The Impact of Logging on Species Richness and Turnover of Field Layer Species in Swedish Boreal Forests

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Abstract: On two occasions, with a 10- or 11-year interval, species occurring in 650 plots (100 m^2) in boreal production forests in Sweden were recorded within a monitoring program. During this interval, many of the plots had been subjected to varying degrees of timber extraction. The presence of 49 vascular plant species or species groups was recorded and we evaluated how species number varied over time. There was an overall increase in species number, probably partly reflecting changing attitudes and strategies for fieldwork. Logging had a modest, but significant positive effect on the change in species number per plot. When analysing individual species, three of 18 showed a differential response along the logging gradient: *Linnea borealis* was more likely to appear at low logging intensities while the opposite pattern was present in *Epilobium angustifolium* and *Calluna vulgaris*. A species turnover index was calculated per plot and used as the dependent variable in a multiple regression with six independent variables. Three of these contributed significantly to the model: turnover increased (i) with decreasing amounts of *Pinus sylvestris* in the tree canopy; (ii) with increasing site productivity; and (iii) with increasing logging intensity. Hence, greatest changes over time occurred in stands lacking *P. sylvestris* (consequently dominated by *Picea abies*) that occurred on fertile soil, and was amplified by logging.

Key Words: Clearcut, monitoring, permanent plots, species richness, succession, Sweden, vascular plants.

1. INTRODUCTION

From the late 1970s onwards, the forestry sector has been influenced by a growing public concern about maintaining biodiversity. In Canada, Finland and Sweden, forestry practices and integrated management plans have been developed to favor maintenance of biodiversity [1, 2]. In Sweden, forestry practices have changed due to the Forestry Act of 1994 [3] and due to influences from the certification of many Swedish landowners by the Forest Stewardship Council (FSC). The questions then become: (i) What measure(s) of biodiversity can be used to evaluate the fulfillment of the bold objective to preserve biodiversity in production forests [4]? and (ii) is there available data from present surveys or inventories that are possible to use? Once a measure has been selected, we would need to know the baseline variation of such a measure, and how it is affected by different forestry practices. One such possible measure is species richness: the number of species per area in the vegetation (excluding tree species, as these are the target for forestry). This vegetation is a dynamic system known to respond not only strongly to logging [5-14] but also to the increasing canopy density of a growing tree stand [15-17]. Hence, in addition to the spatial variation in species richness [17, 18], we should expect a temporal variation. However, the baseline temporal variation in the parameter 'species richness' is poorly known [19], as is its response to logging. In Sweden, the National Forest Inventory (NFI) together with The National Survey of Forest Soils and Vegetation (NSFV) have been running for

many years recording numerous variables, among them vegetation, site productivity and soil data, etc. Similar surveys are being conducted in a number of countries. These surveys have seldom been used for purposes not intended when they started (but see [16, 20]).

In the present study, we investigated if data from the NFI and NFSV was possible to use in evaluating the change in species richness as well as turnover of species in field layer vegetation. Data from 650 permanent monitoring plots resampled after 10 or 11 years in managed boreal coniferous forest were used. We attempted to estimate the impact of the intensity of a single logging event on the apparent loss and recruitment of species. Our objective was to evaluate the extent to which species turnover depends on logging intensity (i.e. percentage volume felled of volume standing before cutting) in comparison with variables known, or suspected to influence the species composition of the field layer flora.

2. MATERIAL AND METHODS

2.1. Data

In 1983-1987, the National Forest Inventory (NFI) of Sweden established permanent plots with an aim to revisit them at 5-year intervals. Parallel to this, the plots were also subjected to a soil and vegetation inventory by the National Survey of Forest Soils and Vegetation (NSFV; www-markinventeringen.slu.se). The Swedish University of Agricultural Sciences (SLU) executed both inventories, and the data are kept in databases managed by the Department of Forest Resource Management at SLU.

For logistical reasons, the sample plots are located along the sides of a quadrate; one quadrate corresponds, in central

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and northern Sweden, to one days work by an inventory team. The distance between quadrates varies from 7 km to 15 km with the greater distances in the northern part of the sampling area [21]. The quadrates side length also differs, from 800 m in the southern to 1000 m in the center and 1200 m in the northern part of the area, a quadrate has one sample plot at each corner of the quadrate and one in the middle of each side, i.e. eight in total with a distance of 400, 500 and 600 m apart [21, 22]. The sample plots are circular, permanently marked with an aluminium pole. The vegetation is surveyed in a plot with a radius of 5.64 m (100-m^2) and the forest variables are collated from plots with radii 10 or 20 m.

The sample plots used in this study were established between 1983 and 1987. The plots were revisited by NFI for the first time in 1988-92, but on this occasion only forestry variables were recorded and no vegetation or soil inventory was made. Plots were then revisited in 1993-98 for a third NFI and a second NSFV recording, the interval between the NSFV inventories being 10 or 11 years.

2.2. Selection Criteria

We decided to concentrate on the boreal coniferous forest of northern and central Sweden (the geographic regions 'southern boreal' and 'middle boreal'; [23]), a vast but still relatively homogeneous area. Coniferous forests dominated by *Picea abies* and *Pinus sylvestris* prevail in this part of Sweden, where it is practically the only managed forest type. In the 'southern boreal' there are some nemoral broadleaves (e.g. *Quercus robur, Tilia cordata, Ulmus glabra*; nomenclature according to [24]) which are lacking further north.

We applied a number of criteria to select appropriate and homogeneous plots for the current study:

i   Plots should be classified as 'forest'.

ii   At least 85% of the standing timber volume at the first inventory should consist of conifers (i.e. *Picea abies* and/or *Pinus sylvestris*).

iii   At the first inventory, the trees should have a mean girth >100 mm at breast height (maturity classes C1- D2; [25]).

iv   To increase the homogeneity of the forest vegetation data, samples from plots classified as 'dry' or 'moist' (see [26]) or occurring on organogenic soils were omitted.

v   Sample plots that were divided by different kinds of boundaries, e.g. between land-use classes, stand-maturity classes, or moisture classes, were excluded.

vi   In a few plots, two separate cuttings had taken place between the inventories, and these were excluded.

vii   One plot was excluded because cutting had not been recorded although some trees had been removed.

viii   The vegetation survey was made for a 'representative area' of the sample plot. This means excluding parts of a sample plot that have been subject to disturbance, like soil scarification, walking tracks, etc. Another reason for using a 'representative area' smaller than the plot size was the presence of, for example, rock outcrops, large boulders, stumps or piles of slash residues. Since the areas omitted could differ between the inventories,

the surveyed areas could differ substantially between the two occasions, making comparisons doubtful. Therefore, sample plots where the area surveyed differed by more than 10 m^2 between inventories were excluded. This limit is arbitrary, but the procedure reflects what users of data from this monitoring system are likely to do to reduce possible bias in data.

These criteria led to 650 sample plots being selected for the present study. These plots were situated in stands of *Picea abies* and/or *Pinus sylvestris* where thinning or final harvesting would be next recommended management practice, and did not exhibit substantial within-plot heterogeneity. Plots were distributed from latitude N59° 15` to N67° 28`. They can be considered to be representative of the typical conifer forests subjected to forestry in northern Sweden, excluding moist and dry sites.

2.3. Species Occurrences

The objective of the NFSV was originally to improve the forest site classification system [27], which is reflected in the pre-determined list of species and groups of species subjected to the inventory. The species are recorded by presence/absence and, for a selection of them, also cover (such data were not used in the present study). In total, 49 species and groups of species had been recorded on the two occasions in the selected plots (Table **1**).

2.4. Other Variables

Numerous variables are recorded by the NFI and NSFV and some of these were used in the present analyses, either directly or indirectly, to calculate new variables (Table **2**). The variables percentage *Pinus sylvestris*, age, temperature sum, volume and productivity came from the survey prior to cutting.

A turnover index (T; [28]) was calculated for changes in species composition in each sample plot from the first to the second inventory:

$$T=(A+DA)/(A+DA+B) \qquad (1)$$

where

T=turnover index

A=number of appearing species;

DA=number of disappearing species;

B=number of species present on both occasions.

If any logging activity had taken place between the two inventories, the time and intensity of the cutting were estimated for each sample plot.

The time was calculated from the two occasions on which forest inventories had been performed. On each occasions the time from cutting was estimated in the field in four classes: current growth season (season 0), previous season (season 1), season 2, or season 3-5 (a season is defined as the time between two subsequent budbreaks, which is easier to determine in the field than whether a tree was felled before or after 1st of January, a particular year).

The intensity of logging (I) was expressed as percentage volume felled of volume standing before cutting. To further

Table 1.   Presence of Species in 650 100-m^2 Sample Plots Surveyed on Two Occasions with 10- or 11-year Interval

Species	Both	Disappeared (D)	Appeared (A)	Absent	"Minimum Detectable Change" (D-A) or (A-D)[1]	McNemar (DF =1)	McNemar P-value	Wald statistic	P-value
Vaccinium myrtillus	631	4	8	7	15	0.75	0.39[2]	0.59	0.44
Vaccinium vitis-idaea	603	7	16	24	23	2.78	0.095[2]	3.3	0.068
Linnea borealis	176	34	178	262	36	96.46	<0.0001***	21.3	<0.0001***
Melampyrum spp.	90	35	250	275	43	161	<0.0001***	0.26	0.61
Empetrum nigrum	253	36	30	331	34	0.38	0.54[2]	0.0065	0.94
Trientalis europaea	48	20	189	393	45	135	<0.0001***	1.7	0.19
Maianthemum bifolium	152	35	63	400	38	7.44	0.0064[2]	0.21	0.65
Calluna vulgaris	173	30	29	418	34	0	1[2]	14	0.0002**
Epilobium angustifolium	53	33	72	492	45	13.8	0.0002**[2]	34.5	<0.0001***
Solidago virgaurea	30	15	111	494	44	71.62	<0.0001***	1.2	0.28
Vaccinium uliginosum	90	22	29	509	32	0.71	0.4[2]	4.4	0.036
Gymnocarpium dryopteris	97	25	18	510	29	0.84	0.36[2]	3.3	0.067
Oxalis acetosella	63	27	21	539	32	0.52	0.47[2]	4.8	0.028
Rhododendron tomentosum	57	9	9	575	23	0.055	0.82[2]	0.22	0.64
Rubus saxatilis	36	19	16	579	39	0.11	0.74[2]	0.26	0.61
Geranium sylvaticum	48	15	3	584	25	6.72	0.0095[2]	5	0.026
Anemone nemorosa	29	7	18	596	37	4	0.046[2]	0.1	0.75
Potentilla erecta	18	13	20	599	46	1.09	0.3[2]	0.23	0.88
Rubus chamaemorus	25	10	11	604					
Viola spp.	17	13	15	605					
Andomeda polifolia Vaccinium oxycoccus	23	3	16	608					
Fragaria spp.	15	3	11	621					
Phegopteris connectilis	14	5	7	624					
Veronica spp.	5	2	17	626					
Pteridium aquilinum	11	4	5	630					
Equisetum palustre	6	6	5	633					
Filipendula ulmaria	11	1	2	636					
Geum rivale	6	4	4	636					
Ranunculus spp.	3	1	9	637					
Cornus suecica	6	2	3	639					
Crepis paludosa	4	1	5	640					
Moneses uniflora	1	3	5	641					
Cirsium helenoides	1	6	2	641					

Species	Both	Disappeared (D)	Appeared (A)	Absent	"Minimum Detectable Change" (D-A) or (A-D)[1]	McNemar (DF =1)	McNemar P-value	Wald statistic	P-value
Anemone hepatica	5	1	2	642					
Paris quadrifolia	4	1	2	643					
Cicerbita alpina	1	2	2	645					
Convallaria majalis	4	0	1	645					
Rumex acetosa	0	2	2	646					
Silene dioica	0	1	3	646					
Mycelis muralis	0	2	2	646					
Aconitum lycoctonum	2	1	0	647					
Alchemilla spp	1	1	1	647					
Angelica sylvestris	1	0	2	647					
Arctostaphylos uva-ursi	0	3	0	647					
Urtica dioica	1	0	1	648					
Parnassia palustris	0	1	1	648					
Selaginella selaginoides	0	0	1	649					
Equisetum hyemale	0	0	1	649					
Tofieldia pusilla	1	0	0	649					
Listera ovata	1	0	0	649					

"Both"=number of plots where the species were present on both occasions; "Absent"=the number of plots where the species were absent on both occasions. The Wald statistic (ordinal multinomial GLZ) evaluates whether the appearance, continued presence and disappearance of a species varied with logging intensity. Calculated P-values are given, and those significant after Bonferroni-correction are indicated with ** $P < 0.01$ and *** $P < 0.001$.
[1]Calculated from data given in [32].
[2]Below the detection level as defined by "mimimum detectable difference".

Table 2.   Description of Environmental Variables Recorded and Used in the Present Study

Variable	Description
Percentage *Pinus sylvestris*	volume *P. sylvestris* divided by total tree volume on the sample plot
Age	age of the stand (mean age of dominating trees)
Temperature sum	sum of temperature $\geq+5$ °C, calculated from climatological data with height above sea level and latitude as independent variables
Volume	volume of all trees ≥ 1.3 m in height on the sample plot
Productivity	productivity of the sample plot is calculated from site index for *Pinus sylvestris* and *Picea abies* - the higher of the two being used ($m^3ha^{-1}year^{-1}$).

enhance the accuracy in determining I, we also used the survey of 1988-92. It was calculated as:

$$I=100*((V_p+G_u*t_t)-(V_a-G_a*t_f))/(V_p+G_u*t_t)$$ (2)

where

V_p=volume at the inventory prior to cutting

V_a=volume at the inventory after cutting

G_u=growth per year from the inventory prior to cutting until cutting [29]

G_a=growth per year from the cutting until the inventory after cutting [29]

t_t=seasons from the inventory prior to cutting until cutting

t_f=seasons from the cutting until inventory after cutting

In some cases, this formula led to negative 'cutting intensity', an artifact due to the problem of determining the time of cutting in the field and of calculating annual growth. Annual growth is based on differences in volume on trees from both occasions with an added variation derived from sample trees, volume is calculated from form height functions and diameter measurements (i.e. basal area). This often results in a negative 'growth' for a sample plot due to error in measurement of diameter (if not allowed, total growth would be biased since measurement errors also can exaggerate differences in diameter).

2.5. Analyses

Five available variables known or suspected to influence ground vegetation (Table **2**) and logging intensity were used in six separate generalized linear models (GLZ) using the identity link function and normal distribution (Statistica 7 software; [30]) with the turnover index (T) as response variable.

A two-sided McNemar test [31] was used to evaluate species-wise changes over time. This type of survey data has a non-negligible error, that vary between species. In a previous study [32], data on errors from the current survey scheme are presented, and based on these data we made species-wise estimates of the "effect size" (i.e. change over time) needed to yield significant results at the 5% level nine times out of ten (power=0.9). We called these effects sizes "minimum detectable differences" and applied them as a filter, to eliminate significant results on species subject to high risk of type I error.

Species-wise responses to logging intensity, that could take the form of +1 (appearance), 0 (continued presence) and -1 (disappearance), were evaluated in GLZs using ordinal multinomial regression (logit link function) with the Statistica 7 software [30].

3. RESULTS

3.1. Change in Species Number

There were substantial differences in species number recorded between the two inventories (Fig. **1b**). Also, there were more gains than losses: 91 plots lost species while 404 gained species. The magnitude of this temporal difference can be estimated from the regression in Fig. (**1b**) ($F_{(1,648)}$= 4.97; y=1.056+0.557*x), where the intercept was 1.1 (SE 0.090). Additionally, the impression from Fig. (**1b**) is that the change in species number is resilient to logging: although the slope was statistically significant (P=0.0262), it explained less than 1% (R^2=0.0076) of the variation in change in number.

3.2. Turnover of Species in Vegetation

Although there was a highly significant relationship between turnover index and logging intensity (Fig. **1c**; $F_{(1,647)}$= 13.7; P=0.00023; y=0.333+0.0903*x), it was weak as only 2% (R^2=0.021) of the variation in the index could be explained by the model. Logging intensity did not significantly affect the number of species found on the second visit ($F_{(1,648)}$=0.00068; P=0.979; Fig. **1a**).

3.3. Factors Affecting Species Turnover

The variable tested with the highest explanatory power for species turnover was percentage *Pinus sylvestris* (Table **3**): higher percentage of *Pinus sylvestris* meant a smaller turnover index of ground layer species. Site productivity was another important factor, while logging intensity seemed much less important (Table **3**). The evaluation of factors affecting species turnover is complicated by correlation between chosen factors. For example, site productivity correlates to both volume (R=0.39) and temperature sum (R= 0.65).

3.4. Species-Wise Responses

Of the 18 most common species (recorded in >50 plots), several were generally more abundant in the second than in the first inventory (Table **1**), as shown by eight having a significant change over time according to the McNemar test. However, after applying the "minimum detectable difference" as a filter, only four species remain reliably significant: *Linnea borealis*, *Melampyrum* spp., *Trientalis europea* and *Solidago virgaurea* (Table **1**). The ordinal multinomial regressions identified only three species whose response varied with logging intensity (Table **1**). At high logging intensity, *Linnea borealis* mainly disappeared while most appearances were at low intensities; in contrast, appearances of *Calluna vulgaris* and *Epilobium angustifolium* were mainly at high logging intensities (Fig. **2**).

4. DISCUSSION

4.1. A Methodological Note

The aim of the inventory, from which the current data were derived, was originally to improve the Swedish system for estimating site productivity by means of easily-assessed variables, among them presence/absence of plant species. This meant that common species with a (suspected) low sensitivity to changes in the environment were chosen. Since the inventory started, the monitoring of biodiversity of field layer flora has been added as an aim and this has probably influenced the field personnel in their work to find species. Therefore, small and inconspicuous species are likely to have been underestimated during the first inventory, and absolute changes in species numbers recorded are suspect. For this reason, we focus the discussion below on the relative differences between species, and put less effort into interpretation of species-wise responses. Another reason for some caution regarding species-wise data is that a substantial number of occurrences are always missed [32]. In the present study, we were fortunate to have species-wise estimates of this detection error [32], enabling us to apply detection limits in the tests used.

4.2. Change in Species Number

The substantial differences in species number recorded between the two inventories (Fig. **1b**), and the fact that there were more gains than losses, suggests a general increase in species richness or, more likely, an increased search effort (see above). The magnitude of this temporal bias can be estimated from the regression in Fig. (**1b**), where the intercept was 1.06 (SE = 0.0897). Apart from showing the magnitude
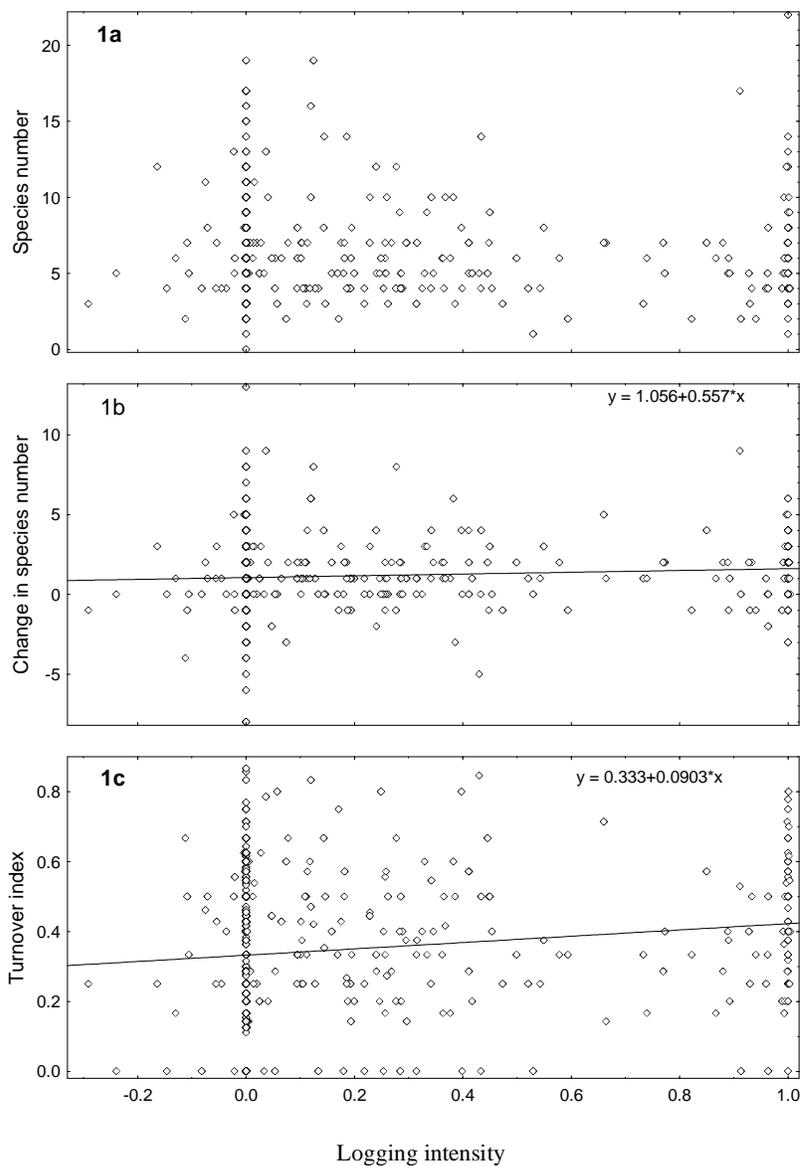
Fig. (1). 1a) Species number on second visit, **1b**) change in species number and **1c**) turnover index for 650 permanent plots, visited on two occasions with an interval of 10 or 11 years, in boreal coniferous forest of Sweden. Turnover index was calculated as T=(A+DA)/(A+DA+B) where A=number of appearing species; DA=number of disappearing species; B=number of species present on both occasions. Logging intensity was calculated from the data on timber volume before and after logging, annual growth and seasons from logging (the formula sometimes led to negative logging intensities because of the problem of determining the time of logging and calculating annual growth). There was a non-significant relationship in 1a and positive relationships in **1b** and **1c**.

Table 3.   Six Separate GLZs, (Normal, Identity Link) Predicting Species Turnover From Various Site Parameters (N=650)

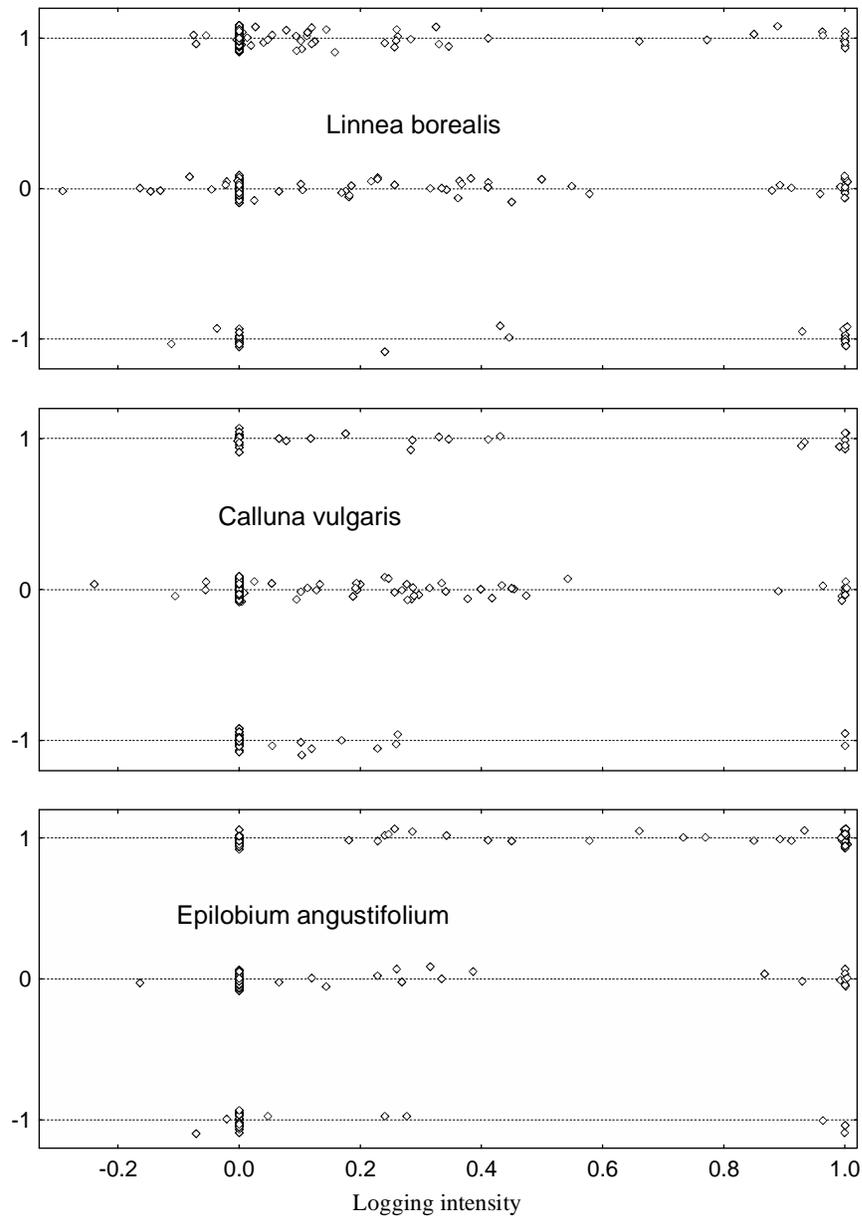|	**Degr. of Freedom**	**Wald Statistic**	**P**	**Direction of Relationship**
Age	1	9.39	0.002183	-
Logging intensity	1	13.73	0.000211	+
Temperature	1	14.14	0.000169	-
Volume	1	31.02	<0.000001	+
Site productivity	1	86.97	<0.000001	+
Percentage Pinus sylvestris	1	97.20	<0.000001	-

Fig. (2). Appearance (1), continued presence (0) and disappearance (-1) in relation to logging intensity for species showing significance in ordinal multinomial GLZ (Table **1**). Data stems from 650 permanent plots visited on two occasions with an interval of 10 or 11 years in the boreal coniferous forest of Sweden. Logging intensity was calculated from the data on timber volume before and after logging, annual growth and seasons from logging; (the formula sometimes led to negative logging intensities because of the problem of determining the time of logging and calculating annual growth). A certain degree of jittering was applied to facilitate the separation of points for the purposes of illustration.

of temporal bias (assuming that there is no large-scale overall increase in species richness), this intercept might also enable the adjustment of species richness data. Additionally, the impression from Fig. (**1b**) is that the change in number of the species subjected to this survey was resilient to logging (the regression line in Fig. (**1b**) had a significant slope, but it explained less than 1% of the variation in change in species number).

4.3. Turnover of Species in Vegetation

Surprisingly, it seems as if cutting intensity had a low impact on species turnover. An analysis of related data [16]

on the change in cover of the important species in the field layer flora showed that cutting intensity has a great influence. So why is there such a difference between cover and species richness? One explanation could be that, with the present sample plot size, small-scale heterogeneity provides habitats for many species even when there is a major perturbation like forest canopy removal. Such small-scale heterogeneity can be created by the shade of stumps, heaps of cutting residues, shrubs, etc. Since most of the species in our study are relatively common in the boreal forests of Sweden, they can be assumed to be relatively resilient, at least on a larger scale, to natural disturbances such as forest fires and

wind-thrown trees [33]. In Scandinavia, bryophytes and lichens (not included in the present study) are more sensitive to logging than vascular plants [34-36].

Pykälä [13] reported a substantial increase in species richness after clear-cuttings in boreal forest, and there can be at least three reasons why our results differ. First, the time period considered differed: time from logging to the post-logging survey was 1-11 years in our data while Pykälä [13] looked at the response 1-2 years after logging. Second, the parts of plots subjected to soil scarification were excluded in our data but not in Pykälä's. Third, site productivity was higher in Pykälä's sites than in ours, and the change in species richness in our data tended to increase with site productivity (data not shown).

Returning to the initial aim of the survey, namely to improve the Swedish forest site classification system, we conclude that the selection of species is appropriate. Even if a few species (*Linnea borealis*, *Calluna vulgaris, Epilobium angustifolium*) varied with logging intensity (i.e. percentage volume felled of volume standing before cutting), they are species with rather little impact on the classification of a site. In contrast, most species seemed resilient to logging. Hence, their potential indicator value for site productivity is not greatly affected by forestry operations (even if individual species might appear/disappear to a surprisingly high degree). For the added aim of monitoring biodiversity, the inventory strategy is less suited. First, 'disturbed' patches (bare soil, rocks, etc.) within plots are omitted from the inventory. This eliminates the recruitment of ephemeral species on bare soil, e.g. annual *Senecio* spp. and *Galeopsis* spp. and also complicates the comparison over time, as the area surveyed might not be of similar size. Second, it is possible that the species chosen might be more resilient to disturbances than average, thereby leading to an underestimation of possible changes in the environment. Third, the size of the sample plot might be less suited to detect changes in the composition of the flora, smaller plots have been demonstrated to better identify changes [19, 37]. Fourth, the presence/absence data exhibited relatively large fluctuations in species number (Fig. **1b**) over time, but nevertheless species richness seemed resilient to a severe impact like canopy removal. Hence, the power to detect a signal of environmental change seems low in the present data. To conclude, the possibility of detecting temporal pattern in this survey will be limited by sample size, and is likely to be useful only for detecting large impact(s), and possibly only over longer time-spans. Its usefulness to detect shifts in species distributions might be more promising.

4.4. Factors Affecting Species Turnover

The most significant variable influencing species turnover was percentage *Pinus sylvestris* (Table **3**): higher percentage of *Pinus sylvestris* meant a smaller turnover index of ground layer species. Site productivity was another important factor, while logging intensity seemed much less important (Table **3**).

Of the two conifers that dominate the boreal forests of Sweden, *Pinus sylvestris* and *Picea abies,* the latter is most common on moist and fertile soils and in areas with higher productivity, and consequently *Picea*-dominated stands generally have longer crowns and denser tree canopies and lower light levels at ground level. There are also architectural differences in crown structure between the two tree species, typical of these two genera, which might also contribute to differences in light regime. Consequently, there are several factors involved in creating differences in vegetation composition between stands dominated by *Pinus sylvestris* versus *Picea abies*. Our results suggest that field layer species are more long-lived in *Pinus*-dominated stands, most likely due to consistent differences in species composition but possibly also due to a slower growth rate [19].

In conclusion, it is clear that the turnover of vascular species in the ground layer flora is mainly affected by what tree species comprise the canopy and by soil fertility. Logging, however, had a surprisingly small effect on our turnover index.

4.5. Species-Wise Responses

A potential bias in the data collection might exist because the scope of the inventories had changed between the first and the second visits (see above). All four species that changed significantly (according to McNemar tests) and that also changed more than the "minimum detectable change" (established on data presented in another study; [32]) were rather small and inconspicuous herbs that increased. For such species, small occurrences are easily overlooked unless carefully searched for.

The ordinal multinomial regressions, which should not be sensitive to the above-mentioned bias, identified only three species whose response varied with logging intensity (Table **1**). At high logging intensity, *Linnea borealis* mainly disappeared while most appearances were at low intensities; in contrast, appearances of *Calluna vulgaris* and *Epilobium angustifolium* were mainly at high logging intensities (Fig. **2**). *Epilobium angustifolium,* a light-requiring species considered as an opportunistic colonizer [38-40] with extreme seed-dispersal abilities [41], appeared on many plots subjected to high logging intensities. At first, our data might seem to suggest that colonization has occurred, implying that the opportunistic occurrences are mainly due to colonization from seed. However, considering the potential bias in data collection (see above), the species might have been overlooked when occurring as scattered and non-flowering shoots. *Calluna vulgaris* was likely to have been recruited from its persistent soil seed bank [42].

5. CONCLUSIONS

Species number per area might be a useful measure in monitoring (e.g. [37], but it is a parameter susceptible to observer error, and potentially also observer bias (c.f. [32, 43-45]), especially when using permanent plots with large size, as in the present survey. Therefore, it is doubtful whether, concerning data from this survey, 'species number' carries the information required for a meaningful evaluation of change. Furthermore, the present study documented changes in species number of surprising magnitude, even in the absence of any forestry operation(s) between the two occasions, this can partly reflect forestry operations taking place before the permanent plots were established (a feature not included in the analyses) as well as changes in search

effort and experience among observers. Consequently, time series with many point in time, or a large number of permanent plots, are needed to discern trends from fluctuations in species number (both real and observer-biased) within a monitoring scheme. Data carrying more information than presence/absence, such as percentage cover of species might be more useful.

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