Long-term impacts of nitrogen and sulphur deposition on forest floor vegetation in the Northern limestone Alps, Austria

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Abstract

Question: Are there effects of long-term deposition of airborne nitrogen and sulphur on the forest floor vegetation from permanent plots collected in 1993 compared to 2005.
Location: Northern limestone Alps in Austria.
Methods: Single species responses were analysed by correlating trends in cover-abundance values, as derived from marginal models, with Ellenberg indicator values. Changes in the species composition of plots were analysed by correlating changes in mean Ellenberg indicator values with the displacement of plots within a multidimensional scaling ordination.
Results: Trends in single species abundance were positively correlated with indicator values of soil pH but were independent of nutrient availability. A general trend towards the homogenisation of vegetation, due to convergent time vectors of the relevés, became obvious. Oligotrophic sites previously situated at the distal ends of ordination axes shifted towards the centre since they were enriched by species preferring mesotrophic conditions. The bulk of plots with intermediate site conditions hardly showed any trends. A concomitant analysis demonstrated that temporal changes in species composition exceed the variation in cover abundance estimates among different field botanists.
Conclusions: N deposition can lead to a homogenisation of forest floor vegetation. Larger limestone areas with diverse soil conditions, such as the Northern limestone Alps in Austria, as a whole are thus negatively affected by airborne N deposition. Nevertheless, the vegetation was at least as strongly affected by an increase of basiphilous species as a result of decreasing S deposition.

Keywords: Acidification; Atmospheric pollution; Eutrophication; Integrated monitoring; LTER-Austria; Multidimensional scaling; Observer error; Soil.

Nomenclature: Adler et al. (1994).

Abbreviations: L = Light value; LTER = Long-term Ecosystem Research Network; M = Moisture Value; nMDS = non-metric Multidimensional Scaling; R = pH value; UN-ECE = United Nations Economic Commission for Europe.

Introduction

Nitrogen (N) and sulphur (S) emissions have increased dramatically during the second half of the 20th century causing excess deposition of N and S on ecosystems (Bouwman et al. 2002; Erisman et al. 2002; Galloway et al. 2004). Nitrogen enrichment has a wide array of detrimental effects on natural and semi-natural ecosystems, including the disruption of the nutrient balance in soils, increased susceptibility to parasite attacks (particularly in forests), increased emissions of nitrogenous greenhouse gases from the soil and elevated nitrate loss to the groundwater (Fenn et al. 1998; Flückiger & Braun 1998; Erisman & de Vries 2000). Significant changes of plant species composition in response to chronic N deposition were particularly found where N is a limiting macronutrient (Diekmann & Dupré 1997; Bobbink et al.1998, 2003). N excess is therefore seen as a major threat to biodiversity, particularly as N emissions are projected to increase globally (Bouwman et al. 2002; Anon. 2005; Suding et al. 2005; Gilliam 2006; Phoenix et al. 2006) or remain high in Europe (Alcamo et al. 2002) for the coming decades. Increased S deposition causing soil acidification, changes in the base saturation and the cation exchange capacity was recognised to be a major environmental problem in the 1970s (Bouwman et al. 2002). Sulphur dioxide is phytotoxic and sulphuric, together with nitrous, acids cause soil acidification; which leads to the depletion of base cations and can cause a leaching of heavy metals from the soil into freshwater ecosystems (Bouwman et al. 2002; Legge & Krupa 2002). Unlike N emissions, S emissions were successfully abated in Europe through internationally ratified protocols (UN-ECE/CLRTAP – United Nations Economic Commission for Europe/ Convention on long range transboundary air pollution) and related measures. Sulphur emmissions have been

decreasing continuously over the last 25 years (Anon. 2006a; Rogora et al. 2006). Nevertheless, it is largely unknown to what extent ecosystems are able to recover (Beier et al. 2003).

The magnitude and the nature of changes of forest floor vegetation due to eutrophication and acidification depend strongly on soil characteristics such as the pH-value, nutrient status and water availability (see Bobbink et al. 2003 for a review on eutrophication; Wittig et al. 1985; Thimonier et al. 1994; Falkengren-Grerup & Diekmann 2003; Mellert et al. 2005; Nordin et al. 2005; Tamis et al. 2005; Clark et al. 2007). The forest floor vegetation showed only a weak or even no response to high N and S input at sites with high buffer capacity against acidifying substances (Zukrigl et al. 1993), as well as on nitrogen rich sites (Kellner & Redbo-Torstenson 1995; Diekmann & Dupré 1997; Falkengren-Grerup & Diekmann 2003; Hédl 2004; Grandin 2004). Forest floor vegetation of limestone areas should, thus, be less at risk to airborne N and S pollution (Clark et al. 2007). However, limestone areas are commonly characterised by a variety of soils (Zukrigl et al. 1963; Ellenberg 1986) which presumably differ in their response to eutrophication and acidification. Since only a handfull of studies focus on limestone ecosystems (Wittig & Neite 1985; Thimonier et al. 1994; Hofmeister et al. 2002), knowledge on the effects of N and S deposition is scarce.

As in many low-cost long-term monitoring schemes plant cover was estimated by simple visual observation. This procedure is known to be subjective (Lepš & Hadincová 1992) with comparably low reproducibility (Klimeš 2003). Misidentification (Scott & Hallam 2002), and failure in detecting the full set of species (Kirkby et al. 1986) respectively, and variation in the assessment of cover values (Kercher et al. 2003) contribute to potentially high 'measurement' errors (observer error, see Karrer 1991). Hence, a concomitant analysis of observer errors was performed to prove whether temporal changes in species composition exceed the variation introduced into the dataset by different field botanists.

In this study, we used observational data from the Austrian Integrated Monitoring (UN-ECE/ICP – International Co-operative Programme Integrated Monitoring) site 'Zöbelboden' to analyse changes in forest floor vegetation in context with trends in N and S deposition during the last 14 years. In particular, we ask (1) if nitrophilous species generally increased and acidophilous species decreased owing to eutrophication and recovery from acidification, (2) if the species composition of individual forest-floor plots changed in a way attributable to airborne N and/or S deposition when accounting for observer errors and (3) if trends in species composition varied with respect to the different soil types of the study area.

Methods

Study area

The Austrian ecosystem monitoring site 'Zöbelboden' (http://www.umweltbundesamt.at/im) was established in 1992 as part of the UNECE International Co-operative Program 'Integrated Monitoring of Air Pollution Effects on Ecosystems' (ICP-IM). The site is also part of the Austrian Long-term Ecosystem Research Network (LTER-Austria). It covers an area of ca. 90 ha and is situated in the northern part of the 'Northern limestone Alps' national park (47°50'30" N, 14°26'30" E) ranging from 550 m to 956 m a.s.l.. The mean annual temperature is 6.7 °C (measured at 900 m a.s.l.). The coldest month at 900 m a.s.l. is January (– 0.9°C) and the warmest is August (15.5 °C). Annual rainfall ranges from 1500 mm to 1800 mm. Monthly precipitation ranges from 100 mm (October) to 230 mm (July). Snow falls between October and May with a mean duration of snow cover of ca. four months, although this is very variable. Temperature and precipitation did not show any major trends between 1992 and 2005.

The main type of bedrock is Norian dolomite (Hauptdolomit) which is partly overlain by limestone (Plattenkalk). The catchment area is divided into a very steep (30°–70°) mainly north to west facing slope at altitudes from 550 m to 850 m a.s.l. and a virtually flat plateau (850 m - 956 m a.s.l.) constituting the top of the mountain.

Throughfall N deposition for two intensively measured plots is 14.8 ± 2.4 kg.ha^{-1}.a^{-1} (mixed *Fagus-Picea-Acer-Fraxinus* forest) and 20.9 ± 2.6 kg.ha^{-1}.a^{-1} (*Picea* dominated forest). When fog, cloud and dry deposition are taken into account, N deposition increases to 28 kg.ha^{-1}.a^{-1} and 43 kg.ha^{-1}.a^{-1}, respectively, depending on forest type (Dirnböck et al. 2007). This is twice the critical load for deteriorating eutrophication effects for temperate deciduous forests (Bobbink et al. 2003) and exceeds by far the estimated background N deposition of 5-10 kg.ha^{-1}.a^{-1} in Europe in the 1950s (Erisman & de Vries 2000). N deposition showed no substantial changes during the years of observation (Dirnböck et al. 2007; Fig. 1). Throughfall SO_4-S deposition was 4.0 ± 1.5 kg.ha^{-1}.a^{-1} (mixed beech-maple-ash-spruce forest) and 7.1 ± 2.0 kg.ha^{-1}.a^{-1} (spruce dominated forest). Taking fog, cloud, and dry deposition into account annual S deposition increases to 10 and 18 kg.ha^{-1}.a^{-1} (Dirnböck et al. 2007) respectively. S deposition decreased from the first measurement in 1996 to 2004 (Fig. 1).

On the slope, Lithic and Rendzic Leptosols (rendsina) predominate. The plateau is characterised by relict loams, forming Dystric Planosols (pseudogley) and at intermediate positions Chromic Cambisols (brown

Fig. 1. Throughfall deposition of N_{tot} and SO_4-S, respectively, in two contrasting forest types of the study area from 1995 to 2004. Intensive plot I: *Picea* dominated forest of the plateau; Intensive plot II: mixed *Fagus-Picea-Acer-Fraxinus* forest typical for the slope area.
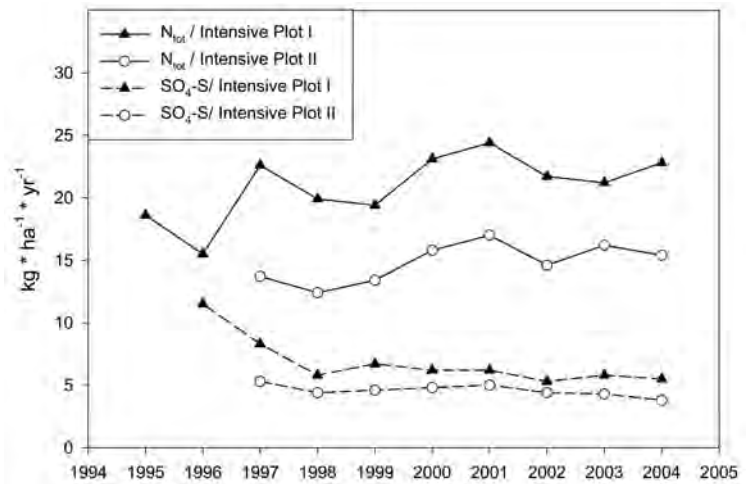
earth) occur. In some rare locations at the plateau Gleyic Planosols (stagnogley) can be found. Humus forms vary considerably, therefore mull, moder and mor occur on all soil types.

Major parts of the study area are covered with soils comparatively rich in N and exhibiting high buffer capacity against acidifying substances (Table 1). Between 1993 and 2005 soil chemical characteristics exhibited temporal changes which can be attributed to the deposition effects of N and S (see Dirnböck et al. 2007 for details). The pH value increased for Leptosols (from 5.3 to 6.0 for the humus layer and from 6.6 to 6.9 for the mineral soil between 0 cm -10 cm), remained stable for Cambisols (5.1 in both years for the humus layer, 6.2 and 6.4 for the mineral soil between 0 cm -10 cm) and

decreased for Planosols (from 4.8 to 4.5 for the humus layer and from 5.3 to 4.9 for the mineral soil between 0 cm -10 cm). The C:N ratio in the humus layer of all soil types narrowed (mean -4.2), indicating enhanced N availability for plants.

The slope is mainly covered by a forest dominated by *Fagus sylvatica* accompanied by *Picea abies*, *Acer pseudoplatanus* and *Fraxinus excelsior* (*Adenostylo glabrae-Fagetum* sensu Willner 2002), whereas *Picea abies* predominates on the plateau owing to plantation after a clear cut around 1910. The potential natural vegetation of the plateau is a mixed *Fagus-Abies-Picea*-forest (*Cardamino trifoliae-Fagetum sensu* Willner 2002). In the decade before the start of the project smaller clear cut areas were set up mainly on the plateau. Since

Table 1. Chemical soil characteristics of the three main soil types (mean and standard deviation; data from 2004; for more details see Dirnböck et al. 2007).

Austrian soil units*	Fels-Auflagehumusboden, Rendzina			Kalkbraunlehm			Typical Pseudogley, Hangpseudogley, Stagnogley		
WRB soil units * mineral soil depth	Lithic and Rendzic Leptosols 13±10			Chromic Cambisols 25±13			Dystric, Haplic or Gleyic Planosols 44±27		
	humus	mineral soil		humus	mineral soil		humus	mineral soil	
		0-5 cm	5-10 cm		0-5 cm	5-10 cm		0-5 cm	5-10 cm
Number of samples	32	32	20	23	23	22	14	14	14
pH (CaCl$_2$)	6.0±0.4	6.8±0.2	7.0±0.2	5.1±0.7	6.3±0.8	6.6±0.7	4.6±0.7	5.1±1.0	5.4±1.1
Total N [%]	1.2±0.3	0.8±0.2	0.7±0.2	1.2±0.3	0.7±0.2	0.5±0.2	1±0.1	0.4±0.1	0.3±0.1
Organic C [%]	33.7±9.6	14.3±4.4	10.5±3.0	35.2±9.1	11.2±2.6	8.2±2.5	30.6±5	6.7±2.4	4.4±2.2
S [mg.kg^{-1}]	1218.9±215.2	1100.1±225.9	933.5±203.9	1155±271.9	850.4±264.0	652.8±241.3	1002.4±157.1	458.7±206.5	318.1±184.5
P [mg.kg^{-1}]	588.3±155.1	749±202.7	720.3±217.8	645.2±125.7	773.8±247.9	659.3±205.7	574.1±108	477.6±206.4	385.7±196.2
Ca [mmol.kg^{-1}]	542.5±116.1	533.9±104.4	432.2±107.0	421.2±99.8	428.4±124.4	361.4±114.9	297.6±113.6	205.5±141.0	172.4±130.0
Mg [mmol.kg^{-1}]	193.8±40.1	182.7±42.9	156.2±44.5	148.3±48.0	165.9±47.2	144.2±44.8	101.4±45.4	89±56.5	75.4±53.3
Na [mmol.kg^{-1}]	0.5±0.3	0.6±0.4	0.7±0.5	0.8±0.4	0.6±0.4	0.7±0.4	0.6±0.1	0.6±0.3	0.5±0.2
K [mmol.kg^{-1}]	14.6±7.3	3.5±1.6	1.9±0.7	13.2±5.1	2.5±0.7	1.7±0.6	16.5±11.4	2.4±0.8	1.6±0.7
Al [mmol.kg^{-1}]	0.3±0.1	0.1	0.1	0.8±1.3	2.0±5.4	1.3±3.7	6.4±16.8	14.7±26.7	11.7±22.3
Fe [mmol.kg^{-1}]	0.1	-	-	0.1±0.1	0.1±0.1	-	0.5±1.1	0.3±0.6	0.1±0.2
Mn [mmol.kg^{-1}]	1.8±1.9	0.5±0.4	0.3±0.0	5.5±2.9	1.9±1.7	1.2±1.4	9.5±3.7	3.5±2.4	2.1±1.8

* Nomenclature according to Nestroy et al. (2000); WRB – World Reference Base for Soil Resources (http://www.fao.org/ag/Agl/agll/wrb/doc/wrb2006final.pdf).

the start of the project in 1992, forest management has been restricted to single tree harvesting in cases of bark beetle infestation.

Permanent plots

Throughout the whole study area, rectangular 10 m × 10 m permanent plots were positioned in a regular 100 m grid. For the present study we only used plots with at least 30% coverage of trees higher than 15 m in both years of observation. In total, 124 plots were marked using metal poles at each corner and surveyed in the year 1993. These plots were revisited in 2005 during the same season (July and August) to assure comparable phenology and coverage of plants (Karrer 1991). A tape measure, fixed at the metal poles, was used to delineate the plots. All plant species present on the plot were recorded and their cover-abundance values estimated on a seven-level ordinal scale (Braun-Blanquet 1964). To reduce erroneous identification of taxonomically difficult species, individuals belonging to *Senecio nemorensis* agg. and *Dryopteris carthusiana* agg. were pooled in the analyses.

Recordings in the two years of observation were carried out by different field botanists. In order to estimate the error in recording cover-abundance values of plant species introduced by different observers, 14 permanent plots were selected randomly. In 2005, these plots were recorded six times by independent observer teams applying the same method as for all other permanent plots.

For each permanent plot the soil type was determined according to Nestroy et al. (2000) and grouped into three soil classes (Leptosols, Cambisols, Planosols) referred to as soil type hereafter. This was either done during soil sampling (7 cm diameter soil cores) 5 m outside the plots (65 plots totally) or by using soil corer (2 cm diameter) directly at the plot (all remaining plots).

Statistical analyses

Changes of forest undergrowth on permanent plots between 1993 and 2005 were evaluated using a single species and a species composition approach. Woody plants were considered only up to a height of 0.6 m. For all statistical analyses we used R 2.2.1 (Anon. 2004).

Single species change

To quantify changes in cover-abundance estimates (Y) of a species across all permanent plots we used marginal models for square contingency tables (Thompson 2004), a statistical framework that accounts for the fact that the two consecutive observations of a species at the same plot form a matched pair. For each species occurring

at least five times in one year of observation, a contingency table of the ordered cover-abundance categories for the two years was calculated (estimates from 1993 were used as columns, estimates from 2005 as rows). The absence of a species was considered as the lowest cover-abundance category. The cells c_{ij} of this table contained the number of plots where the cover-abundance value (Y) of the respective species was estimated to fall into category i in 1993 and into category j in 2005.

Marginal homogeneity occurs when the probability (P) of a species to be estimated in category j in 1993 is equal to the probability to be estimated in the same category in 2005, or $P(Y_{1993} = j) = P(Y_{2005} = j)$. Marginal models compare these probabilities and test for significant deviations from marginal homogeneity, i. e. they provide a test whether the joint probabilities above the diagonal of the contingency table equal those below (symmetry of the table; Thompson 2004). This is done using a likelihood ratio test for the parameter ß of the following model describing the cumulative logits of the ordinal cover-abundance values:

$$\text{Logit}\left[P\left(Y_t \le j\right)\right] = \alpha_j + \beta x_t, \quad t = 1993, 2005; \quad j = 1, \ldots J-1 \quad (1)$$

where x_{1993} 0 and $x_{2005} = 1$. The appropriateness of this model as a definition of the data-generating process was tested with the G^2-statistic (Agresti 2002). The proportional odds structure of this model provides an own intercept α – increasing with j – for every logit, but a common effect β. The odds of outcome $Y_{2005} \le j$ equal e^β-times the odds of outcome $Y_{1993} \le j$. Hence, β is a quantitative measure of the general trend of a species' cover-abundance between 1993 and 2005. $\beta = 0$ refers to marginal homogeneity (= no change), $\beta < 0$ to decreasing, and $\beta > 0$ to increasing cover-abundance over time.

The model was fitted with the MPH.fit function for Multinomial-Poisson homogeneous models (Lang 2002), which gives consistent estimates of regression coefficients regardless of the form of the joint distribution, because marginal and joint parameters are orthogonal.

To facilitate a causal interpretation of cover-abundance trends we used Ellenberg's indicator values for nitrogen (N), soil pH (R), light (L) and moisture (M) (Ellenberg et al. 1992). Ellenberg values indicate the highest probability of occurrence or abundance of species along environmental gradients. Correlation between the parameter β of the marginal models and Ellenberg species values thus allows for testing significant increases or decreases of indicator species groups. We used the Kendall's τ with exact p-value. This analysis was restricted to species with logit-models having G^2-indices with an associated p-value > 0.05, indicating a reasonable fit of the defined logit-model to the data.

Change of the species composition

Changes in species composition between the observations in 1993 and 2005 were evaluated using non-metric multidimensional scaling (nMDS). nMDS is commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin 1987). This ordination procedure reduces a multidimensional space, represented by a dissimilarity matrix comprising pairwise distances between plots, to a configuration with an *a priori* defined number of dimensions (nMDS-space). To minimise the loss of information, nMDS iteratively searches for the best position of plots in the nMDS-space. The quality of this transformation is indicated by the 'stress', which is defined as the square root of the ratio of the sum of squared differences between the input distances and those of the configuration to the sum of squared configuration distances. nMDS, as other iterative algorithms, is susceptible to stick in local minima. To reach the global minimum (i.e the configuration with the lowest stress) calculations were repeated 60 times with random starting arrangements of plots. The model with the lowest stress was chosen as the final configuration. To relax the drawback of indeterminable orientation and scaling of axes, ordination results were post-processed. The configuration was rotated to maximise the variance of points on the first axis using a Principle Component Analysis (PCA). The configuration was centred to the averaged scores of the axes. Additionally, axes were rescaled in a way that one unit represents a halving of community similarity from replicate similarity (Oksanen 2005).

The dissimilarity matrix applied in the nMDS ordination was constructed using Bray-Curtis distances. Vegetation data from both years of observation were included in that matrix. A three dimensional nMDS-space was chosen.

The nMDS was further used to analyse time trends as follows: for each plot, scores of the nMDS-axes derived from its species composition in 1993, were subtracted from the axes scores of the same plot, derived from its species compostion in 2005 resulting in vectors (each with three elements) of distances between each paired plot in the three-dimensional nMDS-space. Overall changes in species composition in time were analysed by using these distance vectors as response in a MANOVA without a grouping variable. A significant deviation of the intercept from zero indicates an overall shift in species composition from 1993 to 2005. For the MANOVA, the Pillai-Bartlett test statistic was applied.

To further investigate the main structure of the nMDS we tested whether plots close to the centre of the first nMDS-axis show less change than plots at the extreme ends. This was done with linear regression between the first elements of the vectors described above and the absolute value of the scores of the first nMDS-axis.

As for single species, inferential evidence for causes of time trends of the species composition were inferred using Ellenberg indicator values. Unweighted mean Ellenberg N, R, L and M indicator values were calculated for each plot. Means derived from observations in 1993 were subtracted from those of 2005. Absolute values of the resulting differences for each Ellenberg indicator were correlated with the absolute values of changes of scores of the first nMDS-axis using Pearson's product moment correlation.

Observer error

To be able to identify the contribution of observer error to the observed temporal shift in species composition, nMDS was applied with the same specifications as for the permanent plot analysis. Data from the observer plots recorded by the six independent teams in the year 2005 together with the corresponding observations of these plots in 1993 were used. The Euclidean distance in the three-dimensional nMDS-space was calculated between the observation in 1993 and the centroid of the six observations in 2005 for each observer plot. Additionally, the mean of all pairwise distances between observations on each observer plot in 2005 were computed. Differences between the temporal shift and the mean distances of observer plots in 2005 were tested for significance using a paired two-sided *t*-test.

Results

Changes of forest floor vegetation

Single species change

For 109 out of 136 species analysed with marginal models, an appropriate fit of the models was reached (see App. 1). Cover-abundance values of 75 species remained unchanged, 21 species significantly decreased in cover-abundance and 13 increased. The mean β of all species was 0.12, indicating a slight increase in cover-abundance of understory vegetation. A significantly positive correlation between the changes of cover abundance estimates of species from 1993 to 2005 (parameter β of the marginal models) with the soil pH (indicated by the Ellenberg R-value) was discovered, whereas no correlation was found for light, moisture or nitrogen (L, M or N-value; Table 2).
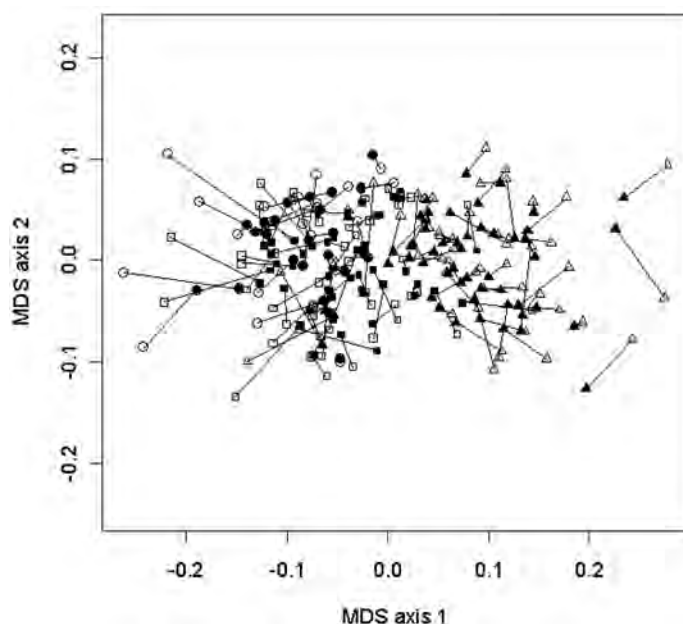
Fig. 2. Changes in species composition on 124 permanent plots of the Austrian Integrated Monitoring site from 1993 to 2005. The graph is spread between the first and the second axis of the three dimensional ordination space derived from an nMDS-space. Filled symbols represent plot position in 2005, open symbols position in 1993. △ = Leptosols, ○ = Planosols and □ = Cambisols. The line between two symbols represents the movement of a site's species composition across the ordination space.

Species compositional change

The stress value (12.88 %) for the nMDS ordination indicates an adequate representation of plots in the (axis-reduced) nMDS space. The first nMDS axis (Fig. 2) clearly represented soil properties so that the species composition of permanent plots grouped according to the three major soil types. Thus, this axis indicated a pattern of nutrient availability with base-rich, dry sites on the right (Leptosols), mesic sites in the centre and moist, acidic sites on the left (Cambisols and Planosols). The changes in species composition from 1993 to 2005 in the nMDS-space are also illustrated in Fig. 2. Overall changes in species composition from 1993 to 2005 were highly significant (MANOVA intercept using the three axes of the nMDS: Pillai = 0.1847, $F_{3,121}$ = 9.1401, $p <$ 0.001). The magnitude of temporal changes of plots along the first nMDS-axis were significantly correlated with their absolute nMDS-scores (linear regression: t = 3.479, $p <$ 0.001). Plots found at the extreme ends of the first

nMDS-axis in 1993 strongly shifted towards the centre in 2005, while for plots located in the centre of the axis in 1993 no clear pattern could be observed.

The magnitudes of temporal change (first axis of the nMDS) significantly correlated with the magnitudes of change of the mean Ellenberg N and R values, while changes of M and L values were independent of the temporal trend (Table 3).

Observer error

The distances between the observation in 1993 and the centroid of the corresponding observations in 2005 on each observer plot (0.088 ± 0.039; mean ± SD) were significantly larger (t-test: t = –4.73, df = 13, $p <$ 0.001) than pairwise distances between independent observers in 2005 (0.039 ± 0.008). The temporal shift of the species composition is therefore larger than the variation in estimates among different observers (Fig. 3).

Table 2. Correlation between the changes in cover-abundance values from 1993 to 2005 (parameter β of species-specific marginal models) and Ellenberg indicator values for nitrogen (N), soil pH (R), light (L) and moisture (M), calculated by means of Kendall's rank correlation with exact p-values for ordinal data (significant values with p-value < 0.05 are given in bold).

Ellenberg indicator	Kendall's τ	p-value
N	0.811	0.418
R	2.715	**0.007**
L	0.380	0.704
M	– 0.808	0.419

Table 3. Correlation between the absolute values of changes of the first nMDS-axis scores and the differences of mean Ellenberg indicator values for nitrogen (N), soil pH (R), light (L) and moisture (M) of plots from 1993 to 2005. Calculations were conducted using Pearson's product moment correlation (significant values with p-value < 0.05 are given in bold).

Ellenberg indicator	Pearson's r	p-value
N	2.016	**0.046**
R	3.739	**< 0.001**
L	-1.660	0.099
M	0.516	0.607

Fig. 3. Comparison of differences between observations by six independent observer teams on 14 plots in 2005 with the changes in vegetation composition on the same plot between 1993 and 2005. The graph is spread between the first and the second axis of the three dimensional ordination space derived from an nMDS-space. Observations in 1993, presented as dots, are connected with the centroid (shown as cross) of the respective plot derived from the data of the six teams in 2005 with a solid line representing the temporal shift of vegetation composition. The radii of the circles were computed as the upper 95% confidence interval of all pairwise distances of observations within each observer plot in 2005. Distances were measured as the Euclidean distances between observations in the three axis of the nMDS-space. Because these distances showed a gaussian distribution, we used an equi-tailed, two-sided, normal approximation to calculate the confidence intervals.
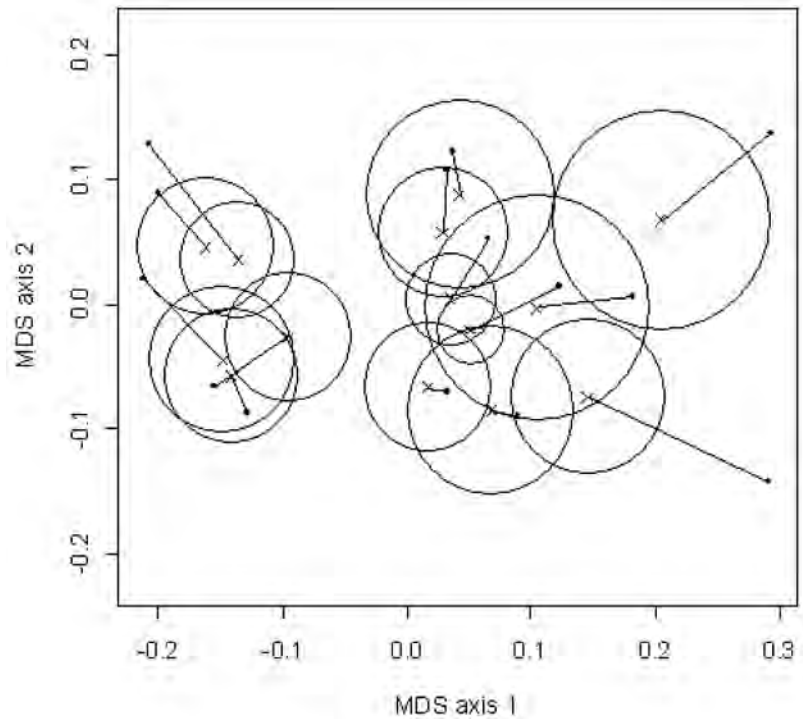
Discussion

Regarding both single species and whole communities, significant temporal changes of the forest floor vegetation between 1993 and 2005 were observed. Although several studies stress the importance of testing the reproducibility of cover estimates in long-term monitoring data (e.g. Helm & Mead 2004), no direct comparisons between temporal changes and the variability in data due to observer errors are available in the literature. In our study, the variation in species composition data recorded by different observers in the same year was generally around half of the variation between observation years (Fig. 3). Due to this significant difference the existence of temporal trends can be confirmed.

Effects of continuously elevated N deposition and decreasing S deposition were ambiguously reflected in the changes of forest floor vegetation. Firstly, the results focusing on single species vs. whole communities differed to some extent with regard to the detected causes responsible for the temporal trend. The changes of the abundance of single species, which was significant for 31% of all species, pointed to an increase of basiphilous species whereas species with a higher nutrient demand did not change (Table 2). On the contrary, the magnitude of temporal changes in species composition was related to both, the increase of basiphilous and, to a lesser extent, nitrophilous species (Table 3). Secondly, the magnitude of changes of the species composition depended on site conditions. The plots at the extreme ends of the base-rich and dry to moist and acidic gradient, shown in the nMDS plot of Fig. 2, exhibited a stronger temporal trend. In addition, the stronger the temporal changes in species composition were the more basiphilous species and species with a higher nutrient demand had increased.

We suspect that the weak overall trend was masked by the diversity of site conditions of the study area. Nevertheless, the changes of forest floor vegetation were related to airborne N and S deposition. Taking the response of single species abundances and the convergence of plots along the first nMDS axis into account, the decreased deposition of acidifying substances and the cumulative deposition of N did affect forest floor vegetation. Although the bulk of permanent plots with intermediate soil conditions remained more or less unchanged, the base-rich, dry and the moist, acid sites exhibited significant changes indicating an erosion of oligotrophic site conditions with the corresponding changes of the species composition at these sites.

How can we interpret the partly ambiguous results of our study? Firstly, methodological limitations exist when inferring from indirect indicators such as Ellenberg values. Secondly, the speed and timing of vegetation changes could not be judged from our data. Thirdly, several processes influencing the forest floor vegetation interacted with the effect of airborne N and S.

Since forest floor species are sensitive to changes in light availability, analysis of Ellenberg indicator values has to be interpreted with caution (Diekmann & Dupré 1997; Englisch & Karrer 2001; Diekmann 2003). As

indicated by hemispherical measurements (Dirnböck et al. 2007), the forests on slopes were more affected by windthrow, slightly increasing light penetration. Whereas on the plateau, light availability on the forest floor has decreased since the first records. Soil conditions were bound to these relief features so vegetation changes which occur due to an interaction of radiation and soil conditions cannot be disentangled entirely using indicator values.

Studies analysing data with comparable site conditions but using longer-term (several decades) monitoring data (Diekmann & Dupré 1997; Hédl 2004; Tamis et al. 2005) showed a much more significant response of forest floor vegetation to either acidification or eutrophication from airborne sources. In our study area, as well as in many forests in Europe, N deposition exceeded background levels many years before the onset of measurements. The same is true for S deposition, which has been decreasing constantly since its peak in the 1980s (Anon. 2006a). Hence, the weak changes of forest floor vegetation in this study might either be due to time-lags or due to changes which already occurred before our observations started. However, our knowledge about the speed of vegetation change following eutrophication and acidification is very limited (Bobbink et al. 2003). Relatively fast responses were found for boreal vegetation, which led Nordin et al. (2005) to state that major vegetation changes occurred in the 1950s when deposition began to rise.

Forest management could, at least in addition to other factors, explain the different responses of the species composition bound to different site conditions. Intensive harvest in the past led to nutritional deficiencies in many central European forests and recovery processes might still be ongoing (e.g. Herman et al. 2001). As an example, Leuschner & Rode (1999) found a significant increase of soil nutrient pools along a 300 year chronosequence from heath to forest. During this succession, airborne deposition of N and S played an increasingly inferior role in comparison to internal nutrient cycles. Hence, the ca. 100 year old clear cut area at the plateau might still affect the nutrient status and acidity of the soils diminishing the effects of later N and S deposition.

A differential effect of eutrophication, with nutrient rich sites remaining relatively unaffected, seems to be typical for forest floor vegetation (Kellner & Redbo-Torstensson 1995; Diekmann & Dupré 1997) and other ecosystem types (Clark et al. 2007). Similarly, acidification and the recovery thereof are tightly linked to soil properties (Falkengren-Grerup 1989; Thimonier et al. 1994; Diekmann & Dupré 1997). Therefore it is not surprising that pooled across all plots of the study area the response of forest floor vegetation to airborne N and S deposition trends remained weak. Recently Gilliam

(2006) hypothesised with reference to N deposition that a decrease in the spatial diversity of N-availability, is a major driver of biodiversity losses in forests. Our results indicate that a homogenization of site conditions which result from long-term high levels of N deposition can lead to a homogenisation of forest floor vegetation. Limestone areas as a whole, if not single sites, with diverse soil conditions such as in the Northern limestone Alps in Austria (Ellenberg 1986) are negatively affected by airborne N deposition. Nevertheless, the vegetation was at least as strongly affected by an increase of basiphilous species as a result of decreasing S deposition during recent decades and, most probably, due to the recovery of soils after clear-cutting of a part of the study area.

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App. 1. Changes in single species cover-abundance on permanent plots from 1993 to 2005 were quantified using marginal models for square contingency tables. Model fit is given as the likelihood ratio statistic G^2 and the p-value, which represents the deviation of the applied model from a model perfectly fitting the data. Consequently, p-values > 0.05 indicate a reasonable model fit, because no significant deviance from a perfect model exists. β is a quantitative measure of the changes in species cover-abundance from 1993 to 2005. $\beta = 0$ refers to constant cover estimation, $\beta < 0$ to decreasing, $\beta > 0$ to increasing cover-abundance. p-values for $\beta < 0.05$ indicate a significant change of cover-abundances ($\beta <> 0$). Degrees of freedom equals six (df = 6) for all models. Models were calculated for all vascular plant species, which occur at least in five plots in one of the observation years.

Species	1993 / 2005[1]	cover[2]	G^2	p	$\beta \pm SE$	z-ratio	p-β
Increasing cover-abundance							
Actaea spicata	2/6	+	5.440	0.489	0.936 ± 0.434	-2.157	0.031
Adenostyles alliariae	0/4	2	0.309	0.999	3.973 ± 1.934	-2.054	0.040
Convallaria majalis	4/12	+	0.396	0.999	1.160 ± 0.373	-3.111	0.002
Euphorbia dulcis ssp. *dulcis*	8/21	+	0.269	1.000	1.149 ± 0.281	-4.095	0.000
Galium lucidum	12/18	1	4.089	0.665	0.569 ± 0.255	-2.232	0.026
Gymnocarpium robertianum	7/16	3	4.569	0.600	0.782 ± 0.298	-2.628	0.009
Hypericum hirsutum	15/22	1	8.488	0.205	0.532 ± 0.267	-1.989	0.047
Knautia maxima	12/19	1	5.775	0.449	0.448 ± 0.218	-2.052	0.040
Lycopodium annotinum	3/8	2	2.451	0.874	0.933 ± 0.385	-2.425	0.015
Molinia caerulea	7/10	5	7.430	0.283	0.36 ± 0.154	-2.339	0.019
Rubus idaeus	44/51	3	4.601	0.596	0.426 ± 0.110	-3.888	0.000
Ulmus glabra	2/9	+	2.759	0.838	1.389 ± 0.513	-2.708	0.007
Veratrum album ssp. *album*	37/49	1	10.257	0.114	0.594 ± 0.150	-3.974	0.000
Unchanged cover-abundance							
Abies alba	20/20	1	2.992	0.81	-0.053 ± 0.220	0.240	0.811
Adenostyles glabra	85/84	3	12.596	0.050	0.081 ± 0.131	-0.619	0.536
Agrostis capillaris	5/2	1	1.270	0.973	-1.107 ± 0.665	1.664	0.096
Ajuga reptans	15/21	1	6.335	0.387	0.286 ± 0.244	-1.176	0.240
Asarum europaeum	6/7	2	1.625	0.951	0.132 ± 0.200	-0.659	0.510
Aster bellidiastrum	8/7	1	1.638	0.950	-0.092 ± 0.316	0.292	0.770
Athyrium filix-femina	38/44	3	4.168	0.654	0.212 ± 0.114	-1.856	0.063
Betonica alopecuros	7/6	1	0.222	1.000	-0.149 ± 0.208	0.715	0.474
Blechnum spicant	19/17	1	2.806	0.833	-0.142 ± 0.078	1.832	0.067
Buphthalmum salicifolium	5/5	1	1.462	0.962	0.000 ± 0.020	-0.012	0.991
Calamagrostis epigejos	3/7	3	0.526	0.998	0.895 ± 0.462	-1.936	0.053
Campanula glomerata ssp. *glomerata*	5/2	1	3.554	0.737	-1.064 ± 0.556	1.914	0.056
Carduus defloratus ssp. *defloratus*	5/7	1	0.251	1.000	0.497 ± 0.345	-1.441	0.150
Carex digitata	15/11	1	10.843	0.093	-0.343 ± 0.261	1.316	0.188
Carex humilis	7/6	3	6.568	0.363	-0.126 ± 0.201	0.628	0.530
Carex leporina	4/0	+	0.050	1.000	-5.529 ± 7.148	0.773	0.439
Carex pallescens	9/6	1	0.162	1.000	-0.329 ± 0.472	0.696	0.486
Carex pendula	8/6	1	3.626	0.727	-0.319 ± 0.270	1.181	0.238
Cephalanthera longifolia	6/8	+	2.519	0.866	0.391 ± 0.480	-0.814	0.416
Cirsium erisithales	19/19	1	12.258	0.056	0.101 ± 0.126	-0.805	0.421
Cirsium palustre	6/3	+	0.020	1.000	-0.583 ± 0.512	1.139	0.255
Dentaria bulbifera	7/6	1	2.174	0.903	-0.211 ± 0.290	0.728	0.467
Deschampsia cespitosa	4/2	1	3.109	0.795	-0.923 ± 0.504	1.833	0.067
Dryopteris filix-mas	31/27	2	4.527	0.606	-0.190 ± 0.152	1.249	0.212
Epipactis atrorubens	6/4	+	3.013	0.807	-0.601 ± 0.530	1.134	0.257
Epipactis helleborine	10/8	+	5.920	0.432	-0.557 ± 0.350	1.59	0.112
Epipactis spec.	1/4	+	0.374	0.999	1.666 ± 1.070	-1.557	0.119
Eupatorium cannabinum	15/16	+	7.466	0.280	0.128 ± 0.224	-0.571	0.568
Fagus sylvatica	77/72	3	7.015	0.319	-0.089 ± 0.151	0.587	0.557
Galium album ssp. *album*	9/4	+	0.887	0.990	-0.820 ± 0.423	1.939	0.052
Galium rotundifolium	20/24	2	10.806	0.095	0.117 ± 0.179	-0.656	0.512
Galium sylvaticum	8/7	1	2.798	0.834	0.117 ± 0.127	-0.923	0.356
Gentiana asclepiadea	7/6	+	0.808	0.992	-0.426 ± 0.232	1.833	0.067
Hedera helix	5/4	+	0.106	1.000	-0.132 ± 0.271	0.487	0.626
Heracleum austriacum ssp. *austriacum*	8/9	+	2.830	0.83	0.206 ± 0.367	-0.562	0.574
Huperzia selago	4/1	+	0.772	0.993	-1.731 ± 0.941	1.839	0.066
Lamiastrum flavidum	10/0	1	0.086	1.000	-5.061 ± 3.861	1.311	0.190
Larix decidua	10/6	+	0.043	1.000	-0.580 ± 0.450	1.289	0.197
Laserpitium latifolium var. *latifolium*	3/5	+	2.613	0.856	0.504 ± 0.393	-1.283	0.199
Lilium martagon	17/18	+	1.206	0.977	0.113 ± 0.208	-0.543	0.587
Luzula luzulina	8/4	1	0.218	1.000	-0.729 ± 0.578	1.262	0.207
Luzula sylvatica ssp. *sylvatica*	6/2	+	0.025	1.000	-0.836 ± 0.544	1.536	0.125
Melica nutans	31/27	2	7.873	0.248	-0.277 ± 0.207	1.337	0.181
Melitis melissophyllum ssp. *carpatica*	7/6	+	1.668	0.948	-0.1 ± 0.414	0.241	0.810

App. 1, cont.

Species	1993 / 2005[1]	cover[2]	G^2	p	$\beta \pm SE$	z-ratio	p-β
Mentha longifolia	4/1	1	2.026	0.917	-1.542 ± 0.803	1.920	0.055
Mercurialis perennis	35/35	3	8.068	0.233	-0.086 ± 0.111	0.774	0.439
Moehringia muscosa	4/2	+	0.580	0.997	-0.852 ± 0.855	0.997	0.319
Mycelis muralis	35/31	2	8.331	0.215	-0.279 ± 0.194	1.442	0.149
Neottia nidus-avis	10/18	+	0.085	1.000	0.694 ± 0.380	-1.827	0.068
Origanum vulgare	5/5	1	1.368	0.968	-0.030 ± 0.246	0.122	0.903
Paris quadrifolia	25/23	1	8.549	0.201	0.211 ± 0.189	-1.114	0.265
Pimpinella major	10/7	2	6.504	0.369	-0.452 ± 0.295	1.533	0.125
Polygonatum multiflorum	9/3	+	0.66	0.995	-1.093 ± 0.566	1.933	0.053
Polygonatum verticillatum	12/13	1	4.275	0.640	0.002 ± 0.217	-0.007	0.994
Polystichum aculeatum	28/25	1	8.198	0.224	-0.149 ± 0.116	1.291	0.197
Pteridium aquilinum	10/10	3	5.211	0.517	0.099 ± 0.086	-1.142	0.253
Pulmonaria officinalis	5/5	+	0.392	0.999	0.046 ± 0.385	-0.119	0.905
Ranunculus nemorosus	17/19	1	2.318	0.888	0.183 ± 0.215	-0.855	0.393
Rhododendron hirsutum	5/3	1	2.496	0.869	-0.317 ± 0.227	1.395	0.163
Rosa pendulina	6/6	+	0.271	1.000	-0.036 ± 0.355	0.102	0.919
Rubus sect. *Rubus*	11/16	2	10.382	0.109	0.301 ± 0.168	-1.790	0.073
Sesleria albicans	32/31	5	7.349	0.290	-0.093 ± 0.089	1.046	0.296
Solidago virgaurea ssp. *virgaurea*	11/17	+	0.310	0.999	0.486 ± 0.339	-1.434	0.151
Sorbus aria	10/12	1	4.141	0.658	0.018 ± 0.325	-0.055	0.956
Sorbus aucuparia ssp. *aucuparia*	3/5	+	0.001	1.000	0.423 ± 0.583	-0.726	0.468
Taraxacum officinale agg.	6/0	+	0.038	1.000	-4.184 ± 7.922	0.528	0.597
Thelypteris limbosperma	11/15	2	5.146	0.525	0.290 ± 0.281	-1.033	0.302
Thelypteris phegopteris	2/2	1	1.787	0.938	-0.333 ± 0.359	0.928	0.354
Vaccinium myrtillus	13/11	2	6.932	0.327	-0.248 ± 0.229	1.085	0.278
Valeriana montana	4/0	1	1.787	0.938	-0.255 ± 0.552	0.462	0.644
Valeriana saxatilis	2/4	+	1.972	0.922	0.461 ± 0.551	-0.837	0.403
Valeriana tripteris ssp. *tripteris*	22/21	2	8.626	0.196	-0.100 ± 0.089	1.128	0.259
Veronica chamaedrys ssp. *chamaedrys*	4/0	1	0.040	1.000	-5.053 ± 5.72	0.883	0.377
Veronica officinalis	10/6	2	1.826	0.935	-0.681 ± 0.435	1.566	0.117
Vincetoxicum hirundinaria	15/14	2	1.700	0.945	-0.095 ± 0.102	0.933	0.351
Decreasing cover-abundance							
Asplenium viride	8/6	1	4.846	0.564	-0.605 ± 0.256	2.358	0.018
Carex brachystachys	10/5	2	5.946	0.429	-0.86 ± 0.404	2.130	0.033
Carex montana	12/2	3	2.964	0.813	-1.649 ± 0.498	3.308	0.001
Carex ornithopoda ssp. *ornithopoda*	13/2	1	1.658	0.948	-1.834 ± 0.583	3.146	0.002
Carex pilulifera	7/1	1	1.766	0.940	-2.250 ± 0.966	2.330	0.020
Carex remota	6/2	1	2.141	0.906	-1.369 ± 0.625	2.190	0.029
Clematis vitalba	25/16	+	1.429	0.964	-0.565 ± 0.284	1.991	0.046
Daphne mezereum	40/31	1	4.672	0.586	-0.394 ± 0.201	1.957	0.050
Digitalis grandiflora	8/5	1	5.263	0.511	-0.663 ± 0.325	2.043	0.041
Dryopteris affinis ssp. *borreri*	9/1	2	4.504	0.609	-1.917 ± 0.671	2.856	0.004
Epilobium montanum	20/3	1	0.495	0.998	-2.051 ± 0.504	4.071	0.000
Euphorbia amygdaloides	52/20	2	12.136	0.059	-1.445 ± 0.209	6.912	0.000
Gymnocarpium dryopteris	12/3	3	3.824	0.701	-1.418 ± 0.486	2.918	0.004
Hypericum maculatum ssp. *maculatum*	31/16	1	6.862	0.334	-0.85 ± 0.229	3.709	0.000
Juncus effusus	8/1	1	0.180	1.000	-2.364 ± 0.949	2.491	0.013
Lonicera alpigena	10/6	+	1.364	0.968	-0.574 ± 0.257	2.236	0.025
Luzula pilosa	4/0	+	2.382	0.881	-1.262 ± 0.621	2.031	0.042
Picea abies	74/61	2	2.360	0.884	-0.655 ± 0.181	3.616	0.000
Polygala chamaebuxus	8/1	1	1.258	0.974	-2.383 ± 0.997	2.389	0.017
Salvia glutinosa	40/30	2	5.511	0.480	-0.480 ± 0.140	3.423	0.001
Scrophularia nodosa	8/1	+	0.208	1.000	-2.361 ± 0.948	2.489	0.013

[1] Values represent the percentage of plots inhabited by a species in 1993 and 2005, respectively.

[2] Given is the maximum cover-abundance value for both years.

Species with inadequate model fit: *Acer pseudoplatanus, Anemone nemorosa, Brachypodium sylvaticum, Calamagrostis varia, Cardamine trifolia, Carex alba, Carex flacca, Carex sylvatica, Cyclamen purpurascens, Daphne laureola, Dentaria enneaphyllos, Dryopteris carthusiana* agg.*, Fragaria vesca, Fraxinus excelsior, Galium odoratum, Helleborus niger* ssp. *niger, Hepatica nobilis, Hordelymus europaeus, Lamiastrum montanum, Lysimachia nemorum, Oxalis acetosella, Phyteuma spicatum* ssp. *spicatum, Prenanthes purpurea, Primula elatior, Sanicula europaea, Senecio nemorensis* agg.*, Viola reichenbachiana.*