also, other studies have reported bryophytes to respond strongly to soil disturbance (e.g., Jonsson and Esseen, 1990; von Oheimb et al., 2007), and probably this effect is most crucial in forest types characterized by strong litter accumulation, as typical in beech forests.

The decline in bryophyte species richness with years since logging is somewhat surprising, but similar results were observed by Müller et al. (2019) who attributed the effect to higher soil disturbance in managed forests related to timber extraction. We also noted a negative correlation between soil pH and bryophyte richness, with the relative proportion of conifers in the canopy being a possible explanation (cf Müller et al., 2019). However, our study context featured minimal conifer presence, and we rather suggest that the relative importance of bryophytes in the field-layer vegetation may increase gradually from high pH mull to acidic mor soils.

4.2. Drivers of species composition

Geography significantly influenced community composition in vascular plants with distinct geographical clusters separated along the principal axis in the NMDS analysis, which were closely related to turnover in soil pH. The gradient roughly separated forest complexes on mor soils developed on sandy and gravelly moraines in central and northern Jutland (clusters 4 and 5) from forest complexes on mull soils developed on clayey moraines and limestone in the southern and eastern parts of Denmark (clusters 2, 3 and 6). Cluster 1 held an intermediate position (Fig. 1). Most of the within-cluster variation for vascular plants was captured by NMDS2 and related to canopy openness and litter and humus layer thickness, indicating their role as crucial drivers of within-site variation in species composition.

Bryophyte community composition showed less clear geographical separation, although soil pH remained the strongest correlated vector along NMDS1. This finding suggests that bryophyte communities in Danish beech forests are less geographically structured than co-occurring vascular plant communities, showcasing larger within-site variation. This difference might be attributed to the better dispersal potential of bryophytes mediated by the wind-dispersal of spores, enabling adaptation to locally favourable soil conditions. To date, few studies have analysed patterns of spatial and environmental turnover in bryophytes, but data analysed by Graco-Roza et al. (2022) suggest that vascular plant communities do indeed exhibit stronger geographical structuring than soil-dwelling bryophyte communities, while patterns of environmental turnover appear comparable.

4.3. Microhabitats and their impact on species composition

All of the surveyed microhabitat types influenced species composition and gamma diversity, each exhibiting specific indicator species

Table 7

Pairwise ADONIS (PERMANOVA) for different pairs of microhabitats in each group. Soil disturbances: a) ditch, b) wheel track, c) soil exposed by a fallen tree; wetland types: d) ditched depression, e) natural depression, f) spring; and canopy gaps: g) from forestry, h) natural.

Pairs	Vascular plants			Bryophytes		
	F	R2	p. adj	F	R2	p. adj
Soil disturbances						
0 - a	**3.962**	**0.01**	**0.006**	**6.329**	**0.02**	**0.006**
0 - b	**2.029**	**0.01**	**0.132**	**3.44**	**0.01**	**0.012**
0 - c	1.631	0.01	0.492	**7**	**0.02**	**0.006**
b - a	**2.453**	**0.03**	**0.036**	**3.534**	**0.04**	**0.006**
b - c	1.662	0.02	0.438	1.853	0.02	0.384
c - a	**3.03**	**0.04**	**0.018**	**2.922**	**0.04**	**0.006**
Wetlands						
0 - d	**4.297**	**0.01**	**0.006**	1.372	0.00	1
0 - e	**3.998**	**0.01**	**0.006**	2.079	0.01	0.168
0 - f	**8.832**	**0.02**	**0.006**	**7.535**	**0.02**	**0.006**
d - f	**3.644**	**0.09**	**0.024**	1.777	0.05	0.366
d -e	1.27	0.04	1	1.243	0.04	1
e - f	**5.181**	**0.1**	**0.006**	**3.346**	**0.07**	**0.006**
Canopy openings						
0 - g	**5.874**	**0.02**	**0.003**	**2.247**	**0.01**	**0.048**
0 - h	**7.989**	**0.02**	**0.003**	**8.089**	**0.02**	**0.003**
g - h	1.748	0.01	0.144	**2.505**	**0.02**	**0.024**

(Table 8 and Appendix B). Wetland microhabitats had few strong indicator bryophytes, but they strongly supported specialised vascular plant communities and thus are large contributors to gamma diversity. Interestingly, the wetland type supporting most indicator species was ditched depressions. However, several of the associated indicators were acquisitive and/or ruderal species (e.g., *Geranium robertianum, Juncus effusus, Poa trivialis, Ranunculus repens* and *Urtica dioica*), indicating nutrient-enriched conditions, suggesting that these modified habitats are attractive for species not naturally occurring in forested wetlands. In contrast, all indicators of natural depressions were typical wetland plants. The Ellenberg indicator values for light and nitrogen further suggested that ditched depressions were more nutrient-enriched and shadier than natural depressions. Spring and stream microhabitats were also associated with plant communities with relatively high nutrient levels and soil pH combined with lower light values. These microhabitats generally supported herbs associated with humid mull soils rather than typical wetland plants.

Soil disturbances were associated with several indicator species in both vascular plants and bryophytes, with ditches supporting most indicators. This observation likely stems from the fact that ditches represent a deep soil disturbance, often exposing mineral soil in both the humid bottom and sides of the ditch and exposed as dug-up soil banks next to it. In that respect, ditches may mimic pit and mound structures from naturally uprooted trees (Ulanova, 2000), but somewhat surprisingly our study revealed only a few shared indicator species (*Ranunculus ficaria, Plagiothecium succulentum/nemorale* and *Dicranella heteromalla*) connecting the two disturbance types. The rather long list of indicator species for ditches contains a mixture of ferns, forbs, graminoids and bryophytes, representing a variety of specialisations, but all can be considered disturbance dependent. In contrast, the two vascular plants indicative of uprooting habitats (*Anemone ranunculoides* and *Hedera helix*) are long-lived perennials. Quite surprisingly, only one bryophyte species (*Pohlia nutans*) was found to be indicative of uprooting habitats, even if this habitat was found to increase local species richness considerably. This result contrasts with those of earlier studies in temperate forests, which have found more bryophytes than vascular plants to be associated with pit and mound habitats (von Oheimb et al., 2007).

Canopy gaps favoured numerous indicator species, but only few had strong indicator values. This pattern suggests that increased light availability in gaps favours plant richness in general, rather than acting as a discrete condition favouring a large set of dedicated gap specialists. Similarly to other studies (e.g. Gálhidy et al., 2006), both natural and forestry gaps were preferred by tall and light flexible vascular plants. The community-mean Ellenberg indicator values for light and nitrogen tended to be higher in forestry gaps, suggesting that these are generally larger and more affected by nitrogen release than natural gaps. This result likely explains why forestry gaps supported ruderal herbs and trees while natural gaps favoured bryophyte communities.

5. Perspectives

Our study casts new light on the intricate relationships between local habitat conditions and patterns of plant and bryophyte diversity influenced by management regimes and natural disturbances. Importantly, our study confirms that the orthodox abandonment of forest management in beech forests leads to reduced plant alpha diversity, at least in the short to medium term, due to increasing shade. This phenomenon expresses the strong competitive effect of forest trees, enhanced by the suppression of natural disturbance regimes, such as wildfires and large herbivores. Further, we were able to show that the most important common limiting factor for plant and bryophyte richness is litter accumulation, while light availability and soil exposure work as key promoting factors for vascular plants and bryophytes, respectively. In addition, small wetland habitats enhanced richness, especially of vascular plants.

Our findings are well-aligned with those of Kaufmann et al. (2017) in Slovakian virgin forest versus managed beech forests, illustrating reversed alpha and beta diversity patterns related to management. By the calculation of species accumulation and extrapolation curves, it was demonstrated that gamma diversity reached similar levels in managed and pristine forests at a sampling area of 2.5 ha (50 plots of 500 m^2), but with a still increasing trend only in the pristine stands. This finding suggests that forest management may have a negative impact on plant gamma diversity at larger spatial scales, in contrast to conclusions often reported (e.g. Paillet et al., 2010) based on small-scale alpha diversity. In our case, a strategic approach to survey microhabitats showed that the stand-scale ecospace was larger in unmanaged than in managed stands based on the overall microhabitat availability, environmental condition variability and NMDS ordination, even if the overall gamma diversity of vascular plants and soil-dwelling bryophytes was not significantly different. This underlines the critical role of scaling issues when evaluating the impact of forest management on biodiversity and warns of potential pitfalls associated with simplistic evaluations of alpha diversity at smaller geographical scales when comparing forests subjected

Table 8

Summary table for indicator analysis for vascular plants and bryophytes in different microhabitats. Besides the total number of indicator species, species with strong associations (phi coefficient > 0.2) are presented. Only groups of three or more species per microhabitat are presented here; the full list, including Ellenberg value of light (L), reaction (R) and nitrogen (N), is available in Appendix B.

Vascular plants				
Microhabitat type	Microhabitat specific	Total indic.	Strong	Indicator species with habitat associations > 0.2
Soil disturbances	Ditch	15	12	*Athyrium filix-femina, Dryopteris filix-mas, Veronica montana, Carex remota, Urtica dioica, Deschampsia cespitosa, Cardamine flexuosa, Milium effusum, Geranium robertianum, Scutellaria galericulata, Circaea lutetiana, Glechoma hederacea*
	Wheel track	5	1	*Stellaria nemorum*
	Exposed by fallen tree	5	2	*Anemone ranunculoides, Hedera helix*
	Ditch, Wheel track	3	1	*Epilobium montanum*
	Total:	28	16	
Wetlands	Ditched depression	19	19	*Glechoma hederacea, Juncus effusus, Carex canescens, Scirpus sylvaticus, Circaea alpina, Poa trivialis, Urtica dioica, Stachys sylvatica, Impatiens noli-tangere, Geranium robertianum, Ranunculus repens, Cardamine flexuosa, Galium aparine, Alnus incana, Carex acutiformis, Carex echinata, Chrysosplenium alternifolium, Equisetum palustre, Lemna minor*
	Natural depression	7	7	*Carex elongata, Agrostis canina, Carex elata, Carex rostrata, Lysimachia thyrsiflora, Phalaris arundinacea, Carex nigra* var. *nigra*
	Spring	6	6	*Ranunculus ficaria, Cardamine bulbifera, Circaea lutetiana, Equisetum telmateia, Carex sylvatica, Anemone ranunculoides*
	Ditched and natural depressions	6	6	*Deschampsia cespitosa, Glyceria fluitans, Scutellaria galericulata, Dryopteris carthusiana, Galium palustre, Calamagrostis canescens*
	Ditched depression, Spring	3	3	*Carex strigosa, Chrysosplenium oppositifolium, Ajuga reptans*
	Any wetland	3	3	*Carex remota, Athyrium filix-femina, Equisetum sylvaticum.*
	Total:	48	48	
Canopy gaps	No gaps	3	-	
	Forestry gap	21	7	*Rubus idaeus, Salix* sp.*, Geranium robertianum, Scrophularia nodosa, Fagus sylvatica, Luzula pilosa, Picea* sp.
	Natural gap	13	1	*Calamagrostis arundinacea*
	Any gap	10	-	
	Total:	47	8	
Bryophytes				
Microhabitat type	Microhabitat specific	Total indic.	Strong	Indicator species with habitat associations > 0.2
Soil	Ditch	9	6	*Kindbergia praelonga, Fissidens bryoides, Plagiomnium undulatum, Oxyrrhynchium hians, Eurhynchium striatum, Rhizomnium punctatum*
	Exposed by fallen tree	4	1	*Pohlia nutans*
	No disturbance, Ditch	2	2	*Thuidium tamariscium, Dicranum scoparium*
	Ditch, Exposed by fallen tree	2	1	*Plagiothecium succulentum/nemorale*
	Wheel track, Exposed by fallen tree	1	-	
	Any soil disturbance	1	1	*Atrichum undulatum*
	Total	19	11	
Wetlands	Ditched depression	2	2	*Calliergonella cuspidata, Plagiothecium latebricola*
	Natural depression	2	2	*Calliergon cordifolium, Lepidozia reptans*
	Spring	1	1	*Fissidens taxifolius*
	Dry areas, Natural depression	1	1	*Hypnum cupressiforme*
	Ditched depression, Spring	1	1	*Kindbergia praelonga*
	Dry areas, Natural depression, Spring	1	1	*Atrichum undulatum*
	Total	8	8	
Canopy	No gaps	3	-	
	Forestry gap	6	1	*Dicranella schreberiana*
	Natural gap	10	5	*Rhytidiadelphus squarrosus, Scleropodium purum, Rhytidiadelphus loreus, Hylocomium splendens, Pleurozium schreberi*
	Total	19	6	

to different management regimes.

While we consider several of our findings to be applicable beyond the study system, we recognise certain limitations. First, our study focuses on the effects of forestry abandonment rather than offering a direct comparison between managed stands and a natural baseline. Almost all study stands, including those classified as long unmanaged, have been subject to shelterwood management in the past, resulting in even-aged canopy structures. The exceptions are a few of the oldest stands, which were never effectively converted to even-aged production stands but originate from older multipurpose forestry systems in which live-stock grazing was an integral element. Since the Forest Protection Act of 1805 in Denmark, this management approach has been banned, leading to the near-complete disappearance of livestock from Danish forests.

This development has resulted in denser canopy structures, promoting timber production (Fritzbøger, 2018). Although deer populations have increased throughout Europe (Burbaitė and Csányi, 2010), increasing grazing pressure and hence promoted plant richness (e.g. Boulanger et al., 2018; Kowalczyk et al., 2021; Kuijper et al., 2009), the effect on forest vegetation is unbalanced compared to that of historical grazing regimes including larger, bulk-feeding grazers (Pringle et al., 2023). Additionally, Denmark's zero-tolerance policy for wild boar means that this key disturbance agent is absent, further impacting soil disturbance in Danish forest ecosystems.

The absence of natural disturbance agents related to larger mammals likely means that the available species pools of vascular plants and soil-dwelling bryophytes in our study system are altered compared to

baseline conditions in natural ecosystems. In tandem, these two factors could explain some of the more surprising results in our study, for example, that several natural disturbances and microhabitat types supported lower richness and fewer indicator species than their human made counterparts. Notably, historical evidence suggests significant changes in plant composition over the last centuries, particularly a decline in species associated with open woodland and forest-grassland ecotones, which were abundant 100–200 years ago (Mortensen, 1872; Finderup Nielsen et al., 2021). Many such species are now listed as threatened on the national red list, and few or none were recorded in our study.

There is currently much focus on restoring forest ecosystems, not only by stopping forestry, but also by restoring hydrology and reintroducing lost disturbance agents, including large herbivores. To date, few if any studies (but see Bernes et al., 2018; Mazziotta et al., 2016) have given detailed insights into how such restoration actions may impact forest plant communities. We find such studies to be a necessary next step to understand the dynamics of communities of vascular plants and bryophytes in temperate forest ecosystems.

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CRediT authorship contribution statement

Anita Atrena: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis. **Gaia Giedrė Banelytė:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Hans Henrik Bruun:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Irina Goldberg:** Writing – review & editing, Investigation. **Carsten Rahbek:** Writing – review & editing, Methodology, Conceptualization. **Jacob Heilmann-Clausen:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122162.

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