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## Spatial pattern and species richness of boreonemoral forest understorey and its determinants—A comparison of differently managed forests

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### Abstract

We compared patterns of understorey vegetation and abiotic factors in old-growth forests with low management intensity and young forests with high management intensity. CCA showed that disturbance gradient was the main axis of community variation, while local light availability (ISF, indirect site factor) and soil conditions (nitrate content) were also of some importance. Young stands demonstrated a significantly higher heterogeneity of vegetation with increased pattern diversity (1 – Jaccard similarity among 1 m × 1 m plots, also called beta diversity), variation in species richness and variation in the cover of both vascular plants and bryophytes. Young stands also showed a higher variation of soil nitrate content and lower average vascular plant cover. We concluded that the understorey vegetation in young stands with high intensity management is, contrary to our literature-based expectation, more heterogeneous in space than that in old stands with low management intensity. The relationship between environmental heterogeneity and diversity has been discussed extensively, but there is a scarcity of quantitative relationships documented in natural vegetation. We found that species richness in 4 m × 4 m plots was positively dependent on the variability of light availability (ISF) within plot. Pattern diversity was positively dependent on the variation of microtopography and the availability of direct radiation (DSF, direct site factor).

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### 1. Introduction

Disturbances in forest ecosystems are important as a driver for biodiversity as they largely determine the characteristics of the habitat mosaic, which in turn, affects the variety of forest-dwelling species that can exist in that environment. Knowledge of forest disturbance and successional processes is a prerequisite for developing ecologically sustainable forest management strategies (Kuuluvainen, 2002). In human-impacted landscapes, forests form a mosaic of different successional stages, representing regeneration after various anthropogenic and natural disturbances (Vellend, 2003; Verheyen et al., 2003). In this paper, we focus on the effects of one of the most common anthropogenic disturbances – clearcut logging – on the forest understorey.

Species composition between unmanaged old growth and successional young managed forests may not differ greatly (Graae and Heskjaer, 1997; Okland et al., 2003; Fraver and White, 2005). Although intensive felling methods may result in a decrease in species richness in the short term (Jalonen and Vanha-Majamaa, 2001), several authors report higher species diversity in recently clearcut areas when compared to old growth (Zobel, 1989; Haeussler et al., 2002; Reich et al., 2001; Small and McCarthy, 2005). Species richness in middle-aged managed forests on former clearcut areas may be lower (Qian et al., 1997; Duffy and Meier, 1992), similar (Okland et al., 2003) or higher (Scheller and Mladenoff, 2002) than that in undisturbed old-growth stands.

While forest management may have a relatively small effect on the gross species diversity and composition of vascular understorey vegetation, logging intensity may be an important driver of changes in understorey plant species cover, at least in the short term (Bergstedt and Milberg, 2001). Also, the specific spatial vegetation structure of old-growth stands is slow to

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recover (Fraver and White, 2005; Scheller and Mladenoff, 2002). The presence and spatial distribution of coarse woody debris (CWD) supplies specific habitats for several species and appears to be important for the maintenance of diversity in old-growth stands, especially with cryptogams and insects (Siitonen, 2001; Miller et al., 2002; Löhmus et al., 2005). Old-growth stands are characterised by an inverse J-shaped age structure of the tree layer (Lorimer et al., 2001) and by the presence of mosaic light conditions due to canopy gaps (Attiwill, 1994). This gives significantly different local environmental conditions compared to those observed in even-aged stands, regenerating after clearcut logging, and may also create differences in spatial structure of understorey vegetation.

However, relatively little is known about the within-stand structure of understorey communities of herbs and small shrubs in differentially disturbed temperate forests (Frellich et al., 2003). Decocq et al. (2004) have reported different beta diversity in differentially coppiced deciduous forests, while Haeussler and Bergeron (2004) recorded no difference in beta diversity between burned and clearcut areas. Qian et al. (1997) showed that the within-stand dissimilarity between vegetation plots was higher in old-growth forest compared to a 40-year-old plantation. Similarly, Bobiec (1998) reported higher structural diversification in old-growth forest.

Despite frequent discussion of the relationship between environmental heterogeneity and diversity in theoretical papers, descriptive quantitative information relating to this relationship in natural ecosystems is very scarce (Wilson, 2000). There is negligible quantitative information about how much the spatial turnover of species composition coincides with heterogeneity in canopy structure, topography and soil properties in differentially managed forest stands.

We aimed to compare the structure of stands representing two different disturbance regimes in a boreonemoral mixed coniferous forest—old growth with low human impact and 20–25-year-old stands established in clearcut areas. Based on the published data, we hypothesised that species composition and diversity do not differ between old and young forest, but that there is a considerable difference in the spatial structure of these ecosystems. In particular, we expected that due to the presence of an uneven-aged tree canopy, both the heterogeneity in abiotic conditions such as surface microtopography, light availability, and soil nitrogen content, as well as spatial turnover in vegetation composition, would be higher in old stands.

## 2. Materials and methods

### 2.1. Study site

The study site was located in Koeru, central Estonia (58°9'N; 26°05'E). It is set within a flat landscape with a mosaic of cultivated arable areas and forest. The climate in the study area is transitional between a maritime and continental climate.

The mean annual precipitation is 700–750 mm. The mean annual air temperature in the region is 4.3–6.5 °C, ranging between –7 °C in January and 17.4 °C in July (Jaagus, 1999).

The study site is a forested patch of 130 ha, representing a *Hepatica* site type (Löhmus, 2004). The soil is a calcareous cambisol with relatively constant soil condition across the study area (cf. Zobel et al., 2007). Norway spruce (*Picea abies*) is the predominant tree species with individuals of *Fraxinus excelsior* and *Acer platanoides* growing in old stands and *Betula pendula* and *Tilia cordata* in young stands. *Corylus avellana* predominates in the shrub layer of old stands. According to the available information the Koeru forest area has not historically undergone arable cultivation: the study area is indicated as forest on the oldest available map (1828). The forest has been managed and clearcutting has repeatedly taken place in patches of approximately 1–2 ha, although part of the forest can still be classified as old growth, with different age classes present and the oldest spruces are 130–140 years old.

We sampled forest ecosystems under low and high intensity management (three dispersed replicates of both low and high intensity managed forest). Old-growth spruce forests with a heterogeneous canopy represented old stands. In these stands, the intensity of forest management has been low, since only scattered selective felling of individual old trees has been practiced. The growing stock is approximately 280–310 m<sup>3</sup> ha, the mean height of trees 28 m, diameter 28–30 cm. Old stands represent ecosystems that are close to their natural state. Early successional stages were represented by young dense stands in areas that were clearcut 20–25 years ago and then planted with Norway spruce. Young stands have been thinned repeatedly since planting, with the aim to both reduce tree density in general and eliminate deciduous trees in particular. The growing stock is about 30–60 m<sup>3</sup> ha, the mean height of trees 5–8 m, the mean diameter 4–8 cm.

### 2.2. Methods

Vegetation sampling was conducted in three old and three young stands. In each stand, we described four 4 m × 4 m plots, divided into 16, 1 m × 1 m subplots. In both large and small plots, percent coverage of all vascular plant species and all bryophytes was recorded. Altogether, 24 large and 384 small plots were described.

In each 1 m × 1 m plot, local environmental conditions were characterised. Since soils over much of the boreal forest biome are characterised by low availability of nitrogen (Tamm, 1991) and soil conditions were rather uniform across all study sites (Zobel et al., 2007), we paid special attention on the availability of nitrogen in study plots. Topsoil samples (1–10 cm) were taken from the center of each plot for the determination of mineral nitrogen content (NO<sub>3</sub><sup>-</sup>-N and NH<sub>4</sub><sup>+</sup>-N). Soils were extracted with 1 M KCl (soil:extractant ratio 1:4) and filtered through Whatman No. 1 filter paper (Wheatley et al., 1989). Then NO<sub>3</sub><sup>-</sup>-N and NH<sub>4</sub><sup>+</sup>-N concentrations were determined colourimetrically on a segmented flow autoanalyser (Skalar Analytical, Breda, The Netherlands). Light availability was estimated from hemispherical photographs (Rich, 1990), taken at a height of 30 cm at the center of each 1 m × 1 m plot. A Nikon CoolPix 950 digital camera equipped with hemispherical lens was used. All photographs were taken at times

when the sun was blocked by clouds to ensure homogeneous illumination of the overstorey canopy and a correct contrast between canopy and sky. We calculated indirect site factor (ISF) and direct site factor (DSF) by using with WinSCANOPY software (Regent Instruments Inc., Canada) assuming Standard Overcast Sky model. ISF and DSF are defined as the proportion of diffuse and direct radiation received below the canopy as a fraction of that received above the canopy (Rich, 1990). As shown by Gendron et al. (1998), the values of transmitted diffuse light can be used as estimates of growing season percentage photosynthetic photon flux density in forests.

The microtopography within 4 m × 4 m plots was characterised by measuring relative elevation of corner points of each 1 m × 1 m plot. We calculated the variation of all measured points for each 4 m × 4 m plot.

All trees with height >1.5 m were identified according to species, mapped, and measured for diameter at ground level. Coarse woody debris (CWD), such as fallen logs (diameter of the thickest end >20 cm, >50 cm long) and stumps, were also mapped.

### 2.3. Data processing

Direct gradient ordination analysis was used to extract the main gradients in understorey species composition on 4 m × 4 m plots in relation to explanatory factors such as management intensity (indicator value), average soil nitrogen (NO<sub>3</sub> and NH<sub>4</sub>) content, light availability (ISF and DSF), variation of microtopography, summed area of CWD and living stems. Canonical Correspondence Analysis (CCA) – the method best suited to community data sets where species responses to environment are expected to be unimodal and where the important underlying environmental variables have been measured – was conducted with PC-ORD ver. 4.36 (McCune and Grace, 2002). Indicator species analysis (Dufrene and Legendre, 1997) of herb layer species composition among managed and old-growth stands was performed with PC-ORD ver. 4.36. The randomness of indicator value distribution within species was tested using Monte Carlo simulation tests (1000 runs) (McCune and Grace, 2002).

We were also interested in average species turnover among adjacent vegetation plots, without considering any environmental or spatial gradients. In recent years, there has been discussion about the components of beta diversity (Vellend, 2001; Veech et al., 2002; Koleff et al., 2003; Ricotta, 2005). Here we follow Pielou (1966), who suggested the use of the term ‘pattern diversity’ for species turnover within a relatively homogeneous environment. In order to measure pattern diversity within 4 m × 4 m plots, we used a metric advocated by Colwell and Coddington (1994): the mean of the total number of unshared species between each pair of 1 m × 1 m plots, divided by the number of species in the two plots combined, i.e. 1 – the Jaccard coefficient of similarity (cf. also Harrison, 1999; Chalcraft et al., 2004; Kluth and Bruelheide, 2004). For each 4 m × 4 m plot, the Jaccard similarity index was calculated based on the data of 16, 1 m × 1 m plots using EstimateS Win 7.5.0 software (Colwell, 2005).

The effect of management intensity on the environmental factors and their variability (coefficient of variation – CV – within each 4 m × 4 m plot, based on data from sixteen 1 m × 1 m plots where a given environmental factor was measured) was analysed with GLM performed in Statistica v.6.0 (StatSoft, 2001), where a random factor ‘site’ was nested within a fixed factor ‘management intensity’.

The effect of environmental factors, their variability, and management intensity on species richness, pattern diversity, the variation of species richness (CV of each 4 m × 4 m plot based on data of 16, 1 m × 1 m plots), total vascular plant cover, the variation of vascular plant cover (CV of each 4 m × 4 m plot based on data of 16, 1 m × 1 m plots), bryophyte cover and the variation of bryophyte cover (CV of each 4 m × 4 m plot based on data of 16, 1 m × 1 m plots) was estimated using the general regression model (GRM). The factors for the model were chosen with backward stepwise procedure. The analysis was performed in Statistica v.6.0 (StatSoft, 2001).

## 3. Results

In total 70 herbaceous and dwarf shrub vascular plant species were recorded in the understorey. *Oxalis acetosella*, *Fragaria vesca*, *Viola mirabilis* and *Hepatica nobilis* were the most abundant vascular plant species, represented in 92–100% of plots. *Dicranum scoparium* Hedw. and *Cirriphyllum piliferum* (Hedw.) Grout were the most common bryophytes.

### 3.1. Direct gradient ordination analysis

The first two axes of CCA described 50.7%, and 2.5% of the total variation of understorey community composition, respectively (Fig. 1a and b). The main source of variation was identified as management intensity—species composition of intensively managed young stands differed from that in less intensively managed old stands. The first axis may thus be interpreted as a management intensity gradient. The second axis, although of considerably lesser importance, was related to both light availability and soil nitrate content, with these factors having an opposing effect on vegetation composition. The second axis thus reflects a complex gradient of the increase of light and the decrease of soil nitrogen availability.

Herbaceous and shrub species tended to segregate along the management intensity axis. Indicator species analysis showed that *Galeobdolon luteum*, *Geum rivale*, *Gymnocarpium dryopteris*, *F. vesca*, *Mycelis muralis*, *O. acetosella*, *Rubus idaeus* and *Sorbus aucuparia* were identified as being the most characteristic to old-growth forests. *Alchemilla* spp., *Anthriscus sylvestris*, *Clinopodium vulgare*, *Galium mollugo*, *Dactylis glomerata*, *Melampyrum nemorosum* and *Viola riviniana* were indicator species for young stands. *Actaea spicata* and *Circaea alpina* occurred only in old stands, *Campanula persicifolia* and *Galium album* only in young stands. *Geranium pratense*, *H. nobilis*, *Paris quadrifolia*, *Rubus saxatilis*, *Veronica chamaedrys* and *V. mirabilis* were the most common species over both management intensity classes.

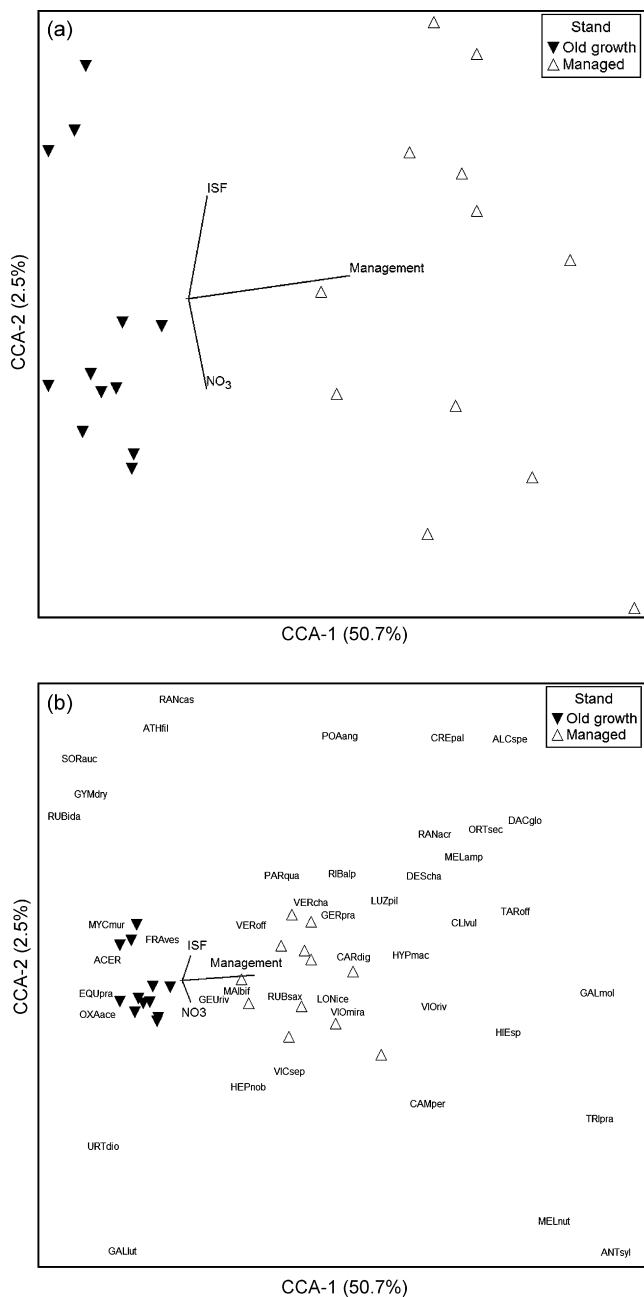


Fig. 1. CCA of forest understorey communities (4 m × 4 m plots) in old growth and young stands and environmental variables in relation to two axes (a) and CCA of forest understorey communities (4 m × 4 m plots) and species in old growth and young stands and environmental variables in relation to two axes (b). ACER, *Acer platanoides*; ALCspe, *Alchemilla* sp.; ANTSyl, *Anthriscus sylvestris*; ATHfil, *Athyrium filix-femina*; CAMper, *Campanula persicifolia*; CARdig, *Carex digitata*; CLIVul, *Clinopodium vulgare*; CREpal, *Crepis paludosa*; DACglo, *Dactylis glomerata*; DEScha, *Deschampsia caespitosa*; EQUpra, *Equisetum pratense*; OXAace, *Oxalis acetosella*; FRAves, *Fragaria vesca*; GALlut, *Galeobdolon luteum*; GALmol, *Galium mollugo*; GERpra, *Geranium pratense*; GEUriv, *Geum rivale*; GYMdry, *Gymnocarpium dryopteris*; HEPnob, *Hepatica nobilis*; HIESp, *Hieracium* sp.; HYPmac, *Hypericum maculatum*; LONice, *Lonicera xylosteum*; LUZpil, *Luzula pilosa*; MAIbif, *Maianthemum bifolium*; MELamp, *Melampyrum pratense*; MELnut, *Melica nutans*; MYCmur, *Mycelis muralis*; ORTsec, *Orthilia secunda*; PARqua, *Paris quadrifolia*; POAang, *Poa angustifolia*; RANacr, *Ranunculus acris*; RANcas, *Ranunculus cassubicus*; RIBalp, *Ribes alpinum*; RUBida, *Rubus idaeus*; RUBsax, *Rubus saxatilis*; SORAuc, *Sorbus aucuparia*; TARoff, *Taraxacum officinale*; TRIpra, *Trifolium pratense*; URTdio, *Urtica dioica*; VERcha, *Veronica chamaedrys*;

In relation to the light-nitrogen axis, *G. luteum*, *H. nobilis*, *Melica nutans* and *Urtica dioica* were located near the ‘nitrogen-rich, shaded’ end of this complex gradient, while, *Alchemilla* spp., *Athyrium filix-femina*, *Crepis paludosa*, *Poa angustifolia*, *Ranunculus cassubicus* and *S. aucuparia* were related to the ‘well-illuminated, nitrogen poor’ conditions.

### 3.2. Abiotic factors and their heterogeneity

The mean ISF ( $F = 3.01$ , d.f. = 1, 18,  $P = 0.100$ ), mean DSF ( $F = 2.67$ , d.f. = 1, 18,  $P = 0.120$ ), mean nitrate content ( $F = 0.34$ , d.f. = 1, 18,  $P = 0.568$ ), mean summed area of living stems at ground level ( $F = 2.854$ , d.f. = 1, 18,  $P = 0.108$ ) and mean cover of CWD ( $F = 1.52$ , d.f. = 1, 18,  $P = 0.234$ ) did not differ between old and young stands. In addition, the variation of ISF ( $F = 0.61$ , d.f. = 1, 18,  $P = 0.445$ ) and DSF ( $F = 0.34$ , d.f. = 1, 18,  $P = 0.569$ ), and the variation of microtopography within 4 m × 4 m plots ( $F = 0.03$ , d.f. = 1, 18,  $P = 0.875$ ) did not differ among old and young forest (Table 1). However, the variation of the soil nitrate content within 4 m × 4 m plots was significantly higher in young forest than in old stands ( $F = 9.20$ , d.f. = 1, 18,  $P < 0.01$ ).

### 3.3. Biotic variability and its determinants

The analysis of the general regression model (GRM) showed that species richness in 4 m × 4 m plots was positively dependent only on the variation of ISF ( $F = 5.32$ , d.f. = 1, 22,  $P < 0.031$ ). Management intensity had no effect on species richness.

The variation in species richness among 1 m × 1 m plots within 4 m × 4 m plots was significantly higher in young forest ( $F = 38.48$ , d.f. = 1, 21,  $P < 0.001$ ). Variation in species richness was positively dependent on the variation of microtopography within 4 m × 4 m plots ( $F = 4.75$ , d.f. = 1, 22,  $P < 0.042$ ) and on the average DSF ( $F = 7.75$ , d.f. = 1, 22,  $P < 0.012$ ), and negatively dependent on the average content of soil ammonium ( $F = 7.35$ , d.f. = 1, 21,  $P < 0.014$ ).

Pattern diversity (1 – mean Jaccard similarity among 1 m × 1 m plots within 4 m × 4 m plots) was significantly higher in young stands compared to old ones ( $F = 41.60$ , d.f. = 1, 20,  $P < 0.001$ ). Also, pattern diversity was higher when the microtopography was more variable ( $F = 15.68$ , d.f. = 1, 19,  $P < 0.001$ ) and when the average DSF was higher ( $F = 18.63$ , d.f. = 1, 19,  $P < 0.001$ ). Pattern diversity was lower in the case of high soil ammonium content ( $F = 9.14$ , d.f. = 1, 19,  $P < 0.007$ ).

The mean cover of vascular plants in 4 m × 4 m plots was significantly higher in old stands ( $F = 110.0$ , d.f. = 1, 21,  $P < 0.001$ ) and smaller in plots where the summed area of living stems at ground level was higher ( $F = 12$ , d.f. = 1, 21,  $P = 0.002$ ). The variation of plant cover among 1 m × 1 m plots within 4 m × 4 m plots was significantly higher in young stands

VERoff, *Veronica officinalis*; VICsep, *Vicia sepium*; VIOmira, *Viola mirabilis*; VIOriv, *Viola riviniana*.

Table 1  
Variables measured in 1 m × 1 m plots, if not specified otherwise

Parameter measured	Old forest stand			Young forest stand		
	Z	Y	W	T	R	S
1 – Jaccard	0.49 ± 0.03	0.48 ± 0.01	0.59 ± 0.03	0.67 ± 0.05	0.61 ± 0.02	0.69 ± 0.06
Species per 4 m <sup>2</sup>	28.00 ± 1.73	23.00 ± 1.08	24.75 ± 3.68	32.25 ± 2.87	24.75 ± 2.75	25.25 ± 2.56
Species per 1 m <sup>2</sup>	11.06 ± 0.61	9.13 ± 0.61	8.75 ± 1.96	11.00 ± 1.44	9.86 ± 2.08	7.78 ± 2.09
Vascular plant cover	59.56 ± 6.45	75.91 ± 5.85	77.81 ± 10.66	24.59 ± 6.04	25.63 ± 7.26	17.98 ± 6.04
Moss cover	38.66 ± 4.71	36.31 ± 3.17	33.63 ± 9.23	50.86 ± 4.69	17.88 ± 9.17	10.39 ± 6.03
CV species number	0.179 ± 0.020	0.261 ± 0.020	0.307 ± 0.041	0.497 ± 0.081	0.430 ± 0.067	0.614 ± 0.117
CV vascular plant cover	0.307 ± 0.039	0.288 ± 0.022	0.374 ± 0.061	0.692 ± 0.145	0.557 ± 0.067	0.919 ± 0.153
CV moss cover	0.503 ± 0.073	0.497 ± 0.061	0.417 ± 0.048	0.395 ± 0.021	1.014 ± 0.178	1.146 ± 0.162
CV DSF	0.333 ± 0.090	0.278 ± 0.056	0.388 ± 0.063	0.400 ± 0.019	0.368 ± 0.044	0.322 ± 0.085
CV ISF	0.178 ± 0.058	0.161 ± 0.047	0.230 ± 0.021	0.260 ± 0.048	0.141 ± 0.043	0.089 ± 0.007
CV NO <sub>3</sub>	0.586 ± 0.038	0.566 ± 0.085	0.528 ± 0.179	0.649 ± 0.090	1.805 ± 0.319	0.424 ± 0.072
CV elevation	0.173 ± 0.064	0.195 ± 0.070	0.363 ± 0.120	0.220 ± 0.057	0.246 ± 0.020	0.235 ± 0.085
DSF	0.285 ± 0.027	0.282 ± 0.024	0.349 ± 0.071	0.331 ± 0.032	0.184 ± 0.011	0.243 ± 0.041
ISF	0.235 ± 0.014	0.226 ± 0.007	0.309 ± 0.037	0.281 ± 0.016	0.293 ± 0.012	0.276 ± 0.004
NO <sub>3</sub>	12 ± 0.9	31.5 ± 3.2	18.5 ± 2.2	14.4 ± 2.3	5.9 ± 2.7	45.7 ± 3.7
NH <sub>4</sub>	1.7 ± 0.5	3.0 ± 1.5	1.7 ± 0.6	3.9 ± 0.7	2.1 ± 0.5	0.1 ± 0.0
Tree basal area	0.040 ± 0.007	0.008 ± 0.007	0.021 ± 0.016	0.008 ± 0.001	0.016 ± 0.008	0.008 ± 0.004
CWD	0.032 ± 0.020	0.013 ± 0.013	0.028 ± 0.015	0.093 ± 0.033	0.008 ± 0.008	0.038 ± 0.031

The letters R, S, T, Z, Y and W denote different study sites. Pattern diversity is measured as 1 – mean Jaccard similarity between 1 m × 1 m plots within 4 m × 4 m plots. CV, coefficient of variation; DFS, direct site factor; ISF, indirect site factor; CWD, coarse woody debris. DSF and ISF are measured as relative values of light availability, basal area of living trees at ground level and CWD are given as cover percentages. The content of NO<sub>3</sub> and NH<sub>4</sub> in topsoil samples is given as μg N g<sup>-1</sup> dry soil. CV of elevation is the variation of relative elevation measures at the corners of 1 m × 1 m plots within 4 m × 4 m plot. Values are represented as mean ± S.E.

( $F = 54.27$ , d.f. = 1, 19,  $P < 0.001$ ). It was positively dependent on average nitrate content in the soil ( $F = 15.71$ , d.f. = 1, 19,  $P < 0.001$ ) and on DSF ( $F = 8.21$ , d.f. = 1, 19,  $P < 0.010$ ), and negatively dependent on the total area of living stems at ground level ( $F = 10.14$ , d.f. = 1, 19,  $P < 0.005$ ).

The mean coverage of bryophytes in 4 m × 4 m plots was higher in the case of higher variation of ISF ( $F = 22.91$ , d.f. = 1, 21,  $P < 0.001$ ) and lower in the case of higher variation of microtopography ( $F = 13.27$ , d.f. = 1, 21,  $P < 0.002$ ). Variation of the cover of bryophytes among 1 m × 1 m plots within 4 m × 4 m plots was significantly higher in young stands compared to old ones ( $F = 18.30$ , d.f. = 1, 20,  $P < 0.001$ ). Variation in the cover of bryophytes was negatively dependent on the content of ammonium in the soil ( $F = 10.70$ , d.f. = 1, 20,  $P < 0.004$ ) and on the amount of CWD ( $F = 5.61$ , d.f. = 1, 20,  $P < 0.029$ ).

#### 4. Discussion

There were clear differences in species composition between young and old forests clearly differentiated along the first axis on CCA. There were particular species that occurred exclusively or more commonly either in young or old stands. The more frequent occurrence of species like *R. idaeus* or *U. dioica* in old growth is evidently correlated with local small-scale disturbances due to tree uprooting (Okland, 2000).

Former studies have indicated that differences in species composition and richness between intensively managed young forests and less managed old stands are relatively small (e.g. Graae and Hesckjaer, 1997; Okland et al., 2003). The clear difference of understorey community composition in differently managed forests in Koeru is thus a little unexpected. It

may, however, be explained by two factors. First, the community species pool in the herb-rich Koeru forest is relatively large with a consequent potential for marked vegetation change. Second, the management disturbance in young stands has been rather strong—planting has resulted in dense young coniferous stands, with an additional effect caused by the selective removal of spontaneously grown deciduous trees and thinning of spruce trees from these plots has causing additional disturbance of the soil surface, and evidently also changes in soil properties.

Species richness in 4 m × 4 m plots did not differ among the young and old stands with differential intensity of management disturbance, although the cover of understorey vascular plants was higher in old stands. Species richness was not related to absolute values of measured environmental variables, and depended positively only on the variation of light conditions within 4 m × 4 m sample plots. It is well established that both vegetation composition (Goldblum, 1997) and species richness (Beatty, 1984; Peterson and Campbell, 1993) differ between shaded canopy and gap microsites. Also, it is generally accepted that small-scale environmental heterogeneity may support higher species richness (Huston, 1994; Wilson, 2000). Surprisingly, the field evidence demonstrating small-scale richness values related to variability of measured environmental characteristics is scarce and contradictory—Lundholm and Larson (2003) report positive relationship between environmental microheterogeneity and richness, Palmer (1991) and Richard et al. (2000) no relationship and Kleb and Wilson (1997) an inverse relationship. Our results clearly show that, in herb-rich spruce forest ecosystems, variability in light availability within 4 m × 4 m plots provide the main determinant of richness on this scale. However, richness in a

larger scale may depend on different set of variables (Palmer, 1990; Wilson, 2000).

The mean values of measured environmental factors and their variability did not differ between old and young stands, except for the spatial heterogeneity of soil nitrogen content, which was higher in young stands. Some authors have shown a historical effect of logging on soil parameters (Fraterrigo et al., 2005), therefore the higher variations in soil  $\text{NO}_3^-$ -N concentrations reported for the young stands is likely to be connected to an uneven distribution of decomposing plant material from recent thinning activities.

The understorey vegetation in young stands was more heterogeneous in space than in old stands—variation of species richness among  $1\text{ m} \times 1\text{ m}$  plots, variation of the cover of vascular plants and bryophytes, as well as pattern diversity were significantly higher. This result is in contradiction to our expectations, based on published evidence. Old-growth plots have been characterised by a high spatial variability of canopy structure (Fraver and White, 2005), microtopography (Miller et al., 2002) and light conditions (Scheller and Mladenoff, 2002). There is, however, less firm evidence about the spatial heterogeneity of understorey vegetation. Bobiec (1998) reported higher turnover of synusia and Scheller and Mladenoff (2002), smaller community patch size and larger compositional heterogeneity in old-growth forests. In both these cases, old-growth forests had practically no logging history.

We found that pattern diversity, characterising species turnover in space, was higher in plots with more variable microtopography. Also, pattern diversity was higher in gap environments with higher availability of direct radiation. Although the possible measures of beta diversity *sensu lato* have been thoroughly discussed in recent years (Oksanen and Tonteri, 1995; Vellend, 2001; McCune and Grace, 2002; Koleff et al., 2003; Legendre et al., 2005), we are not aware of any previous attempts to relate pattern diversity to measured environmental variables.

Vegetation heterogeneity in Koeru was partly explained by the variability of abiotic factors and only the vascular plant cover was dependent on a biotic factor—the stem area of living trees. In addition to the abiotic and biotic determinants of the vegetation structure addressed here, there may be other biotic mechanisms responsible for understorey vegetation heterogeneity, which we have not described. For example, nucleation – the development of a community through chance establishment or persistence, followed by vegetative expansion from these nuclei – might be a factor causing the patchiness of the understorey vegetation in young successional forest. Data about species mobility in space is needed to validate this explanation in the future.

## 5. Conclusions

Species composition of understorey vegetation in herb-rich mixed coniferous forest was strongly dependent on the management intensity. At the same time, our results indicate that disturbance due to forest management did not influence

small-scale species richness, but resulted in a spatially more heterogeneous understorey vegetation in intensively managed young forest, compared to lightly managed old forest. Young stands differed by significantly higher heterogeneity of vegetation with increased pattern diversity (1 – Jaccard similarity among  $1\text{ m} \times 1\text{ m}$  plots), variation in species richness and variation in the cover of vascular plants and bryophytes. Consequently, if there is any degree of patchiness in the understorey vegetation of old-growth stands, it may be expressed at a different spatial scale than the  $4\text{ m} \times 4\text{ m}$  plots used here. Finer-grained patch structure in old-growth forest as opposed to middle-aged forest was recognised, for example, by Scheller and Mladenoff (2002). Our data show that the recovery of understorey vegetation after management disturbance may be described as a change from ‘temporary patchiness’ to ‘elaborated uniformity’.

Although the relationship between species richness, pattern diversity and environmental heterogeneity has frequently been discussed, there is little quantitative evidence. We found that in the case of forest understorey vegetation, species richness in  $4\text{ m} \times 4\text{ m}$  plots was positively dependent on the variability of diffuse radiation within a plot. Pattern diversity of understorey vegetation was positively dependent on the variation of microtopography and the average level of the availability of direct radiation. Our results provide novel information for further discussion of an area which has, to now, mainly concerned theoretical models with limited experimental data.

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