Author(s): Kepfer-Rojas, Sebastian; Ovaskainen, Otso; Møller, Peter Friis; Johannsen, Vivian Kvist; Byriel, David Bille; Justesen, Mathias Just; Riis-Nielsen, Torben; Hansen, Aslak Kappel; Gottlieb, Lasse; Schmidt, Inger Kappel

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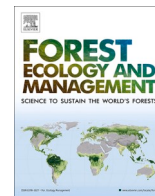
Beyond species richness: Forest structure and edaphic conditions have similar importance but different effects on multi-taxon biodiversity

Sebastian Kepfer-Rojas [a,*], Otso Ovaskainen [b,c], Peter Friis Møller [d], Vivian Kvist Johannsen [a], David Bille Byriel [a], Mathias Just Justesen [a], Torben Riis-Nielsen [a], Aslak Kappel Hansen [e], Lasse Gottlieb [a], Inger Kappel Schmidt [a]

[a] Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, Copenhagen 1958, Denmark
[b] Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35 (Survontie 9C), Jyväskylä FI-40014, Finland
[c] Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, Helsinki 00014, Finland
[d] Geological Survey of Denmark and Greenland, Copenhagen K 1350, Denmark
[e] Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, Copenhagen 2100, Denmark

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ABSTRACT

Managed forests represent a major fraction of the global forest area and are known to host impoverished biodiversity compared to natural forests. The effect of forest management has focused mainly on aggregated community metrics such as species richness of single taxa and on simplistic managed vs. unmanaged comparisons. However, the effect of forest management is expected to vary among species and taxa and to be contingent on site-specific conditions. In this study, we focus on fine-scale multi-taxon biodiversity patterns to disentangle the impact of forest management on the forest structure and the abiotic soil conditions of the stands. We base our comparisons on carefully selected pairs of managed and unmanaged stands to minimize regional differences that could confound the effects of management. We found that the total effect of forest management on alpha diversity was positive on plants and rove beetles, neutral on ground beetles and mosses, and negative on crane flies, fungi, and lichens. However, using joint species distribution modeling we show that individual species' responses to the local underlying soil conditions can be as important as the forest structural changes induced by management, but this varied among the different taxa. Based on these responses we disclose synergies and trade-offs among some of the taxa. Our results indicate that the balance between forest management and abiotic conditions can shape the patterns of forest multi-taxon biodiversity. Considering these conditions can be important in predicting the response of biodiversity to forest management and act as key criteria when prioritizing areas for the conservation of biodiversity.

1. Introduction

Managed forests comprise a significant proportion of the total global forest area and provide multiple goods and ecosystem services (FAO, 2020; Messier et al., 2015). Despite these benefits, forestry practices alter structural elements of the forest and typically result in homogeneous stands in terms of age classes, vertical structure, canopy cover, deadwood, and tree species composition. Because many forest-associated species depend on these elements and their variability, simplified and homogenized forests generally support impoverished assemblages of forest-associated taxa (Lindenmayer et al., 2006).

Increased focus on sustainability and biodiversity in Europe has led to changes in forest management over the last decades (Messier et al., 2015). Recognizing the impact of forestry on biodiversity, several management systems have been adopted with varying degrees of management intensity and thus varying degrees of impacts on biodiversity (Brunet et al., 2010; Chaudhary et al., 2016; Schall et al., 2018). One extreme of this gradient is the abandonment of forestry practices and subsequent designation of strict forest reserves, where forest management is prohibited (i.e. unmanaged forests). For this to be effective, prioritization of areas for unmanaged forests requires an understanding of the direct and indirect impacts of forest management across different

taxa, and of the relative importance of the changes induced by management to those of local site conditions (Moilanen et al., 2011).

Forest management can affect species communities in different ways. The most obvious is through the effects of changes in forest stand structure, either due to the choice of the planted tree species or by tree harvesting and deadwood removal. Numerous studies in Europe and elsewhere have demonstrated the impact of forestry practices on biodiversity across multiple taxa (Dieler et al., 2017; Paillet et al., 2010; Schall et al., 2018). Although these studies generally agree that leaving forests unmanaged has a positive effect on biodiversity, they have also found contradicting results regarding the overall effects of management across various taxa (Schall et al., 2020). A possible reason for this is that most studies have used simplistic comparisons of management categories (i.e. managed vs unmanaged) or have only considered the structural features of the stands. However, forest management involves simultaneous changes in multiple forest features which might not be captured by simple forest management classifications (Nolet et al., 1995). In addition, managed and unmanaged sites typically differ in developmental stages, time since abandonment, and management intensity, which complicates using reference sites and drawing conclusions from comparisons of simplified categories (Trentanovi et al., 2023).

Besides the structural features, forest management can affect the physical, chemical and biological properties of the soil due to compaction, nutrient depletion, and drainage and are expected to correspond to management intensity (Roy et al., 2021). Soil properties such as nutrient availability and moisture can determine the community structure of species assemblages (Byriel et al., 2020b; Graae and Heskjær, 1997; Sebastià et al., 2005) but have rarely been considered in studies assessing the impacts of forest management and few studies have directly assessed their relative importance in comparison to structural changes in multi-taxon biodiversity assessments (Janssen et al., 2018; Tinya et al., 2021). Although local soil conditions can vary due to regional and historical differences or to the direct impact of management (Blondeel et al., 2018), accounting for their effects is necessary when assessing the effect of forest management.

To improve predictability in the response of ecological communities to forest management it is then necessary to quantify the importance of different factors. A complement to using forest management categories is to tease apart the importance of single elements or groups of elements and assess their relevance for biodiversity (Gossner et al., 2014; Grevé et al., 2018). Furthermore, disentangling the impact of structural and abiotic soil conditions among different taxa, can improve our understanding of the underlying drivers of the distribution and abundance of forest-associated species and thus provide guidelines for prioritization of areas for forest conservation or optimizing management and restoration by targeting these specific components (Felipe-Lucia et al., 2018).

Multi-taxon biodiversity assessments are emerging as a comprehensive tool to evaluate the effects of forest management (Burrascano et al., 2023). To date, most of these studies are based on aggregated community or diversity metrics such as species richness or distance-based compositional differences. Although aggregated community measures are useful, they can in some cases lead to equivocal results or preclude more nuanced insights (Hillebrand et al., 2018). Furthermore, these metrics do not allow explicitly considering the sensitivity of different species to changing environmental conditions like the ones induced by forestry practices. Hierarchical models of species distributions (Ovaskainen et al., 2017) belong to the family of joint-species distribution models and are gaining popularity when studying the responses of multiple species to environmental and spatial factors. This family of models allows us to simultaneously estimate the responses at the levels of individual species and communities when assessing changes in biological communities (Jackson et al., 2012; Warton et al., 2015).

In this study, we investigate the impact of forest management on the small-scale community patterns of ground beetles, rove beetles, crane flies, vascular plants, epiphytic lichens, mosses, and wood-inhabiting

fungi. We focus on the relative importance of forest structure, soil physicochemical properties, and soil moisture as these are recognized drivers of the distribution and abundance of multiple taxa in forest ecosystems and because management can have differential impacts on each of these features. We considered the following questions and hypotheses:

1) What is the overall effect of forest management across taxa? 2) What is the relative importance of forest structure, soil properties, and soil moisture on the community structure of different taxa? 3) Are there similarities in the response of species to these factors across taxa?

We hypothesize that the effect of management will differ among taxa and it is mainly driven by structural elements of the forest. However, regional differences in abiotic soil properties can be more important, especially on sessile autotrophic organisms (Brunbjerg et al., 2020). Finally, we expect that forest specialists, due to their affinities to forest microhabitats and resources, are more sensible to changes in the structural elements of the forest as induced by management.

2. Material and methods

2.1. Site description and data collection

The study was conducted on the island of Zealand in eastern Denmark, characterized by a temperate climate and post-glacial sandy loam soils. The landscape consists mainly of agricultural fields, cultural grasslands, forest plantations, and some natural forest stands. Seventeen broadleaved forest stands were selected based on a biodiversity survey from 1994 (Møller, 1997), with pairs of managed and unmanaged stands chosen to minimize differences in various factors. The unmanaged stands are all mature forest (> 150 years) stands where forestry operations have ceased, at least 100 years before the time of sampling. The managed stands are high forests in mature stages that have been logged by either selective or clear-cutting differing in the time since the last intervention, and thus represent a gradient of management intensity (Møller, 1997). (Supplementary Table S1). Data was collected between July 2015 and May 2016, using a systematic sampling design based on plots placed at the intersections of a 100×100 m grid for measurement of forest structure, species composition assessment and collection of soil samples. Forest structures were quantified using field measurements and LiDAR data in circular plots (15 m radius), while deadwood was sampled using transects (10×50 m) and plot-based (15 m radius) methods. Soil properties including pH, carbon, nitrogen, and moisture content were assessed in the intersections of the 100×100 m grid. Soil moisture measurements were conducted at different depths (for details see Supplementary Methods and Data Analysis).

2.2. Species sampling

Biodiversity data was collected using the subset of plots where the environmental factors were available using the same 100×100 m grid, as in the soil sampling. We used established methods for each taxon and collected the data between March 2015 and May 2016 (Supplementary Methods and Data Analysis). The investigated taxa included understory vascular plants, mosses, lichens, fungi, crane flies, and ground and rove beetles (Table 1).

2.3. Data preparation

Soil samples were taken in 137 plots across all stands (Supplementary Table S2). Missing values in some of the soil properties were filled out using a random forest model from the 'missForest' package in R (Stekhoven and Buehlmann., 2012). We used all soil and structural variables and the plot coordinates to obtain predictions for the missing values. We grew 100 forests with 10 iterations achieving an out-of-bag

Table 1

Overview of taxa surveyed, number of species, abundance, number of plots, and species sampling design across all sampling units aggregated by management category (MAN = managed, UNM = unmanaged) for all species and forest specialists (in parenthesis). n.a. = not available.

Taxon	Species richness		Abundance		No. of plots		Method
	MAN	UNM	MAN	UNM	MAN	UNM	
Ground beetles	45 (14)	39 (13)	6540 (2542)	7285 (3255)	55	59	Pitfall traps; four in 10 m radius plot; 3 collections; abundance
Rove beetles	48 (9)	40 (8)	3200 (68)	4015 (28)	55	60	Pitfall traps; four in 10 m plot; 3 collections; abundance
Craneflies	72(n.a.)	81(n.a.)	1801(n.a.)	2835(n.a.)	57	66	Sweep nets in 15 m plots; 10 minutes; 3 collections; abundance
Vascular plants	87 (28)	70 (27)	n.a.	n.a.	60	75	Visual percentage cover estimation in $2 \times 1 \, m^2$ quadrats; spring and summer
Wood-inhabiting fungi	93 (55)	110 (54)	381 (257)	636 (421)	55	62	Fruit body survey on deadwood and trees in 10×50 m transects starting at the center of the sampling plots, 1 registration; occurrence
Epiphytic lichens	50 (6)	49 (7)	669 (59)	895 (165)	54	62	Visual survey on trees with DBH > 40 cm (lower when only small trees present) and deadwood in 5 m plots, 1 registration; abundance
Mosses	51 (13)	44 (11)	n.a.	n.a.	58	65	Visual survey in 15 m plots; occurrence

normalized mean root squared error (NMRMSE) of << 0.001, indicating that the model adequately predicted the missing values.

We constructed three separate principal component analysis (PCA) on forest structure, soil, and water availability variables (Table 2). The first two components of the PCA explained 61 %, 73 % and 70 % of the respective variation and were selected for the analysis. The first axis of the PCA for the structural features (STRU1) represents the forest development showing positive loadings for variables that increase with forest age such as tree size, number of large trees, and basal area. The second axis (STRU2) was mainly determined by decreasing canopy cover and increasing dead wood volumes and vertical heterogeneity, representing a management abandonment gradient increasing along this axis. From the soil PCA, axis 1 (SOIL1) mainly represents a gradient of soil density and carbon and nitrogen content, increasing with decreasing values of bulk density and increasing values of C and N concentrations. The second axis (SOIL2) represents a fertility gradient with increasing values of pH and decreasing values of C:N. The two axes of the water PCA are related to hydrology and soil moisture, increasing along axis 1 (WATER1). The second axis (WATER2) increases with decreasing values of moisture in the litter layer. There were no strong correlations among these axes (all < 0.25)

Statistical analysis

Table 2

Description of variables included in a Principal Component Analysis of structural and edaphic variables. The values are the loadings describing the contribution of the individual variables to each axis. *DBH = Diameter at breast height.

Variable code	Variable Description	Axis 1	Axis 2
Structure			
dbhm	Mean DBH*	0.253	−0.178
dbhsd	Standard deviation of DBH	0.382	0.181
dbhmax	Maximum DBH	0.411	0.156
Nlarge	Number of large trees (DBH > 60 cm)	0.384	−0.116
bhatot	Basal area	0.382	–
ccmean_lid	Canopy cover (LiDAR)	0.316	−0.350
h95m_lid	Height (95th percentile, LiDAR)	0.349	−0.145
h95sd_lid	Standard deviation of height (LiDAR)	–	0.573
dwptot	Deadwood volume (706 m² plot)	0.139	0.565
dwhat	Deadwood volume (500 m² transect)	0.292	0.316
Soil properties			
N	Nitrogen content	0.480	0.418
C	Carbon content	0.532	0.245
CN	C:N ratio	0.377	−0.488
pH	pH	−0.298	0.633
BD	Bulk density	−0.494	−0.153
OH	Depth of organic layer	0.104	−0.321
Soil moisture			
Twimean	Topographic wetness index	0.294	0.546
Theta1.mean	Soil water content	0.416	0.102
H20.LITTER	Litter moisture	0.261	−0.813
H20.05	Soil moisture (0–5 cm depth)	0.464	−0.112
H20.515	Soil moisture (5–15 cm depth)	0.489	–
H20.1530	Soil moisture (15–30 cm depth)	0.467	0.137

2.4. Total effect of management on species richness and environmental predictors

We compared the total number of species and the PCA environmental axes between forest management classes using generalized and general linear mixed-effects models. Species from the different taxa were classified as forest specialists based on published lists (Supplementary Table S3). Crane flies were not classified since we couldn't find a classification. For each taxon, we used separate models for all species and forest specialists. The models included forest management class (managed vs unmanaged) as a fixed factor and plot nested in stand, and stand nested in area, as random factors to account for possible spatial dependencies in the observations. Models were fitted using a Normal and a Poisson distribution for environmental predictors and species richness, respectively, in the lme4 package (Bates et al., 2015). Models' residuals were visually inspected for violation of assumptions.

2.5. Analysis of Individual and community responses

A Hierarchical Modeling of Species Communities (HMSC) framework was used to analyze the response of species to management and environmental factors. Separate analyses were performed for each taxon. The response variables varied depending on the taxa, including counts, cover, or presence-absences of the species in plots (Supplementary methods and data analysis). Depending on the type of response, we modeled the count and cover data sets with a hurdle approach, where we first fitted a probit-regression to presence-absence data, and then a linear model to log-transformed abundance data conditional on presence. Explanatory variables included management category, vegetation cover, forest structure, soil properties, and soil moisture. The latter 3 were represented by the first two axis of the PCAs, described above. Variance partitioning was performed to examine the relative roles of different environmental and spatial factors in influencing species communities. The response to explanatory variables across taxa was quantified for each taxon, and a PCA was used to visualize and compare the response of species from the different taxa in the parameter space.

3. Results

3.1. Total effects of management on species richness, forest structure, and edaphic conditions

We registered 608 species from the 7 taxa, varying from 51 species of ground beetles to 140 of vascular plants. Across all plot observations, there were 446 species in the managed (n = 394) and 433 in the unmanaged plots (n = 449). Except for fungi and crane flies, we registered more species in managed plots, despite there being 14 % more plot observations in unmanaged areas. We recorded 25,676 specimens from the three insect groups considered, and 1017 and 1564 observations of fungi

and lichens respectively, all of which were higher in unmanaged stands (Table 1). At the plot level, the number of species of crane flies, fungi, and lichens were significantly higher in unmanaged sites, whereas plants and rove beetles were significantly higher in the managed plots, and ground beetles and mosses showed a similar number of species (Fig. 1). Of the recorded species, 153 are considered forest specialists (Supplementary Table S3). Like the comparisons of "all species", alpha diversity of forest specialists was significantly higher in unmanaged stands for fungi, lichens, and mosses while for plants and rove beetles, alpha diversity was significantly higher in the managed stands (Supplementary Figure S1).

The effect of management was more evident in the structure of the forests, as both PCA components were markedly different between management types (Fig. 1). Unmanaged stands were characterized by having higher: maximal DBH, number of large trees, basal area, canopy cover, and deadwood volumes. The variability in tree sizes and canopy height was also higher in unmanaged plots. Soil characteristics did not differ markedly between management types except for bulk density, which was higher in managed stands, and water availability (average across all depths) which was higher in unmanaged stands (Supplementary Table S2). On the other hand, most of the edaphic factors showed a large variability mainly due to differences among the study areas rather than management.

3.2. Explanatory power and variable importance

The explanatory power of the HMSC models (i.e. the percentage of the total variance) varied widely between species within and among the different taxa (Fig. 2). For species' occurrences, the total explained variation (Tjur's R^2) ranged from 15 % for fungi to 29 % in plants. For species' abundances, R^2's ranged from 75 % for lichens to 88 % in plants. The explanatory power of the models was similar between forest specialists and non-specialists. However, when considering lichens, the models demonstrated higher explanatory power among forest specialists, and in the case of plants, the opposite trend was observed. (Supplementary Figure S2).

Comparing taxa, soil properties, soil moisture, and forest structure accounted for a larger but similar share of the total variation in the occurrence and abundance of species for most taxa. An exception was the occurrence of plants and mosses, for which the soil was the most important factor. Similarly, soil and water had the largest explanatory power for the plant species' cover. Understory cover and management

were the least important across taxa for both community metrics (Fig. 2). There were no consistent patterns on the explanatory power for the models for forest specialists and with very few exceptions, they followed the patterns obtained for the models including all species.

3.3. Effects of forest structure and edaphic factors on species

The influence of abiotic and biotic factors on the occurrence of species varied widely across taxa. For instance, the average response of plants was influenced in a statistically supported manner by 5 predictors, whereas mosses responded only to 1. Most predictors influenced the occurrence patterns of multiple taxa. Four of the 5 taxa responded on average to SOIL1 and STRU1 and no taxa responded to WATER2 (Fig. 3) and is therefore not considered further. The proportion of species with statistically supported effects (i.e. where at least 90 % of the credibility intervals did not overlap 0), was higher for STRU1 and SOIL2 and lowest for WATER2. A similar variability was observed in the abundance models, but the magnitude of the responses was lower, and less than 5 % of the species showed statistically supported responses for any of the factors (Fig. 4). Across taxa, only plants responded to more than 1 predictor. All the parameter estimates for individual species can be found in Supplementary Document 1.

On species' occurrences, the effect of STRU1 was consistently positive across taxa, except for plants, where it was negative for almost all species. STRU2 had negative effects on most plant species, but positive on fungi. SOIL1 was negative for plants, mosses, craneflies, and ground beetles; positive for lichens, and had no effect on rove beetles or fungi. The effect of SOIL2, was more variable, and across taxa, roughly the same percentage of species responded positively and negatively. However, when considering only forest specialists, the effect of SOIL2 was positive for all autotrophic taxa (Supplementary Figure S3). The average species' occurrences of craneflies and ground beetles increased with VEGCOV, whereas averaged responses were negative for lichens and mosses. WATER1 had strong positive effects on mosses, crane flies, ground beetles, and plants. After accounting for the effects of other factors, the effect of abandonment of forest management (UNMANAG) was positive for craneflies and fungi and negative for plants and rove beetles. However, few species showed significant effects, except for rove beetles where 37 % of the species showed a higher probability of occurrence in managed plots. For forest specialists, the occurrence of mosses was associated with unmanaged forests, after accounting for the other variables (Supplementary Figure S3).
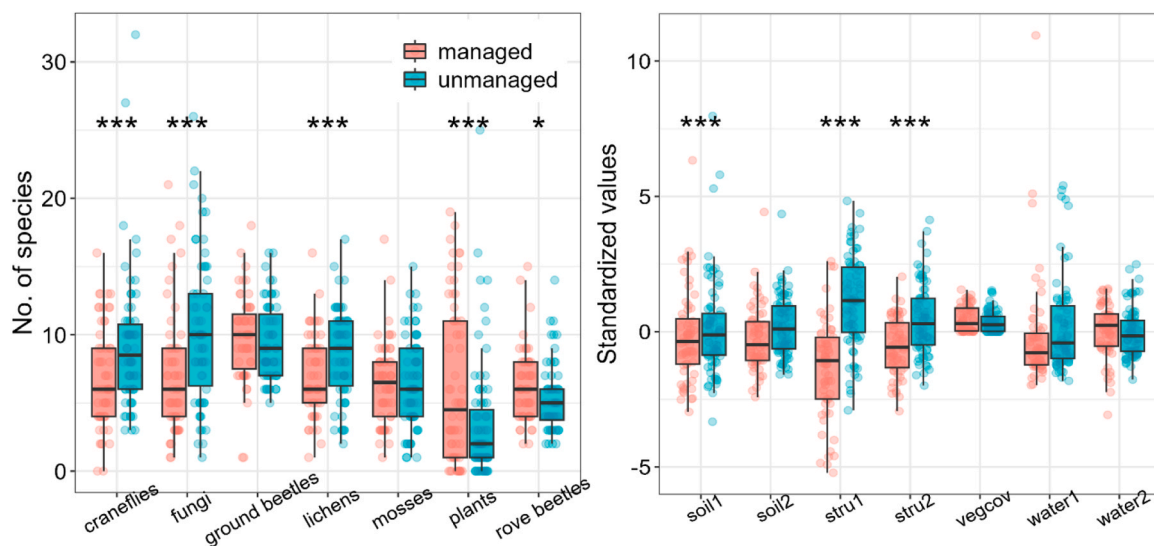

Fig. 1. Mean number of species per plot (left) and PCA scores for the environmental variables (right) in managed and unmanaged forests. Stars show significant differences estimated with a mixed-effects model.
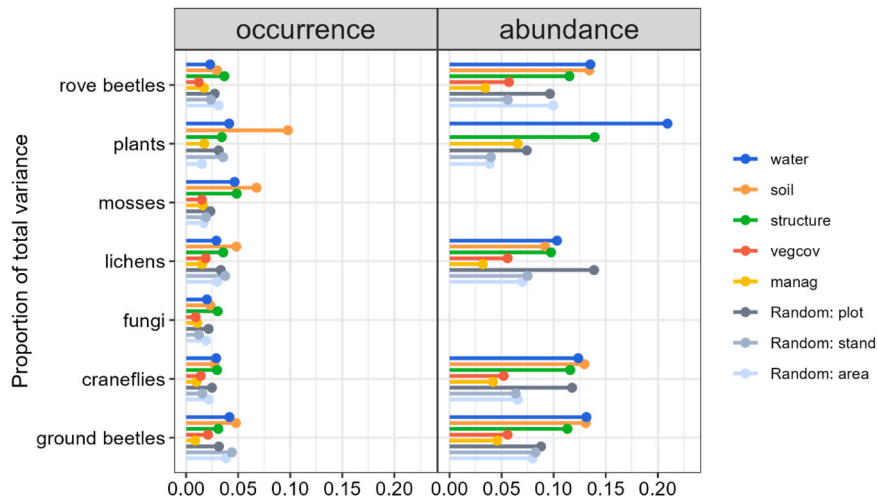
Fig. 2. The average proportion of total variance in the occurrence and abundance (conditional on presence) of species explained by understory vegetation cover, management, soil properties, hydrology, forest structure and random factors at different scales.
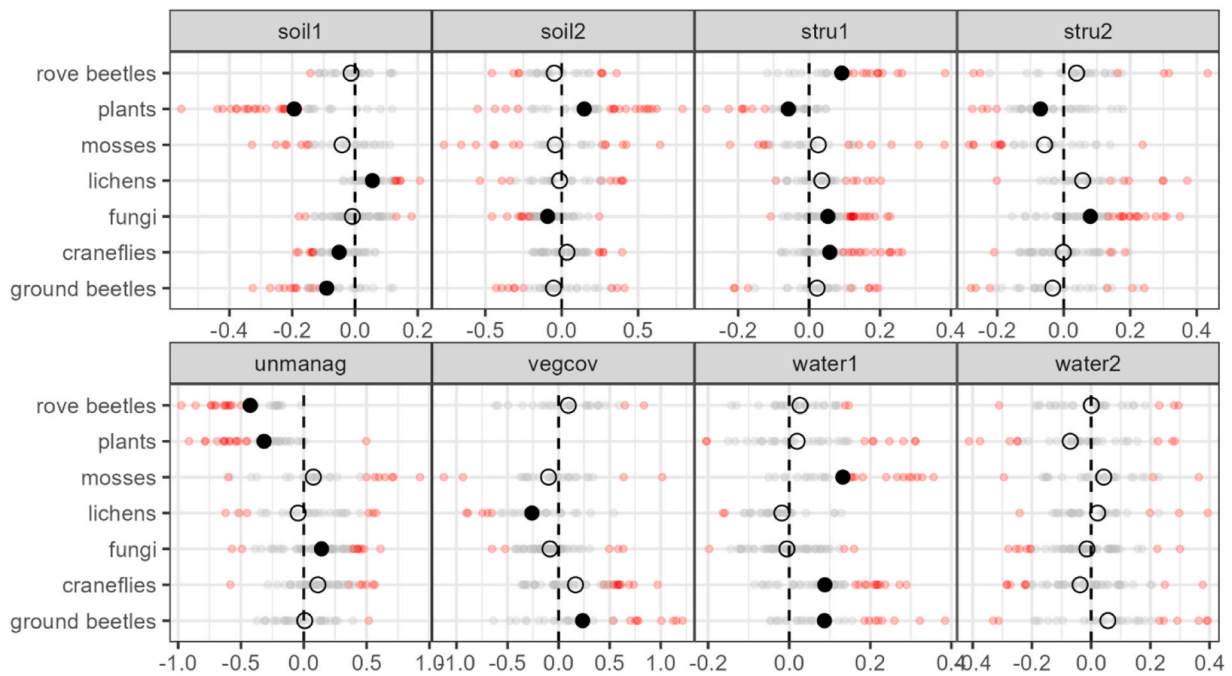

Fig. 3. Estimates of the marginal effects (after accounting for all other effects) of forest structure, soil properties, soil moisture, and ground vegetation cover the OCCURRENCE of species from different taxa. The small dots show the posterior mean response of each species. The responses are colored red when supported by at least the 90 % posterior probability. The large dots (posterior mean) show the mean response across all species from each taxon. The filled, black responses are supported by at least the 90 % posterior probability.

For species' abundances, there were only a few general responses to the explanatory variables, except for plants that responded mostly to edaphic variables (Fig. 4).

3.4. Coordinated responses among taxa

The first two PCA axes for the responses of species occurrences to environmental factors explained 45 % of the variation. The first axis correlated positively with the species' responses to STRU1 and SOIL1 and negatively with VEGCOV and SOIL2. The second axis correlated positively with WATER1 and negatively to UNMANAG. The species responses aligned on a gradient from species responding positively to STRU1 and SOIL1 (Fig. 5). Fungi and lichen species increased along this gradient and plants, in the opposite direction. The centroid of the

remaining groups occupied a more central position in the ordination space. For species' abundances, PCA axis 1 captured a gradient of species' responses to soil moisture and Axis 2 was mainly related to management, explaining 48 % of the variation. Three groups appeared on the first axis, with plants on the high soil moisture and lichens and crane flies on the opposite side, which was also related to soil properties. Beetles occupied the center of the ordination indicating no general association to any of these gradients (Fig. 5).

4. Discussion

4.1. Total effect of forest management on multi-taxa diversity

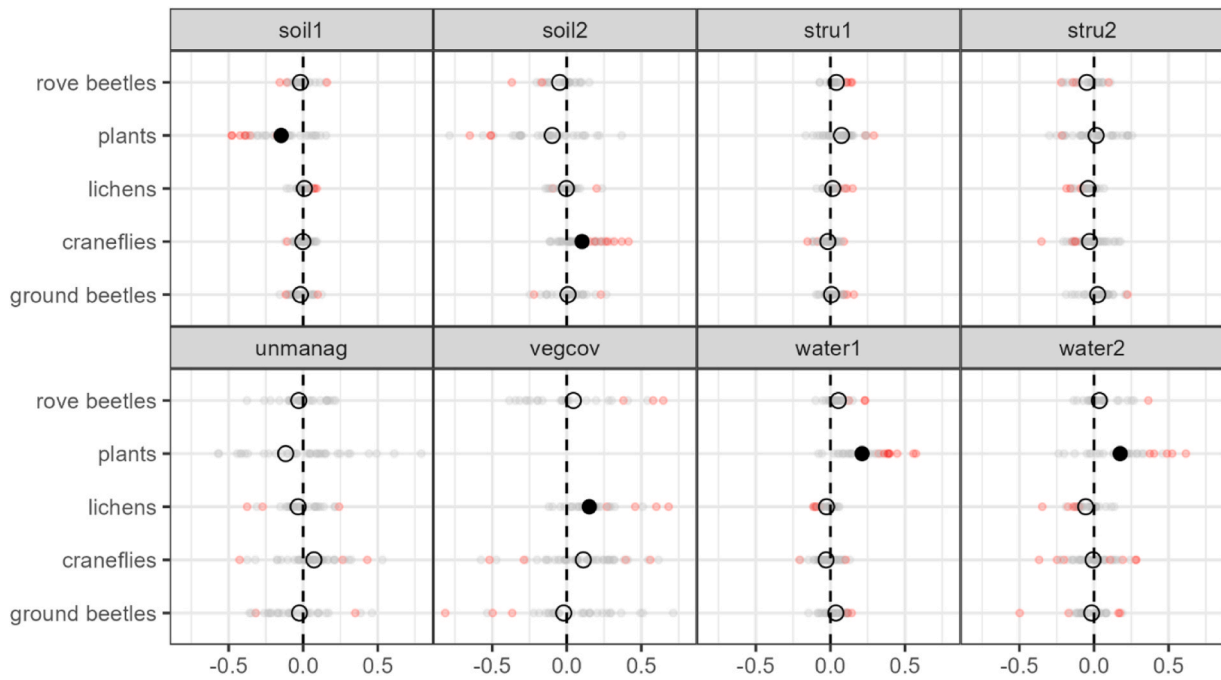Our multi-site pairwise stand comparison showed that forest

Fig. 4. Estimates of the marginal effects (after accounting for all other effects) of forest structure, soil properties, soil moisture, and ground vegetation cover the ABUNDANCE (conditional on presence) of species from different taxa. The responses are colored red when supported by at least the 90 % probability. The large dots (posterior mean) show the mean response across all species from each taxon. The filled, black responses are supported by at least the 90 % probability.
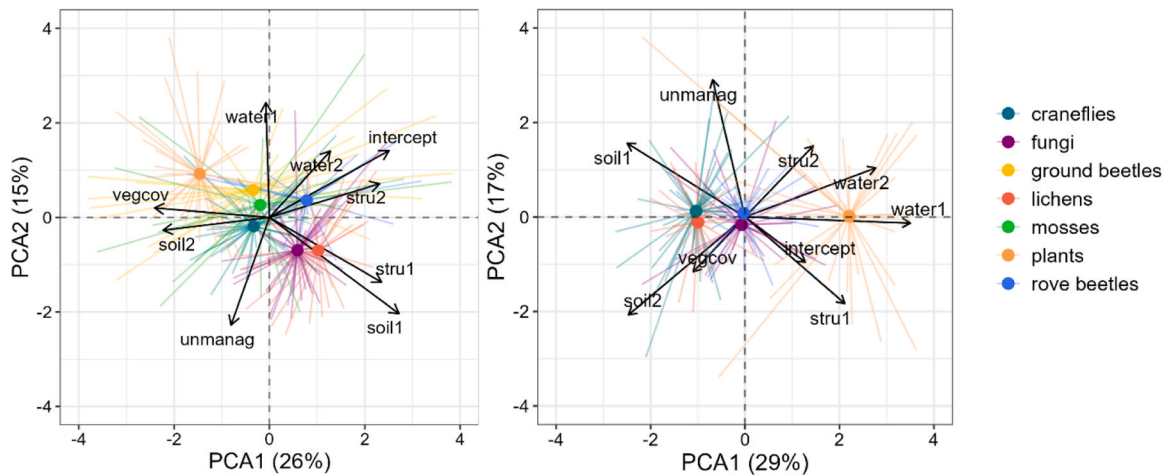

Fig. 5. PCA ordination of species based on the species responses to environmental factors and management for occurrence (left) and abundance/cover (right). The colored dots represent the average responses of each taxon to environmental predictors and each colored line links to an individual species. The estimate for vegetation cover was set to 0 for plants, as it was not included in the model.

management has taxon-specific effects on alpha diversity and that the structural characteristics and the underlying edaphic conditions of forests have on the occurrence and abundance of single species at the plot scale across a range of organisms. The effect of forest management was more evident in the structural attributes of the forest such as tree size, canopy cover, and dead wood amount, whereas the edaphic factors were mainly related to the underlying biophysical conditions of the different study areas.

Similar to other studies (Gossner et al., 2014; Paillet et al., 2010; Tinya et al., 2021), we found a wide range in the sensitivity of species richness to forest management *per se*. Taxa such as lichens, fungi, and crane flies, which are related to elements found in forests with high continuity, responded positively to the abandonment of management. Plants and rove beetles showed negative responses, and mosses and

ground beetles did not show any differences. Contrasting other studies, classifying species into forest specialists, changed these patterns only slightly (Supplementary Figure S1).

4.2. Sensitivity and effects of explanatory variables

Structural attributes and edaphic conditions shaped the individual and community responses, but the magnitude and direction of their effects varied across taxa. Studies on the effect of forest management on biodiversity have typically focused on broad management categories and use species richness as an indicator (Ryabov, 2018). Although this approach can give a quick and simple quantification, it offers a limited explanation of how the specific elements of the forest are affected by management and how they, in turn, affect individual species across taxa.

By disentangling the different components of the forest and by focusing on individual species' responses, our analysis sheds important insights. First, we were able to make a distinction between the relationships among species and the different components of the forest. For some factors (SOIL1, STRU1, STRU2, WATER1), most of the species within a taxonomic group responded in a similar direction, leading to an overall positive or negative effect. However, for SOIL2, the directionality in the within-taxa responses was variable, which translated into neutral or weakly positive or negative average responses. Importantly, this variable had the highest share of species with significant responses. Similarly, the number of ground beetle species was not different between management classes but 20 % of species responded strongly to the structural variables affected by management (Supplementary Document 1). Because a similar number of ground beetle species showed negative and positive responses, there was no overall effect of management on the averaged effect or the total number of species. Together, these results demonstrate that the importance of some variables can be overlooked in analysis based on average responses or species richness, which can ultimately obscure the effect of forest management.

Secondly, our approach allows identifying patterns in the species' responses to specific variables related to management and/or edaphic characteristics and how they relate to the patterns of species richness. For instance, increasing structural features related to forest age or tree size (STRU1), decreasing soil carbon and nitrogen content (SOIL1), and increasing soil moisture (WATER1) had generally positive effects on the occurrence of species from most taxa. Compared to the results of species richness between management types, the taxa that responded positively to a more complex forest structure showed higher richness in the unmanaged forests as expected. An exception were the rove beetles, which, despite the positive response of many species to a more natural forest structure, showed a higher number of species in managed stands. The reason for the higher association to managed sites is not clear but it could be a response to the more complex understory vegetation in managed sites or to other site-specific factors not accurately captured in our study. For the taxa that responded positively to a more complex forest structure, sustainable forest management practices that increase structural heterogeneity, expand the rotation period, and retain more deadwood can be beneficial.

Lichens, plants, mosses, and ground beetles responded more strongly to soil factors than structural variables. This contrasts with other studies showing that light availability mediated by forest structure is an important driver of the diversity patterns of autotrophs (Gossner et al., 2014; Hilmers et al., 2018; Schall et al., 2018), and ground beetles (Lange et al., 2014). Likely, the lower relative effect of the forest structure in this study can be explained by the developmental stage of the stands. Although management had an impact on the forest structure, the high canopy cover across all our stands caused light conditions to be generally low for both management types. Another factor likely contributing to the difference in the importance of soil conditions among taxa is the scale of our study. Soil and biodiversity sampling was done in the same, small-scale plot to capture the effect of the direct within-stand variability of soil and structural factors on biodiversity. At this fine scale, sessile autotrophic organisms can be expected to be better coupled to underlying soil conditions to a larger extent than mobile insects.

After accounting for forest features, management type did not explain much of the variation in the occurrence of species from different taxa suggesting that the effect of management acts upon changes in the structural attributes of the forest. This supports the use of forest features as predictors instead of discrete management categories, as they capture different dimensions of the requirements of different species (Gossner et al., 2014; Tinya et al., 2021). An exception was the positive effect of the abandonment of management *per se* had on average on fungi, and on some species of crane flies (*Dicranophragma sp.*, *Paredelphomyia senilis*), lichens (*Pyrenula nitida*), and mosses (*Brachythecium, salebrosum, Homalothecium sericeum, Isothecium myosuroides, Plagiothecium succulentum subsp. nemorale*). That the structural and abiotic factors did not

mediate the management effects completely, suggests that factors not considered explicitly in this study might be driving these effects. One possibility is forest continuity, whereby older stands could have a higher probability of accumulating poor-dispersing species like crane flies (Byriel et al., 2020), or species with specific habitat requirements, e.g. different decay stages of dead wood, such as fungi (Tomao et al., 2020).

On the contrary, rove beetles and plants had higher average probabilities of occurrence in managed stands. Previous studies have argued that vascular species richness is a poor indicator of old-growth beech forests because plant species richness generally increases in managed stands (Lelli et al., 2019; Sabatini et al., 2016). Our results confirm this observation. However, among the studied taxa, vascular plant species were the most responsive taxa with the most significant responses and congruent patterns among species. For example, the occurrence of *Carex pilulifera, Juncus effusus, Poa trivialis, Rubus idaeus, Urtica dioica* and *Veronica hederifolia*, was negatively related to the forest structures related to abandonment of forest management. Similarly, *Carex pilulifera, Dactylis glomerata* subsp. *lobata, Avellana flexuosa, Hordelymus europaeus, Juncus effusus, Moehringia trinervia, Poa annua,* and *Poa nemoralis* were negatively associated with unmanaged forest stands, after accounting for the other variables. These individual species can potentially serve as indicators of high forest management intensity or disturbances, but this will need to be further explored in a wider range of forest types and regions.

4.3. Congruence among taxa, specialization, and community properties

Previous studies assessing inter-taxa congruences have found little agreement, scale dependencies, or functional group dependencies in the correlations between species richness among taxa. By focusing on individual species and multifactorial drivers, we disclosed some general patterns. For lichens and fungi, the species that responded positively to forest structures characteristic of mature stands (STRU1) also responded positively to soils with higher carbon and nitrogen content (SOIL1). Plants, including forest specialists, occupy the opposite side of this gradient responding negatively to these factors, thus revealing a trade-off between these taxa. The averaged responses from heterotrophic mobile taxa and mosses showed a more central position in the ordination space. In the case of beetles and mosses, this was due to the wider range of the species' affinities to the environmental factors, and in the case of crane flies, due to the weaker responses of the species to these factors.

Furthermore, our analysis showed that even when the predictive power of the models for the species' abundances was generally high, species responses to the explanatory variables were only weak or neutral. Even though abundance and cover are informative population-level parameters, their usefulness as indicators of management practices seems to be constrained in our case. This limitation can be related to the multifactorial and markedly variable nature of abundance drivers within certain groups. Furthermore, identifying relationships between taxa and environmental factors can be difficult for mobile and heterotrophic insect species at the small scale of the sampling units of this study.

5. Conclusions

Our study design allowed us to identify the environmental and structural variables that respond locally to forest management from those that vary at larger scales (i.e. among study areas). The balance between the inherent abiotic conditions and management determines the distribution of different species. By disentangling the contribution of different components of the forest, we disclosed relevant messages for management and conservation: Forest structure and soil moisture are more amenable to active management or restoration than soil properties such as pH or bulk density. Because of the wide regional variation of these underlying soil properties, selecting sites with the appropriate soil conditions can aid in designing management plans tailored to these conditions. Finally, focusing on individual species' responses can allow

us to identify indicator species and the specific environmental factors to which they react. Balancing the selection of sites with appropriate conditions and implementing management actions on the forest structure can ultimately lead to more targeted conservation and management plans.

CRediT authorship contribution statement

Inger Kappel Schmidt: Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Lasse Gottlieb:** Writing – review & editing, Formal analysis. **Aslak Kappel Hansen:** Writing – review & editing, Investigation, Data curation. **Torben Riis-Nielsen:** Writing – review & editing, Methodology, Data curation. **Mathias Just Justesen:** Writing – review & editing, Investigation, Data curation. **David Bille Byriel:** Writing – review & editing, Methodology, Data curation. **Vivian Kvist Johannsen:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Peter Friis Møller:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Otso Ovaskainen:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Sebastian Kepfer Rojas:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **sebastian Kepfer rojas:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, 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.

Acknowledgments

Author contributions

[Vivian Kvist Johannsen] [Inger Kappel Schmidt][Torben Riis-Nielsen] and [Peter Friis Møller] conceived the ideas and designed methodology; [Sebastian Kepfer-Rojas], [Inger Kappel Schmidt][Torben Riis-Nielsen] [David Bille Byriel], [Mathias Just Justesen], [Torben Riis-Nielsen], [Aslak Kappel Hansen], and [Irina Goldberg] and collected the data; [Sebastian Kepfer-Rojas] [Otso Ovaskainen] and [Lasse Gottlieb] analyzed the data; [Sebastian Kepfer-Rojas] led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122230.

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