Spatial diversity of ground layer vegetation as a sensitive indicator of forest naturalness

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Abstract: In this paper we tested if diversity measures of forest floor assemblages can be used as an indicator of forest naturalness. We compared vascular and bryophyte vegetation of two habitat types in an unmanaged beech-dominated reserve and five nearby managed stands of different ages. Different diversity measures were calculated from systematically collected data for four spatial scales obtained by successively aggregating neighbouring quadrats.

Species richness not always differentiated near natural sites from managed sites, and the observed difference depended very much on the spatial scale used.

The behaviour of Shannon-Wiener diversity function can only be understood if both the species richness and the evenness components are taken into consideration. Near natural plots had high Shannon-Wiener diversity values even at the finest spatial scale not only because of high number of species, but also because of high evenness.

We found that a simple measure of spatial variation was the most effective in differentiating the diversity of plots with different levels of naturalness. The absolute values of spatial variance in the forest floor vegetation were the highest in those plots, where the characteristics of important limiting ecological factors were generated by natural disturbance.

Vascular and bryophyte species responded differently to tree stand structural characteristics. The diversity of vascular vegetation was determined mainly by the spatial variation of light availability, whereas that of bryophyte vegetation responded to the amount and spatial heterogeneity of appropriate substrates (dead wood, rock).

The use of pattern sensitive diversity measures is necessary to reveal diversity-naturalness relationships. We suggest that all diversity descriptors should be calculated for different spatial scales, since their change with spatial scale was as informative as their actual values.

Introduction

Herbaceous and bryophyte species that inhabit forest interior have adapted to those special circumstances that characterize natural woodlands. Under moist continental climate these include uneven-aged mixed tree stands with considerable amounts of snags and lying dead wood, the presence of large old (up to 300-400 years) tree individuals, pits and mounds around tipped rootplates, deep shade and/or special sunfleck patterns (Peterken 1996, Hunter 1999, Voller and Harrison 1998). Most of these structural features are missing from managed forest stands in large parts of Europe.

Another important peculiarity of these temperate forests is their natural disturbance regime, which is characterized by small-scale gap formation that creates a fine-scale mosaic of different developmental phases (Koop 1989, Korpel 1995, Peterken 1996). However, in many European countries (including Hungary) the standard silvicultural practices (clearcutting or uniform shelterwood systems) create large cleared areas within a short time and at relatively young tree ages (80-120 years), then these areas are regenerated either naturally or artificially (Matthews 1991). As a result, natural and managed woodlands are different in the spatio-temporal distribution and also in the intensity of disturbances. Managed forest landscapes are characterized by relatively homogenous even-aged tree stands that can be quite different from each other. Natural woodlands are structurally more heterogeneous at the stand scale and they possess several features (e.g. large old trees, dead wood, rootplates, etc.) that are almost completely missing from managed forests (Peterken 1996).

We hypothesize that the above features influence the richness of herbaceous and bryophyte vegetation inhabiting natural versus managed forests. To test this hypothesis one needs a comparative approach. We also want to investigate which vegetation characteristics indicate best those structural differences of the tree stands that reflect differences in disturbance regime in unmanaged versus managed stands.

Implicitly these questions concern the problems of defining how forest management affects original forest biodiversity, and how naturalness is related to biodiversity. To be able to deal with these problems one needs to find those attributes of biodiversity that effectively indicate the biological quality (conservation value, naturalness, sustainability) of forests (Ferris and Humphrey 1999, Noss 1990, Simberloff 1998). It is assumed that forest floor vegetation is affected by the different tree stand structures found in managed and unmanaged stands. However, it is less straightforward to estimate what ecological characteristics are the most sensitive indicators of these differences.

There is a legion of recent literature on the importance, different levels and measurement techniques of forest diversity (e.g. Bachmann et al. 1996, 1998, Boyle and Boontawee 1995, Noss 1999, Larsson et al. 2001). Kaennel (1998) excellently analyses the ‘diversity’ of ways how diversity and related concepts have been used and defined. Here we concentrate on discussing the potential limits of species based diversity measures as potential indicators of naturalness in forest vegetation.

Species richness and classical diversity indices, as the simplest but most widely (and often exclusively) used diversity measures, are potentially misleading and insufficient descriptors of forest naturalness. There are three main objections against using them as absolute criteria.

Firstly, they are value independent, i.e., they do not differentiate among species. However, the origin (natural geographic and ecological range) of the species is of utmost importance in interpreting species lists and/or diversity indices (Pielou 1995). Without this, statements like natural forests are (not) more diverse than managed

ones are of disputable value. The interpretation of species list in terms of functional types (Grime et al. 1988, During 1979, Peterken and Game 1984, Graae 1997, Hermy et al. 1999) can also help in assessing conservation value of forests.

Secondly, the level of diversity is not necessarily a useful indicator of 'high quality' in forest communities, which are often naturally species poor. While evaluating the status of a forest, one need a biological standard, a reference of the given community with which comparison could be sensible. This reference, ideally, would be the 'natural' or 'original' forest. However, in most of Europe it is impossible to find such forest. As a result, we can compare our managed forests with either the believed (but not proved) 'original', or with some documented 'best possible' status.

Thirdly, a major disadvantage of these simple diversity measures, that they disregard the spatial aspects of diversity. The simplest way to illustrate the spatial component of diversity concept is to study how the value of any diversity index depends on the size of the sampling unit used (Podani et al. 1993). These indices are also insensitive to the spatial variation in the arrangement of the elements. Considering forest naturalness this aspect is of absolute importance, since natural disturbances often create characteristic patterns of stand structures (gaps, mosaic of different developmental stages, coarse woody debris, etc.) at much finer spatial scales than regular management. Spatial variation in the importance (abundance, frequency or cover) of individual species reflects variation in the conditions affecting their establishment and success in surviving. Consequently, any measure that summarizes this spatial variation for all species at a given spatial resolution (i.e., sampling unit size) can serve as a simple descriptor of the spatial element of diversity.

In this paper we investigate different diversity measures of forest floor vegetation to test how they indicate structural differences of the tree stands. We do this by presenting a case study that illustrates how habitat and stand structural heterogeneity are reflected in the richness, diversity and spatial heterogeneity of forest herb and bryophyte assemblages at different spatial scales.

Materials and Methods

Study area

The study was carried out in the Kékes Forest Reserve and in five nearby managed stands. Kékes, in the Mátra Mts., is the highest point in Hungary (1014 m). Climate is relatively continental with 5.7 °C mean annual temperature, low winter (-4.7 °C in January) and high summer temperatures (15.5 °C in July). Precipitation is ca. 840 mm of which 480 mm falls during the growing season. The bedrock is andesite and the topography is extremely steep, scree slopes being characteristic. The shallow brown forest soils are mainly covered by montane beech wood (*Aconito-Fagetum* Soó). Mixed maple-ash-lime woodland (*Phyllitidi-Aceretum subcarpaticum* Soó) occurs in the most humid and rocky patches of the reserve (Kovács 1968).

The Kékes Forest Reserve (63 ha) is one of the last vestiges of near-natural Central-European montane beech woods in Hungary. The stand is a mosaic of different forest developmental phases, with trees older than 200 years occurring together with many younger age classes. It is also a mosaic of two community types, which differ in stand structure. Large trees that form a closed canopy with a few small gaps dominate montane beech wood patches (RESB). The amount of decaying logs is cc. 34 m^3/ha. In contrast, in mixed maple-ash-lime patches (RESA) large canopy trees are virtually missing in many parts, since large gaps with many large fallen

logs (cc. 290 m^3/ha) predominate. The amount of rocks is much higher in this site than in the other parts of the reserve. It is assumed that regeneration is slower, and gaps are larger because of extreme site conditions. Species composition indicates ravine-like habitats with high humidity.

The understorey layer is scarce in the, consisting mostly of advanced regeneration of beech and *Daphne mezereum*. *Sambucus racemosa* and *Ulmus glabra* grow on scree sites. In the ground layer, *Galium odoratum, Mercurialis perennis, Dentaria bulbifera, Viola sylvestris* and *Oxalis acetosella* are the most frequent vascular species, together with seedlings of *Fagus sylvatica* and *Acer pseudoplatanus*. In the scree sites *Urtica dioica, Impatiens noli-tangere, Solanum dulcamara* and *Athyrium filix-femina* are the dominant species. Bryophytes occur mainly on rocks and on decaying logs. Accumulations of coarse woody debris (CWD) are characteristic of this near-natural stand, which, along with rocky outcrops, accounts for rich epixylous and epilithic bryophyte vegetation (Ódor 2000, Ódor and Standovár 2002). Most common species on exposed rocks are *Hypnum cupressiforme, Grimmia hartmanii, Isothecium alopecuroides* and *Paraleucobryum longifolium*. More species occur in humid and shaded fissures of outcrops (eg. *Dicranum scoparium, Plagiochila porelloides, Plagiothecium spp., Metzgeria furcata*). On logs *Lophocolea heterophylla, Hypnum cupressiforme, Brachythecium rutabulum, Rhizomnium punctatum* are the most abundant species, but a lot of regionally rare species also occur on them.

All the five managed stands, chosen for comparisons, have as similar topography as possible (northeasterly aspect, similar steepness) to that of the Kékes Reserve, though they are situated at a bit lower elevation - between 600 and 800 m a. s. l. Stand structure, including dead wood, was described in all studied stands (Gálhidy 1999, Ódor and Standovár 2001). All of them are almost pure beech stands. The youngest stand (26D) is ca. 25 years old, mean diameter at breast height (DBH) is 10.1 cm, the amount of dead wood is cc. 3 m^3/ha. This stand is now part of the reserve that was created after this part had been clear-cut, but it means that no thinning and tending cuts have been done recently. Site conditions are similar to those in the RESB habitat type of the old-growth stand. There are two ca. 40-year-old stands. One of them (31B) was thinned in 1997 (mean DBH is 18.6 cm, dead wood 73 m^3/ha), whereas the other (29D) has not been thinned recently (mean DBH is 11.8 cm, dead wood 10 m^3/ha). Older managed forests are represented by two 80-90-year-old stands (34C, 36D). Mean DBH is 28.7 cm and 31.1 cm, respectively, the amount of dead wood is cc. 30 m^3/ha in both stands. The amount of stones in the forest floor is similar in the five managed stands to the level found in the RESB habitat type in the reserve - mean stone cover is about 10%. However, the RESA habitat type differs from them in having much more stones on the surface (mean cover cc. 40%), often in larger pieces. The amount of CWD in RESB is similar to what is found in the old managed stands, but much smaller (about ten times) than in RESA. The distribution of size classes and decay phases is more equal in both reserve stands than in the managed ones. The volume of CWD is relatively large in 31B – about twice as high as in older managed stands – because of recent thinning, but thin (DBH <20 cm) logs predominate. Information on dead wood in the investigated stands is based on Ódor & Standovár (2001).

Data collection

In each investigated stand a 40 x 40 m plot was selected. Vegetation was systematically sampled in 64 0.5 x 0.5 m quadrats that were set out on a grid at 5 m intervals. Vegetation cover (vascular plants and bryophytes separately) was estimated. In addition, cover was estimated for each vascular plant species separately.

Bryophytes were recorded in nine systematically distributed circular plots of 100 cm². Presence/absence was recorded, so for each 0.5 x 0.5 m quadrat a local frequency value was obtained for the bryophyte species. Nomenclature follows Simon (1992) for vascular plants, Corley et al. (1981) and Corley and Crundwell (1991) for mosses and Grolle (1983) for liverworts.

Data analyses

The following measures of diversity were calculated for each unit at all spatial scales:

1. Species richness, expressed as number of species

2. Species-dominance diversity using the Shannon-Wiener index:

$$H = -\sum_{i=1}^{S} p_i \log_2 p_i ,$$

where S = the number of species; p_i = the proportion (cover or frequency of individuals) of species i in the total sample.

3. Shannon-Wiener evenness:

$$E = \frac{H}{H_{\max}},$$

where $H_{\max}$ = the possible maximum of Shannon-Wiener diversity at given species richness; H = actual value of Shannon-Wiener-index.

4. Spatial variance was calculated among quadrats within merged samples as follows (Podani 2000):

$$VAR_A = \frac{SSQ}{m_A} = \frac{\sum_{i=1}^{n} \sum_{j \in A} \left(x_{ij} - \bar{x}_{iA} \right)^2}{m_A},$$

where VAR_A = variance within group A; SSQ= sum of squares; m_A = number of quadrats in group A; x_{ij} = cover (or frequency) of species i in quadrat j; $\bar{x}_{iA}$ = mean cover (or frequency) of species i in quadrats belonging to group A. This function was not calculated in first spatial step (individual quadrats of 0.25 m²).

5. Average cover or frequency

6. To exclude the effect of differences in average cover (or frequency), spatial variance (see above) was also calculated from standardized data. Cover (or frequency) values were divided by the respective maximum for each species.

For data analyses we used the above measures at four spatial scales, by successively aggregating four neighbouring quadrats (Fig. 1). The spatial resolutions used and the calculated parameters were as follows:

- 64 individual quadrats (0.25 m² samples representing 25 m²; mean, standard error and standard deviation, Fig. 1a);
- 16 groups of 4 aggregated quadrats (1 m² sampled representing 100 m²; mean, standard error and standard deviation, Fig. 1b);
- 4 groups of 16 aggregated quadrats (4 m² sampled representing 400 m²; mean, standard error and standard deviation, Fig. 1c);
- 1 large group of 64 aggregated quadrats (16 m² sampled representing 1600 m²; mean, Fig. 1d).

With these aggregations cover (for vascular species) and frequency (for bryophytes) values were added. Differences among sites were tested by Kruskal-Wallis ANOVA and non-parametric multiple comparison (Zar 1999) for all indices used and for all spatial scales studied.

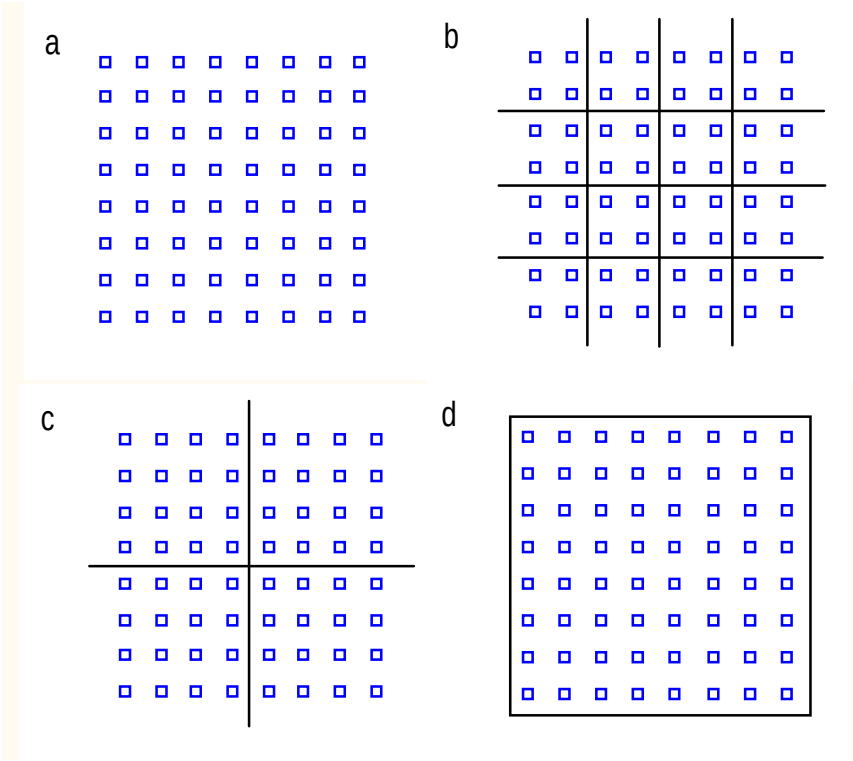

Figure 1. Sampling and data merging design within the investigated 40 by 40 meter plots. a: 64 individual quadrats, 0.25 m^2 each quadrat represents 25 m^2; b: 16 groups of 4 merged quadrats, each group represents 100 m^2; c: 4 groups of 16 merged quadrats, each group represents 400 m^2; d: 1 group of 64 merged quadrats representing 1600 m^2.

Results

Vascular plants

The whole sample contains 47 vascular species, of which 39 occur in the two unmanaged plots (RESA, RESB) and 23 in the five managed plots (26D, 29D, 31B, 34C, 36D). The 24 species that occur exclusively in the reserve samples have intermediate frequency. Most of them are also present in the unmanaged stands, but at much lower frequency, i.e., only a much more intensive sampling (larger area covered) could have contained them in the managed stands.

Both plots in the unmanaged reserve (RESA and RESB) contain significantly more species than any of the managed stands for all spatial scales studied (Fig. 2a, Tab. 1). The larger the sampling unit, the larger this difference between unmanaged and managed plots. Species richness in RESA always exceeds that of in RESB, but this difference is not significant (Tab.1). Managed stands of different ages contain about the same number of species at all spatial scales studied.

If one compares the Shannon-Wiener-diversity values calculated for all sites at all spatial scales, the differences are not as striking as in the case of species richness (Fig. 2b, Tab.1). We found the most pronounced difference between unmanaged and managed sites at finer spatial scales. The differences are much smaller when the coarsest spatial scale is considered, especially in the case of old managed stands (34C, 36D). The reason why we observed relatively small difference in species-cover diversity - in spite of large difference in species richness - becomes clear if one investigates the values describing the second aspect of species-cover diversity, evenness. As Fig. 2c and Tab. 1 show, at finer spatial scales the vegetation in RESA and RESB has significantly higher evenness than in any of the managed stands. In unmanaged stands evenness values do not increase with sampling unit size, whereas they do increase considerably in managed stands, approaching the values found in unmanaged stands (differences are not significant at the coarsest scale, cf. Tab. 1). These changes of diversity and evenness with spatial scale show, that the vegetation in the unmanaged reserve can be characterised as fine-grained, composed of species rich small patches, whereas in managed stands vegetation is composed of large patches with sparse vegetation dominated by one or two species. For this reason in managed stands evenness values increase with sampling unit size.

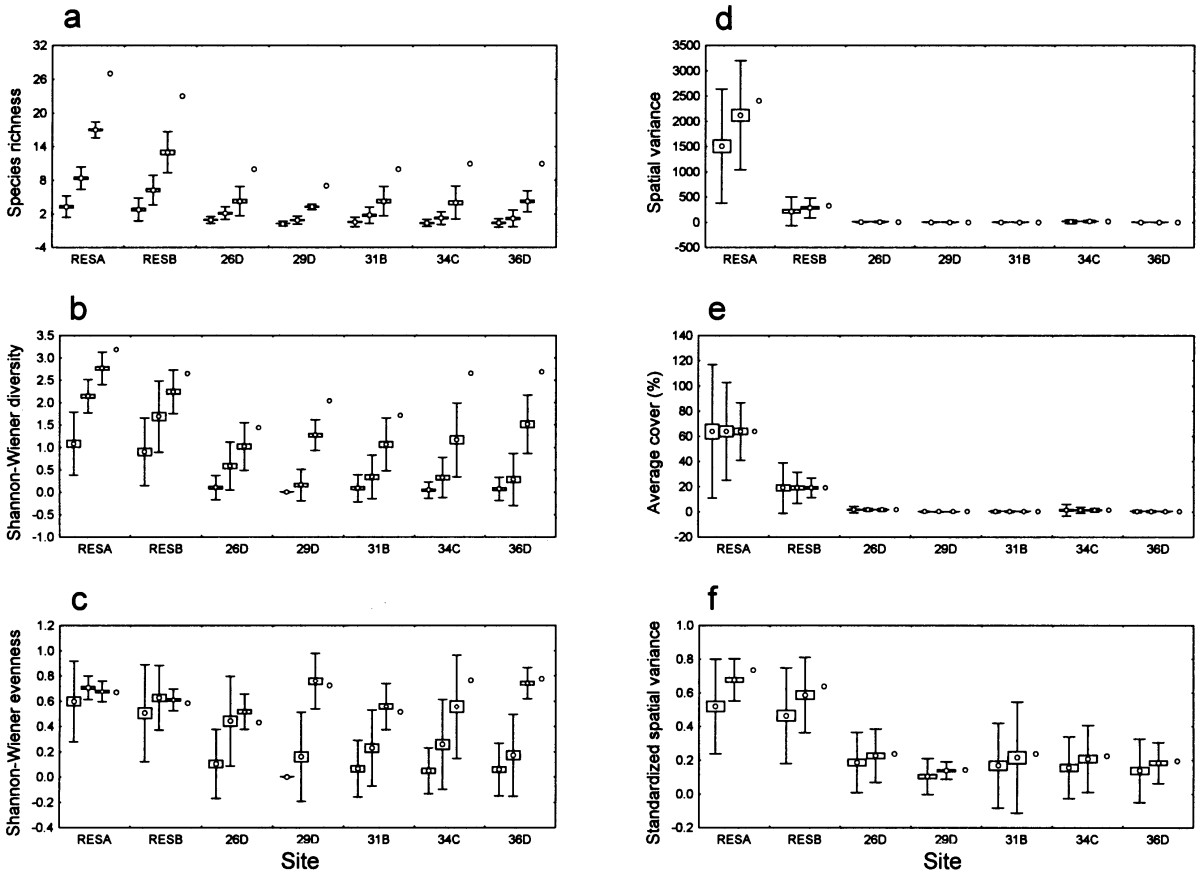

Figure 2. Mean, standard error (box) and standard deviation (whiskers) of different vegetation characteristics of vascular vegetation. In each site, these statistics are calculated in the following spatial scales: 25 m^2, 100 m^2, 400m^2, 1600 m^2 (only the mean). a: species richness; b: Shannon-Wiener diversity function; c: Shannon-Wiener evenness function; d: spatial variance (not calculated for the first spatial scale); e: average cover; f: spatial variance standardized for maximum cover (not calculated for the first spatial scale).

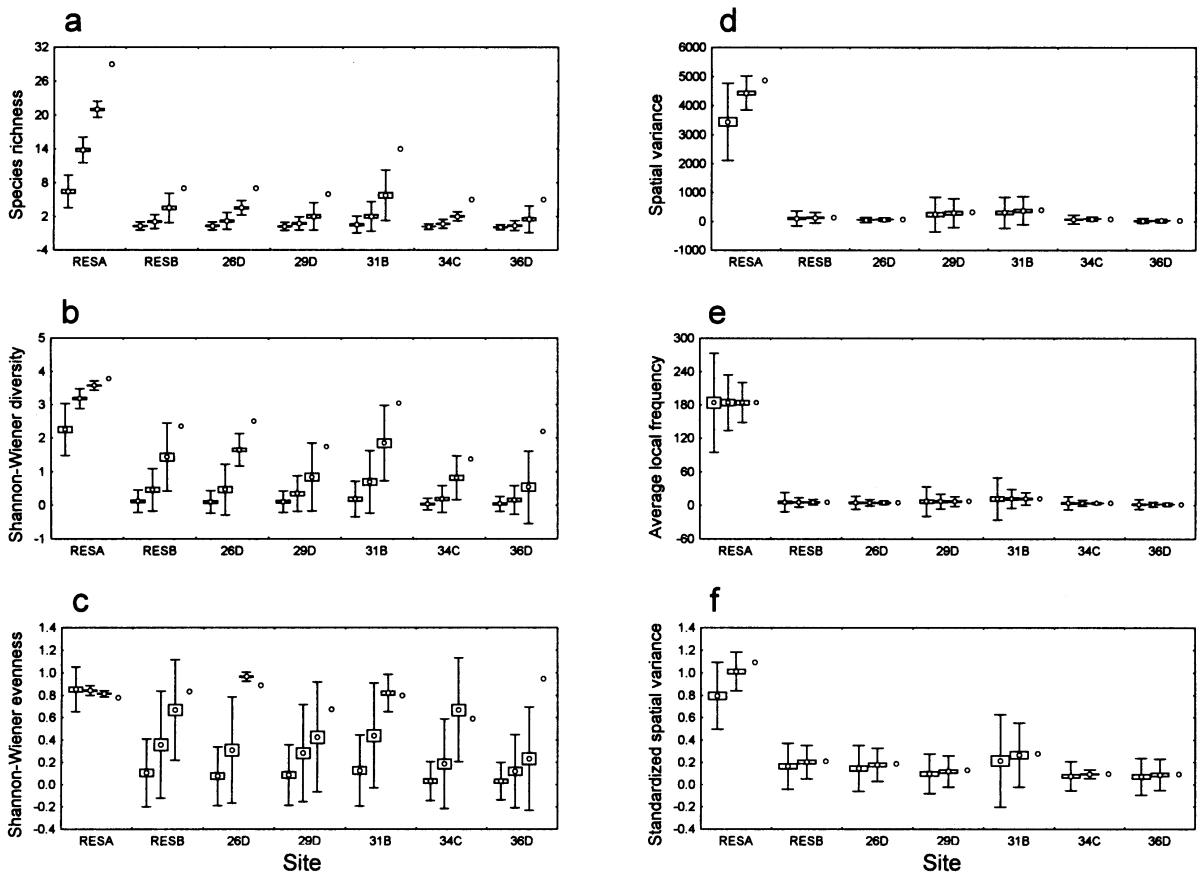

Figure 3. Mean, standard error (box) and standard deviation (whiskers) of different vegetation characteristics of bryophyte vegetation. In each site, these statistics are calculated in the following spatial scales: 25 m^2, 100 m^2, 400m^2, 1600 m^2 (only the mean). a: species richness; b: Shannon-Wiener diversity function; c: Shannon-Wiener evenness function; d: spatial variance (not calculated for the first spatial scale); e: average local frequency; f: spatial variance standardized for maximum frequency (not calculated for the first spatial scale).

	p of Krukal-Wallis test	Non-parametric multiple comparisons						
		RESA	RESB	26D	29D	31B	34C	36D
Vascular vegetation								
Species richness 25 m^2	p<0.001	a	a	b	c	c	c	c
Species richness 100 m^2	p<0.001	a	a	b	b	b	b	b
Species richness 400 m^2	p<0.01	a	a	a	a	a	a	a
Shannon-Wiener diversity 25 m^2	p<0.001	a	a	b	b	b	b	b
Shannon-Wiener diversity 100 m^2	p<0.001	a	a	a/b	b	b	b	b
Shannon-Wiener diversity 400 m^2	p<0.05	a	a	a	a	a	a	a
Shannon-Wiener evenness 25 m^2	p<0.001	a	a	b	b	b	b	b
Shannon-Wiener evenness 100 m^2	p<0.001	a	a	a/b	b	b	a/b	b
Shannon-Wiener evenness 400 m^2	n.s.	-	-	-	-	-	-	-
Spatial variance 100 m^2	p<0.001	a	a	a/b	b	b	b	b
Spatial variance 400 m^2	p<0.01	a	a /b	a/b	b	b	a/b	a/b
Average cover 25 m^2	p<0.001	a	a	b	c	c	c	c
Average cover 100 m^2	p<0.001	a	a	a/b	b	b	b	b
Average cover 400 m^2	p<0.01	a	a /b	a/b	b	b	a/b	a/b
Standardized spatial variance 100 m^2	p<0.001	a	a	a/b	b	b	b	b
Standardized spatial variance 400 m^2	p<0.05	a	a	a	a	a	a	a
Bryophyte vegetation								
Species richness 25 m^2	p<0.001	a	b	b	b	b	b	b
Species richness 100 m^2	p<0.001	a	b	b	b	b	b	b
Species richness 400 m^2	p<0.05	a	a	a	a	a	a	a
Shannon-Wiener diversity 25 m^2	p<0.001	a	b	b	b	b	b	b
Shannon-Wiener diversity 100 m^2	p<0.001	a	b	b	b	b	b	b
Shannon-Wiener diversity 400 m^2	p<0.05	a	a	a	a	a	a	a
Shannon-Wiener evenness 25 m^2	p<0.001	a	b	b	b	b	b	b
Shannon-Wiener evenness 100 m^2	p<0.01	a	a/b	a/b	a/b	a/b	a/b	b
Shannon-Wiener evenness 400 m^2	n.s.	-	-	-	-	-	-	-
Spatial variance 100 m^2	p<0.001	a	b	b	b	b	b	b
Spatial variance 400 m^2	p<0.05	a	a/b	a/b	a/b	a/b	a/b	b
Average local frequency 25 m^2	p<0.001	a	b	b	b	b	b	b
Average local frequency 100 m^2	p<0.001	a	b	b	b	b	b	b
Average local frequency 400 m^2	p<0.05	a	a/b	a/b	a/b	a/b	a/b	b
Standardized spatial variance 100 m^2	p<0.001	a	b	b	b	b	b	b
Standardized spatial variance 400 m^2	n.s.	-	-	-	-	-	-	-

Table 1. Significance level of Kruskal-Wallis test and non-parametric multiple comparison for all investigated indices at all studied spatial scales. The different letters (a, b, c) in multiple comparisons (in rows) indicate significantly different plots at p<0.05 significance level.

Spatial variance of vegetation is extremely high in RESA, and it increases with the area of sampling units (Fig. 2d). This increasing trend of spatial heterogeneity is also characteristic for RESB, though the absolute level is much lower. Managed stands are significantly different from both unmanaged sites (Tab.1), because spatial variance does not increase with sampling unit size, and spatial variance values are extremely low.

Since spatial variance values are affected by the absolute values of cover, it is worthwhile seeing how average cover differs among sites. As Fig. 2e shows, average cover is the highest in RESA (above 60%), about the third of that in RESB, and significantly lower in all the managed stands (Tab. 1). The high cover in RESA can be attributed to the combined affect of available light, decomposing organic material and high relative humidity in the large gap of the ravine like mixed maple-ash-lime woodland.

To check if the higher spatial variance observed in the unmanaged stands is caused merely by differences in average cover, we repeated the calculations with standardized data. As Fig. 2f shows when data were standardized for maximum cover, the two unmanaged sites (RESA, RESB) have similar level of variance. This verifies, that it is not different spatial structure, but the difference in average cover that differentiates RESA from RESB in Fig. 2d. The pattern of increasing variance with increasing sampling unit size is similar to what is shown in Fig. 2d. Managed sites have lower variance at all spatial scales, however, unlike in Fig. 2d, variance increases with sampling unit size in all managed sites. The difference between unmanaged and managed sites is significant only at fine spatial scale (Tab.1).

Bryophytes

The whole sample contains 30 bryophyte species, of which 29 occur in RESA. The other unmanaged plot (RESB) contains only 7 out of the 29 species found in RESA. Managed plots are much poorer in species than RESA, altogether 16 species occur in the managed plots.

As Fig 3a and Tab. 1 show, RESA plot in the unmanaged reserve is significantly the richest in species at all spatial scales, which is caused by the large amount and even spatial distribution of dead wood and large rocks. Species richness in RESB is about ¼ of that, and is similar to most of the managed stands. The only exception is 31B, where the species richness of bryophytes is the double of what we can find in RESB. The reason for this is the high amount of dead wood left in the stand after thinning, allowing for the appearance of some epiphytic and epixylous species.

If one compares the Shannon-Wiener-diversity values calculated for all sites at all spatial scales, a similar pattern can be observed (Fig. 3b, Tab. 1). Bryophyte vegetation in RESA has much higher diversity than in any other studied stand, though the difference between RESA and others decreases as sampling unit size increases. Similarly to what we observed for herbaceous vegetation, in spite of the large difference in species richness, the behaviour of evenness values explains the pattern shown in Fig. 3b. At finer spatial scales the vegetation in RESA has significantly higher evenness than in RESB or any of the managed stands (Fig. 3c). In RESA evenness values do not increase with sampling units, whereas they do increase significantly in RESB and all the managed stands, approaching the values found in RESA (though differences are not significant at the coarsest scale, cf. Tab. 1). These patterns of diversity and evenness indicate, that as a result of high abundance of appropriate substrates (dead wood, rock) the bryophyte vegetation in RESA is fine-grained, composed of species rich small patches. This is also reflected in small standard deviation of evenness in spite of high mean frequency

values, even at the finest spatial scale. On the other hand, in RESB and in managed stands suitable substrates are much scarcer, so the increase in sampling unit size results in the inclusion of new species. For this reason in these stands evenness values increase with sampling unit size.

Spatial variance of vegetation is extremely high in RESA, and it increases with the area of sampling units (Fig. 3d). RESB and all the managed stands are significantly different from RESA (Tab. 1), since spatial variance does not increase with sampling unit size, and the values observed are extremely low. As it is shown above (Figs. 2d-f), spatial variance values are affected by the overall amount of vegetation, so average frequency was also calculated for bryophytes. As Fig. 3e shows, average frequency of bryophytes is extremely high in RESA compared to other stands. However, even when frequency data are standardized for maximum frequency, spatial variance is still significantly higher in RESA than in the other stands (Fig. 3f, Tab. 1). The trend of increasing variance with sampling unit size is also characteristic. Consequently, the higher observed spatial variance of bryophyte vegetation in RESA is caused by more heterogeneous spatial structure, not only by higher average frequency. RESB and all the managed sites have lower variance at all spatial scales, however, the increase of variance with sampling unit size is more expressed than in Fig. 3d.

Discussion

In this study we aimed at comparing different diversity measures of forest floor vegetation by their sensitivity for those stand structural features that reflect differences in the disturbance regimes found in near-natural and managed forests.

Our results showed that species number, as the simplest diversity measure, not always differentiated near natural sites from managed sites (cf. Fig. 3b). Also, the observed difference depended very much on the spatial scale used.

The behaviour of Shannon-Wiener diversity function can only be understood if both the species richness and the evenness components are taken into consideration. The most diverse plots had high Shannon-Wiener diversity values even at the finest spatial scale not only because of high number of species, but also because of high evenness (cf. e.g., Figs. 3b and 3c). In these plots (RESA and RESB for vascular plants and RESA for bryophytes) evenness hardly increased with spatial scale, whereas it increased considerably in the less diverse managed plots. This behaviour reflects the much finer grained spatial vegetation pattern found in near-natural plots.

Of the used diversity descriptors spatial variance is the only measure that reflects a spatial component of diversity in the forest floor vegetation at each spatial scale studied. This function measures the average variation per quadrat in species' importance (expressed as cover for vascular species and local frequency for bryophytes) within a group of quadrats representing a given spatial scale. In our study this measure was the most effective in differentiating the diversity of plots with different levels of naturalness. The absolute values of spatial variance in the forest floor vegetation were the highest in those plots (RESA and RESB for vascular plants and RESA for bryophytes), where the characteristics of important limiting ecological factors (light patterns on the forest floor and the amount and quality of different substrates) are generated by natural disturbance. This held true even when data were standardized for maximum cover/frequency of each species to exclude the effects of overall differences in the amount of forest floor vegetation (Figs. 2d-f and 3d-f). Another strong feature we found was that the increase of spatial variance with spatial scale was much steeper in the same plots.

Vascular and bryophyte species respond differently to tree stand structural characteristics. The diversity of vascular vegetation was higher in the unmanaged reserve than in any of the managed stands. The diversity values measured in the two habitat types (RESA and RESB) were rather similar. On the contrary, the diversity of bryophyte vegetation was very high in RESA, whereas it was much lower in RESB, resembling the values obtained in the managed stands. These statements held true for all used descriptors of diversity.

In RESB vascular vegetation was composed of typical Central-European beech forest species, like *Galium odoratum, Mercurialis perennis, Dentaria bulbifera, Viola sylvestris* and *Oxalis acetosella.* The multilayered canopy and the presence of differently sized gaps and regeneration patches produced much more heterogeneous light conditions in this plot than in the managed stands with homogenous stand structure. This resulted in the high diversity of vascular vegetation. Many studies emphasized the importance of light conditions in generating the diversity and pattern of vascular vegetation on the forest floor (e.g., Collins et al. 1985, Collins and Pickett 1987, Diekmann 1994, Fekete 1974, Standovár 1998, Uemura 1993). Our results also nicely showed, that the diversity of vascular vegetation was determined mainly by light conditions, since site differences caused change only in composition, not in diversity values. In RESA the dominant species were *Urtica dioica, Solanum*

dulcamara, Athyrium filix-femina, Impatiens noli-tangere and *Sambucus racemosa* reflecting the higher nutrient and moisture content of the shallow soil accumulating among the large rocks and logs characteristic of this habitat type.

On the contrary, for forest dwelling bryophytes the most important ecological factor is the amount and proportion of potential substrate types (Smith 1982). In temperate deciduous forests bryophytes are restricted to rock outcrops and to living and dead trees. In Central European beech forests the bryophyte layer is usually missing from the forest floor, because of litter accumulation. The frequency of terricolous species is low, they are restricted to root plates and other disturbed places. Where relative air humidity is not high enough, the epiphytic bryophytes are much more abundant on bark of lying dead logs than on standing trees (Ódor and van Hees unpubl.).

Because of the abundance of large rocks and dead logs of different decay classes, many regionally rare bryophytes (*Blepharostoma trichophyllum, Nowellia curvifolia, Calypogeia suecica)* occurred in habitat type RESA. In addition to the rich epiphytic and epixylous bryophyte vegetation, in this habitat type a species rich epilithic assemblage also developed in wet rock crevices, since high organic matter accumulation from CWD and high air humidity were characteristic. There was an overlap between the species pool of humus rich outcrops and that of dead wood, which resulted in a fine grained diverse bryophyte vegetation in RESA (Ódor and Standovár 2002). The amount of potential substrates for bryophytes (CWD and rocks) in RESB was much lower than in RESA (ten times less CWD), but it was the same as in the studied managed stands. As a consequence, the diversity of bryophyte vegetation in RESB and in the managed stands was also similar. The only exception was 31B, where the amount of CWD was higher because of recent thinning. As a consequence, the diversity of bryophyte vegetation was also higher. Although thinning of young stands provides only thin, hence rapidly decaying woody material, it can be important for bryophyte diversity in managed forests (Kruys and Jonsson 1999, Ódor and Standovár 2001). Light conditions, which were more heterogeneous in RESB than in the managed stands, proved to be less important for the amount and diversity of bryophyte vegetation than the availability of potential substrates.

In conclusion we can state that appropriately chosen diversity measures of forest floor assemblages can be used as an indicator of forest naturalness. We emphasize that diversity-naturalness relationships are much less straightforward when the spatial component of diversity, like spatial variance were not considered. We also stress that all descriptors should be calculated for different spatial scales, since their change with spatial scale was as informative as their actual values. Finally, we showed that it is of utmost importance to elucidate the ecological factors that determine the distribution of the chosen indicator groups, since different organisms respond in their own ways, hence they can not be used in a similar way to indicate the effects of natural versus human induced processes.

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