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RESEARCH PAPER

Diversity and composition of moss guilds on uprooted trees in Central European mountain forests: effects of uprooting components and environmental variables

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Abstract

- ***Key message*** **The size of the structural components of the root–pit–mound complex was crucial for high moss species richness. Root plates, pits, and mounds were similar in terms of moss species composition, which was mostly determined by forest type.**
- ***Context*** Uprooted trees may be colonized by different terricolous mosses including common species and specialists.
- ***Aims*** The main aim of the present study was to analyze the relative effects of tree uprooting on mosses.
- ***Methods*** We used the parametric ZIGLMM and GLMM models to explain the richness and abundance of the moss species and double constrained correspondence analysis (dc-CA) to analyze species composition.
- ***Results*** The size of components of RPM complexes had a positive effect on moss species richness. The species cover of mosses was positively correlated with elevation. Species richness was partly dependent on forest type and species cover on component type and age of the RPM complex. The most important factor diversifying species composition was the type of forest. Species traits were also related to forest communities.
- ***Conclusion*** Uprooted trees are worth keeping in forest community, especially large ones. Moreover, the conservation value of uprooted trees in woodlands is higher if they are dispersed in different forest types.

Keywords Uprooted tree · Species diversity · Bryophytes · Species-area relationship · Forest types · Karkonosze Mts · Sudetes Mts

1 Introduction

Tree uprooting is an important process changing the functioning of forest ecosystems, because it impacts both the structure and dynamics of plant communities and soil profile (Faliński 1978; Schaetzl et al. 1989a; Jonsson 1990; Simon et al. 2011; Šebková et al. 2012; Plotkin et al. 2017). It also influences many chemical, physical, and

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Contribution of the co-authors Monika Staniaszek-Kik: carried out field activities, literature review, and paper draft and revision.
Jan Żarnowiec: conceived the idea and approach, modification of the manuscript, and overall supervision.
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biological processes in forest soils and has a significant role in nutrient cycling and water retention (Valtera and Schaetzl 2017). Tree uprooting diversifies the forest floor and enriches its heterogeneity with exposed tree root plates (R) and additional topographic elements, i.e., pits (P) and mounds (M) (Schaetzl et al. 1989b; Šamonil et al. 2016). These components may be several meters in diameter, and they may be visible on the forest floor for 200 to 500 years (Schaetzl and Follmer 1990; Šamonil et al. 2010; Pawlik 2012). In addition, the temporary gap in the forest canopy formed above the uprooted tree changes the microclimate conditions, i.e., insolation and humidity (Schaetzl et al. 1989b). Moreover, pits formed after tree uprooting are periodically filled with stagnant water (Żarnowiec 1995; Valtera and Schaetzl 2017). Finally, the uprooted trees provide new niches available for colonization, where competition does not exist or competitive relationships are weak (Schaetzl et al. 1989a; Jonsson and Essen 1990; Jonsson and Dynesius 1993; Šebková et al. 2012).

Uprooted trees are a structural element crucial for high bryophyte diversity (Jonsson and Essen 1990; von Oheimb et al. 2007). This is because the richness and species composition of mosses in forest communities depend on the diversity of substrates and microhabitats (Vellak and Paal 1999; Mills and Macdonald 2004; Lõhmus et al. 2007), and uprooted trees provide such elements. The components of a tree uprooting, i.e., a root plate, pit, and mound, offer a variety of substrates, including mineral soil, roots, humus, fine fragments of wood debris, and stones. Moreover, each of them has slightly different ecological conditions (Schaetzl et al. 1989a, b; Jonsson 1990; Jonsson and Essen 1990; von Oheimb et al. 2007). Such heterogeneity is especially favorable for mosses, which, due to their low competitive potential, often colonize substrates inaccessible to vascular plants (e.g., bark on trunks of trees and rocks) or temporary habitats (e.g., decaying wood and newly exposed patches of mineral soil) (Jonsson and Essen 1990; Márialigeti et al. 2009; Evans et al. 2012; Madžule et al. 2012). Tree uprootings are usually overgrown by common species with a broad ecological spectrum, which are able to colonize various substrates in the new area in a relatively short time (Kimmerer 2005; von Oheimb et al. 2007). Diversity of microsites within uprooted trees may be a driver for taxonomic composition which may be diversified in terms of functional traits of settled species (Jonsson and Essen 1990). Bare soil may be a beneficial substratum for colonists and short-lived shuttles which diaspores are deposited in soil bank (Jonsson 1993). The participation of species representing different life strategies may also depend on forest type (von Oheimb et al. 2007; Caners et al. 2009). Finally, the moss species richness and composition of sites disturbed by tree uprootings are influenced by the age of the uprooted tree, its size, tree stand composition, and the distance to similar objects (Jonsson 1990; Żarnowiec 1995; Ulanova 2000; von Oheimb et al. 2007).

The impact of natural uprootings has been studied intensively. However, most studies were conducted on large areas affected by natural disasters where the forest canopy had been removed (e.g., Ilisson et al. 2007; Sass et al. 2018; Khanina et al. 2019). We therefore decided to focus on uprooted trees dispersed randomly within not disturbed forest and to pay special attention to their structural components, i.e., root plates, pits, and mounds. We also chose mountain forests, because uprooted trees are more frequent in mountain ecosystems than in lowlands.

The main aim of the present study was to analyze the relative effects of different microhabitat conditions created by tree uprooting (root plates, pits, and mounds) while taking into account the size and the age of the uprooted tree and also habitat conditions, i.e., forest type, tree canopy cover, and elevation (Ulanova 2000; von Oheimb et al. 2007). We aimed to assess the diversity and composition of mosses on uprooted trees.

We hypothesized that species richness is positively correlated with the size of the uprooted tree components according to the well-known species-area relationship (Jonsson 1990; Rosenzweig 1995). Moreover, we supposed that species richness, cover, and composition may differ on root plates, pits, and mounds, because these components are different in terms of ecological conditions (Żarnowiec 1995; Ulanova 2000). Probably, species traits have significant effects on species composition and may be correlated with component type and/or forest communities (During 1979; Darell and Cronberg 2011; Zielińska et al. 2018). As we studied well-structured and different (deciduous versus coniferous) forest types, our last hypothesis was that there was a difference in the moss species composition of the uprooted trees between forest types (Faliński et al. 1996).

The following detailed questions were put forward:

(1) How did the different microhabitat conditions created by tree uprooting (RPM component, size, and age) and larger-scale habitat conditions (stand type, elevation) influence moss richness, abundance, and species composition, and which drivers are more influential?

(2) What moss traits explain community response to tree uprooting-related microhabitat and to larger-scale habitat conditions?

2 Material and methods

2.1 Study area

Field work was carried out in southern Poland, in the Karkonosze Mts (50°49′02″N 15°26′00″E, 50°44′50″N 15°49′28″E), which is the highest range of the Sudetes Mts. The study area is located within the borders of Karkonosze National Park and its buffer zone. This area is characterized by a harsh mountain climate with long cold winters and short cool summers (Table 1).

Almost 90% of the forest area is covered by *Picea abies* stands. *Fagus sylvatica* stands account for about 3%, and other tree species, i.e., *Abies alba*, *Larix decidua*, *Acer pseudoplatanus*, and *Pinus sylvestris*, cover extremely small areas as dominant species or they are admixed components of the stands, with the average age of trees being more than 90 years. Tree stands older than 200 years have survived only on ca. 1000 ha (Bugajski and Nowiński 1985; Danielewicz et al. 2002). There is a typical, zonal vegetation reflecting the climate and soil conditions. The lower montane forest belt (500–1000 m a.s.l.) is mostly occupied by recent spruce forests mostly planted in habitats of beech forests. *Picea abies* is the predominant and often the only component of the tree stands, with a minor admixture of *Larix decidua*. This belt is also occupied by small, well-preserved patches of natural forest types: beech forests on acid soils *Luzulo luzuloidis-Fagetum* Meusel 1937. On fertile soils, there are small patches of rich beech communities *Hordelymo-Fagetum* Kuhn 1937. Additionally, fir-spruce forest *Abieti-Piceetum abietis* Szafer et al. 1923 occupies the poorest sites in the lower montane forest belt: flat slopes with skeletal soils, elevations between streams, and steep, narrow valleys with a cool microclimate. Forest stands of the upper montane forest belt (1000–1250 m) are dominated by a subalpine reedgrass spruce forest *Calamagrostio villosae-Piceetum abietis* Schlüter 1969. The subalpine belt (1250–1450 m) is dominated by thickets, *Pinetum mugo sudeticum* W. Mat. 1960 and *Empetro-Vaccinietum* Br.-Bl. 1926 communities (Danielewicz et al. 2002). Considerable areas are covered by herb and grass communities, including grasslands *Carici-Nardetum* (Zlatn. 1928) Jenik 1961. The highest parts of the Karkonosze Mts are occupied by the alpine belt (1450–1603 m) with fragmented patches of rocky grasslands (Żołnierz and Wojtuń 2013).

All forest types in the Karkonosze Mts occupy 13,505.03 ha, of which almost 30% is protected as Karkonosze National Park (KNP) (Bugajski and Nowiński 1985; Raj 2014). In the 1970s and 1980s, the synergistic effect of several factors (including acid rain and outbreaks of insects) led to an ecological disaster in the Karkonosze Mts associated with large-scale dieback of spruce stands. During that period, 67% of the forests in KNP suffered damage. For several decades, silvicultural treatments have been done in the Karkonosze Mts to change the species structure of tree stands, mainly in the lower montane forest belt. Over that period, forestry services have managed to significantly increase the proportion of beech (Raj 2014).

2.2 Data collection

Several components characterized by unique microclimatic and sedimentation-erosion conditions can be distinguished in the structure of sites disturbed by uprooting (Šebková et al. 2012). These include a fallen log with the crown, root plate (R), pit (P), and mound (M); the latter three form the root plate–pit–mound complex (RPM complex) (Fig. 1). The present study investigated only mosses (division Bryophyta) on RPM complexes (Staniaszek-Kik 2021). Mosses growing on the logs of uprooted trees were the subject of other analyses of epixylic flora (e.g., Chmura et al. 2016; Staniaszek-Kik et al. 2016). Analyses were carried out in the main types of forests in the Karkonosze Mts, i.e., in three communities of coniferous forests: spruce-fir forest of the lower

Table 1 Climatic features of selected stands in the Karkonosze Mts (Staniaszek-Kik and Żarnowiec (2018) based on Głowicki (2005); period 1991–2000)

	Jelenia Góra (342 m a.s.l.)	Karpacz (575 m)	Jakuszyce (860 m)	Śnieżka (1603 m)
Mean annual temperature (°C)	7.4	2.7	4.3	1.0
Absolute minimum temperature (°C)	−29.5	−20.9	−28.9	−24.9
Absolute maximum temperature (°C)	35.8	32.2	30.1	23.5
Mean annual precipitation (mm)	684	1042	1360	1102
Seasonal average of days with snow cover (in months IX–VI)	70.1	85.8	154.1	198.7

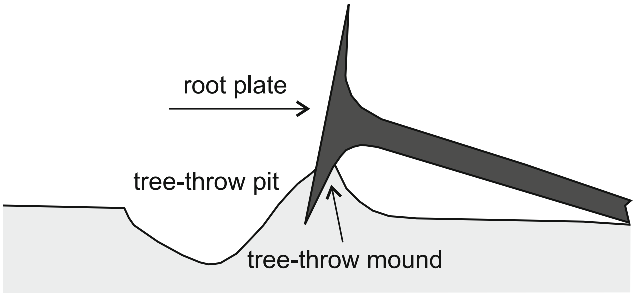

Fig. 1 Schematic draft of the root plate (R), pit (P), and mound (M) complex (RPM complex)

montane belt, *Abieti-Piceetum abietis* (AP); plantations of spruce *Picea abies* in the lower montane belt (PA-PF); spruce forest of the upper montane forest belt, *Calamagrostio villosae-Piceetum abietis* (CVP); and *Fagus sylvatica* forests of the lower montane belt, *Luzulo luzuloidis-Fagetum* (LF) (Table 2). RPM complexes in all forest types were studied in square plots size 10×10 m. These plots were established using random-stratified sampling (Chmura et al. 2016). Within the plot, we studied one or more uprooted trees (max. 5 per plot). In addition, to obtain a similar number of uprooted trees in individual types of communities, randomly selected RPM complexes outside the study plots were analyzed. Overall, 160 RPM complexes were studied. Each particular RPM complex was represented by one, two, or three components. Because of the age of the uprooted trees, as well as habitat conditions, not every complex comprised all three components. Overall, 260 components were investigated (R—112, P—77, and M—71). The following parameters of RPM complexes were measured: for R: height and length; P: length, width, and depth; M: length, width, and height. We used the degree of decomposition of the fallen log as an acceptable proxy of the age of RPM complexes (Lõhmus et al. 2010). A five-degree scale was used for that purpose: 1: fresh windthrows not decomposed, a knife can only penetrate a few millimeters into the wood; 2: wood is quite hard, a knife can penetrate about 1–2 cm deep into the log; 3: wood quite soft, a knife can easily penetrate about 3–5 cm deep into the wood; 4: log in advanced decomposition, soft wood, a knife easily penetrates deep into the wood; 5: very soft wood, almost completely decayed, easily falls apart in the fingers, a knife easily passes through the log (Staniaszek-Kik and Żarnowiec 2018). The altitude above sea level (elevation) and geographical coordinates of the examined sites were determined using a GPS receiver. Light conditions were determined based on visual estimates of the tree canopy above the RPM complex. We used a 5-degree scale (1: <30% of canopy cover, 2: 30–40%, 3: 40–60%, 4: 60–80%, and 5: >80%). A floristic survey of moss species was carried out for each component within an RPM complex, and the cover (abundance) for each species was estimated using the 10-point Londo scale (Londo 1975): 1: species covers 5–10% of the R, P, or M; 2: 11–20%; 3: 21–30%; 4: 31–40%; 5: 41–50%; 6: 51–60%; 7: 61–70%; 8: 71–80%; 9: 81–90%; 10: 91–100%. For species cover < 5%, additional points were used: 0.1 for cover <1%; 0.2: 1–3%; 0.4: 3–5% (Londo 1975). Nomenclature of mosses follows Ochyra et al. (2003).

2.3 Data analysis

The total and mean numbers of species (species richness) were calculated for all RPM complexes and separately for each of their components R, P, and M. The mean species cover (species abundance) was calculated only for R, P, and M. First, we calculated cover of all species on each individual component and then we calculated mean value of species cover on R, P, and M. For calculations, we transformed the degrees of the Londo scale into the mean

Table 2 Characteristics of the studied forest communities

Belt	Elevation (m)	Community	Forest stand	Soils	Number of uprooted trees	
					Within study plots	Outside study plots
Lower montane forest belt	500–1000	*Luzulo luzuloidis-Fagetum* (LF)	Beech stand	Acidic brown mountain soils, cryptopodzolic or rankers	2	51
	500–1000	Plantations of spruce *Picea abies* (PA-PF)	Spruce stand	Acidic brown soils, podzolic and cryptopodzolic soils	15	5
	850–1000	*Abieti-Piceetum abietis* (AP)	Fir-spruce stand	Skeletal soils, brown podzolic soils, or poorly developed podzols, very acidic in the upper layer	19	1
Upper montane forest belt	1000–1250	*Calamagrostio villosae-Piceetum abietis* (CVP)	Spruce stand	Podzolic soils and rankers	24	43

percentage cover (i.e., 0.1 = 1%, 0.2 = 2%, 0.4 = 4%, 1 = 10%, and 2 = 20%).

The size of R was calculated using the formula for the area of the ellipse $P = \pi ab$, where a is the ½ of R diameter and b is the ½ of R height. The size of P and M was calculated using the formula for the total area of the spherical cap $P = 2\pi Rh$, where h is the depth of P or height of M and R is the ½ of diameter calculated from the arithmetical mean of the measured shorter and longer diameter of P or M.

To identify factors influencing species richness and abundance on the components of RPM complexes, we calculated generalized linear mixed-effects models using R language and environment (Bates et al. 2015; R Core Team 2019). In the models, study plot (site) and RPM complex were regarded as random effects because the location of a study plot was random, and from one to five RPM complexes were to be found within a study plot. The predictors, treated as fixed effects, were as follows: type of component of RPM complex, component size, age of uprooted trees, forest type, canopy cover, and elevation (altitude above sea level). For species richness as a response variable, we performed a zero-inflated generalized linear mixed model (ZIGLMM) because several RPM complexes had no bryophyte species (Brooks et al. 2017). In this model, the Poisson distribution for species richness was assumed. For the generalized linear mixed-effects model (GLMM) with species abundance (cover) as a response, Gamma distribution was assumed. Due to the fact that negative values including zeros are not appropriate for Gamma distribution, cases without species were removed from the analysis. Diagnostics of distribution was done using the "descdist" function of the *fitdistrplus* package and comparison of goodness of fit by means of the Akaike information criterion (AIC) and Bayesian information criterion (BIC). Due to high numbers of categories in RPM components and forest types, no interaction was considered. Both models were used to generate best-fit models with the lowest corrected (AICc) and delta (Δ) values (Table 5 in Appendix). In order to indicate strong evidence for the model, among 64 generated models for ZIGLMM and 32 generated models for GLMM, the criterion with $\Delta < 2$ was included using the "dredge" function (package *MuMIn*). The significance of the final model with the presentation of Wald chi-square statistics and p values of each covariate was done using the *car* package. The package *lsmeans* was adopted with the *post hoc* procedure using the Tukey test after GLMMs in order to examine differences among studied groups.

To check if there was any floristic specificity of components of RPM complexes, we calculated species fidelity, percentage frequency, and cover. As the measure of fidelity, the phi coefficient was adopted. The phi coefficient is a statistical measure which considers species presence and absence and shows the relationship between species and a defined category (Chytrý et al. 2002), i.e., R, M, and P in our study. Its values range from −1 to 1, but for the identification of diagnostic species, positive values are of particular importance. For better presentation, the phi coefficient was also multiplied by 100 (Tichý et al. 2010). The phi coefficient provides no information about statistical significance, so Fisher's exact test is additionally used before finally assessing the fidelity. In our analysis, values of fidelity were significant with $p<0.01$. For R, P, and M, on the basis of the species fidelity, frequency, and cover, we identified three groups of species: diagnostic species (min. fidelity = 10), constant species (min. frequency 30%), and dominant species (min. cover 20% and at least 10% frequency). This analysis was done using JUICE software (Tichý et al. 2010).

Functional composition of moss guilds was explained through the ordination method. We used double constrained correspondence analysis (dc-CA) to relate environmental variables and species functional traits through species composition. The analysis was performed in Canoco software (Šmilauer and Lepš 2014), in its newest version 5.12 (ter Braak et al. 2018). dc-CA is based on an ordination of a rectangular table of response data in which the scores of rows (samples) and columns (species) are constrained by linear combination of predictor variables: environmental variables and species traits (ter Braak et al. 2018; Peng et al. 2021). The advantage of the method is that it takes into account both correlation among environmental variables and correlation among traits. We included only species with frequency higher than 1%. Predictors (explanatory variables) for samples and species were arranged in an additional two tables. Predictors for the samples were environmental variables, and predictors for the species were species traits. The environmental variables were component type (RPM), component size, age of uprooted tree, forest type (AP, CVP, LF, and PA-PF), canopy cover, and elevation. Species traits were light and moisture indicator values (Düll 1991), growth form (orthotropic, plagiotropic), and life strategy (Dierβen 2001; Hill et al. 2007). In the case of life strategy, we combined some strategies provided by Dierßen (Dierβen 2001) and finally used 4 groups: colonists (colonists and pioneer colonists), perennials (competitive perennials, stress-tolerant perennials, and perennials), long-lived shuttles, and short-lived shuttles. In the dc-CA, besides the three aforementioned tables (species, environmental variables, and functional traits), we also used an additional table which was the transpose of the first table, i.e., the response data table with species and samples. This fourth table is necessary to perform dc-CA. The transpose table allows us to test for the significance of the trait effects on the response data and for the explanation of the variation in the species composition (ter Braak et al. 2018; Peng et al. 2021). We performed the analysis in six steps according to the procedure provided by Peng et al. (2021): step 1—a canonical correspondence analysis (CCA) constraining the species composition by environmental variables, step 2—a weighted RDA explaining constrained species scores of step 1 by functional traits, step 3—a CCA constraining the transposed species composition table by functional traits, step 4—a weighted RDA explaining constrained sample scores of step 3 by environmental variable, step 5—a CA to find scores for samples and species for maximizing the fourth corner correlation without any constraints, and step 6—calculation of dc-CA scores. A detailed description of steps was provided by Peng et al. (2021). We applied logarithmic transformation of species cover. Effects of predictors were tested with the Monte Carlo permutation test (number of permutations=499).

3 Results

3.1 Species richness, abundance, and species composition

A total of 50 moss species were found in RPM complexes (35 on R, 37 on P, and 29 on M; Table 6 in Appendix). The total number of mosses in RPM complexes in individual forest types varied in the following sequence: CVP (34 species) > PA-PF (29) > LF (28) > AP (25). The mean species number of a single RPM complex was 5.1. The mean species number on R, P, and M varied in the range of 4.2–4.4 and in forest types in the range of 3.7–5.9.

The RPM components were smallest in the spruce forest CVP in the upper montane forest belt and largest in beech forests LF (Table 7 in Appendix). There was a significant positive correlation between species richness and the size of the RPM component (Table 3, Fig. 2a, Table 8 in Appendix). The mean number of moss species was highest in plantations of spruce *Picea abies* (PA-PF) (Fig. 2b). Species cover differed significantly between class 1 of age of RPM complexes and other classes (2–5) (Fig. 2c). The cover was also positively correlated with elevation (Table 3, Table 9 in Appendix) and dependent on the RPM component, i.e., moss species cover on mounds and root plates was significantly higher (Fig. 2d).

Species found on all three components of the RPM complex accounted for 42% of the moss flora; seven of them were characterized by high frequency: *Atrichum undulatum*, *Dicranella heteromalla*, *Dicranodontium denudatum*, *Plagiothecium laetum*, *Pohlia nutans*, *Polytrichastrum formosum*, and *Tetraphis pellucida* (Table 6 in Appendix). The floristic specificity of components of the RPM complex was low. Some species were recorded only on one component type (on R, P, or M). They accounted, respectively, for 18%, 20%, and 6% of total moss composition. At the same time, these species had very low frequency (mostly 1%). Species recorded only on one component type were not necessarily statistically diagnostic species. The highest numbers of diagnostic moss species were found on P, while single ones were found on R and M (Table 4). Constant species for all three components of RPM complexes included *Dicranella heteromalla* and *Polytrichastrum formosum*. M were characterized by high cover of the constant species *Atrichum undulatum*.

Table 3 Results of the best-fit models for species richness and species abundances of moss community

Response	Covariate	Wald χ^2	df	p value
Species richness	Size	24.5237	1	<0.00001
	Forest type	25.9108	3	<0.00001
	Elevation	3.5381	1	0.05997
Species abundance	Type of RPM component	30.8429	2	<0.00001
	Elevation	5.4506	1	0.01956
	Age	2.6896	1	0.10101

3.2 Moss traits and functional composition

It was found by CCA constraining the species composition by environmental variables (step 1 of dc-CA) that environmental variables had significant effects on species composition. Both the first constrained axis and all constrained axes were significant (F=1.9, p=0.002, F=4.1, p=0.002, respectively; Table 10 in Appendix, Fig. 3). The environmental variables accounted for 14.92% of variation (adjusted R^2=11.29%). LF, elevation, and CVP explained, respectively, 6.9%, 5.5%, and 4.6% of the variation when they were analyzed separately in the model (Table 11 in Appendix). When the correlation of variables was taken into account, LF and CVP had the most important effects (6.92% and 2.18%). By the CCA constraining the transposed species composition table by functional traits (step 3), it was revealed that species traits also had significant effects on species composition. The first constrained axis was not significant (F=0.3, p=0.076). However, all constrained axes were significant (F=1.2, p=0.034, Table 10 in Appendix, Fig. 3). Species traits accounted for 28.73% of variation (adjusted R^2=4.97%) in species composition. Perennial strategy and also light preferences explained, respectively, 7.2% and 6.0% of the variation when they were analyzed separately in the model and 7.2% and 5.3% when the correlation of variables was taken into account (Table 11 in Appendix). In the last step

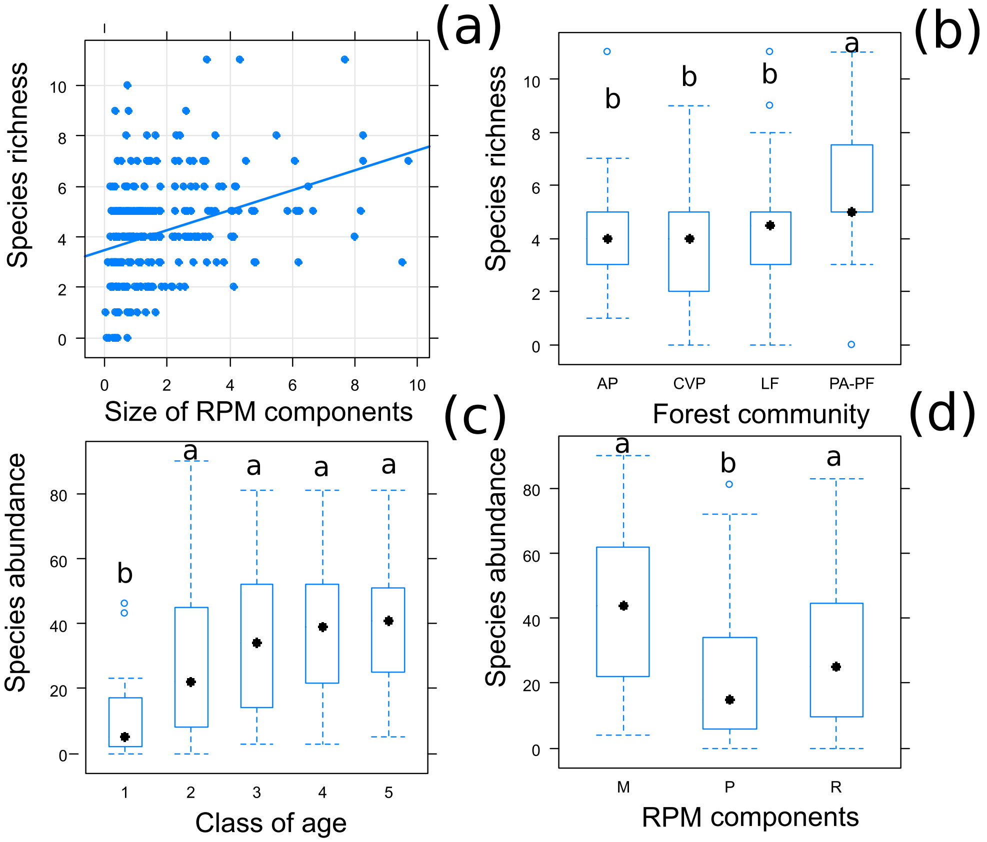

Fig. 2 The effect of selected environmental factors on moss species richness and abundance on components of RPM complexes. Forest communities: *AP Abieti-Piceetum abietis*, *PA-PF* plantations of spruce *Picea abies* in the lower montane forest belt, *CVP Calamagrostio villosae-Piceetum abietis*, *LF Luzulo luzuloidis-Fagetum*; class of age: 1–5 degrees of decomposition; RPM components: *R* root plates, *P* pits, *M* mounds

of dc-CA, we found that the association of environmental variables and species traits reduced the explained variation, and both selected environmental variables and species traits accounted for 6.74% (adjusted R^2=5.78%) of variation in species composition (Table 10 in Appendix). Among environmental variables and traits which are the most important and significant in the model, the community CVP is correlated with perennial life strategy, and the community LF is correlated with light preferences of species (Fig. 3).

4 Discussion

4.1 Drivers of moss richness, abundance, and species composition

Species richness within RPM complexes was influenced by the size of the components, and this is consistent with the SAR concept (species-area relationship) (Rosenzweig 1995). In Karkonosze forests, the mean size of individual

Table 4 Diagnostic, constant, and dominant species on components of RPM complexes

	Diagnostic	Constant	Dominant
Root plates	*Tetraphis pellucida* 17.5	*Dicranella heteromalla* 70 *Pohlia nutans* 39 *Polytrichastrum formosum* 71 *Tetraphis pellucida* 37	*Polytrichastrum formosum* 24
Pits	*Buckiella undulata* 20.4 *Polytrichum commune* 21 *Sphagnum girgensohnii* 26.3	*Dicranella heteromalla* 62 *Polytrichastrum formosum* 75	*Polytrichastrum formosum* 23
Mounds	*Pseudotaxiphyllum elegans* 19.9	*Atrichum undulatum* 38 *Dicranella heteromalla* 59 *Pohlia nutans* 34 *Polytrichastrum formosum* 68 *Pseudotaxiphyllum elegans* 38	*Atrichum undulatum* 18 *Polytrichastrum formosum* 30

Explanations: *diagnostic species* phix100 >10 (statistically significant values are presented, according to Fisher's exact, p>0.01), *constant species* frequency >30%, *dominant species* cover >20% with a min. of 10% frequency

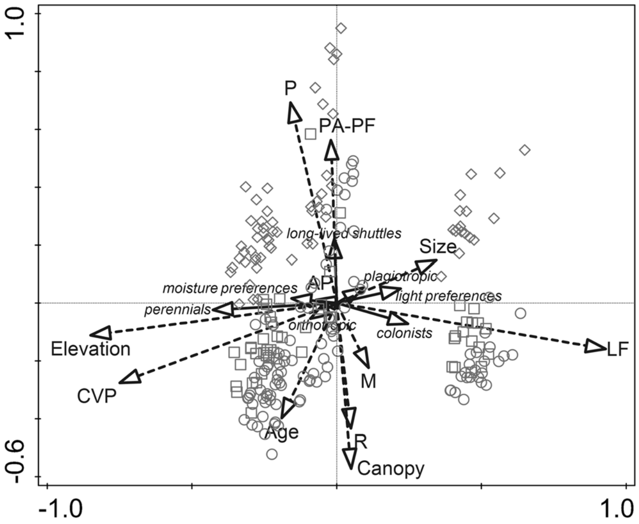

Fig. 3 Plot of dc-CA showing floristic associations among components of RPM complexes in relation to environmental variables and species traits. Explanations: symbols indicate the components of RPM complexes: *circles* root plates (R), *rhombus* pits (P), *squares* mounds (M), *solid line arrows* environmental variables, *AP Abieti-Piceetum abietis*, *PA-PF* plantations of spruce *Picea abies* in the lower montane forest belt, *CVP Calamagrostio villosae-Piceetum abietis*, *LF Luzulo luzuloidis-Fagetum*, *Elevation* altitude above sea level, *Age* age of uprooted trees (measured by degree of decomposition), *Canopy* cover of tree crowns, *Size* size of the components of RPM complexes, *dashed line arrows* species traits

components of the RPM complexes is in the range 1.7–2.1 m^2, and the largest components are over 9 m^2. For small cryptogams, such as mosses, treefall disturbances therefore create considerably large niches, with low competitive pressure (Kimmerer 2005; von Oheimb et al. 2007). As our research has shown, a single RPM complex can be a habitat for up to 12 moss species (5.1 on average). Considering all four types of forest communities, the highest species richness of mosses was found on R and M in managed of *Picea abies* plantations. A conclusive explanation for this is difficult. It could be associated with the size of the RPM components, which were usually larger than their counterparts in other types of communities, e.g., in the spruce forest in the upper montane forest belt. Accessibility to diversified substrates is essential for mosses (Lõhmus et al. 2007), and with a constant inflow of propagules from less transformed communities, the degree of forest naturalness may be less important.

Our results indicated that the cover of mosses on RPM complexes increased with increasing elevation. Elevational trends in terricolous bryophyte richness have been reported in many studies from different regions (Bruun et al. 2006; Grau et al. 2007; Stehn et al. 2010). As the altitude increases, microclimatic conditions change, i.e., the precipitation increases and snow cover lasts longer. Such conditions are favorable for the development of mosses. Forest types in the mountain regions are strongly related to elevation gradient; however, these two drivers affect moss guilds separately and significantly (Stehn et al. 2010). We also found that moss cover on the components of age class 1 of the RPM complex was significantly lower than on older (more decomposed) components. This means that after colonization of the new habitats provided by the tree falls, the species cover is quite stable. Our observation was partly consistent with previous findings by Kimmerer (2005), who reported that moss species cover increases with treefalls' age and at the same time composition and diversity did not change with age. Colonization of uprooted trees is not a typical succession, and early successional species may persist on the disturbed sites for up to several years (Jonsson and Essen 1990).

Despite the diversity of microhabitat conditions within sites disturbed by uprooted trees (Schaetzl et al. 1989a, b), as much as 42% of moss species indifferently occurred on all three components of the RPM complex, and the individual structural components are characterized by comparable species richness of moss flora. This is largely due to the fact that the R, P, and M form an integrated spatial complex, and species potentially capable of colonizing these sites originate from the same sources, i.e., the soil bank of propagules, vegetative fragments, clonal growth on the forest floor, and newly transported propagules (Rydgren and Hestmark 1997; Kimmerer 2005; von Oheimb et al. 2007).

Within the RPM complex, diagnostic species can be identified for each component of the uprooted tree. For example, *Tetraphis pellucida* is a diagnostic moss for R. This species prefers wood at an advanced stage of decay (Dierβen 2001), so it grows on R, specifically on decomposing roots and deposited humus. Other authors also point to the fact that epixylic moss species are common on sites affected by uprooting (von Oheimb et al. 2007). Compared to other components of the RPM complex, P are characterized by higher moisture and are periodically filled with stagnant water (Żarnowiec 1995; Valtera and Schaetzl 2017). This topographic element of the mountain slopes influences the accumulation and outflow of rainwater and the accumulation of snow and modifies surface runoff (Schaetzl and Follmer 1990). Therefore, P on uprooted sites are a habitat for hygrophytic and boggy mosses, e.g., *Polytrichum commune* and *Sphagnum girgensohnii*, but also for *Buckiella undulata*, which has low tolerance to drying out. These three species are constant components of upland and mountain spruce forests (Matuszkiewicz 2001b). On steep slopes, large surface runoff does not promote the growth of hygrophytic species, so for this group of mosses P may play an important role, since they are sites where rainwater is retained for a longer time (Valtera and

Schaetzl 2017). Compared to P, M are characterized by higher insolation, higher temperature, lower moisture, and lower content of organic matter, and in deciduous forests, the surface of M is also free from the thick layer of litter formed by leaves from deciduous trees (Schaetzl et al. 1989a, b; von Oheimb et al. 2007; Valtera and Schaetzl 2017). In our case, *Pseudotaxiphyllum elegans* was a diagnostic moss for M. In mountain forest communities, it mainly grows on exposed soil (Żarnowiec and Stebel 2014). It forms multiple slender branchlets acting as vegetative propagules and can quickly overgrow the surface of M.

4.2 Functional composition as a response for tree uprootings

Our research showed that the type of forest community was the most important variable for the species composition of mosses within the RPM complexes. In particular, natural beech forests and spruce mountain forest are different in terms of moss composition. This results from the fact that the moss flora of the uprooted trees is determined by the surrounding vegetation and mesoclimate (Faliński et al. 1996). Beech forests are characterized by a small share of the mosses in the ground layer (Matuszkiewicz and Matuszkiewicz 1973; Matuszkiewicz 2001a). Undecomposed leaves of *Fagus sylvatica* usually form a dense layer on the forest floor, which prevents the colonization of substrates by epigeic mosses or makes this process difficult (von Oheimb et al. 2007). More exposed places, like mounds, have a thin litter cover (Schaetzl et al. 1989a, b) and can be sites suitable for the growth of mosses. Our results indicated that the species composition of RPM components in beech forests (LF) was significantly determined by a species trait of light preferences. In beech forests, epigeic mosses are rare. However, many of them showed a positive correlation with light (Tinya et al. 2009). This might be explained by specific habitat conditions in beech forests where light regimes are significantly affected by canopy architecture (Canham et al. 1990). In these communities, during a growing season, light transmittance is strongly limited by the dense tree canopy layer. Disturbances like tree uprootings significantly change microhabitat conditions, especially improving local light availability (Gálhidy et al. 2006). Light-demanding species immediately take advantage of such an improvement. Along with the increase in altitude, the share of *Picea abies* in the tree stand gradually increases, and the share of *Fagus sylvatica* decreases, which has a clear effect on the cover and composition, and of epigeic mosses. In coniferous communities, the different architecture of tree crowns and canopy provides better (stable and continuous) light transmittance, so there are no special conditions favorable for light-demanding mosses.

In coniferous forests, the layer of epigeic mosses is more developed than in beech forests (Stebel 2006; Żarnowiec and Staniaszek-Kik 2008). As the moss layer is an indicative and permanent structural element of natural coniferous forests on oligotrophic substrates, the moss species composition is dominated by long-lived and competitive species. Our results indicated that perennial species are associated with RPM components in natural spruce forests (CVP). As within the group of perennials, there are species occurring on the forest floor (During 1992), so their diaspores are constantly available to colonize the uprootings. Moreover, perennials are characterized by rapid clonal growth, so they can dominate newly formed niches within uprooted trees (Jonsson and Essen 1990).

5 Conclusions

Uprooted trees are specific objects of complicated structure which provides various substrates for different species including mosses. As a result, storage of uprooted trees is an element of the protection of natural resources in forests and an indicator of a good conservation status of a forest community (Baran et al. 2020). Our study has shown that an object size, component type, elevation, and forest community influence different aspects of diversity and composition of mosses on the root–pit–mound complex. These results provide an important guideline for nature conservation and diversity maintenance. A single uprooted tree is worth keeping in forest community, because it is complicated itself by being a complex of root plates, pits, and mounds. Additionally, a large uprooting has a special value, because the bigger size the larger surface is available for organisms and the higher richness is possible. Moreover, large objects of decaying wood have a longer duration time in ecosystems and are available for species for a long time. Finally, the conservation value of uprooted trees in woodlands is higher if they are dispersed in different forest types.

Despite the fact that uprooted trees are a common phenomenon in forests, they still require a lot of detailed research, mainly regarding their number per unit area and the distance between objects. Such characteristics are crucial for the dispersion of groups of cryptogams (Jonsson and Essen 1990). In the future, this knowledge may lead to the implementation of retention patches (Perhans et al. 2009) with uprooted trees in managed and commercial forests.

Appendix

Table 5 Base and best-fit models of two responses species richness (SR) and species abundance (SC) with site and RPM complex treated as random effects. Selected models had the lowest corrected Akaike information value (AICc) and the lowest delta value (Δ)

Response variable	Type of model	Model	AICc	Δ
SR	ZIGLMM (base model), Poisson distribution	SR ~ size + plant_com + RPM + canopy + elevation + age + (1|site) + (1|RPM)	1107.6	36.99
	ZIGLMM (best-fit model), Poisson distribution	SR ~ size + forest_com + + (1|site) + (1|RPM)	1076	0
SC	GLMM (base model), Gamma distribution	SC ~ size + plant_com + RPM + canopy + age + (1|site) + (1|RPM)	2227.7	12.59
	GLMM (best-fit model)	SC ~ RPM+ age+(1|site) + (1|RPM)	2215.1	0

ZIGLMM Zero-inflated generalized linear mixed effects models, *GLMM* Generalized linear mixed-effects models

Table 6 List of mosses growing on RPM complexes

No.	Name of species	Frequency (%)			Mean cover (%)			Growth form	Life strategy
		F_R	F_P	F_M	A_R	A_P	A_M		
1	*Amblystegium serpens*	0.9	–	–	0	–	–	pl	p
2	*Atrichum undulatum*	27.7	29.9	38.0	2.2	1.5	10	o	s
3	*Brachydontium trichodes*	–	2.6	–	–	0	–	o	c
4	*Brachytheciastrum velutinum*	0.9	–	–	0	–	–	pl	p
5	*Brachythecium rutabulum*	–	1.3	–	–	0.1	–	pl	cp
6	*Brachythecium salebrosum*	0.9	–	–	0	–	–	pl	cp
7	*Buckiella undulata*	0.9	14.3	5.6	0	0.4	0.1	pl	pc
8	*Callicladium haldanianum*	–	1.3	1.4	–	0	0	pl	p
9	*Ceratodon purpureus*	1.8	–	–	0	–	–	o	c
10	*Dicranella cerviculata*	3.6	3.9	1.4	0.1	0.1	0	o	c
11	*Dicranella heteromalla*	69.6	62.3	59.2	3.3	1.5	5	o	c
12	*Dicranodontium denudatum*	21.4	24.7	21.1	2.1	0.7	1.3	o	pc
13	*Dicranum fuscescens*	2.7	–	–	0	–	–	o	pc
14	*Dicranum scoparium*	11.6	15.6	11.3	0.6	0.3	0.7	o	pc
15	*Diphyscium foliosum*	–	–	1.4	–	–	0.3	o	f
16	*Ditrichum lineare*	1.8	–	1.4	0	–	0	o	c
17	*Herzogiella seligeri*	9.8	11.7	5.6	0.1	0.1	0.1	pl	ps
18	*Hypnum andoi*	–	–	1.4	–	–	0	pl	ps
19	*Hypnum cupressiforme*	1.8	1.3	4.2	0	0	0.2	pl	ps
20	*Leucobryum glaucum*	–	–	1.4	–	–	0.1	o	p
21	*Mnium hornum*	16.1	22.1	15.5	0.4	0.7	0.5	o	l
22	*Oligotrichum hercynicum*	0.9	2.6	1.4	0	0.3	0	o	cp
23	*Orthodicranum montanum*	11.6	1.3	7.0	0.2	0	0.1	o	pc
24	*Plagiomnium affine*	–	1.3	1.4	–	0	0	o	pc
25	*Plagiothecium curvifolium*	8.0	20.8	15.5	0.2	1	0.4	pl	pc
26	*Plagiothecium denticulatum*	0.9	5.2	4.2	0	0.1	0	pl	pc
27	*Plagiothecium laetum*	27.7	26.0	19.7	0.5	0.4	0.3	pl	ps
28	*Pleurozium schreberi*	0.9	–	–	0	–	–	pl	pc
29	*Pogonatum aloides*	9.8	5.2	12.7	1.1	0.1	0.5	o	c
30	*Pogonatum urnigerum*	5.4	5.2	1.4	0.9	0.1	0.1	o	c
31	*Pohlia nutans*	39.3	23.4	33.8	0.9	0.3	1.6	o	cp

Table 6 (continued)

No.	Name of species	Frequency (%)			Mean cover (%)			Growth form	Life strategy
		F_R	F_P	F_M	A_R	A_P	A_M		
32	*Polytrichastrum alpinum*	2.7	2.6	7.0	1	0.1	1.4	o	pc
33	*Polytrichastrum formosum*	70.5	75.3	66.2	15.3	13.6	20.3	o	pc
34	*Polytrichastrum pallidisetum*	1.8	5.2	–	0	0.2	–	o	ps
35	*Polytrichum commune*	–	6.5	–	–	0.2	–	o	pc
36	*Polytrichum juniperinum*	0.9	–	–	0.1	–	–	o	ps
37	*Polytrichum piliferum*	0.9	–	–	0	–	–	o	ps
38	*Pseudotaxiphyllum elegans*	19.6	19.5	38.0	0.5	0.3	2.9	pl	cp
39	*Rhizomnium punctatum*	2.7	5.2	2.8	0	0.1	0	o	l
40	*Sanionia uncinata*	1.8	–	–	0	–	–	pl	ps
41	*Schistostega pennata*	–	1.3	–	–	0	–	o	c
42	*Sciuro-hypnum oedipodium*	0.9	2.6	–	0	0.3	–	pl	pc
43	*Sciuro-hypnum starkei*	–	2.6	–	–	0.1	–	pl	ps
44	*Sphagnum capillifolium*	–	1.3	–	–	0	–	o	l
45	*Sphagnum denticulatum*	–	1.3	1.4	–	0.1	0.6	o	l
46	*Sphagnum fallax*	–	1.3	–	–	1	–	o	l
47	*Sphagnum fimbriatum*	–	1.3	–	–	0.1	–	o	l
48	*Sphagnum girgensohnii*	2.7	11.7	–	0	0.6	–	o	l
49	*Straminergon stramineum*	–	2.6	–	–	0	–	pl	pc
50	*Tetraphis pellucida*	36.6	18.2	21.1	1.8	0.3	0.7	o	cp

Explanations: F_R Frequency on root plates, F_P Frequency on pits, F_M Frequency on mounds; we obtained the frequency by dividing the number of species records by the number of R, P, or M and multiplied by 100%. A_R abundance on root plates, A_P abundance on pits, A_M abundance on mounds; 0 cover means value <0.01%; *o* orthotropic, *pl* plagiotropic, *c* colonist, *cp* pioneer colonists, *d* dominant, *f* fugitives, *l* long-lived shuttle, *p* perennials, *pc* competitive perennials, *ps* stress-tolerant perennials, *s* short-lived shuttle

Table 7 Size of components of RPM complexes in forest communities

	Forest community	*N*	Size (m^2)			
			Mean	Min	Max	SD
Root plates	Forest communities combined	112	2.11	0.04	8.27	2.07
Pits		77	1.60	0.08	9.72	1.74
Mounds		71	1.67	0.20	8.03	1.47
Root plates	AP	20	2.88	0.04	8.27	2.86
	CVP	44	1.57	0.16	6.22	1.35
	LF	29	2.39	0.13	6.68	2.15
	PA-PF	19	2.11	0.26	8.27	2.15
Pits	AP	11	1.68	0.36	3.44	1.01
	CVP	33	1.03	0.10	2.83	0.72
	LF	24	2.37	0.08	9.72	2.74
	PA-PF	9	1.49	0.68	2.40	0.65
Mounds	AP	6	0.45	0.22	1.06	0.31
	CVP	31	1.15	0.20	4.72	1.04
	LF	31	2.43	0.56	8.03	1.57
	PA-PF	3	1.67	0.42	4.07	2.08

Explanations: *N* number of cases; forest communities: *AP Abieti-Piceetum abietis*, *PA-PF* plantations of spruce *Picea abies* in the lower montane forest belt, *CVP Calamagrostio villosae-Piceetum abietis*, *LF Luzulo luzuloidis-Fagetum*

Table 8 The model coefficients of fixed effects for species richness of moss community on RPM components

	Estimate	SE	*z*	*p* value
(Intercept)	1.25377	0.09291	13.494	0.0000
Size	0.06626	0.01565	4.235	2.29*e*-05
Forest_com [CVP]	-0.04951	0.10067	-0.492	0.622877
Forest_com [LF]	0.06940	0.09970	0.696	0.486341
Forest_com [PA-PF]	0.41607	0.11222	3.708	0.000209

Table 9 The model coefficients of fixed effects for species abundance of moss community on RPM components

	Estimate	SE	*z*	*p* value
(Intercept)	0.047757	0.008216	5.813	6.14*e*-09
RPM [P]	0.014828	0.003951	3.753	0.000174
RPM [R]	0.006788	0.003166	2.144	0.032003
Age	−0.005241	0.002236	−2.344	0.019093

Table 10 Results of successive steps of double constrained correspondence analysis (dc-CA)

	Variation explained by explanatory variables	Eigenvalues of axes	Explained variation of axis	Monte-Carlo permutation test of the first axis	Monte-Carlo permutation test of all axes
Step 1: CCA constraining species composition by environmental variables	R^2 = 14.92%	Axis 1=0.4234	Axis 1=7.56	F=1.9	F=4.1
	adjR^2=11.29%	Axis 2=0.1226	Axis 2=2.19	p=0.002	p=0.002
Step 2: RDA explaining constrained species scores by functional traits	R^2 = 48.16%	Axis 1=0.332	Axis 1=33.2	F=1.5	F=2.8
	adjR^2= 30.88%	Axis 2=0.0712	Axis 2=7.12	p=0.004	p=0.004
Step 3: CCA constraining transposed species composition table by functional traits	R^2= 28.73%	Axis 1=0.4528	Axis 1=8.39	F=0.3	F=1.2
	adjR^2= 4.97%	Axis 2=0.3039	Axis 2=5.63	p=0.076	p=0.034
Step 4: RDA explaining constrained sample scores by environmental variables	R^2= 24.86%	Axis 1=0.1669	Axis 1=16.69	F=4.7	F=7.8
	adjR^2= 21.65%	Axis 2=0.0398	Axis 2=3.99	p=0.002	p=0.002
Step 5: CA		Axis 1=0.6939	Axis 1=12.4	–	–
		Axis 2=0.5721	Axis 2=10.21		
Step 6: calculation of dc-CA scores	R^2= 6.744%	Axis 1=0.2536	Axis 1=4.7	–	–
	adjR^2=5.781%	Axis 2=0.0605	Axis 2=1.12		

Explanations: R^2 the squared correlation coefficient (proportion of the variance), *adj*R^2 adjusted R^2

Table 11 Effects of environmental variables and species traits on species composition obtained in steps of double constrained correspondence analysis

	Explained variation %	*F*	*p*
Step 1 of dc-CA: CCA constraining species composition by environmental variables			
Simple term effects			
LF	6.9	16.3	0.002
Elevation	5.5	12.8	0.002
CVP	4.6	10.6	0.002
Age	1.8	4	0.002
P	1.8	3.9	0.002
PA-PF	1.5	3.3	0.002
Size	1.4	3.1	0.006
Canopy	1.1	2.4	0.004
R	1	2.3	0.004
AP	1	2.2	0.004
M	0.6	1.3	0.138
Conditional term effects			
LF	6.92	16.3	0.002
CVP	2.18	5.2	0.002
P	1.58	3.8	0.002
Age	1.3	3.2	0.002
Canopy	0.85	2.1	0.016
Elevation	0.73	1.8	0.012
PA-PF	0.58	1.4	0.114
Size	0.43	1.1	0.338
M	0.36	0.9	0.604
Step 3 of dc-CA: CCA constraining transposed species composition table by functional traits			
Simple term effects			
Perennials	7.2	1.8	0.002
Light preferences	6	1.5	0.002
Colonists	4.9	1.2	0.166
Long-lived shuttles	4.6	1.1	0.22
Moisture preferences	3.6	0.9	0.694
Orthotropic	3.4	0.8	0.734
Plagiotropic	3.4	0.8	0.742
Conditional term effects			
Perennials	7.2	1.8	0.002
Light preferences	5.3	1.3	0.044
Long-lived shuttles	4.8	1.2	0.164
Colonists	4	1	0.3
Orthotropic	3.8	1	0.438
Moisture preferences	3.7	0.9	0.598

Explanations: *F, p* values of statistics obtained in Monte Carlo permutation test, *R* root plates, *P* pits, *M* mounds; forest communities: *AP Abieti-Piceetum abietis*, *PA-PF* plantations of spruce *Picea abies* in the lower montane forest belt, *CVP Calamagrostio villosae-Piceetum abietis*, *LF Luzulo luzuloidis-Fagetum*; *Elevation* altitude above sea level, *Age* age of uprooted trees, *Canopy* cover of tree crowns, *Size* size of the components of RPM complexes, *Conditional term effects* the effects of the correlated variables, *Simple term effects* the effects of the separate variables

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Data availability The datasets available during and/or analyzed during the current study are available in the Zenodo repository, https://doi.org/10.5281/zenodo.4632197.

Declarations

Ethics approval We obtained the approval of Karkonosze National Park for conducting the study—license number: 5/2003 (366).

Conflict of interest The authors declare no competing interests.

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