



## The impact of forest management on forest floor vegetation evaluated by species traits

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**Abstract:** This study investigated if ecological traits of forest floor vegetation could be used as indicators of naturalness of beech forest in Hungary, by comparing near-natural unmanaged stands with managed ones. Seventeen patches in the unmanaged Kékes Forest Reserve were compared with 11 subcompartments of different ages in the surrounding managed forest. In each stand, the character state distributions of 9 ecological species traits were calculated based on presence/absence data of plants. Averages for unmanaged versus managed stands were compared. Significant effects of management were shown. The characteristics of herbaceous plants with higher frequency in managed stands include late start and longer duration of flowering, overwintering canopy, and small epizoochorous seeds. Unmanaged stands are richer in plants that bear leaves from spring to autumn, start flowering early or flower very shortly, produce large seeds. Relevance of this method is discussed for Central Europe, where in large areas intensive forest management rather than fragmentation or break in forest continuity is the major human disturbance.

**Nomenclature:** Simon (1992) for vascular plants, Kovács (1975) for plant associations.

### Introduction

Forest management influences original forest structures and composition in many ways. Some of these impacts (e.g., on tree species composition, age structure, tree shape) are intentional, whereas others (e.g., soil erosion, loss of biodiversity) are just negative side effects. The traditional view of treating forests simply as resource for timber, game and later pulp has changed recently. As a result, public awareness and political concern for the loss of forests and for the deterioration of forest biodiversity have increased. New principles for national forest and conservation policies and international agreements are all signs of this process (UNCED 1992, for a summary see Larsson et al. 2001). To implement these policies it is important to collect relevant information and to develop methods for maintaining and, where necessary, reconstructing original biodiversity. To be able to do so, one needs simple methods for measuring diversity components in order to get ecologically meaningful information

(e.g., Noss 1990, Simberloff 1998, Bachmann et al. 1998, Larsson et al. 2001).

Species richness *per se* and deviations from “optimal” species composition are straightforward candidates as measures of forest naturalness. However, for many groups of organisms it is rather unrealistic to collect this information especially on large areas. In addition, simple assessments on the regional or national scales could be obstructed by differences in species composition caused by differences in biogeographic status, bedrock, nutritional status, etc. One possible solution is to use species' ecological traits that reflect adaptation of species to prevailing natural and human induced disturbance regimes and ecological conditions.

Several authors have studied how different levels of human impacts are reflected in the representation of certain ecological traits of vegetation. It is generally assumed that in ancient or primary forests species adapted to stable environments are more abundant than in intensively altered managed forests, where species adapted to frequent

disturbance flourish. Species of stable environments are characterized by slow growth, stress tolerator strategy, early and short flowering, vegetative spread, large non-persistent seeds dispersed by ants and transient seed bank. Species of disturbed habitats are usually therophytes, with ruderal strategy, with flowers all year round, having small epizoochorous and resistant seeds (Foster and Janson 1985, Schmidt et al. 1991, Graae and Heskjaer 1997, Graae and Sunde 2000).

It is widely recognized that these traits are not independent from each other. Seed dispersal is correlated with seed size and plant height (Thompson and Rabinowitz 1989, Leishman et al. 1995, Graae and Sunde 2000). Relationship between seed size and life-form is also noteworthy (Peart 1984, Thompson et al. 1998). Flowering duration and seed weight are also correlated (Graae and Sunde 2000). Shaded conditions of dense forests select for large seeds (Foster and Janson 1985, Venable and Brown 1988, Leishman et al. 1995, Graae and Sunde 2000) and also affect plant height and leaf phenology (Givnish 1982). These relationships should be considered while interpreting the results of studies on the distribution of ecological species traits.

In this paper, we want to investigate if we can use ecological traits of herbaceous plants in assessing the naturalness (*sensu* Peterken 1996) or conservation value of forest stands under different management. Unlike previous studies, this work concentrates on the effects of forest management. Many studies that compared herbaceous vegetation in forests with different histories investigated the effects of fragmentation (Peterken and Game 1984, Dzwonko and Loster 1988, Dzwonko and Loster 1989, Dzwonko 1993, Matlack 1994) and interruption of forest continuity (Newell and Tramer 1978, Peterken and Game 1984, Halpern 1988, Halpern 1989, Matlack 1994). Differences in species richness and in some cases in species composition were shown. However, the effects of forest management on forest floor vegetation are less straightforward. Aude and Lawesson (1998) showed management-related difference in species composition. Attempts to show differences in the distribution of ecological traits, however, did not give significant results (Graae and Sunde 2000).

To eliminate the effects of fragmentation and break in forest continuity, for this study we chose an area, where managed stands are in direct contact with near-natural, unmanaged stands, and they grow under similar conditions (slope, aspect, fertility). These managed stands have uninterrupted continuity, they were clear-felled only once. Hence, effects of management (clear-felling,

changes in tree patterns caused by uniform tending, forest operations) can be readily tested.

## Materials and methods

### Study area

The study was carried out on the northerly slopes of Kékes, Mátra Mts (47°55' N, 20°05' E), which is the highest point (1014 m) in Hungary. Mátra belongs to the inner volcanic ring of the north-western Carpathians. The bedrock is andesite and the topography is extremely steep, scree slopes being characteristic (Székely 1964). The shallow (40-80 cm) brown forest soils are moderately acid with pH between 5.0 and 5.7 (Kovács 1975).

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. Snow cover lasts for 3-4 months.

The investigated stands lie between 750 and 900 m above sea level. Potential vegetation is montane beech wood (*Aconito-Fagetum*) at the highest points and submontane beech wood (*Melittio-Fagetum*) at lower elevation. Mixed maple-ash-lime woodland (*Phyllitidi-Aceretum subcarpaticum*) occurs in the most humid and rocky patches on periglacial scree (Kovács 1968, 1975).

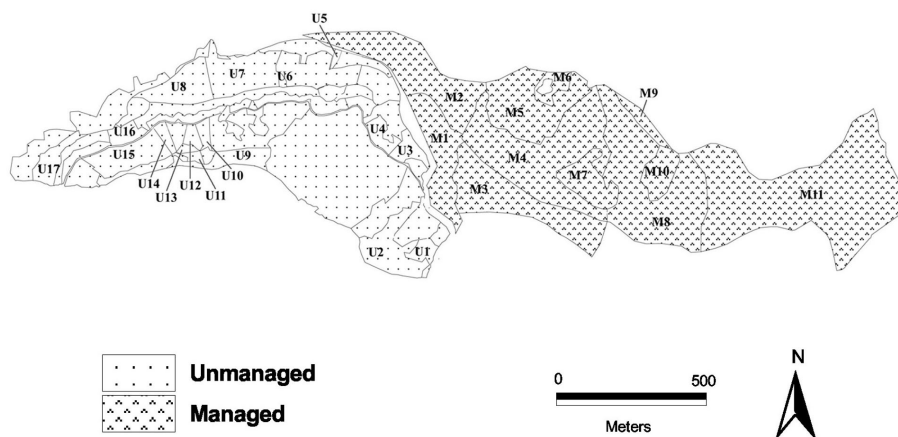
The whole area belonged to the Károlyi family until 1945, then it became state-owned. Before 1945 the Károlyi family used the area as a hunting area (game enclosure), which also means that timber extraction was not practised. The extent of near-natural forests was 2000 hectares in 1943, which dropped dramatically to less than 50 hectares after 1950. The original near-natural forest is a mosaic of different forest developmental phases, with trees older than 200 years occurring together with many other age classes. It is also a mosaic of the two community types (beech wood and mixed maple-ash-lime woodland). The last relic is now protected as a forest reserve. For our comparative study we used the Kékes Forest Reserve and the surrounding stands that were all cut and regenerated only once, so forest continuity was not disrupted. The managed stands are of different ages and have been managed by uniform shelterwood system with short regeneration period (Matthews 1991).

### Data collection

In summer 2000, the list of all vascular plant species was created by intensive investigation and intentionally uniform coverage for 11 managed subcompartments (Fig. 1, Table 1). We chose stands that are close to the unman-

**Table 1.** Age, size and species richness of studied subcompartments.

Site code	Management	Age (year)	Mixing ratio of beech (%)	Size (ha)	Number of species
M1	managed	160+13	100	3.67	76
M2	managed	50	96	6.14	87
M3	managed	50	71	5.87	47
M4	managed	45	100	9.31	58
M5	managed	75+50	94	4.99	62
M6	managed	119+59	22	0.68	33
M7	managed	145	100	2.05	18
M8	managed	50	100	10.01	72
M9	managed	90	100	0.68	26
M10	managed	145	100	1.42	11
M11	managed	55	100	17.84	75
U1	unmanaged	mixed	100	0.75	18
U2	unmanaged	mixed	100	3.26	59
U3	unmanaged	mixed	100	0.93	63
U4	unmanaged	mixed	100	0.83	57
U5	unmanaged	mixed	100	0.17	22
U6	unmanaged	mixed	95	0.16	31
U7	unmanaged	mixed	100	3.75	31
U8	unmanaged	mixed	100	2.71	25
U9	unmanaged	mixed	100	1.66	91
U10	unmanaged	mixed	100	0.42	16
U11	unmanaged	mixed	80	0.46	47
U12	unmanaged	mixed	100	0.45	37
U13	unmanaged	mixed	100	0.19	12
U14	unmanaged	mixed	100	0.43	56
U15	unmanaged	mixed	90	2.66	58
U16	unmanaged	mixed	90	0.82	35
U17	unmanaged	mixed	100	1.23	70

**Figure 1.** Map showing the locations of the study sites.

aged reserve, have similar aspect and steepness. To exclude the effects of forest roads, wide paths, temporary watercourses and scree, we made separate species lists along them within each subcompartment, and these are not used for this analysis. We only used the data collected from the forest interior (minimum 15 meters from edges and roads) for the present study. Altogether the species lists of 62.66 hectares of managed forests were created. For characterising the flora of the unmanaged beech forest in the reserve we used the data collected by Pászty while she produced the vegetation map of the reserve (Pászty 1998). In addition to phytosociological relevés, in her thesis she also presented species lists for each mapping unit she distinguished. For our analyses, we excluded the data

describing extreme rocky sites, so we used the summer species lists of 17 patches (20.88 ha, Fig. 1., Table 1.) representing beech dominated forest interior habitats. Sampling intensity warrants detection of species in all cases.

We then collected data for characterizing species traits. We had to consult several references to complete the species by species traits database. When it was available we preferred Hungarian sources because species might have different behaviour in different regions. As far as it was possible we tried to use category systems where we could code species straightforwardly, but in some cases (e.g., seed dispersal) mixed categories were also used. For some traits data were not available for all species. This effect was accounted for during the analyses of

**Table 2.** Analyzed species traits and codes for each trait used in figures and tables. Sources of the attributes given in brackets.

Trait (source)	Categories	Details
Life-history (Soó 1964; Grime et al. 1988, inferred from life-form) Raunkiaer life-form (Horváth et al. 1995)	P	Perennial
	B	Biennial
	A	Annual
	Ph	Phanerophyte
	Ch	Chamaephyte
	H	Hemicryptophyte
	G	Geophyte
	Th	Therophyte
	TH	Hemitherophyte
	E	Epiphyte
Plant height – maximum value of the given range is coded into the given categories (Rothmaler 1988; Graae and Sunde 2000; Grime et al. 1988; Simon 1992)	0-20	0-20 cm
	21-40	21-40 cm
	41-60	41-60 cm
	61-80	61-80 cm
	81-100	81-100 cm
	101-150	101-150 cm
	151-1000	151-1000 cm
Leaf phenology (Lindacher 1995)	>1000	>1000 cm
	E	Canopy evergreen
	Sh	Canopy seasonal, hibernal
	Sa	Canopy seasonal, aestival
	Sv	Canopy seasonal, vernal
Clonality (Klimes et al. 1997)	0	no clonality
	1	" <i>Trifolium pratense</i> " type
	2	" <i>Alliaria petiolata</i> " type
	3	" <i>Rumex acetosella</i> " type
	4	" <i>Ranunculus ficaria</i> " type
	5	" <i>Lycopodium annotinum</i> " type
	6	" <i>Festuca ovina</i> " type
	7	" <i>Rumex obtusifolius</i> " type
	8	" <i>Rumex alpinus</i> " type
	9	" <i>Dactylis glomerata</i> " type
	10	" <i>Aegopodium podagraria</i> " type
	11	" <i>Fragaria vesca</i> " type
	12	" <i>Caltha palustris</i> " type
	13	" <i>Galium odoratum</i> " type
	15	" <i>Lycopus europaeus</i> " type and " <i>Adoxa moschatellina</i> " type
	16	" <i>Corydalis solida</i> " type
	20	" <i>Allium montanum</i> " type
Dispersule weight [g/1000 seeds] (Csontos 2000; Graae and Sunde 2000; Grime et al. 1988)	s	spore
	1	0,20 g/1000 seeds
	2	0,21-0,50 g/1000 seeds
	3	0,51-1,00 g/1000 seeds
	4	1,01-2,00 g/1000 seeds
	5	2,01-4,00 g/1000 seeds
	6	4,01-10,00 g/1000 seeds
	7	10,01-50,00 g/1000 seeds
	8	> 50,00 g/1000 seeds
Seed dispersal (Csontos et al. 2002)	ANIM	Zoochorous
	AUTO	Autochorous
	ENDO	Endozoochorous
	EPI	Epizoochorous
	MYR	Myrmecochorous
	WIND	Anemochorous
	UNSP	Unspecialised dispersal (more than two dispersal agent)
	EN+M	Endozoochorous + myrmecochorous
	EN+W	Endozoochorous + anemochorous
	EP+W	Epizoochorous + anemochorous
Earliest flowering time (Soó 1964; Simon 1992)	II	February
	III	March
	IV	April
	V	May
	VI	June
	VII+	July or later
	Flowering duration (Soó 1964, Simon 1992)	2
3		3 months
4		4 months
5+		more than 4 months

individual traits. Details of references used and coding of the 9 traits (life-history, Raunkiaer life-form, plant height, leaf phenology, clonality, dispersule weight, seed dispersal, earliest flowering time, flowering duration) are shown in Table 2.

#### Data analyses

For each subcompartment  $A$ , we calculated the relative importance of species with the trait state  $i$ :

$$A_i = \frac{n_i}{n_{total}},$$

where  $n_i$  is the number of species with trait state  $i$ , and  $n_{total}$  is the total number of species in subcompartment  $A$  which have been given any trait state (Graae and Sunde 2000). With this calculation we could compensate for the effects of differences in species richness and size among the study sites. Mean proportions of trait states were calculated and plotted for unmanaged and managed subcompartments. Among managed sites, averages were also calculated for young (tree age < 50 years) and old (tree age > 50 years) subcompartments separately. Statistical comparisons of unmanaged versus managed and young versus old managed sites were carried out using Mann-Whitney U-test.

To get comparable results, we used similar methods as Graae and Sunde (2000) to elucidate important associations among traits. We analysed the species by traits matrix using likelihood ratio  $\chi^2$  for comparing traits on nominal scale, Spearman rank correlation for traits on ordinal scale and Kruskal-Wallis-test for comparing traits on nominal versus ordinal scales. Relationships among traits are shown in a plexus graph.

We used data of only herbaceous species for all these calculations, because woody species composition is strongly affected intentionally by forest management.

## Results

The whole sample included 164 herbaceous species. In the sampled unmanaged sites Pászty recorded 120 summer species, whereas samples collected from managed stands included 104 species. Average species richness was 33.53 and 39.45 in unmanaged and managed stands, respectively. Since managed subcompartments are larger than the selected unmanaged patches average species richness/hectare was also calculated. Unmanaged stands are much richer in this respect (50.82 versus 11.81 species/ha).

### Herbaceous plants in unmanaged versus managed stands

Results of all U-tests are given in Table 3. Altogether 65 tests were performed, of which 22 gave significant result ( $p < 0.05$ ). In a random dataset, the expected number of significant correlations would be only 3.25.

Most of the species (>80%) are perennial both in unmanaged and managed sites, though this proportion is significantly higher in managed stands (Fig. 2a).

The analysis of Raunkiaer life-forms showed that hemicryptophytes dominate (>60%) in these stands (Fig. 2b). We found that the proportions of chamaephytes and epiphytes are significantly higher in managed stands. However, because of low frequency values in these categories it might be only chance effect.

Species are well distributed among plant height categories, but species belonging to height category 21-40 cm have the highest proportion (>20%). Small plants (0-20 cm) and plants that are higher than 1.5 meters are significantly more important in the managed stands, whereas plants of intermediate size (81-150 cm) are more frequent in the unmanaged stands (Fig. 2c).

Leaf phenology comparisons resulted in significant differences (Fig. 2d). Overwintering (Sh) species have higher relative frequency in the managed stands. Species with aestival canopy (Sa) give higher proportion of the herb layer in unmanaged stands. Since our dataset did not contain some of the early spring geophytes with vernal canopy (Sv), this category is almost empty.

The distribution among clonality categories is shown in Fig. 2e. There are three categories where species number is not too low and significant differences were obtained. Managed stands are richer in *Festuca ovina* type plants with long-lived below-ground stems (formed above-ground) and slow vegetative spread, and also in *Fragaria vesca* type plants with short-lived above-ground stems. Unmanaged stands are richer in *Aegopodium podagraria* type plants with long-lived below-ground stems and fast vegetative spread.

As Fig. 2f shows, all dispersule weight categories have considerable importance in the studied stands. Species with small seeds (0.21-0.50 g/1000 seeds) are significantly more important in managed stands, whereas species with large seeds (4.01-10.00 and 10.01-50.00 g/1000 seeds) have significantly higher frequency in the unmanaged stands.

The distribution of seed dispersal categories is not much different in the two stand types (Fig. 2g). Epi-

**Table 3.** Results of Mann-Whitney U tests (z, p) comparing unmanaged versus managed forests (—: not significant; \*: p<0.05; \*\*: p<0.01; \*\*\*: p<0.001).

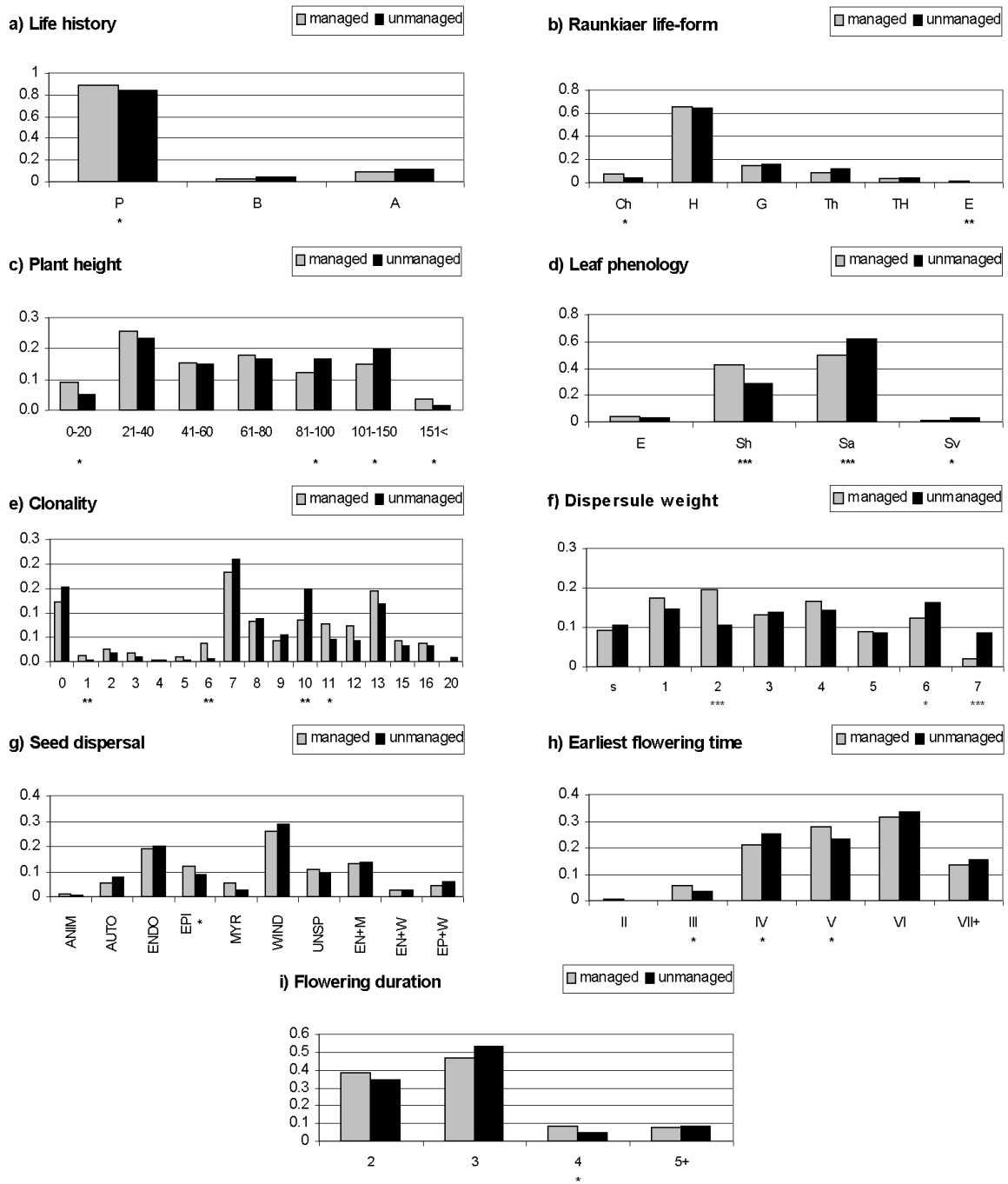
	Z	p-level		Z	p-level
<b>Life history</b>			<b>Dispersule weight</b>		
P	-2.1186	0.0341 *	s	0.9177	0.3588 --
B	1.1242	0.2609 --	1	-1.1530	0.2489 --
A	1.0602	0.2891 --	2	-3.4368	0.0006 ***
<b>Raunkiaer life-form</b>			3	0.9649	0.3346 --
Ch	-2.3174	0.0205 *	4	-1.5057	0.1322 --
H	-0.5181	0.6044 --	5	-0.2355	0.8138 --
G	0.4001	0.6891 --	6	2.3059	0.0211 *
Th	1.0602	0.2891 --	7	4.4055	0.0000 ***
TH	1.1242	0.2609 --	<b>Seed dispersal</b>		
E	-2.9933	0.0028 **	ANIM	-0.8790	0.3794 --
<b>Plant height</b>			AUTO	1.3885	0.1650 --
0-20	-2.4945	0.0126 *	ENDO	0.3294	0.7418 --
21-40	-1.8351	0.0665 --	EPI	-2.2366	0.0253 *
41-60	-0.3530	0.7241 --	MYR	-1.7465	0.0807 --
61-80	0.4001	0.6891 --	WIND	1.7417	0.0816 --
81-100	2.2601	0.0238 *	UNSP	-1.1533	0.2488 --
101-150	2.2827	0.0225 *	EN+M	-0.2355	0.8138 --
151-1000	-2.0236	0.0430 *	EN+W	-0.2427	0.8083 --
<b>Leaf phenology</b>			EP+W	0.9936	0.3204 --
E	-0.0476	0.9620 --	<b>Earliest flowering time</b>		
Sh	-3.7423	0.0002 ***	II	-1.0917	0.2750 --
Sa	3.4594	0.0005 ***	III	-1.9924	0.0463 *
Sv	2.0837	0.0372 *	IV	2.3778	0.0174 *
<b>Clonality</b>			V	-2.4582	0.0140 *
0	1.1536	0.2487	VI	1.3653	0.1722 --
1	-2.6284	0.0086 **	VII+	0.4943	0.6211 --
2	0.4815	0.6301	<b>Flowering duration</b>		
3	-1.0952	0.2735	2	-1.3888	0.1649 --
4	-0.3091	0.7572	3	1.9054	0.0567 --
5	-1.5072	0.1318	4	-2.1430	0.0321 *
6	-3.1498	0.0016 **	5+	0.0235	0.9812 --
7	0.8000	0.4237			
8	0.2353	0.8140			
9	1.0645	0.2871			
10	2.7310	0.0063 **			
11	-1.9681	0.0491 *			
12	-1.8596	0.0629			
13	-0.8710	0.3838			
15	-0.1177	0.9063			
16	0.0708	0.9436			
20	1.7001	0.0891			

zoochorous species have significantly higher relative frequency in managed stands.

The analysis of earliest flowering time showed that most species (>80%) start flowering between April and June (Fig. 2h). The proportion of species that start flow-

ering in April is significantly higher in the unmanaged stands. The proportion of species that start flowering in May is higher in the managed stands. There is no significant difference in the frequency of species that start flowering in June. We also found that species that start flowering in March are more important in the managed stands.





**Figure 2.** Occurrence of species traits of the herbaceous plants in unmanaged versus managed stands. Diagrams show the mean proportions for each species trait and the level of significance for a Mann-Whitney U test between unmanaged and managed forests (\*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ ).

We found slightly significant differences between unmanaged and managed sites in the distribution of species among categories describing flowering duration (Fig. 2i). Though species that flower for 3 months have slightly higher frequency in the unmanaged reserve, the only significant difference is that managed stands have more species that flower for 4 months.

*Intercorrelations of species attributes*

Intercorrelations among species attributes are depicted in a plexus graph (Fig. 3). Of the 36 possible pair-wise intercorrelations 15 are significant ( $p < 0.01$ ). Since we carried out many non-independent pair-wise tests, we accepted only intercorrelations with  $p$ -level  $< 0.01$  to decrease the chance of type one error. Moreover, the aim of

producing this plexus graph was not to test special hypotheses, but only to help interpreting the result of other analyses. Intercorrelations among reproductive traits are stronger than those among vegetative traits.

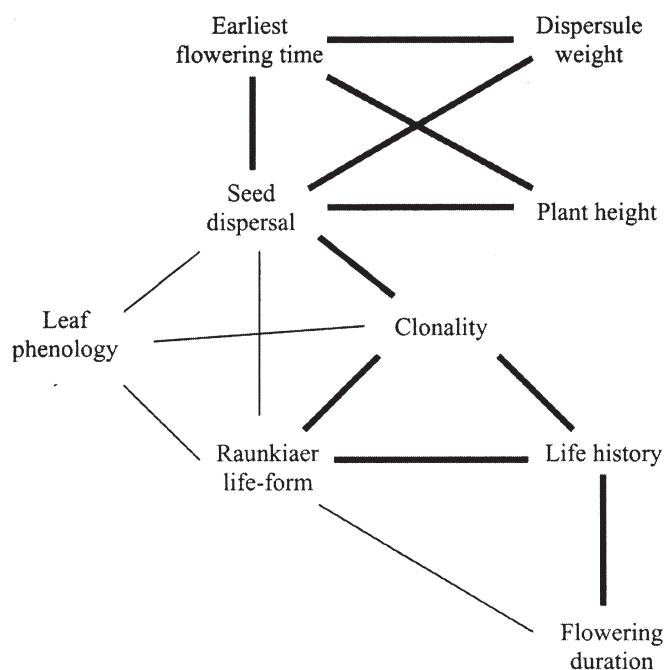
### Discussion

This study suggests that forest management, i.e., application of uniform shelterwood system, exerts important influence on the distribution of specific ecological species traits of forest floor vegetation. To avoid erroneously interpreting the effect of stand age as effect of management intensity, we tested if we could find the same differences between young (< 50 years) and old (> 50 years) managed stands as shown between unmanaged and managed stands. Altogether 64 tests were performed, of which only 4 gave significant result ( $p < 0.05$ ). In a random data set, the expected number of significant correlations would be 3.2. Most significant differences were found in categories with low values, where chance effect can be important. So, we concluded that the differences shown between unmanaged and managed stands are not caused by differences in stand age.

While interpreting the findings of this study we were aware of the fact that the species traits are not independent from each other (Fig. 3.). In spite of different species pool, information sources and coding used, the intercorrelations of species traits shown in Fig. 3 are rather similar to those published in the literature (Thompson and Rabinowitz 1989, Leishman et al. 1995, Thompson et al. 1998, Graae and Sunde 2000). However, it is generally found

that intercorrelations among vegetative traits are stronger than among reproductive traits (Shipley et al. 1989, Leishman and Westoby 1992, Grime et al. 1997, Díaz et al. 1998). Our results show the opposite.

If one concentrates on traits describing the vegetative body of plants, managed stands contain more plants that are perennial, have overwintering leaves and are small (*Ajuga reptans*, *Carex digitata*, *Fragaria vesca*, *Prunella vulgaris*, *Taraxacum officinale*, *Veronica officinalis*). Some very tall perennials (*Atropa belladonna*, *Cirsium arvense*, *Eupatorium cannabinum*, *Rumex obtusifolius*) are also more frequent in managed stands. However, except for *Rumex obtusifolius*, these species have summer-green leaves and they require lot of light and nitrogen, and they usually find place for establishment along the disturbed and locally more humid small paths. Unmanaged stands are richer in moderately tall (81-150 cm) plants with aestival canopy (*Aegopodium podagraria*, *Athyrium filix-femina*, *Campanula rapunculoides*, *Chelidonium majus*, *Lilium martagon*, *Lunaria rediviva*, *Polygonatum multiflorum*, *Polygonatum verticillatum*, *Scrophularia nodosa*). As our results show, perennial species dominate both in managed and unmanaged stands. This is in harmony with the observation of several authors (Newell and Tramer 1978, Bierzychudek 1982, Falinski 1986, Dzwonko 1993, Peterken 1996), who claimed that many herbaceous species of temperate deciduous forests are perennial and are capable of vegetative spread. These species allocate only small proportion of resources for reproduction (Newell and Tramer 1978). Once they have estab-



**Figure 3.** Plexus graph showing significant intercorrelations of species traits (thick line:  $p < 0.001$ ; thin line:  $p < 0.01$ ).



lished, they spread by rhizomes or stolons (Dzwonko 1993). This is demonstrated by a detailed study that showed successful survival and active vegetative spread of large sterile ramets of *Allium tricoccum* (Nault and Gagnon 1993). The proportion of plants capable of vegetative spread is around 20% both in our unmanaged and managed stands. The higher importance of *Aegopodium podagraria* type species (e.g., *Capmanula rapunculoides*, *Mercurialis perennis*, *Polygonatum multiflorum*, *P. verticillatum*) in unmanaged stands can be attributed to the advantage of having long-lasting stems that permit fast vegetative spread and grow below-ground. The higher importance of *Fragaria vesca* type plants (e.g., *Veronica officinalis*, *Prunella vulgaris*, *Moehringia trinervia*) in managed stands can be interpreted as successful adaptation to regular uniform disturbance of stands. The individual ramets connected by short-lived above-ground stems can survive independently after being separated from the rest of the genet.

Our observations concerning leaf phenology are in agreement with the assumptions that in crowded situations tall summer-green species have advantage, whereas in sparse forest floor vegetation longer light utilization and small size is beneficial (Regehr and Bazzaz 1976, Givnish 1982). Observations that in primary old-growth forests herbaceous vegetation has higher cover than in secondary forests support this thread of thoughts (Duffy and Meier 1992). Differences in plant height between unmanaged and managed stands could become more interpretable if plant height would be coded differently. Species with rosettes or with tall inflorescence but low canopy behave more like small plants. Examples are *Campanula persicifolia*, *Carex sylvatica*, *Geum urbanum*, *Hieracium sylvaticum*, *Lapsana communis*, *Luzula luzuloides*, *Mycelis muralis*, *Rumex obtusifolius*, *Sanicula europaea*.

In terms of the closely linked reproductive traits unmanaged and managed stands differ greatly. The most pronounced difference was shown in dispersule weight. Unmanaged stands contain more species that produce large seeds (4.01-10.00 and 10.01-50.00 g/1000), whereas managed stands are much richer in species with small seeds (0.21-0.5 g/1000). Large seeded species that are more frequent in the unmanaged stands include *Actaea spicata*, *Lathyrus vernus*, *Lilium martagon*, *Lunaria rediviva*, *Melica uniflora*, *Mercurialis perennis*, *Polygonatum multiflorum*, *P. verticillatum*. Small seeded species characteristic of our managed stands are *Carex digitata*, *Cardamine impatiens*, *Fragaria vesca*, *Hieracium sylvaticum*, *Luzula luzuloides*, *Lysimachia nummularia*, *Stellaria media*, *Taraxacum officinale*, *Tussilago farfara*.

This finding is in good harmony with the results of several authors who argued that species of undisturbed habitats produce fewer and larger propagules than those of disturbed sites (Foster and Janson 1985, Schmidt et al. 1991, Graae and Heskjaer 1997, Graae and Sunde 2000). It is also assumed that small seeds are more resistant, which can be advantageous under the more disturbed conditions of managed forests.

Earliest flowering time also differentiated between unmanaged and managed stands. Characteristic species of unmanaged stands that start flowering in April include *Arum maculatum*, *Galeobdolon luteum*, *Lamium maculatum*, *Mercurialis perennis*, *Scopolia carniolica*. The proportion of species that start flowering in May (e.g., *Ajuga reptans*, *Cardamine impatiens*, *Hieracium sylvaticum*, *Luzula luzuloides*, *Prunella vulgaris*, *Ranunculus repens*, *Sanicula europaea*) is higher in the managed stands. Other works that showed that early flowering species are more abundant in ancient forests (e.g., Graae and Sunde 2000) supports this finding. This difference in earliest flowering time is most probably the result of the correlation between seed size and earliest flowering, since more time is needed to produce large seeds. Early start and/or short duration of flowering can be the solution to achieve successful production of large seeds. We also found that plants that start flowering in March are more important in the managed stands, but most of these species (e.g., *Carex digitata*, *Chrysosplenium alternifolium*, *Stellaria media*, *Taraxacum officinale*) are small, have small seeds and dispersed by ants. It is not straightforward to interpret the slight difference we found between unmanaged and managed sites in terms of flowering duration. While coding this trait, one can mix the effects of two phenomena: the length of flowering of an average individual and the length of the time period when different individuals start flowering. The ecological interpretation of these two aspects should be different. Unfortunately, available data usually describe the average behaviour of populations.

Seed dispersal is treated as a crucial trait limiting the success of many ancient forest species in inhabiting secondary and/or managed forests (Peterken and Game 1984, Whitney and Foster 1988, Matlack 1994). Myrmecochory is generally regarded as an important means of seed dispersal in nemoral deciduous forests, where this trait is often characteristic of up to 30% of forest herbs (Beattie and Culver 1981, Beattie 1983, Dzwonko and Loster 1989, Lanza et al. 1992, Hermy et al. 1999). However, we found that myrmecochorous species are less important in our sample. One could have assumed that unmanaged stands are richer in myrmecochorous species than managed stands if the analogy with primary and secondary

forests was valid. However, we found more myrmecochorous (not significant) and epizoochorous species in our managed stands. These results contradict assumptions, but need careful interpretation. The relative importance of myrmecochorous species can be the result of limited success of wind-dispersed species in managed stands caused by the continuously closed dense canopy. Many myrmecochorous species are capable of vegetative spread, so they can survive and then spread in the managed stands in vegetative form.

## Conclusions

In this study, we investigated if herbaceous plants' ecological traits could differentiate between unmanaged and managed forests. As for many traits we showed differences in character state distribution, this kind of analyses could possibly be applied in developing indicators of the naturalness and/or conservation value of forests. The search for management sensitive indicators is relevant in our study region, since in many areas it is not forest fragmentation or the lack of forest continuity that deteriorate forest quality, but the widespread use of a silvicultural system that creates artificial spatial and temporal patterns of disturbance in these temperate deciduous forests.

Our major findings show that - unlike in the Northwestern part of Europe (Brunet et al. 1996, 1997, Kirby 1990, Graae and Sunde 2000) - we found significant and long lasting effects of management on the distribution of certain ecological traits of plants making up the forest floor vegetation. The importance of herbaceous plants that tolerate disturbance, start flowering late, flower longer, have overwintering canopy and small epizoochorous seeds is higher in managed stands. Unmanaged stands are richer in plants that bear leaves from spring to autumn, start flowering early or flower very shortly, produce large seeds.

A possible explanation for this different response of forest floor vegetation across Europe can be the change in continentality of climate with increasing distance from the Atlantic Ocean. In Central Europe, where climate is more continental, management induced changes in stand structure can cause more dramatic changes of habitat characteristics. As a result, plants adapted to the special habitat characteristics provided by the complex tree canopy of a natural forest (Crawford 1989), have to face more dramatic changes in Central Europe than in Northwest Europe, where prevailing oceanic climate provides less extreme relative humidity and temperature patterns outside the closed forest. This can also explain that some of the species (e.g., *Anemone nemorosa*, *Majanthemum bifolium*, c.f. Graae and Sunde 2000) that exclusively grow

in closed forests in Central European submontane zone, can also occur in extensively managed habitats (grassland or heathland) in West Europe.

While interpreting our results one should remember that only presence/absence data were used for each sub-compartment. We assume that the strength of this method could be improved by applying more intensive quantitative sampling of vegetation.

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