

Understorey Vegetation Stability and Dynamics in Unmanaged Boreal Forests Along a Deposition Gradient in Sweden

Ulf Grandin

Abstract The aims of this study were to investigate spatial patterns and temporal changes in understorey vegetation at four forest catchments forming a depositional gradient. Inventories of the bottom and field layers were carried out in the 1990s and repeated after 5–14 years, depending on catchment. It was hypothesized that changes and patterns in ground vegetation would be related to changes and patterns in N and S deposition. The data were analyzed using Ellenberg indices and multivariate methods. All catchments showed temporal changes in species composition. Analyses of the bottom layer were confounded by a change of field staff, but after accounting for this observer effect, differences in species composition between the catchments remained. Within catchments, the changes in species composition were unrelated to N or S deposition. Relationships between environmental factors, expressed as Ellenberg indices, and compositional patterns differed between catchments although Ellenberg indices showed small temporal changes.

Keywords Long-term · Bryophytes · Vascular plants · Observer effect · Ellenberg

INTRODUCTION

The species composition of forest floor vegetation is determined by several factors, including regional and local (micro) climate (Bailey 2009; Sang and Bai 2009), tree species composition, and the local species pool (Barbier et al. 2008; Cornwell and Grubb 2003). Anthropogenic factors such as forest management practice (Paillet et al. 2010) and atmospheric deposition of N and S (van Dobben and de Vries 2010; Lee 1998) can also influence species composition. Strongly decreasing emissions of S and

moderately decreasing emissions of N have resulted in decreasing levels of N and S deposition throughout Europe (Benedictow et al. 2009). In Sweden, patterns of N and S deposition show a latitudinal gradient, with the highest levels in the south west and the lowest in the north (Sjöberg et al. 2006).

The eutrophication and acidification of terrestrial ecosystems related to long-term N deposition has been shown to alter nutrient balances and change the species composition of plant communities (Bobbink et al. 2003). As N emissions are expected to remain at current levels, with only a weak decreasing trend (Reis et al. 2009), eutrophication from N deposition is expected to persist (Erisman and de Vries 2000). Excess N deposition favors nitrophilous species and leads to the homogenization of understorey plant communities (Gilliam 2006). However, there is evidence that species composition, diversity and ecosystem functions are affected at relatively low levels of N deposition (Bobbink et al. 2010), although the effects of N deposition have been shown to be most pronounced where N is limiting (Bobbink et al. 2003). Nordin et al. (2005) concluded that while understorey vegetation reacts quickly to increasing N levels, recovery is a very slow process. In addition, we can anticipate that the recovery after reduced N deposition may be delayed since N deposition is still higher than pre-industrial levels. There are also reasons to assume that the response to changing N deposition will be faster for bryophytes than for vascular plants. Bryophytes have no root system, resulting in a more direct uptake of compounds from precipitation (Brown and Bates 1990), while uptake by vascular plants is from the soil solution which is affected by soil–water interactions (Bache et al. 1984).

Sulfur deposition is known to be a major threat to mosses and lichens (Liska and Herben 2008). Vascular

plants in the field layer appear to be less affected by acid (sulfur) deposition and edaphic, climate, and tree species composition factors are of greater importance (van Dobben and de Vries 2010). However, sulfur emissions, in contrast to nitrogen emissions, have decreased significantly in the last few decades (Benedictow et al. 2009), and the recovery of at least S-sensitive plants is anticipated. The responses to changes in S deposition may differ between bryophytes and vascular plants due to differences in their sources of nutrient uptake.

The current study is based on the repeated survey of the bottom and field layer vegetation at the four Swedish Integrated Monitoring (IM) sites (UN-ECE-International Co-operative Program on Integrated Monitoring of Air Pollution Effects on Ecosystems). The Swedish IM program has been ongoing since the 1990s, a period when emissions of S began decreasing while N emissions have remained high. Due to the low levels of N and S deposition in the northern part of the country, it was expected that temporal trends in plant species composition of the field layer at the northernmost IM site would be unrelated to deposition. In contrast, since the west coast of Sweden has experienced significant decreases in deposition (Grandin 2011), it has been hypothesized that shifts in ground vegetation species composition there would be related to changes in N and S deposition. In an earlier study of the changes in the understorey vegetation carried out at the Swedish IM catchments, Grandin (2004) found temporal changes in the understorey vegetation, even though understorey vegetation has been shown to respond only slowly to changes in deposition (Strengbom et al. 2001; Zechmeister et al. 2007).

The aims of this study were to use two inventories of the bottom and field layer vegetation recorded on the permanent plots in the four Swedish IM catchments in order to: (a) assess whether species occurrence and composition have changed, (b) to assess whether any changes found exhibit temporal trends or spatial patterns, and (c) whether changes are related to the levels and changes in the deposition of N and S. Establishing such cause-and-effect relationships between the abiotic and biotic components of ecosystems are important for the validation of air pollution abatement policy.

MATERIALS AND METHODS

Vegetation data from permanent plots at the four Swedish IM catchments (Fig. 1; Table 1) was collected as part of the UN ECE ICP-Integrated Monitoring program. The catchments are located along a climatic and depositional gradient, with the mildest climate and highest levels of deposition in the south west and close to pre-industrial

levels of deposition at the northernmost catchment (Table 1). The small headwater catchments are entirely forested, mainly with Norway spruce (*Picea abies*), and have an understorey dominated by *Vaccinium* sp. and a few grasses and herbs. A few plots located on open *Sphagnum*

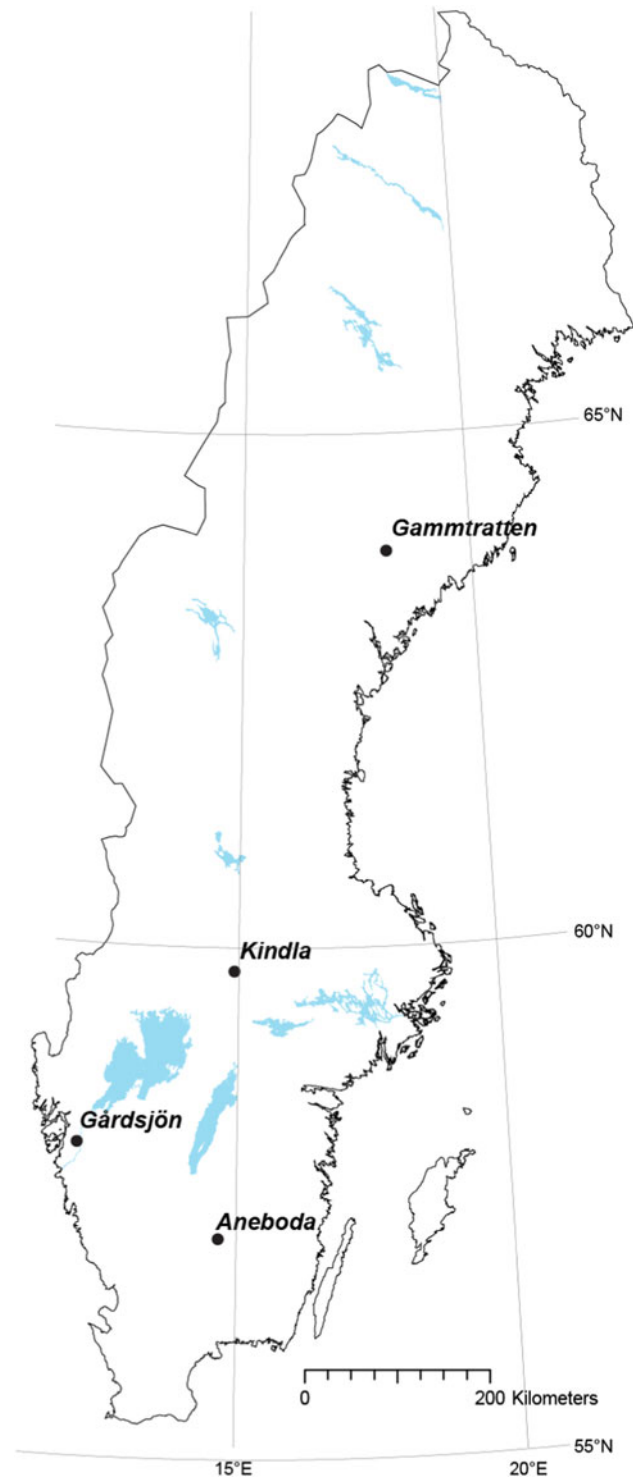


Fig. 1 Locations of the four study sites

Table 1 Catchment characteristics of the four catchments included in this study, ordered from south to north

	Aneboda	Gårdsjön	Kindla	Gammtratten
Size (ha)	18.9	3.7	20.4	45
Annual mean temp (°C) ^a	5.8	6.7	4.2	1.2
Precipitation (mm year ⁻¹) ^a	750	1000	900	750
N dep. Survey 1	5.7	11.9	5.5	4.0
N dep. Survey 2	7.0	8.5	5.0	2.2
S dep. Survey 1	4.1	9.1	4	3.7
S dep. Survey 2	3.2	4.7	2.8	1.7

All figures for deposition are given in kg ha⁻¹ year⁻¹

^a 30-year mean values

mires were not included in this study. All four of the catchments are located in protected nature reserves, with a long history (>100 years) of absence of management.

At each catchment, all plant species in 100 m² circular plots were recorded twice: in 1996 and 2006 (Aneboda), in 1999 and 2004 (Gammtratten), in 1991 and 2005 (Gårdsjön), and in 1998 and 2003 (Kindla). The plots were located at the interstices of a 50 × 50 m grid, except at Gammtratten where the grid was 100 × 100 m. All data can be downloaded from [http://info1.ma.slu.se/veg/www_veg.acgi\\$Project?ID=Intro](http://info1.ma.slu.se/veg/www_veg.acgi$Project?ID=Intro). The number of plots per catchment was dictated by the size of the catchment. For this study, data from both inventories were available for 17 plots at Aneboda, 32 at Gammtratten, 17 at Gårdsjön, and 16 at Kindla.

In July or August, species abundance was recorded as percentage cover. In the first inventory at Aneboda, however, cover was estimated using percentage cover classes (see below). The trained field staff responsible for making the inventories spent between 1 and 3 h surveying each plot. The species were divided into bottom, field, shrub, and tree layer species. This study, however, focuses on the bottom and field layers only. The first set of surveys was performed by the same observer for both layers at all four sites. In the second survey, however, two new observers were engaged, one to analyze the bottom layer and another to analyze the field layer.

Statistical Analyses

During the first Aneboda inventory, cover estimates for individual species were made using an ordinal four degree semi-logarithmic scale (described as: “0 = absent; 1 = scattered occurrence; 3 = frequent occurrence; and 2 = between 1 and 3”), while the total cover of a vegetation layer was recorded using percentage cover. Transformation

of the ordinal scale data into percentage cover values was accomplished by testing different percentage cover values as candidates for cover class 3 for each species and layer, and then comparing the sum of these tested percentage cover values to the recorded total cover of that layer (Fig. 2). In the summations, cover class 2 was replaced by 3% for the bottom layer and 2% for the field layer, and for both layers class 1 was replaced by 1% (equivalent to cover up to 1 m²). The sum of all modeled individual percentage cover values should be greater than, or at least equal to, the total recorded percentage cover. In the Aneboda 2006 inventory, when the percentage cover values for all species were recorded, the mean difference between recorded total cover and sum of individual cover percentages was 2.2% for the field layer species, and 18% for the bottom layer species. Using these values and the regressions shown in Fig. 2, cover class 3 data from 1996 was converted into a percentage cover value of 3% for field layer species and 12% for the bottom layer species.

For each plot, taxon richness, Shannon diversity and evenness (Magurran 2004), and weighted Ellenberg indices (Ellenberg et al. 1991) for soil nitrogen (N), soil acidity (R), soil moisture (F), and light (L) were calculated. The weighted Ellenberg values were calculated as $I_E = \text{sum}(x_i \times E_i) / \text{sum}(x_i)$, where x_i is the cover of species i , and E_i is the Ellenberg indicator value for species i . The Ellenberg indicator values were developed for central Europe. Some studies have shown minor deviations in the indicator values outside this region, however, the deviations are significant for only a few species (e.g., Diekmann 2003).

Differences between catchments and over time were tested for using a repeated measure ANOVA model followed by Student's t post hoc tests in cases where the ANOVA model was significant. Univariate statistical tests were performed using JMP version 9.0.0 (JMP 2010).

Community structure and correlations with explanatory environmental variables were analyzed using the meta-NMDS and EnvFit (999 permutations) packages as implemented in the “vegan” package (Oksanen 2006) for the software package R (R Development Core Team 2010). The similarity matrix for the NMDS was calculated using the Bray–Curtis index. Explanatory variables were the diversity metrics and Ellenberg indices described above, and the following forest stand variables: number of trees <5 cm diameter at breast height dbh (Sapl), sum dbh of trees >5 cm (Diam), number of fallen logs (Logs), and number of deciduous trees (Decid), all calculated per monitoring plot. In all ordinations, the understorey data were transformed into presence/absence values and species occurring in less than 5% of the plots in a given catchment omitted. To test whether temporal changes had a common direction in the ordination spaces, or whether the directions

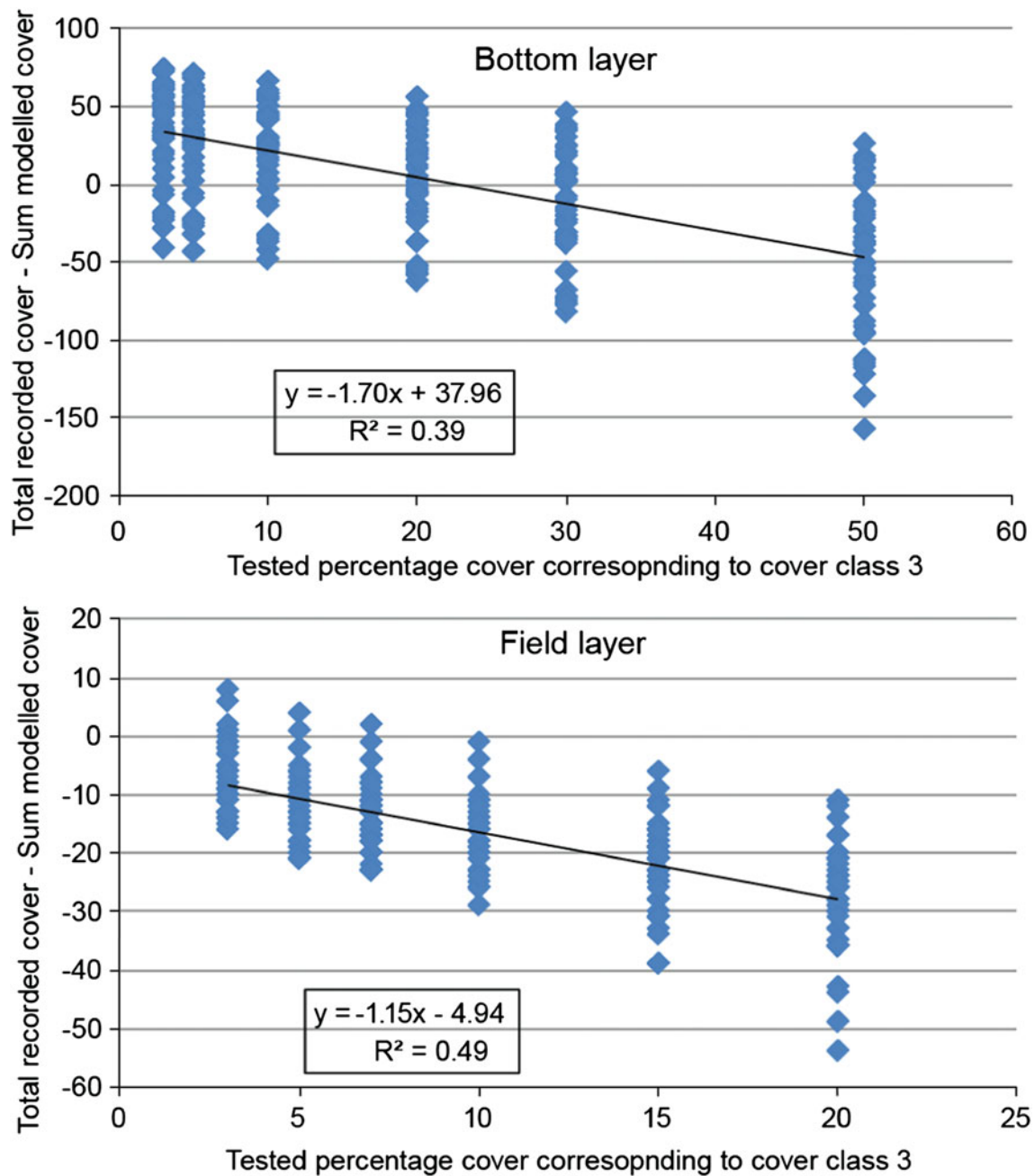


Fig. 2 Comparisons of the difference between the sums of modeled percentage cover of each species and total cover for the vegetation layer recorded in the field (y-axis) for different assumptions of the percentage cover corresponding to cover class 3 in an ordinal scale (x-axis)

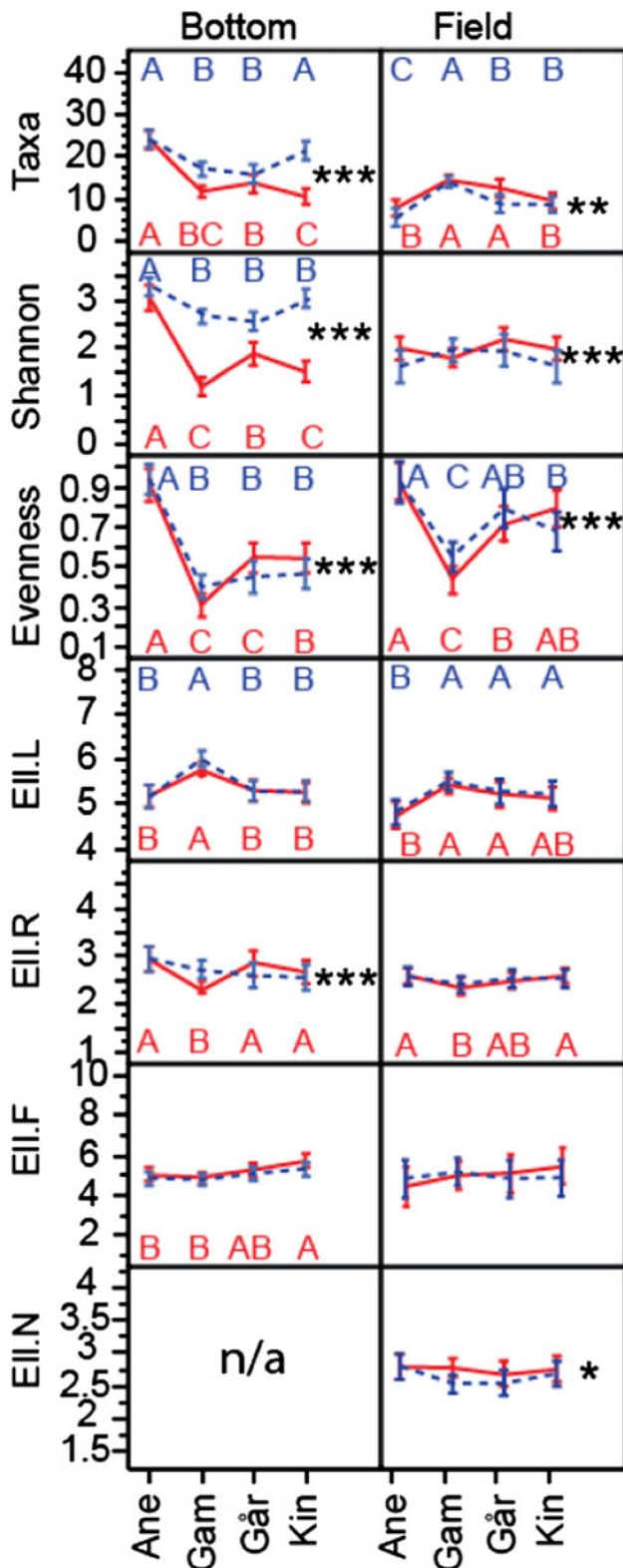
of the temporal trajectories connecting the two surveys of the same plot were randomly distributed, Rayleigh's R statistic was used (Greenwood and Durand 1955).

Changes in the cover of individual species between the two surveys were assessed using Wilcoxon's matched pairs test (Zar 1999). To decrease the risk of inflation of type I errors, only changes with a p value less than 0.01 was considered to be significant. A nonparametric test was used because there are many zeros in the data causing a skewed distribution.

RESULTS

Diversity Patterns

There were clear differences in species diversity in the bottom layer between the sites. The most striking result was that, in the first survey at Aneboda, there were about twice as many species as recorded at the other catchments (Fig. 3). The second survey showed smaller differences in number of species between catchments. The Shannon



diversity index showed similar spatial patterns (Fig. 3). The high evenness in species distribution among all the plots at Aneboda showed that diversity was high and evenly distributed.

Fig. 3 Spatiotemporal patterns in the vegetation at four Swedish IM sites as indicated by a set of response variables. Analyses are divided into bottom (left column) and field (right) layers, and into first (solid lines) and second (dashed lines) surveys. In each subfigure, letters at the bottom indicate significant differences (Student's *t* on least square means differences after significant ANOVA) between catchments in the first survey, and letters at the top indicate differences in the second survey. Significant temporal differences are indicated by asterisks between pairs of lines (****p* < 0.001, ***p* < 0.01, **p* < 0.05). Error bars show 95% confidence intervals. The lines connecting the catchments are to improve visual perception of the patterns and have no ecological meaning

Comparisons over time showed that the number of taxa in the bottom layer increased at all four catchments (Table 2). For Kindla, the number of species more than doubled between the two inventories. There was also high species turnover rate in the bottom layer, with many species unique to the first inventory (Table 2). The mean species number per plot in the bottom layer showed significant changes between the two inventories at all four catchments (Fig. 3). The most marked mean changes were found at Gårdsjön (mean decrease of 3.1 species) and at Aneboda (mean decrease of 1.4 species).

For the field layer, differences in diversity between the four sites were less pronounced than for the bottom layer. The highest diversity was found at the northernmost catchment, Gammtratten. The other three catchments had approximately similar numbers of species, although Aneboda had a statistically significantly lower number than the other catchments (Fig. 3). However, the differences between the four sites in the number of taxa were not reflected in Shannon diversity. The evenness index showed considerable between-catchment variability, with high evenness at Aneboda and much lower evenness at the three other catchments. Temporal differences in the field layer were less pronounced than for the bottom layer. The greatest change was observed at Gårdsjön (a decrease of 10 species). Species turnover was also much lower for the field layer compared to the bottom layer, with few species being found only during the second inventory (Table 2).

Despite striking changes in diversity, only a few species showed significant changes in abundance. In total 20 out of

Table 2 Total number of observed taxa and number of taxa unique per inventory for bottom and field layers at the different catchments

Catchment	Number of taxa (unique number of taxa)			
	Bottom layer		Field layer	
	Inv. 1	Inv. 2	Inv. 1	Inv. 2
Aneboda	77 (26)	81 (30)	24 (7)	24 (7)
Gammtratten	53 (16)	82 (45)	63 (5)	61 (3)
Gårdsjön	41 (4)	53 (16)	42 (11)	33 (2)
Kindla	37 (4)	79 (46)	36 (2)	37 (3)

Table 3 Significant (Wilcoxon, $p < 0.01$) changes in species cover between two inventories of vegetation in 100 m² plots at four catchments

Species	Mean change (m ²)			
	Aneboda	Gammtratten	Gårdsjön	Kindla
<i>Brachythecium oedipodium</i>	–	0.31	–	1.1
<i>Brachythecium starkei</i>	n/a	–	–	0.88
<i>Chiloscyphus profundus</i>	–	–	–	0.62
<i>Chiloscyphus</i> sp.	–	n/a	1.5	n/a
<i>Dicranum drummondii</i>	n/a	0.25	n/a	–
<i>Hylocomium splendens</i>	–	–	3.8	–
<i>Hylocomium umbratum</i>	n/a	–	n/a	0.56
<i>Lophozia</i> sp.	–	0.28	n/a	–
<i>Plagiothecium curvifolium</i>	–0.76	0.38	–	–
<i>Plagiothecium</i> sp.	0.11	0.25	n/a	–
<i>Pleurozium schreberi</i>	–	–	5.2	–
<i>Ptilidium ciliare</i>	–	0.44	–	–
<i>Sphagnum capillifolium</i>	–	1.4	2.4	–
<i>Sphagnum girgensohnii</i>	–	–8.8	–	–
<i>Sphagnum russowii</i>	n/a	4.1	–	–
<i>Tetraphis pellucida</i>	–	n/a	–	0.5
<i>Leparia incana</i>	–0.47	n/a	n/a	n/a
<i>Deschampsia flexuosa</i>	–	–	–	2.5
<i>Linnaea borealis</i>	n/a	0.83	–	–
<i>Vaccinium vitis-idaea</i>	–	–	–	5.7

“n/a” indicates that the species was not found. The table is arranged with the bottom layer species first

270 species showed a significant temporal change in abundance (Table 3). All species showing a significant change were present in both inventories. Most of these significant changes were increases, with only three species showing a decrease. Four of the species changed at two catchments, while all other significant changes were unique to only one of the catchments. The significant changes in cover could not be explained by any of the Ellenberg values for light or for soil moisture, fertility or acidity (Kendall's τ , $p > 0.05$ for all combinations of catchments and Ellenberg values).

Environmental Variables

Except for N at Aneboda, the deposition of N and S decreased between the inventories (Table 1). However, over a longer timescale there is also a decreasing trend in N deposition at Aneboda (Grandin 2011). The decreasing trends in deposition were only partly reflected in the Ellenberg indices (Fig. 3). For the bottom layer, there was an overall decrease in the Ellenberg index for soil acidity, although the northernmost catchment showed an increase.

The field layer vegetation showed a small but significant decrease in Ellenberg values for soil fertility, but not for soil acidity. Although statistically significant, the temporal changes in Ellenberg N indices for the field layer were very small and, ecologically, probably of little relevance.

The Ellenberg indices also differed little between the catchments (Fig. 3). Most Ellenberg indices varied within one Ellenberg unit. These small differences indicate a set of species present at all catchments having similar ecological preferences regarding N and S deposition, even though the catchments span a phytosociological gradient from boreo-nemoral, close to the nemoral zone, to true boreal (Sjörs 1956). The most conspicuous results were the slightly higher light indices for both vegetation layers at the northernmost catchment (Fig. 3), indicating a more open forest than at the other catchments.

Compositional Patterns

Ordinations revealed that factors other than N and S were also important for the composition of the plant communities and that temporal effects were few and weak (Fig. 4a, b; Table 4). When all four catchments were included in the same ordination of the bottom layer vegetation data (Fig. 4a), the northernmost catchment was clearly separated from the other three, while the two southernmost catchments were only weakly separated. The Ellenberg light indices and Shannon diversity index were the most important factors explaining differences between the catchments, while the Ellenberg values for soil moisture was the most important factor explaining the variation within catchments (Fig. 4). The Ellenberg index for soil acidity was also significant and had a similar relationship to the species composition as the diversity variables. Forest stand variables were generally weakly, albeit significantly, correlated with the floristic patterns of the bottom layer (Table 4).

In the ordination of the field layer for all four catchments together, there was a significant effect of catchment (Fig. 4b). The most important factors separating the plots were the number of taxa and the Ellenberg indices for soil acidity. The number of taxa was related to the order of the catchments in the ordination space, whereas the Ellenberg R indices separated the plots within the catchments. As was the case with the bottom layer, the Ellenberg L indices were most strongly related to the northernmost catchment and it can be inferred that it is less dark under the canopy in this catchment. The Ellenberg N indices were only weakly related to the vegetation patterns (Table 4). The forest stand parameters were more strongly related to the ordination of the field layer species than they were for the bottom layer species, but the relationships were still quite weak compared to the importance of the Ellenberg R, L, and F indices.

Fig. 4 NMDS ordinations on vegetation in circular plots at four Swedish IM sites surveyed twice between 1991 and 2005. The bottom layer (a), (stress value = 21.8) and field layer (b), (21.1) were analyzed separately. *Vectors* represent significant ($p < 0.05$) explanatory variables fitted to the ordination space, and catchment names represent centroids of each catchment. *Polygons encircle* all plots belonging to the same catchment

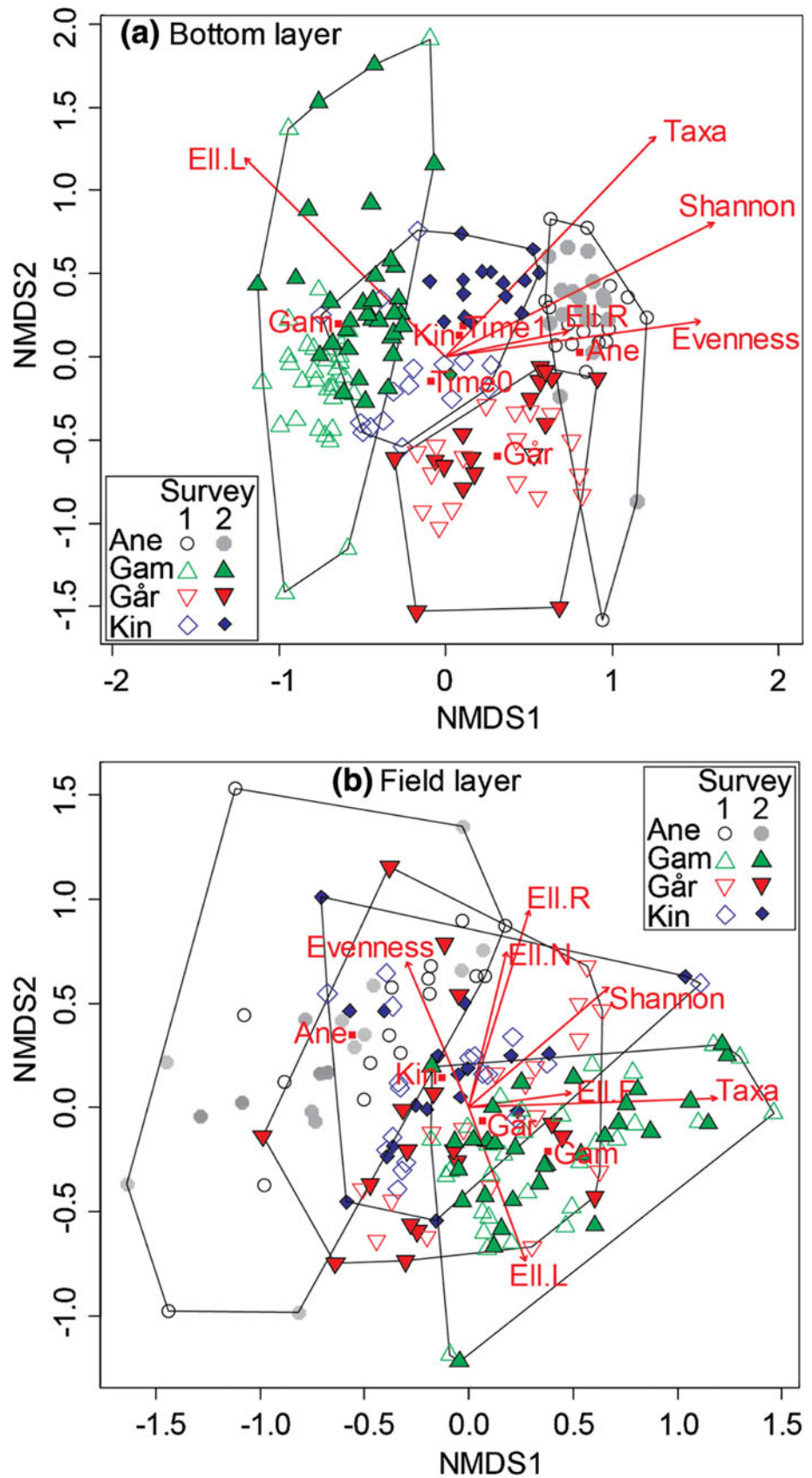


Table 4 NMDS stress values and significant ($p < 0.001$) relationships (r^2) between explanatory variables and NMDS ordinations, for all catchments together and each catchment individually, and divided into bottom and field layer

Explanatory variable	Coefficient of determination (r^2)									
	Bottom layer					Field layer				
	All	Ane	Gam	Går	Kin	All	Ane	Gam	Går	Kin
NMDS stress	21.4	16.4	19.1	18.9	18.6	21.0	21.1	12.9	22.7	12.4
Catchment	0.48	–	–	–	–	0.45	–	–	–	–
Time	–	0.13*	0.17	–	0.23	–	–	–	–	–
Taxa	0.28	–	0.52	0.50	0.68	0.70	0.55	0.81	–	0.92
Shannon	0.43	0.21*	0.55	–	0.62	0.31	0.57	0.66	0.34**	0.64
Evenness	0.40	–	0.16**	0.20*	–	0.41	–	0.38	0.36**	0.43
Ellenberg L	0.41	–	–	0.58	0.53	0.41	0.44**	0.75	–	0.36
Ellenberg R	0.28	0.22*	0.29	0.41	0.33	0.54	0.53	0.62	0.69	0.61
Ellenberg F	0.41	0.76	0.74	0.51	0.32	0.40	0.60	0.54	0.48	0.43
Ellenberg N	–	–	–	–	–	0.11	0.36**	0.34	0.49	0.55
Sapl	0.056*	–	0.22**	–	0.28	–	–	0.21**	–	–
Diam	0.19	–	–	0.33**	0.22**	0.15	–	0.55	–	0.19*
Logs	0.088	–	–	0.34**	0.40**	0.19	–	0.27**	0.23*	0.43
Decid	0.086**	–	0.33	–	–	0.13	–	–	–	0.35

P values based on 999 permutations

–, Not significant

* $p < 0.05$, ** $p < 0.01$

Separate ordinations of each catchment and vegetation layer (diagrams not shown but results presented in Table 4) revealed significant plot-wise temporal changes in species composition between the surveys at each catchment except Gårdsjön (despite 14 years between inventories) for the bottom layer, but not for the field layer ($p > 0.4$). Additional tests on the directions of significant changes in the NMDS ordination spaces showed that the directions of the changes between the two surveys were nonrandom at all catchments except Aneboda (Rayleigh's R , $p < 0.001$). However, despite the results from Rayleigh's tests of direction and the multivariate analyses, which both indicated systematic and significant plot-wise changes in species composition, the causes of the changes were not obvious. Moreover, the shift in centroid position in the ordination space between the inventories for each catchment (calculated as the Euclidean distance) was not correlated with the change in N or S deposition (Kendall's τ , $p > 0.5$) for either vegetation layers at any of the catchments. Fitting available explanatory variables to the ordinations resulted in significant ($p < 0.001$) fits for both diversity variables (number of taxa and Shannon diversity index) and Ellenberg indices in both vegetation layers, with the exception of the Ellenberg indices for soil pH in the bottom layer at the northernmost catchment and light in the field layer at the catchment on the west coast (Table 4). The forest stand parameters were either weakly correlated

or uncorrelated with the floristic patterns in the ordinations, indicating that the characteristics of the forest stand had little influence on the species composition of both the bottom and field layers.

DISCUSSION

The observed increase in the number of species in the bottom layer may well be attributed to the change of observer between the two inventories (cf. Magurran et al. 2010), even though both observers were skilled and experienced bryologists. A long-term study of similar catchments in Sweden by the same observer found no changes in number of species over a 16-year period (Köchy and Bråkenhielm 2008). Many studies have acknowledged the importance of training of field staff and consistency between them (e.g., Ahrends et al. 2011; Milberg et al. 2008; Vittoz and Guisan 2007), and this study further emphasizes the need for consistency and calibration. Nilsson and Nilsson (1985) used the term “pseudoturnover” to describe false changes in species assemblages as an effect of species being missed during field work. In this study, unique species were found during both the first and the second inventories, but a substantial increase was noted during the second inventory. Many of these apparent species replacements are therefore probably pseudoturnovers.

Unfortunately, there is no direct way to distinguish between observer and ecological/environmental effects on species turnover in our study, as causes of the large increase in number of bryophyte species. An indirect test would be to determine whether the new bryophyte species in the second inventory have different ecological preferences from those of species recorded the first inventory. Plot-wise paired comparisons of Ellenberg indices from the first inventory and for species unique to the second inventory revealed that most of the indices based on the new species in the second inventory did not differ from the indices calculated for the first inventory (paired t tests, $p > 0.05$). However, significant increases were detected in the Ellenberg indices for soil moisture at Aneboda (mean change = 0.72, $p < 0.01$), Gammtratten (1.0, $p < 0.001$) and Kindla (0.28, $p = 0.05$), and for light at Gammtratten (0.66, $p < 0.01$). The new species that appeared in the second inventory are thus not indicative of a depositional change. Unfortunately, bryophytes lack Ellenberg indicator values for N, so the possibility that there was an effect of decreasing nitrogen deposition for these species cannot be ruled out, although this is less likely as the decrease in N deposition is low. The few significant changes detected indicate an increase in species showing a preference for moisture and, for Gammtratten, also for light conditions. These changes in Ellenberg indices could partly be an effect of the observed increase in the number of *Sphagnum* species; species that are typical of open mires and wetlands and therefore have high Ellenberg light values. The number of *Sphagnum* species increased from 5 to 9 at Aneboda, from 5 to 16 at Gammtratten, and from 11 to 17 at Kindla. However, a high turnover of bryophytes has been observed in a study of the bottom layer at the Austrian IM site, in the absence of any assumed systematic error (Zechmeister et al. 2007). Some of the turnover observed in this study may therefore be due to natural variability.

Other studies comparing differences between field workers have concluded that species that are overlooked are often those with low cover (Vittoz and Guisan 2007). In this study, the new *Sphagnum* species in the second inventory had a mean cover value of 5.7% (SD = 8.0), while the other species unique to the second inventory had a mean cover of 1.1% (0.32); 1% was the lowest cover value used in this study. Hence, the new *Sphagnum* species were probably not missed, but misidentified in the first inventory.

However, an observer effect is probably not the only explanation why the Ellenberg light indices were the highest at Gammtratten (0.8 units higher, on average, than the other catchments). The higher light indices at this northern catchment are probably an effect of the tree structure. Spruces at this latitude typically have short branches, as an effect of natural selection for individuals with short sturdy

branches that do not break when covered with large amounts of snow (Geburek et al. 2008; Jalkanen and Konopka 1998). This crown architecture forms a more open and light forest compared to spruce forests at the three southerly catchments which have much wider crowns.

Although changes in bottom layer species between the repeated surveys were observed, the effect of time was small when tested as an explanatory variable in the ordinations. The non-significant temporal effect in the bottom layer vegetation at Gårdsjön indicated that this catchment still 14 years after the first inventory had not changed its species composition since the early 1990s when S deposition was high. As the other sites with lower levels of deposition have changed their species composition, it is likely that the bottom layer vegetation at Gårdsjön still is affected by deposition, or that the recovery has not proceeded as far as at the other sites.

The weak temporal changes in species composition in the bottom layer may be related to the omission of species occurring in less than 5% of the plots. The omitted rare species were mainly found in the second survey and thus probably an effect of the change of observer. However, the analyses of direction of change showed that the temporal trajectories connecting the two analyses of the same plot in the ordination spaces had nonrandom directions, both for all catchments together and also (with the exception of Aneboda) when the catchments were analyzed individually. Thus, although the causes are not obvious, nonrandom temporal changes were detectable even when rare species were omitted. Furthermore, an ordination made using all species resulted in a significant ($p < 0.05$) effect of time, although it only explained 7% of the variation in the species data. Weak temporal changes over 5 years in boreal understorey were also found by Økland and Eilertsen (1996). The weak temporal effect is not surprising as the catchments span a broad biogeographical gradient, from boreo-nemoral to true northern boreal, and factors other than within-catchment temporal variation are expected to be important over such a gradient (Salemaa et al. 2008). The importance of spatial variation in the bottom layer was also confirmed by the relatively strong effect of 'catchment' in the combined analysis of all catchments.

The ordinations of the field layer vegetation did not show a significant effect of time. The strongest descriptors of the ordination patterns were catchment and diversity variables, closely followed by the Ellenberg indices, while the forest stand variables showed weak correlations with the floristic patterns for the field layer. In a more extensive study of forest understorey vegetation in Norway, Økland and Eilertsen (1996) concluded that the plant communities were affected by both catchment location and soil acidification, but not by N deposition, and the present study supports this conclusion.

CONCLUSIONS

Changes in species occurrence and composition of the bottom and ground vegetation layers were found, but the changes showed no clear or consistent direction. For the bottom layer, much of species turnover was ascribed to observer effects, underlining the importance of observer consistency in such studies. Nevertheless, the results showed clear differences between the catchments in species composition and that the drivers of the observed temporal changes differ between the catchments. However, it was not possible to unequivocally attribute the differences in the bottom and ground vegetation between catchments and changes over time to patterns and trends in N and S deposition. The Ellenberg indices showed very small temporal changes and the magnitudes of changes for the species that showed a significant change were not correlated with their Ellenberg values.

From the results in this study, it can be concluded that internal catchment factors outweigh temporal change for both bottom and field layers, and that soil acidity for the field layer and soil moisture for the bottom layer, both indicated by Ellenberg indices, are the factors most strongly influencing species composition within catchments. Natural dynamics in long-established boreal forests are characterized by gap regeneration (Hytteborn and Verwijst 2011), with wind, fire, and insect attacks being the most important factors for gap creation (Messier et al. 2009). The protected and unmanaged forests at the Swedish IM sites were at a mature stage, even by the time of the first inventory, and gaps were rare. However, in 2005 the forest at Aneboda suffered from a severe storm and a subsequent mass infection of bark beetles, and large changes in the vegetation can be anticipated. The stable conditions prior to 2005 meant that the canopies at all catchments were relatively closed resulting in rather similar understorey light regimes and micro-climates at all four catchments, overriding the effect of decreasing deposition.

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AUTHOR BIOGRAPHY

Ulf Grandin (✉) is a researcher and lecturer at the Swedish University of Agricultural Sciences. His research interests include vegetation dynamics in boreal forest ecosystems and long-term ecological research.

Address: Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Box 7050, 750 07 Uppsala, Sweden.

e-mail: ulf.grandin@slu.se