



## **Vegetation of beech forests in the Rychlebské Mountains, Czech Republic, re-inspected after 60 years with assessment of environmental changes**

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### **Abstract**

From 1941–1944 nearly 30 phytosociological relevés were completed by F. K. Hartmann in the Rychlebské Mountains, a typical mountainous area in northeastern Czech Republic. Of the original plots still covered with adult grown beech (*Fagus sylvatica*) forest, 22 were resampled in 1998 and 1999. In order to describe the recent vegetation variability of the sites 57 relevés were recorded. Changes in vegetation were estimated using relative changes in species density and ordinations (PCA, RDA). Environmental changes were assessed using Ellenberg indicator values when no direct measurements were available. A decline in species diversity has been documented, particularly, many species occurring frequently in deciduous forests with nutrient and moisture well-supplied soils around neutral have decreased. In contrast, several light-demanding, acid- and soil desiccation-tolerant species have increased. Natural succession, quantified as forest age, contributed slightly to these changes. In Ellenberg indicator values, a decline in F (soil moisture), R (soil calcium) and N (ecosystem productivity), and an increase in L (understorey light) were shown. This is interpreted as the influence of modified forestry management and of airborne pollutants. Intensified logging caused the canopy to open and soil conditions to worsen. The latter is most likely also due to acid leaching of soil cations (Ca, K, Na). This caused a decline in soil productivity, thus the effect of nitrification could not be detected. The original relevés may have differed in size influencing the results.

### **Introduction**

Environmental changes in contemporary Central Europe are driven both by natural processes and human activities. Forests experience changes both in abiotic and biotic conditions. In general, contributing factors may be considered as (compare Puhe and Ulrich 2001): abiotically originated changes, like weathering, fires, frosts or droughts (e.g., Haas and McAndrews 2000); endogenous vegetation changes, natural succession or aging (e.g., Lichter 1998; and Økland 2000); pests and diseases, sometimes having disastrous effects (e.g., Hubbes 1999); direct human influ-

ence, forestry management and non-forestry use; indirect human influence over the last decades in particular.

Excluding strictly maintained forest reserves, the two latter groups of factors are of key importance. Forestry management is primarily represented by logging of various types and intensities (Meier et al. 1995; Brunet et al. 1996). Combined with liming, drainage, soil tillage etc., it alters the state of the forest's ecosystem (Demchik and Sharpe 2001). Non-forestry use such as litter removal, cattle grazing, etc., leads to the thinning of sites (Brockway and Lewis 2002). Three kinds of indirect human influence have

been of particular importance: (i) the sustainment of dense populations of game herbivores leads to eutrophication, inhibited tree species renewal and selective suppression of many herb species (Chytrý and Danihelka 1993; Reimoser and Gossow 1996; Reimoser et al. 1999). (ii) air-borne deposits of sulfur oxides, nitrogen oxides, and ammonia have a twofold effect; acidification and eutrophication. (iii) climatic warming can play a great role in the near future, weakening of the ecophysiological constraints causing changes in species composition is reported even in European temperate forests (Walther and Grundmann 2001; Walther 2002).

Fluxes of sulfur and nitrogen acids have led to the leaching of exchangeable cations (Ca, Mg, K, Zn, Na) from soils and a consequent decline in soil reaction. Aluminum was released, Ca/Al and Mg/Ca ratios decreased rapidly. In forests, these processes were described e.g. by Federer et al. (1989); Billett et al. (1990); Huettl (1993); Likens and Bormann (1995); Likens et al. (1996). Nitrogen enrichment has, on the other hand, caused eutrophication of many ecosystems (Bobbink et al. 1998; Diekmann et al. 1999). Plants are good indicators of these processes, especially in a long-term perspective. As observed in several European countries, species demanding higher soil reaction decrease, while acid-tolerant and nitrophilous species increase or even expand (e.g., Ellenberg 1985; Kuhn et al. 1987; Falkengren-Grerup and Tyler 1991; Falkengren-Grerup 1995; Vacek et al. 1999).

In this study, I attempt to assess changes in vegetation and environment of beech forests in the Rychlebské Mountains, northeastern Czech Republic. Their state in the 1940s is described with phytosociological relevés by F. K. Hartmann, a forester who had visited the territory of the former Sudeten region regularly from the 1930's until 1944. In my subjective field experience, I noted that Hartmann's original vision of beech forest vegetation could no longer be found. I hypothesize, however, that no changes in the vegetation and environment of the beech forests took place between the 1940s and the 1990s. Phytosociological relevés serve as the main source of data when comparing the past and present state of vegetation.

Phytosociological relevés represent a great potential for studies of long-term vegetation dynamics (Wittig 1992). Their number is estimated at nearly one million worldwide (Ewald 2001), covering a period of approximately eighty years since 1920. For the most part they are presently stored in electronic

databases. The only serious disadvantage is a characteristic feature of phytosociological relevés: imprecise localization. In studies of long-term vegetation dynamics, relevés can be an interesting alternative to permanent plots (Bakker et al. 1996), which rarely span a period of several decades (e.g., Dodd et al. 1995). Sampling and data analysis methods, considering the imprecise localization of phytosociological relevés, have not yet been thoroughly tested.

In the Rychlebské Mountains' forests, both the history of management and influence of airborne pollutants have to be considered. The landowner has changed since the end of the 1940's. All of the forests studied were possessed by the Archbishopric of Breslau (Wrocław in what is today Poland) until 1948, after which, they were taken over by the Czechoslovak state (see Roering 1999). I consulted previous forest use with Mr. V. Hédl (my grandfather), who has worked as a forester at the local forestry directory in Javorník since 1947. We can assume the important factors are:

1. *Forestry use.* Light and substrate conditions change with the forest's age, which is reflected by plants (e.g., Lichter 1998). Natural succession is, however, under full control of forestry management today. Cutting period and size of clearings are key aspects here. The cutting period has not changed since World War II; approximately 100–150 years. The size of clearings is difficult to quantify. Regardless, small clearings were common in the pre-war period and there wasn't extensive deforestation at that time. Forestry management was accomplished more carefully since heavy machinery wasn't used. In state forests, clear-cuts, tens of hectares large became frequent; heavy logging techniques were frequently in use. Liming, drainage, or soil tillage was never applied. With the exception of the Norway Spruce (*Picea abies*) plantations, forest recovery was mostly left to spontaneous rejuvenation; no deciduous tree species was ever planted extensively. Deer and roe-deer density may have been greater in the 1940's since the numbers were diminished in the 1990's.

2. *Non-forestry use.* Local inhabitants have not promoted forest grazing and litter removal in the Archbishopric forests or in state forests. This dates at least to the mid-18<sup>th</sup> century taking in to consideration the laws established by the empress Maria Theresa (Nožička 1957). Extensive wood collection or even stub grubbing wasn't practiced as was in more densely inhabited and mainly forest-free parts of the country until the 1950's (Nožička 1957).

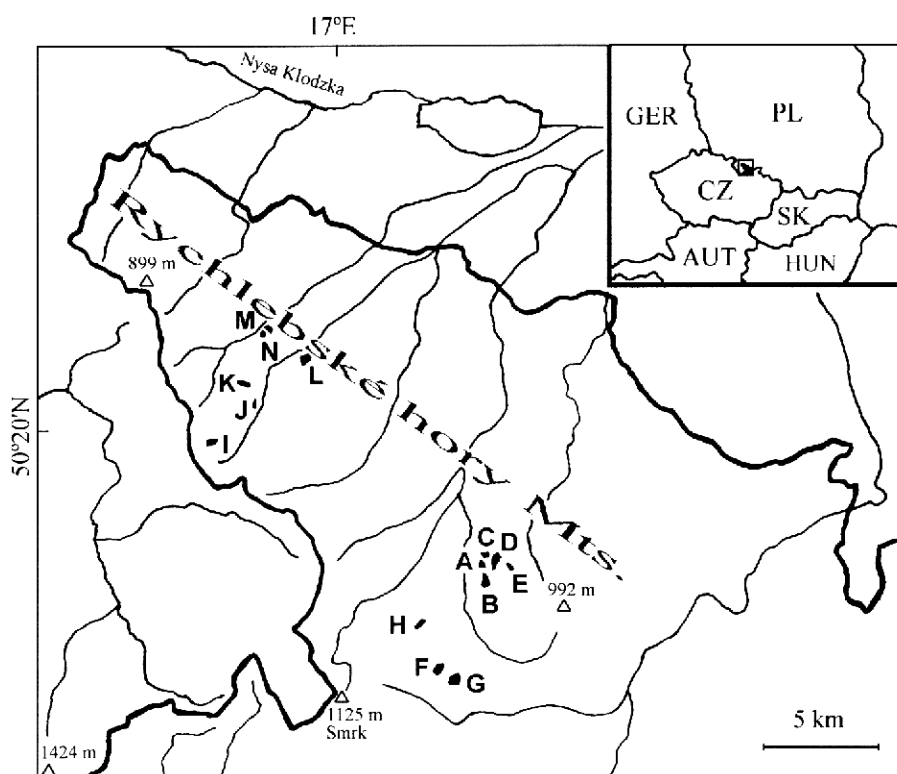


Figure 1. Map of the study area. Forest detachments are marked A to N (see Table 1)

3. *Airborne pollutants.* The Central European region is among territories with the greatest amount of air-borne pollutants (Berge et al. 1999). The area studied receives low to intermediate amounts of deposits within the Czech Republic. In 1996 it was 1,0–2,0 (–3,0)  $\text{g.m}^{-2}.\text{year}^{-1}$  for total sulfur, 0,1–1,0  $\text{g.m}^{-2}.\text{year}^{-1}$  for total nitrogen (ČHMÚ 1997). Vast forest die-off, as is apparent in the northwestern parts of the country (Kubíková 1991), did not result. There are no detailed measurements of pollutant loads for the concerned territory and environmental processes cannot be quantified by a reliable comparison with measurements from the past either. Although Hartmann analyzed about five soil profiles in the Rychlebské Mountains (see Hartmann and Jahn 1967), the repeated measurements done in 1998 by the author (not published) cannot be considered as worthy evidence. The profiles are too few, are not exactly localized, and the laboratory instruments are different today. However, all of the repeated measurements of soil pH have shown a significant decrease in value by a maximum of 1.5 points. Hence, these processes are assessed only indirectly using Ellenberg indicator values.

Objectives of the study are: (1) to describe the temporal changes in vegetation in the 1940's and 1990's regarding particular species and vegetation overall (2) to determine the role of natural forest dynamics (quantified as forest age) to the overall temporal change (3) to assess the environmental changes based on indirect information provided by Ellenberg indicator values (Ellenberg et al. 1991) (4) to assess the role the size difference of Hartmann's relevés and those used for the study plays.

## Material and Methods

### Study Area

The Rychlebské Mountains (Reichensteiner Gebirge in German) are 276  $\text{km}^2$  (Demek 1987) and are part of the eastern Sudetan Uplands, today the mountainous area of northeastern Czech Republic defining the Czech-Polish border (Figure 1). Elevations range from 350 to 1,125 m above sea level, averaging 645 m (Demek 1987). Moderate mountain ranges and steep valley slopes are characteristic landscape

Table 1. Overview of the forest detachments marked A to N (see also Figure 1). The former locality names are all within the Archbishopric Forests of Breslau, the current names within the Czech State forests, Javorník headquarters. Several detachments consist of parts of different ages. The last two columns give minimal, average and maximal number of species per relevé

For. det.	Hartmann's locality name (1940s)	Recent locality name (1990s)	Number of relevés		Forest age (years)		Nr. species (min./) aver. (/max.)	
			old	new	1940s	1998	1940s	1990s
A	Setzdorf 91a	Vápenná 454 B6	1	5	117	57	20	9/ 24 /38
B	Setzdorf 84b	Vápenná 433D6, 456B6a, 456B15/1	2	8	90	58/149	34/ 40 /46	10/ 22 /32
C	Setzdorf 99b	Vápenná 455A6	4	5	110/113	58	33/ 39 /42	11/ 18 /32
D	Setzdorf 92, 92a	Vápenná 455B16/2	4	14	100/106	154/158	24/ 31 /38	1/ 14 /31
E	Setzdorf 86	Vápenná 460A5	1	2	120	49	24	4/ 9 /14
F	Setzdorf 38a	Vápenná 422C5	1	4	125	46	38	14/ 21 /27
G	Setzdorf 46a	Vápenná 423B6	1	4	130	61	36	20/ 27 /38
H	Setzdorf 6c	Vápenná 405E7	1	3	100	66	12	13/ 19 /26
I	Johannisberg 54a	Javorník 256C12b/1c	1	2	67	121	49	6/ 7 /7
J	Johannisberg 51	Javorník 254C7	2	1	128	63	25/ 32 /38	32
K	Johannisberg 37b	Javorník 219C11	1	2	59	110	42	23/ 32 /40
L	Johannisberg 21c	Javorník 251D15/4b, 251D4a	1	3	104	36/148	45	17/ 18 /20
M	Jauernig 12a	Javorník 204B5	1	2	120	48	41	19/ 23 /26
N	Jauernig 12c	Javorník 204B5	1	2	100	48	30	13/ 17 /21

features. The predominate bedrock has an acidic character. It is made up of silicates, mainly gneiss, mica schist, granite, granodiorite, amphibolite, and phyllite. Crystalline limestone is only found locally (ČGÚ 1992a, 1992b, 1995, 1997). Vegetation cover is primarily formed by forests with dominant Norwegian Spruce (*Picea abies*) plantations. In Jeseník district 67% of forest composition is spruce, 18% European beech (*Fagus sylvatica*) – (ÚHÚL 2003). Potential vegetation are eutrophic (*Dentario enneaphylli-Fagetum*) and acidophilic (*Luzulo-Fagetum*, *Calamagrostio villosae-Fagetum*) beech and spruce (*Calamagrostio villosae-Piceetum*) forests (Neuhäuslová and Moravec 1997; Neuhäuslová 1998; Moravec et al. 2000).

#### Reference Records

Reference records include phytosociological relevés carried out by German forest ecologist Friedrich K. Hartmann from 1941–1944 using Braun-Blanquet's (1964) approach. They were published as part of a comprehensive study of Central European forest vegetation (Hartmann and Jahn 1967). The sites that were sampled were chosen subjectively using a preferential sampling design (Podani 1984). Relevés were localized by Hartmann within forest detachments (Abteilung). Detachments are spatial units used in forestry management, each covering from one to several hectares, usually regularly shaped. Boundaries

between the detachments have remained the same since the 19<sup>th</sup> century. Their identification numbers were changed, however, and so identification had to be made according to the historical forestry maps located at the State Archive in Opava (Zemský archiv v Opavě). Hartmann supplemented the relevés with descriptions of the slope aspect, exposition, altitude, topography, and forest age. However, he did not mention the size of his relevés anywhere. I decided not to utilize all of Hartmann's records. Two criteria were applied: (i) deciduous or mixed stand were not to have been replaced by a Norwegian Spruce plantation (ii) the forest shouldn't be younger than 45 years old. Of the 27 relevés and 19 forest detachments available, 22 relevés and 14 detachments complied with the criteria. There was the exception of one 36 year old forest area (Table 1). These relevés are from here on referred to as 'old relevés', numbered 1 to 22 in the Table of relevés (Appendix).

#### Resampling Method

Hartmann's relevés were not exactly localized. The changes at each site cannot be judged by recording one new relevé alone, by executing a parallel comparison. This approach would be appropriate if there were permanent plots (Bakker et al. 1996). If the exact position is unknown, recent spatial variability mingles with the desired temporal variability unidentifiably. In our case the position of the reference

relevé is identified approximately within a forest detachment. If we describe the recent spatial variability of vegetation within each detachment, the vegetation variability from the 1940's can then be related to it.

Relevé subsets can, however, be selected following different criteria (e.g., relative similarity). In general, two factors influence the results. (i) We cannot identify the previous vegetation variability completely. Therefore, we cannot quantify the temporal change accurately and all the results will be regarded rather as an estimate. (ii) Observer's bias, which is inevitable, may play a role but is not the most significant source of error (Lepš and Hadincová 1992). I described the recent vegetation variability of the forest detachments studied with 57 phytosociological relevés using the preferential sampling design (Podani 1984). 51 relevés were recorded in 1998 and 1999 and another 6 relevés which were completed in 1994 were added. They are numbered 23 to 79 in the Table of relevés (Appendix), from here on referred to as 'new relevés'. The number of relevés per detachment (Table 1) was determined by subjectively observed vegetation variability. I considered this approach the most suitable since rare vegetation types (possibly those sampled by the phytosociologist Hartmann) could have been better recorded. The samples are circles measuring approximately 10m in radius, i.e. about 315 m<sup>2</sup>. Sample size and shape had to be determined arbitrarily since no such information had been provided by Hartmann. The compared plots were to be equally sized as species diversity increases with area size (e.g., May 1975). Vegetation composition was described using Braun-Blanquet's (1964) 7 grade abundance-dominance scale. Current forest ages were obtained from the Czech State Forest's local directory in Javorník (Lesy České republiky, lesní správa Javorník).

#### Data Handling and Editing

Relevés were stored in the database program Turboveg for Windows (Hennekens 2002) in the form they were published (Hartmann and Jahn 1967) or recorded in the field (my own relevés). Nomenclature of the phanerogams follows Kubát (2002), cryptogams were not considered because they were mostly omitted during sampling. For woody species, tree layer (represented by T), shrub layer (S) and seedlings (juv.) were taken into consideration. Before the analyses, relevés were edited with the program Juice (Tichý 2002). Some taxa had to be merged into one

taxon, either because two different names obviously denoted one species or because some species groups were distinguished with a varying accuracy; if the species status was unclear, an aggregative species name was used.

Hartmann's species names are denoted with a 'H' and mine with a 'R'; so *Bromus ramosus* (H) and *B. benekenii* (R) were merged into *Bromus ramosus* agg. *Carex digitata* (H) was considered *Carex pilulifera* (R), a misinterpretation of calciphilous *Carex digitata* is feasible so it was connected to acidiphilous *Carex pilulifera*. A recent discovery of *Dryopteris affinis* (R) was connected to *D. filix-mas* (H, R). *Dryopteris carthusiana* (H, R), *D. dilatata* (R) and *D. expansa* (R) were all merged into *Dryopteris carthusiana* agg. *Epipactis* species (R) was connected to *Epipactis helleborine* (R). *Galeobdolon luteum* (H), *G. luteum* agg. (R), and *G. montanum* (R) were merged into *Galeobdolon luteum* agg.; all records are most likely related to *G. montanum*. *Pulmonaria officinalis* (H) was connected to *Pulmonaria officinalis* agg. (R), since most likely only *P. obscura* occurs in the study area. *Rubus fruticosus* agg. (H), *Rubus* species (R) and *R. hirtus* s.l. (R) were merged into *Rubus fruticosus* agg.; most forest brambles in the territory are probably within *R. hirtus* s. l.

When analyzing species composition changes (frequency changes and ordination methods), rarely occurring species were excluded. Recording a species once or twice can be to a great extent due to imprecise localization of the plots, not an actual change, which might distort the verity of results. Rarely occurring species are present in a maximum of one old (frequency = 4.5%) and two (frequency = 3.5%) new relevés. The limits were set arbitrarily. This concerns 52 species of 152 in total. Therefore, 100 species were included in the analyses.

#### Data Analyses

##### Changes in species frequency

In order to observe the change of a particular species occurring over time, frequencies in both the old and new relevés datasets are related. Relative change of the species frequency, *C*, is computed, based on species frequency, *F* [%]:

$$C = \pm \left( 100 - \frac{F_b}{F_a/100} \right) [\%]$$

$F_a$  is frequency in the group where the species frequency is greater than in the other group (i.e., frequency in old relevés if the species decreased or frequency in new relevés if it increased).  $F_b$  is frequency in the second group. The 'minus' sign is used for a decline in a species, a 'plus' sign for an increase in a species. To visualize the trend of change regarding the commonness of the species from the 1940's,  $C$  is plotted against  $F$  in old relevés, fitted with a non-linear trend.

#### *Multivariate methods*

Ordinations (Jongmann et al. 1987) are applied to determine the difference between groups of old and new relevés and the influence of environmental factors (general temporal change and forest age) on the vegetation and particular species. Analyses based on the linear species response are chosen because the number of species was low (100) and the data set didn't seem to be very heterogeneous. The criterion based on the length of the longest gradient from DCA (ter Braak and Šmilauer 1998) is not possible to apply; SD is between 3 and 4. Thus, Principal Components Analysis (PCA) and its constrained counterpart, Redundancy Analysis (RDA) are applied using the CANOCO for Windows 4.0 program package (ter Braak and Šmilauer 1998).

To estimate the influence of environmental factors, the eigenvalues of the corresponding ordination axes from unconstrained (PCA) and constrained (RDA) analyses shall be compared (Lepš and Šmilauer 1999) and vectors of species versus environmental factors read in ordination biplots (Jongmann et al. 1987) shall be observed. The role of two environmental factors are considered separately. These factors are *time* (the time span of the record from the 1940's or the 1990's) and *age* (the current forest age in years). Time constrains the first ordination axis in  $RDA_{time}$ , age does the same in  $RDA_{age}$ .  $RDA_{old}$ , analogous to  $RDA_{time}$ , deals only with forests untouched by a clear-cut since the 1940's. They belong to detachments B, D, K, I, and L, including 9 old and 22 new relevés. To see the relationship between the two factors, a linear regression between both and linear regressions between the species scores on the first ordination axes from  $RDA_{time}$ ,  $RDA_{age}$ , and  $RDA_{old}$  have been carried out.

To partially reduce the influence of spatial variability, relevés are compared only within the corresponding forest detachments. For this purpose, 14 covariables (ter Braak and Šmilauer 1998; compare also Sokal and Rohlf 1995:499), each representing one

detachment, are used in both analyses. Rare species are excluded as described in 'Methods'. In RDA's, scaling is focused on species correlations in order to facilitate visibility of species positions in biplots. Suchlike is the focus on sample distances in a PCA-scatterplot (Lepš and Šmilauer 1999). Species scores are divided by standard deviation. Species covers are transformed using the formula  $y = \log x + 1$  (applied to intermediate percentage values of Braun-Blanquets scale classes: 1, 2, 3, 13, 38, 63, and 88). Neither centering nor standardization is used for samples. Centering, but not standardization is used for species. Statistical significance of constrained axes is determined using the Monte Carlo permutation test, with 1,999 permutations, reduced model, unrestricted permutations; blocks are defined by covariables.

$RDA_{loc}$ , with the exception of one parameter, identical with  $RDA_{time}$ , aims to restrict recent overall vegetation variability. The criterion was the most probable position of the old relevés. For 14 of them (in 11 detachments) information regarding slope aspect, altitude and site topography was provided by Hartmann. 17 new relevés could be matched as located closest to those. 38 rare species (located at maximum in 1 old and 1 new relevé) were excluded. 14 covariables have been created, one for each old relevé.

#### *Assessment of environmental conditions*

Analyses were performed based on Ellenberg indicator values (source: Ellenberg 1996). Six parameters were considered: understorey light 'L,' temperature 'T,' continentality 'K,' soil moisture 'F,' soil reaction 'R' and soil nutrients 'N.' Parameters R and N should be regarded as the total calcium (important in acid to neutral parts of acidity gradient) and biomass productivity values respectively (Schaffers and Sýkora 2000). Tree species are excluded with the exception of tree seedlings. Relevés with less than 5 species with a given indicator value were excluded. I follow Sokal and Rohlf (1995) in the statistical approach.

The first analysis relates indicator values for relevés computed as a mean of indicator values for species present in relevés between old and new relevés. Species are not weighed by their abundance (compare Diekmann 1995; Schaffers and Sýkora 2000). Because of abnormal distribution and the relatively low number of cases (22 old relevés), non-parametric tests were performed. The Mann-Whitney test is applied to all old and new relevé

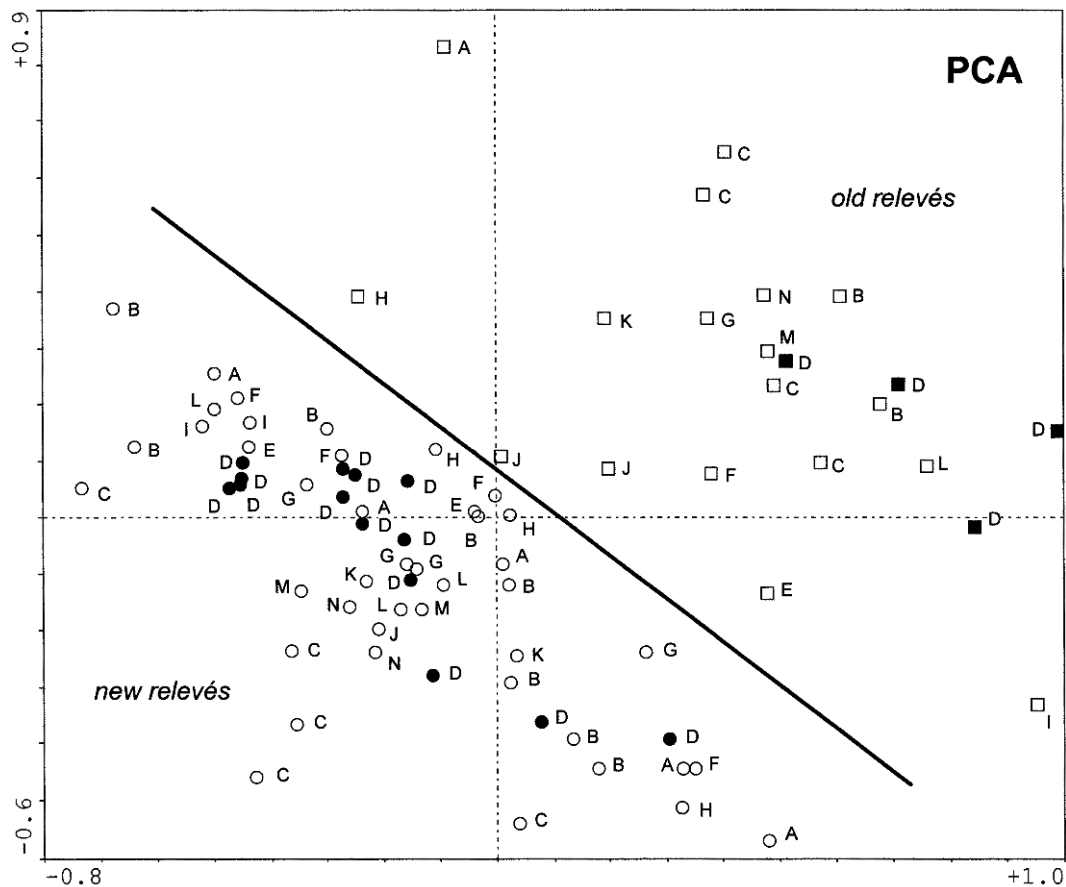


Figure 2. PCA with 22 old (squares) and 57 new (circles) relevés. Letters denote forest detachment (see Table 1). Scaling is focused on intersample distances. Distinct separation of the two groups is demarked with a solid line. Black-marked detachment D exemplifies variability within one locality

groups. A signed-rank test is applied to pairs of old and new relevés which were most similar within the detachments, determined by Euclidean distances between the relevés.

The second analysis relates the scores of 100 species from  $RDA_{time}$  (i.e. quantified species response to overall change) with species indicator values. A distance-weighted least squares fit shows the trend in six scatterplots for L, T, K, F, R, and N. The number of cases depends on the number of species indicator values available.

#### Size of relevés

The size of the old relevés is unknown. The only method to attain an estimate is by comparing the number of species per old and new relevé. Species diversity is also governed by forest age, but the factors are impossible to separate in this case. Statistical

distribution (Sokal and Rohlf 1995) of the number of species per relevé and forest age are compared between the old and new relevés. The number of species is further correlated with forest age.

## Results

### *Species and Vegetation Changes*

PCA scatterplot (Figure 2) indicates distinct differences between old and new relevés so that both groups can be separated by a line. The basic characteristics of ordination analyses are resumed in Table 2. A comparison of eigenvalues of the first ordination axes ( $\lambda_1$ ) from PCA and  $RDA_{time}$  shows that about 3/4 (72%) of the vegetation variability along with the main floristic gradient can be attributed to temporal

Table 2. Results of ordinations.  $N_{rel}$  denotes number of relevés,  $N_{spec}$  number of active species, env var environmental variables, covar co-variables (two types of locality).  $\lambda_1$  and  $\lambda_2$  are eigenvalues of the first and the second ordination axes, in %. Axes constrained with environmental variable are in bold print. F-stat is the F-statistics of Monte Carlo permutation test, with its p-value (1,999 permutations)

analysis	$N_{rel}$	$N_{spec}$	env var	covar	$\lambda_1$	$\lambda_2$	F-stat	p-value
PCA	79	103	–	loc1	15,9	6,7	–	–
RDA <sub>time</sub>	79	103	time	loc1	<b>11,4</b>	10,6	12,80	0,0005
RDA <sub>age</sub>	79	103	age	loc1	<b>3,4</b>	9,5	4,02	0,0005
RDA <sub>old</sub>	31	85	time	loc1	<b>22,0</b>	10,8	11,41	0,0005
RDA <sub>loc</sub>	31	93	time	loc2	<b>11,3</b>	6,2	5,27	0,0005

change. Permutation test of the constrained axis is highly significant. Eigenvalues of RDA<sub>loc</sub> and RDA<sub>time</sub> are almost identical. Therefore, localizing the old relevés more precisely would not yield a substantial difference in results. Frequency changes  $C$  for the 100 most frequent species are given in Table 3. Dependence of  $C$  on species frequency in old relevés is pictured in Figure 3. Species once most frequent have declined in general, but this trend is even more striking for species with intermediate frequency in the 1940's (20 to 40%). On the contrary, an increase has been noted primarily for several formerly least abundant or absent species. While there are 81 species which have decreased in frequency or have become extinct, only 19 species have increased in frequency or have appeared for the first time at the sites (Table 3). The RDA<sub>time</sub> biplot shows the same disproportion between the number of species that have declined (40, right side), and those that have increased (10, left side), see Figure 4.

The species that have decreased most significantly are indigenous to nutrient-rich and moisture-stable temperate forests. They are frequently found in beech-dominated forests, such as *Dentaria enneaphyllos*, *Galium rotundifolium*, *Veronica montana*, *Paris quadrifolia*, *Bromus ramosus* agg., *Milium effusum*, *Hordelymus europaeus*, *Mycelis muralis*, *Pulmonaria officinalis* agg., *Scrophularia nodosa*, *Campanula trachelium*, *Actaea spicata*, *Asarum europaeum*, or *Mercurialis perennis*. Other species that have declined in frequency which are related with nutrient-rich conditions, mainly of forests, are e.g. *Geranium robertianum*, *Ranunculus lanuginosus*, *Circaea lutetiana*, *Galeopsis pubescens*, *Impatiens noli-tangere*, *Urtica dioica*, *Sanicula europaea*, *Stachys sylvatica*, or *Primula elatior*. Several species tending to thrive in more acidic conditions such as *Epilobium montanum*, *Phegopteris connectilis*, *Fragaria vesca*, *Polygonatum verticillatum*, *Carex pilulifera*, have also decreased significantly. Species

that have experienced an increase are mainly acid-tolerant grasses, e.g. *Calamagrostis villosa*, *C. arundinacea*, *Luzula luzuloides*, *Avenella flexuosa* and other species tolerating acidic soils such as *Rubus fruticosus* agg., *Veronica officinalis*, *Dryopteris carthusiana* agg. or *Maianthemum bifolium*. Most tree and shrub species have decreased, e.g. *Ulmus glabra* T, *Sambucus racemosa* S, *Acer platanoides* T, *Daphne mezereum* S, *Larix decidua* T and *Picea abies* T. The most striking decrease affected *Abies alba* (in T, S as well as juv.). On the other hand, *Fagus sylvatica* currently thrives. Tree seedlings that have increased in frequency are *Acer platanoides*, *Picea abies*, and *Fagus sylvatica*.

#### The Most Depleted Species

Of the 100 most frequent species, 12 were not rediscovered presently (Table 3,  $C = -100\%$ ). *Abies alba* T, once present in 3/4 of the sites, was not discovered in the present study at all. Other species that were not rediscovered include *Sambucus racemosa* S, *Campanula trachelium*, *Circaea alpina*, *Cardamine impatiens*, *Lonicera nigra* S, *Pulmonaria officinalis* agg. or *Atropa bella-donna*. Another 22 species were depleted by more than 80%; *Epilobium montanum*, *Dentaria enneaphyllos*, *Galium rotundifolium* and *Fragaria vesca* showed the most striking decrease. Of the 52 rare species, 21 (40%) could not be discovered. Each of them was indicated once in the 1940's.

#### Role of Forest Aging

The RDA<sub>age</sub> biplot shows the clear influence of forest age (Figure 5). A majority of species tend to older (30, left side) than younger (21, left side) forests. Herbs (*Hieracium murorum*, *Prenanthes purpurea*, *Phegopteris connectilis*, *Epilobium montanum*, *Rubus idaeus*, *Veronica montana*, *Bromus ramosus* agg., *Lilium martagon*, *Festuca altissima*), several acidophil-

Table 3. Frequencies (F) and frequency change (C) for 100 most common species

	Species		Change
	F [%]		C [%]
	old	new	
<i>Extinct species:</i>			
Abies alba T	77	0	-100
Sambucus racemosa S	23	0	-100
Campanula trachelium	23	0	-100
Circaea alpina	23	0	-100
Cardamine impatiens	18	0	-100
Lonicera nigra S	14	0	-100
Agrostis capillaris	14	0	-100
Pulmonaria officinalis agg.	14	0	-100
Chrysosplenium alternifolium	14	0	-100
Atropa bella-donna	14	0	-100
Abies alba S	9	0	-100
Chaerophyllum hirsutum	9	0	-100
<i>Decreased species:</i>			
Epilobium montanum	45	2	-96
Dentaria enneaphyllos	41	2	-96
Galium rotundifolium	32	2	-94
Fragaria vesca	32	2	-94
Veronica montana	45	4	-92
Galeopsis pubescens	23	2	-92
Phegopteris connectilis	23	2	-92
Paris quadrifolia	64	5	-92
Asarum europaeum	27	4	-87
Ranunculus lanuginosus	14	2	-87
Geranium robertianum	50	7	-86
Abies alba juv.	55	9	-84
Impatiens noli-tangere	64	11	-83
Polygonatum verticillatum	41	7	-83
Actaea spicata	73	14	-81
Circaea lutetiana	36	7	-81
Ulmus glabra T	27	5	-81
Carex pilulifera	27	5	-81
Galeopsis speciosa	18	4	-81
Acer platanoides T	9	2	-81
Allium ursinum	9	2	-81
Primula elatior	9	2	-81
Bromus ramosus agg.	32	7	-78
Daphne mezereum S	14	4	-74
Lilium martagon	14	4	-74
Mycelis muralis	82	23	-72
Milium effusum	55	16	-71
Larix decidua T	18	5	-71
Sanicula europaea	41	12	-70
Scrophularia nodosa	41	12	-70
Urtica dioica	64	21	-67
Festuca gigantea	32	11	-67
Picea abies T	82	30	-64
Rubus idaeus	50	19	-61
Stachys sylvatica	45	18	-61
Moehringia trinervia	41	16	-61
Ajuga reptans	27	11	-61
Anemone nemorosa	14	5	-61
Aegopodium podagraria	9	4	-61

Table 3. Continued.

	Species		Change
	F [%]		C [%]
	old	new	
Hieracium murorum	45	19	-58
Poa nemoralis	59	30	-50
Dentaria bulbifera	59	30	-50
Petasites albus	14	7	-49
Galeopsis tetrahit	14	7	-49
Carex remota	14	7	-49
Gymnocarpium dryopteris	77	40	-48
Ulmus glabra juv.	18	11	-42
Polystichum aculeatum	9	5	-42
Polygonatum multiflorum	9	5	-42
Viola reichenbachiana	55	32	-42
Hordelymus europaeus	59	35	-41
Carex sylvatica	55	33	-39
Mercurialis perennis	77	51	-34
Senecio ovatus	95	68	-28
Athyrium filix-femina	95	70	-26
Galium odoratum	73	54	-25
Acer pseudoplatanus juv.	77	58	-25
Dryopteris filix-mas	95	72	-25
Galeobdolon luteum agg.	86	67	-23
Acer pseudoplatanus T	55	42	-23
Fraxinus excelsior T	23	18	-23
Stellaria nemorum	9	7	-23
Luzula pilosa	9	7	-23
Prenanthes purpurea	68	54	-20
Festuca altissima	86	74	-15
Oxalis acetosella	95	82	-14
Lysimachia nemorum	45	40	-11
<i>No or little change:</i>			
Maianthemum bifolium	18	18	-4
Melica nutans	9	9	-4
Fraxinus excelsior juv.	45	46	0
Solidago virgaurea	23	25	7
Sorbus aucuparia juv.	23	25	7
<i>Increased species:</i>			
Fagus sylvatica T	86	98	12
Fagus sylvatica S	36	42	14
Dryopteris carthusiana agg.	55	65	16
Fagus sylvatica juv.	59	77	23
Veronica officinalis	5	7	35
Calamagrostis villosa	14	26	48
Calamagrostis arundinacea	9	19	53
Acer platanoides juv.	9	25	63
Luzula luzuloides	9	26	65
Rubus fruticosus agg.	18	67	73
Brachypodium sylvaticum	5	23	80
<i>Newly appeared species:</i>			
Glechoma hederacea	0	5	100
Calamagrostis epigejos	0	7	100
Galeopsis species	0	7	100
Avenella flexuosa	0	19	100
Picea abies juv.	0	33	100

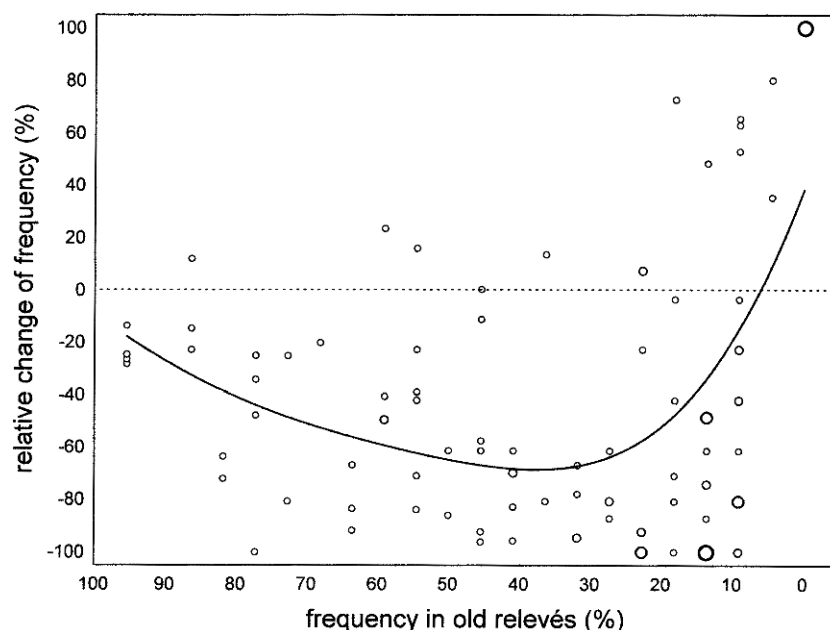


Figure 3. Relationship between species frequency in old relevés and relative change of species frequency. A distance-weighted least squares fit (stiffness 0,4) indicates a strong decrease of formerly middle-abundant and increase of the least abundant species. Points are sized according to the number of cases represented (1 to 5)

ous grasses (*Calamagrostis arundinacea*, *C. villosa*, *Luzula luzuloides*) and woody species (*Fagus sylvatica* S and juv., *Abies alba* T and juv., *Picea abies* T, *Larix decidua* T and *Lonicera nigra* S) are characteristic for matured forests.

Common beech-forest herbs (e.g. *Carex sylvatica*, *Dryopteris carthusiana* agg., *Viola reichenbachiana*, *Galeobdolon luteum* agg., *Dentaria bulbifera*, *Cardamine impatiens*, *Luzula pilosa*) and woody species (*Fraxinus excelsior* T and *Fagus sylvatica* T) are characteristic for younger forests.

The results of  $RDA_{old}$  show that forests uncut since the 1940's have changed even more than the whole set (Table 2). The species that have increased most are *Fagus sylvatica* T, S and juv., *Rubus fruticosus* agg., *Picea abies* juv., *Calamagrostis villosa*, *C. arundinacea*, *Luzula luzuloides*, *Avenella flexuosa* and *Acer platanoides* juv. The species that have decreased most are *Paris quadrifolia*, *Carex sylvatica*, *Actaea spicata*, *Mycelis muralis*, *Abies alba* T, *Viola reichenbachiana*, *Milium effusum*, *Oxalis acetosella*, *Dentaria enneaphyllos*, *Mercurialis perennis*, *Sanicula europaea*, *Geranium robertianum*, *Dentaria bulbifera* and *Hordelymus europaeus*. This corresponds with results of  $RDA_{time}$  well; the trend of overall species change is most pronounced in the oldest forests.

Results of linear regressions between species scores on the first ordination axes from  $RDA_{time}$ ,  $RDA_{age}$  and  $RDA_{old}$  are in Table 4. Forest age depends on the overall time change relatively little and very loosely, see the low R-square (the first correlation). The same shows a correlation between the two factors alone; the correlation coefficient is  $-0,2594$ . Hence, the recent forests (represented by increased species with a negative score) are younger (positive score regarding forest age) as a whole. The oldest forests follow the overall trend near to perfect (the second correlation). This is not much surprising because it is a subset of the total dataset. We can resume that mostly the oldest forests contributed the observed global change. Forest age correlates with time change of oldest forests well (the third correlation) which contradicts a poor and negative relationship between time and forest age. It might be due to absence of younger forests in  $RDA_{old}$  so this result is valid for the oldest forests only.

#### Assessment of Environmental Conditions

Statistical test results for differences between relevé indicator values are presented in Table 5. Soil moisture F, calcium R and site productivity N considering all relevés, and R considering relevé pairs, show

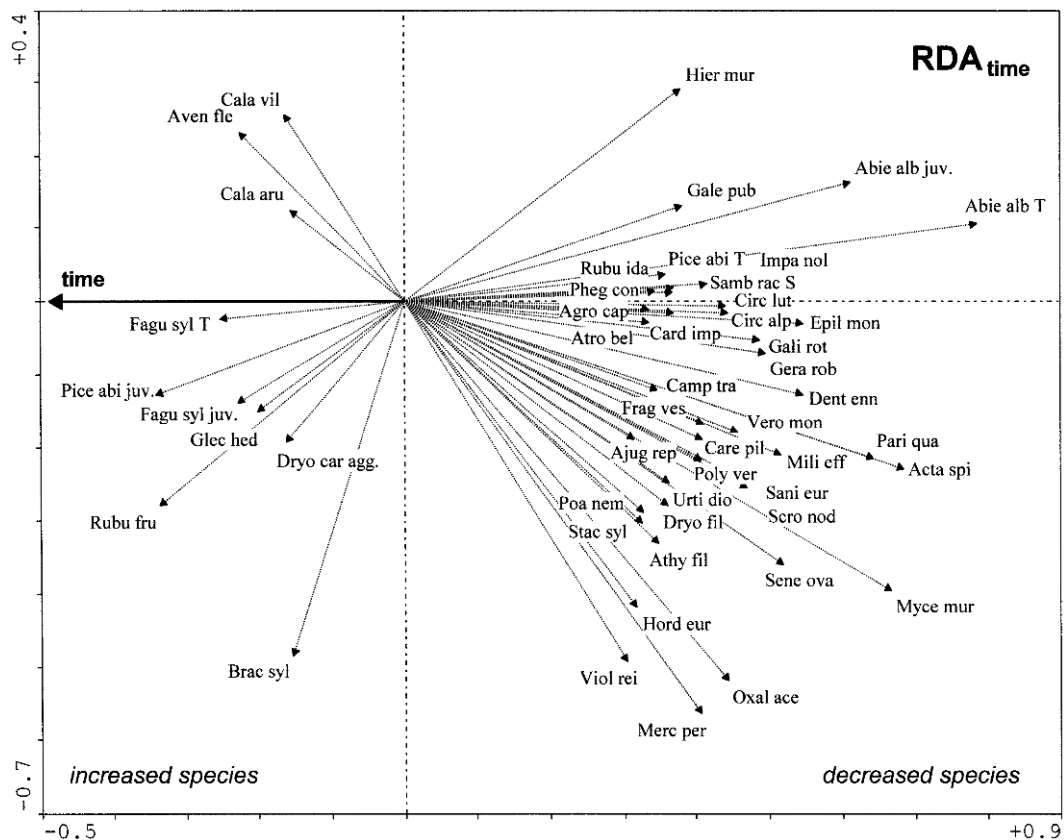


Figure 4. RDA<sub>time</sub> constrained with factor "time" (scaled by 0.5), reflecting the overall vegetation change. On the left side are increased, on the right side decreased species. Only the most correlated half of the species is pictured. For the full species names see Table 3

highly significant statistics. These indicator values have declined since the 1940's. Light L, temperature T and continentality K do not differ significantly. Value distribution can be seen in Figure 6. In all parameters, distribution has widened. When relating the species response to temporal change and species indicator values (Figure 7), course of the fit shall be observed. The trend is most obvious for R and N, indicating that almost all species with the lowest R and N values (2 and 3) have increased (negative y-axis values), while the species with greater indicator values (5 to 8) have decreased in general (positive y-axis values). In L the trend runs from a decrease of species with low L values to an increase of species with high L values. K tends to have higher values, T somewhat lower values. There is no clear trend in F which would contradict the results mentioned above.

#### Number of Species

Species richness in the old records is clearly greater than that in the new ones (Figure 8a). The average number of species is 35 and 19 (medians 37 and 18), respectively. Several old relevés contain from 40 to 50 species, while new relevés includes no more than 40 species. Several new relevés, but none of the old relevés, include less than 10 species. Species richness is the highest in 90–120 year old forests (Figure 8b), most frequently within the old relevés (Figure 8c); mostly 40–60 and 140–160 year old recent forests are somewhat species poorer.

#### Discussion

##### Resampling bias

The resampling of any records is a difficult task for the results can be easily biased. There are a number

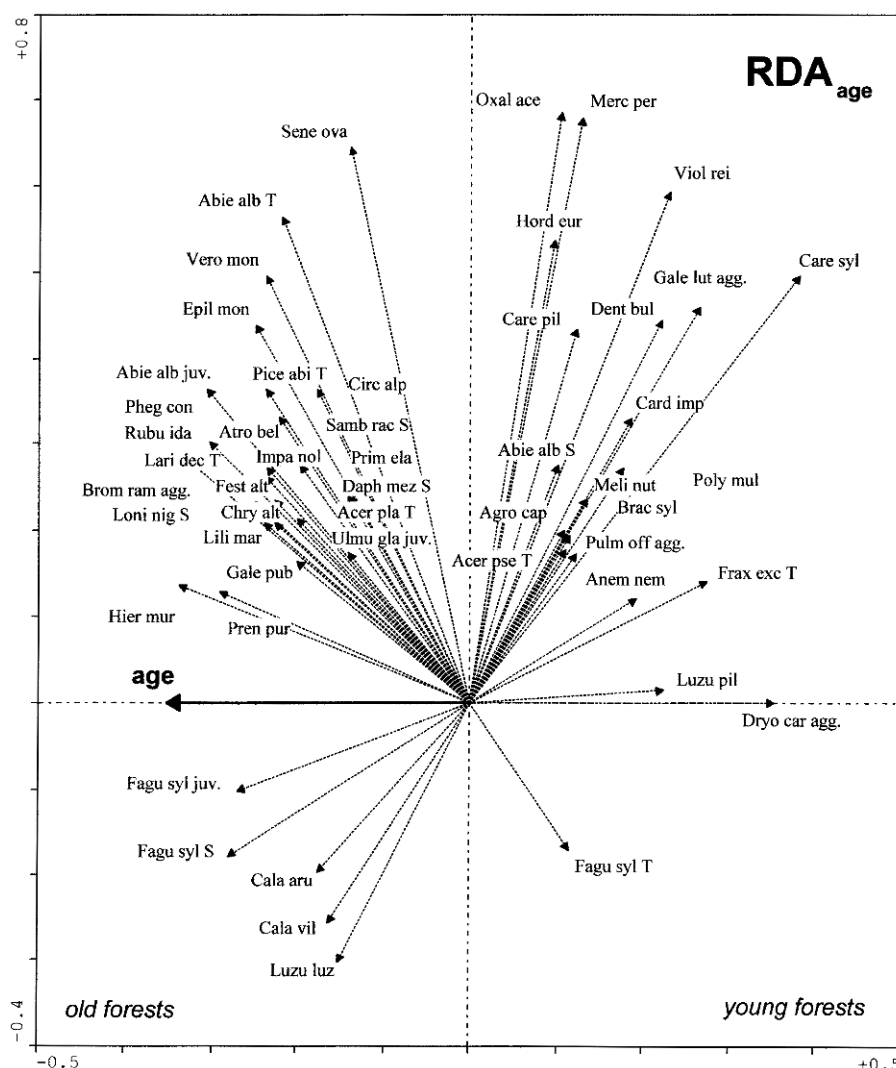


Figure 5.  $RDA_{age}$  constrained with factor "forest age" (scaled by 0,5), reflecting the pure influence of forest age. Increase of forest age runs from the right to the left. Only the most correlated half of the species is pictured. For the full species names see Table 3

Table 4. Linear regressions of species scores on first ordination axes from three RDA-analyses. Ordination axes are constrained with factors time ( $RDA_{time}$ ), age ( $RDA_{age}$ ), and time only for the oldest forests ( $RDA_{old}$ ). Regression outputs are B-coefficient (B-coef.), R-square (R-sq.), F-statistics (F-stat.) and its p-value

Regression	B-coef.	R-sq.	F-stat.	p-value
Time/age	-0,13	0,04	3,9	0,0509
Time/old	1,16	0,70	181,9	0,0000
Old/age	0,83	0,14	13,1	0,0005

of studies concerned with observation bias and with data analysis methods (e.g., Gotfryd and Hansell 1985; Nilsson and Nilsson 1985; Lepš and Hadincová

1992). The role of imprecise re-localization of reference records is seldom examined, as did Fischer and Stöcklin (1997). In the present study the most disputable fact is the distinctly higher species density of Hartmann's relevés. Possible reasons could be: (1) real depletion in species density since the 1940's due to the described environmental processes (2) larger size of the old relevés (3) selective sampling of the species-rich parts of the forest detachments.

It was shown that phytosociologists used to make larger relevés in the past (Chytrý 2001). If this is correct, the higher species number of the old relevés in Hartmann's case could be at least partly due to this. Species number per plot increases with the plot size,

Table 5. Differences in indicator values between old and new relevés. Mann-Whitney test is applied to all relevés containing five or more species with a given indicator value. Signed-rank test is computed for the most similar old / new relevé pairs (criterion is Euclidean distances), within the forest detachments. Highly significant statistics are printed in italics.

Parameter	Mann-Whitney test				Signed-rank test			
	Nr. old/new	U-stat.	Z-stat.	p-value	Pairs	stat. %	Z-stat.	p-value
L	22/54	580	0,15	0,88	21	28,6	1,75	0,081
T	22/49	530	1,36	0,17	21	38,1	0,87	0,383
K	22/54	517	- 0,89	0,37	21	57,1	0,44	0,663
F	22/52	350	2,63	<i>0,008</i>	21	42,9	0,44	0,663
R	22/53	308	3,20	<i>0,001</i>	21	23,8	2,18	<i>0,029</i>
N	22/52	384	2,22	<i>0,026</i>	21	33,3	1,31	0,190

which is a well-studied phenomenon (May 1975). Because the size of Hartmann's relevés was impossible to assess, the size of the new relevés were set in order to describe the current vegetation variability. If they were larger, the differences between relevés would probably be effaced within one forest detachment. If the high species density of the old relevés were caused by size alone, the relevés must have been extremely large, possibly many thousands of square meters.

It is also probable that Hartmann sampled the parts of the forest that were species rich since it can hardly be expected that there was no species-poor forest vegetation at that time. Nevertheless, none of the new relevés contain 40 to 50 species, as a great deal of old relevés do. Hence this explanation does not solve the problem itself.

When the records compared were reduced to relevés from forests untouched by a clear-cut (RDA<sub>old</sub>) or to the topographically closest relevé pairs (RDA<sub>loc</sub>), the results were very similar as when considering all new relevés. In addition, PCA separated old and new relevés into two distinct groups. Distances and scattering of the points reflect similarity between the relevés directly within the displayed ordination axes (Lepš and Šmilauer 1999). Probably uneven distribution of old and new relevés on the pattern of species density can either be problematic when relating species frequency changes *C* between both groups. However, a great number of species decreased by 70% or more which must be considered a real process, not only a methodological bias.

#### Changes in Vegetation Composition

Significant changes were found in vegetation species composition. The most notable trend is the decrease in the variety of species characteristic for Central Eu-

ropean deciduous forests (compare Ellenberg 1996; Moravec et al. 2000). They mostly demand an approximate neutral soil reaction and a good supply of nutrients such as *Pulmonaria officinalis* agg., *Veronica montana*, *Galeopsis pubescens*, *Paris quadrifolia*, *Asarum europaeum*, *Impatiens noli-tangere*, *Stachys sylvatica*, *Dentaria bulbifera*, *Galeobdolon luteum* agg. or *Gymnocarpium dryopteris*. Some of them tolerate more acidic conditions, such as *Epilobium montanum*, *Phegopteris connectilis*, *Polygonatum verticillatum*, *Mycelis muralis*, *Moe-hringia trinervia* or *Galium rotundifolium*. Soil acidity plays a key role in species distribution in temperate forests as demonstrated by Falkengren-Grerup and Tyler (1993); Falkengren-Grerup et al. (1995b); Falkengren-Grerup et al. (1995c). Cations content is closely linked with soil reaction, in particular at the margins of the acidity gradient. The anticipated increase of nitrophilous species did not occur, which contradicts many studies (review by Bobbink et al. 1998). There was no increase found in thermophilous species (as reported e.g. by Walther 2002). A small group of increased species is mostly made up of light-demanding, acid-tolerant species. Let's look closer at some species and species groups now.

*Dentaria enneaphyllos* is a species characteristic for Czech beech forests (Moravec et al. 1982; Moravec et al. 2000). *D. enneaphyllos* was present in 40% of the old relevés, presently it has become extremely rare. As a vernal geophyte, it is sensitive to modification in logging practices (Meier et al. 1995). Mapping of its populations within the entire study area shows that *D. enneaphyllos* occurs of late merely in leeward valleys and lower parts of the slopes (not published). These sites are obviously rich in nutrients transported from the slopes above. Most of the popu-

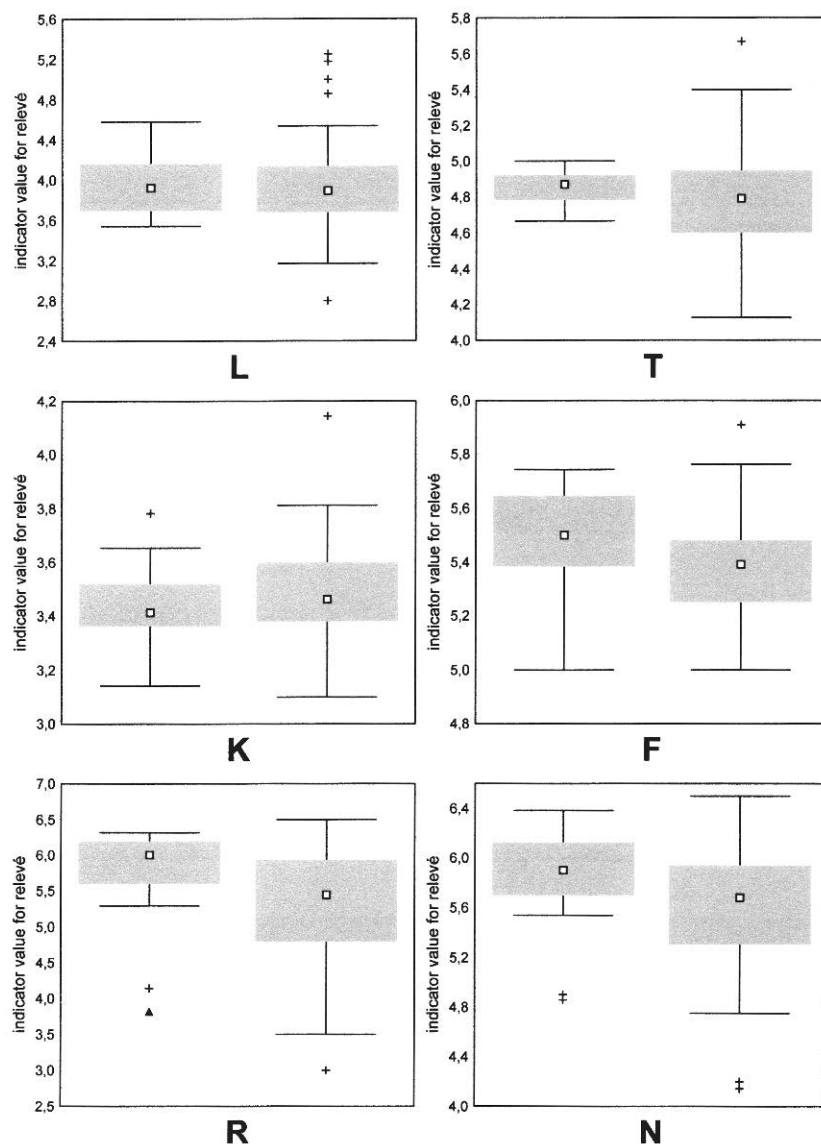


Figure 6. Distribution of indicator values for relevés considering six Ellenberg indicator parameters. Left-side boxplots represent old relevés, right-side boxplots new relevés. Major differences show soil moisture F, soil calcium R, and site productivity N. Distributions are broader in new relevés. Open squares indicate median, grey boxes interquartile range, whiskers non-outlier range (coefficient 1). Outliers are denoted with crosses, an extreme (at R) with triangle (coefficient 1,5)

lations are restricted to calcareous substrate, which is rare in the Rychlebské Mountains.

*Bromus benekenii*, *Hordelymus europaeus*, *Milium effusum*, and *Festuca altissima* are grasses typical for beech-dominated forests. In the Czech Republic (Moravec et al. 1982), *Bromus* occurs frequently in mesophilic deciduous forests (order *Fagetalia*), being diagnostic for lime-beech forests (*Tilio cordatae-Fagetum*). *Milium* behaves similarly, appearing most

frequently in herb-rich beech forests (sub-alliance *Eu-Fagenion*). *Hordelymus* is a diagnostic species for alliance of mesotrophic beech-dominated forests *Fagion* (contra acidic *Luzulo-Fagion*). *Festuca* defines association *Festuco-Fagetum* which is on the transition to acidic beech forests (Ellenberg 1996: 198–199). *Bromus*' and *Milium*'s frequencies were lowered by 70 to 80%, *Hordelymus* by 40%. Brunet and Neymark (1992) and Falkengren-Grerup et al. (1995a)

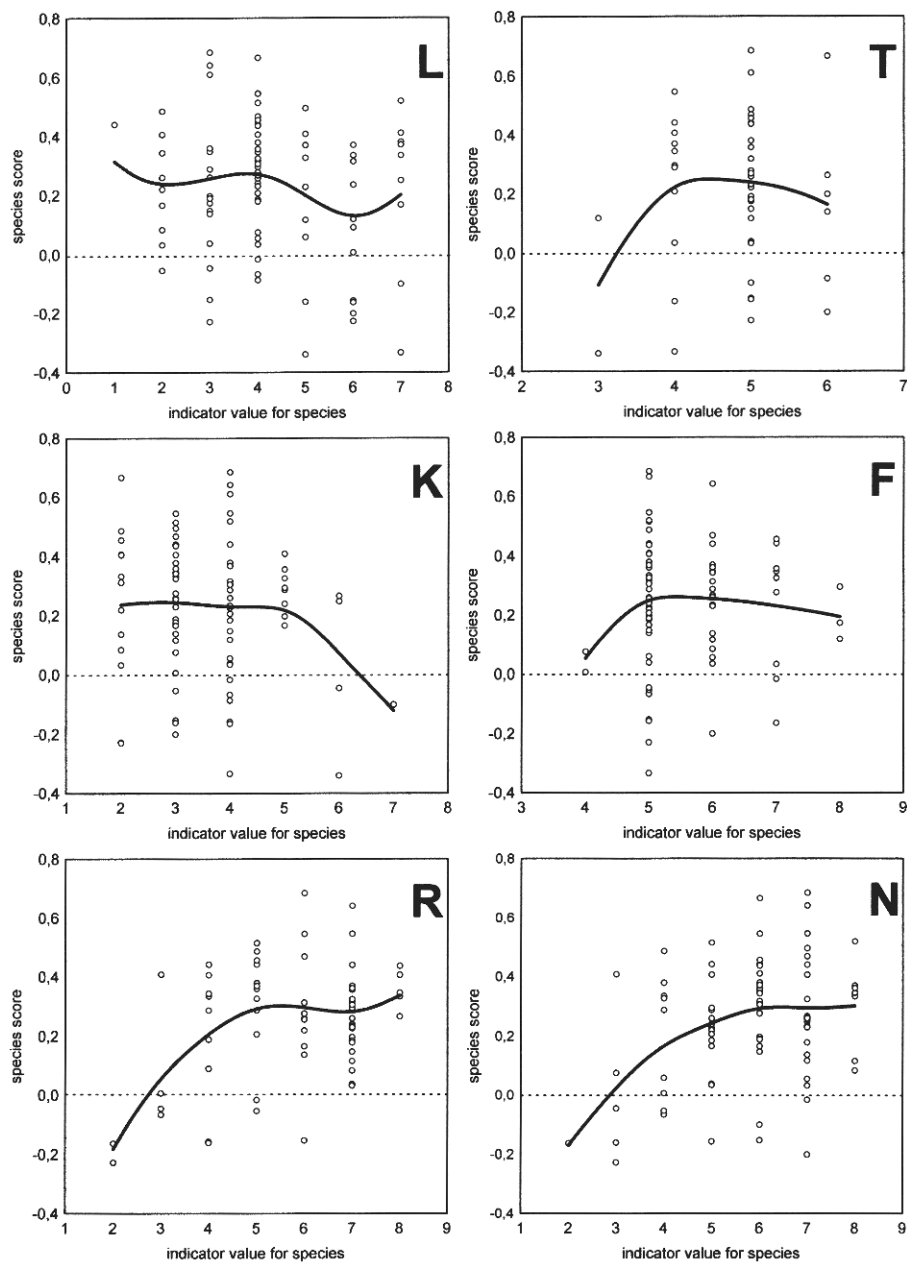


Figure 7. Relationship between indicator values for species and species scores on first ordination axis from  $RDA_{time}$ , considering six Ellenberg indicator parameters. Decreased species obtained a positive score, increased species a negative score. A distance-weighted least squares fit, stiffness 0,3, shows the trend. It is the most apparent in soil calcium R and site productivity N

have proven how sensitive they are to acidification in southern Swedish beech forests. *Festuca*, the most acid-tolerant, is still common and decreased only by 15%.

*Mycelis muralis*, *Rubus idaeus*, *Poa nemoralis*, *Stellaria nemorum* and *Urtica dioica* are reported to have increased in European nitrogen polluted forests

(Bobbink et al. 1998). *Urtica*, in particular, is a species requiring high levels of nutrients, although it tolerates a wide pH-range. It is characteristic for nitrogen rich sites (Šrútek and Teckelmann 1998). However, all of these species have retreated significantly from the study sites. *Urtica dioica* character-

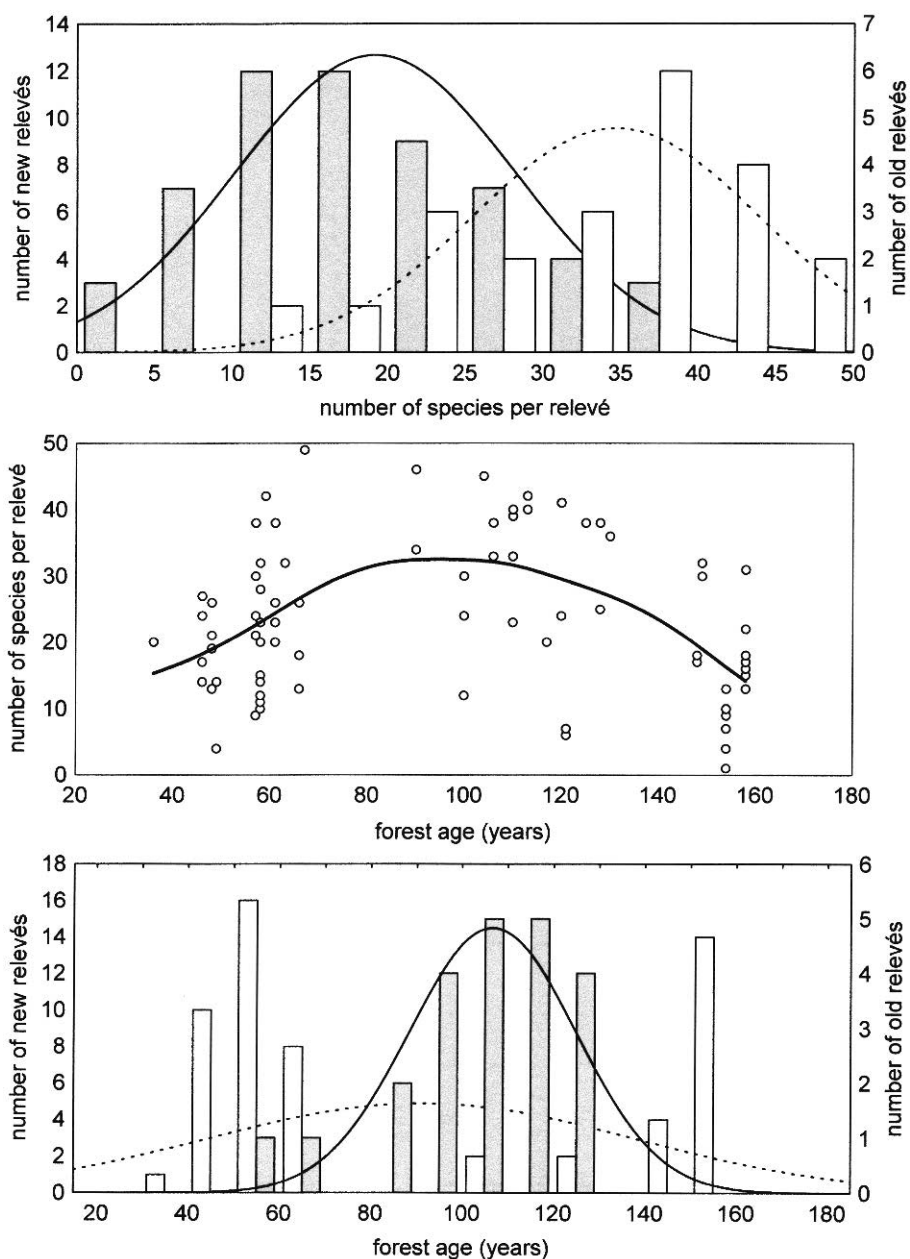


Figure 8. a) (upper diagram) Distribution of the number of species in old (grey bars) and new (white bars) relevés. Normal distribution curves are fitted. b) (centre) Species number in relevé and forest age. Distance-weighted least squares fit shows the relationship. c) (below) Distribution of forest ages in old (grey bars) and new (white bars) relevés, with normal distribution curves

izes foothills in the Rychlebské Mountains as of late, areas with an accumulation of nutrients.

The previous method of forestry management, smaller clearings and horse logging, was replaced with extensive cut-offs and the use of heavy machinery. The direct effect of forest management is a decline of species number in the tree layer. Of the most

common species, this concerns not only *Abies alba*, which was affected most, but also *Ulmus glabra* T, *Acer platanoides* T, *Larix decidua* T, *Picea abies* T and *Fraxinus excelsior* T. On the other hand, *Fagus sylvatica* may have relatively expanded in all layers.

Changes in logging practices have, most probably, resulted in changes in soil properties, such as loss of

humus and drying, and caused generally lighter conditions on the forest floor. Currently drier conditions are reflected in the decrease of the hygrophilous species *Circaea alpina*, *C. lutetiana*, *Cardamine impatiens*, *Chrysosplenium alternifolium*, *Chaerophyllum hirsutum*, *Festuca gigantea*, *Carex sylvatica*, *Petasites albus* as well as others. The decrease of several shade-demanding forest species such as *Mercurialis perennis* and *Oxalis acetosella* could indicate an opening of the canopy. On the other hand, light-demanding *Senecio ovatus* and *Rubus idaeus* showed a decrease as well, although they prefer forest clearings and even expand extensively on vast deforested areas (personal observation). This can be explained by their relatively high nutrient requirements, which have begun deficient in soils. *Atropa bella-donna* is a species demanding half-shady sites with nutrient-rich and moist soils (Slavík 2000), often preferring smaller clearings with a release of nutrients in the early phases of forest succession. Such habitats are rare now; *Atropa* has therefore currently become restricted to a few places.

A conspicuous increase of *Rubus fruticosus* agg., now abundantly occupying 2/3 of the plots, contrasts with the decline of *R. idaeus*. Abundance of both species depends on light conditions (Janík 1997). Their biomass is very low in shady, non-managed forests. Consecutively the clear-cut, biomass grows rapidly (Ellenberg's L is 7 for both). While *R. idaeus* became an expander in deforested sites, *R. fruticosus* agg. expanded in forest sites with favorable conditions.

Other species that have shown an increase are mainly grasses, either demanding light conditions (*Brachypodium sylvaticum*, *Calamagrostis arundinacea*, *C. epigejos*), tolerating much lower soil reaction and fewer nutrients than the other species (*Avenella flexuosa*, *Luzula luzuloides*), or the combination of both (*Calamagrostis villosa* in particular). *Calamagrostis villosa* and *C. arundinacea* are successful expanders in deforested areas (e.g., Pyšek 1993), successfully absorbing nitrogen, Ca, and Mg from the substrate (Fiala et al. 2001).

#### *Environmental Processes*

A decline in F, R and N and an increase in L were detected. Changes of L (understorey light) and F (soil moisture) can be interpreted relatively easily as opening of the canopy and substrate drying. The most probable reason is changes in forestry management

although the lowered soil moisture could also be related to worsened humus properties. Slightly decreased T values show a tendency toward colder conditions which can be attributed to an intrinsic ecosystem process.

Changes in R and N are, on the contrary, difficult to interpret. As proven by van Dobben et al. (1999), N increases when nitrogen increases, R increases with liming, both decrease with acidifying almost linearly. However, as found by Hill and Carey (1997) and Schaffers and Sýkora (2000), N values correlate poorly with soil nitrogen (with nitrogen mineralisation in particular, with nitrogen content in biomass somewhat better). Correlation of R with soil pH is not clear, but a strong relation was proven for total calcium (exchangeable and in carbonates) in the acidic to neutral pH-range. Thus, a decrease in R probably reflects a decrease in soil calcium content. This is probably closely linked with the content of other cations. A decrease in N reflects a decline in ecosystem's productivity.

Both parameters seem to be interrelated. Soil productivity was most likely decreased by the loss of cations, although humus deterioration due to changed logging methods played an important role at many sites. Substantially high airborne nitrogen deposits may not, therefore, improve productivity. Nitrogen amelioration can even have a negative effect regarding tree growth. Because calcium and magnesium were mostly leached from the soil organic-mineral complexes, tree growth enhanced by nitrogen is not supported with other necessary nutrients (Schulze 1989; Katzensteiner et al. 1992). In Scandinavian forests, not affected as much by acidification as Central Europe, such nitrogen fertilization really does increase tree productivity (Binkley and Högberg 1997).

An alternative explanation might be acidification in the course of forest succession (Lichter 1998; Sogn et al. 1999; but see Yanai et al. 2000). This explanation is not completely valuable for the forests studied because influence of the forest age does not correlate with the overall changes. However, forests let to age since the 1940's (included in RDA<sub>old</sub>) follow the observed trends in vegetation and environment most strongly. There are only five such forests, while there are 11 recorded to have been clear-cut soon after the 1940's, now in the early to mid-succession phases. Besides this, tree dominants influence the soil chemistry substantially (e.g., Nihlgård 1971; Augusto et al. 1998). Although beech (*Fagus sylvatica*) has slowly

prevailed over other species, this change should not affect soil properties significantly.

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