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Plant species richness in managed boreal forests—Effects of stand succession and thinning

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ABSTRACT

Disturbance is a key factor affecting plant species richness and it has been hypothesized that species richness reaches a peak some time after disturbance occurs. Managed boreal forests are characterized by large scale disturbance in the form of clear-cuttings, which partly resembles natural disturbance regimes. The young stands however, which may be important to many plants, are often homogenous and dense compared to naturally regenerated stands. We examined previously unstudied effects of disturbance, succession and management practices on plant species richness in boreal forests. Survey data covering the northern and central parts of Sweden (4465 plots) were used to compare species richness and composition in four stand maturity classes—“cutting”, “young”, “pre-mature” and “mature”, and two fertility classes—“rich” and “poor”. In addition, the effect of thinning was examined in young and pre-mature forests.

In both pine and spruce forests species richness was higher in the “cutting” and “young” classes than in the “pre-mature” and “mature” classes. In pine forests, the difference in species richness between young and mature forests was greater in “rich” than in “poor” fertility classes. Spruce forests grow on somewhat richer sites than pine forests, but there was no significant effect of site fertility within these stands. A few Ericaceous species were dominant, although this trend is slightly relaxed in favor of pioneer species in the “cutting” and “young” classes, which results in higher species richness. Plant communities were also affected by thinning. Stands thinned in the “young” maturity class exhibited higher species richness in both the “young” and “pre-mature” classes than did unthinned stands. Thinning in the “pre-mature” class had no effect on species richness.

We conclude that a peak in plant species richness was recorded in early forest succession stages, especially in fertile sites. Moreover, early pre-commercial thinning seems to promote and sustain this diversity. Hence, young stands and their management may play a central role in the preservation of plant diversity in boreal production forests. We suggest that thinning practices could be developed to support plant diversity, for example the creation of larger gaps in lush young forests.

1. Introduction

The role of disturbance for plant species richness has been a central theme in ecology for several decades (Connell, 1978; Chesson and Warner, 1981; Higgins et al., 2000; Haeussler et al., 2002; Sheil and Burslem, 2003). Many studies agree that high local species richness is a transient property, dependent on an appropriate disturbance regime for its maintenance (Connell, 1978; Huston, 1979; Sheil, 1999; Shea et al., 2004). One of the best known of the disturbance-based theories, the intermediate disturbance hypothesis (Connell, 1978), states that the maximum species richness is found at intermediate levels of disturbance or at an intermediate stage of development since the last major disturbance event (Cordonnier et al., 2006). If communities remain undisturbed for long periods, they will be dominated by a few competitively superior species and pioneer species are driven to extinction. High levels of disturbance will favor fast reproducing pioneers over long-lived stress tolerant plants. At an intermediate stage between these two extremes both types of species will be able to survive, resulting in an increase in the number of co-existing species. Many theoretical and empirical studies have shown an increase in species richness at intermediate levels of disturbance, however, several studies have also shown other types of relationships, including negative and bimodal patterns (Halpern and Spies, 1995; Schwilk et al., 1997; Mackey and Currie, 2000; Johst and Huth, 2005).

One important factor thought to affect disturbance—diversity relationships is productivity (Grime, 1979; Grace, 1999; Kondoh,

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2001; Kadmon and Benjamini, 2006). Grime (1979) suggested that on rich sites, which contain a wider array of plant types and life histories, disturbance has the potential to create opportunities for more species to co-exist, and thereby increase diversity. Low productivity sites, on the other hand, contain few species, most of which have stress tolerant life history traits. At these sites diversity will not increase with disturbance.

Despite the fact that boreal forests are subjected to major disturbances, in form of fire, wind and clearfelling (Parviainen, 1996; Ruokolainen and Salo, 2006), few studies have been concerned with plant diversity in early forest successions and how this is affected by management (But see Hart and Chen, 2008). Traditionally, research on forest diversity has mostly been concerned with the diversity associated with old growth forests. In recent years, however, processes such as disturbance and succession have become more central to the development of sustainable forest management strategies (Angelstam, 1998; Askins, 2001; Bergeron et al., 2002; Kuuluvainen, 2002; Junninen et al., 2006). Plant succession is known to follow major disturbance to the crown cover (Halpern and Spies, 1995; Nygaard and Odegaard, 1999; Pykälä, 2004; Ruokolainen and Salo, 2006), with pioneer species colonizing the open stages and with stress tolerant species tending to become more dominant as the forests mature (Bråkenhielm and Liu, 1998; Nygaard and Odegaard, 1999). Studies have also shown that the number of species may increase after disturbance (Nygaard and Odegaard, 1999; Pykälä, 2004). However, little is known about how species density, i.e. the number of co-existing species per unit area, changes with forest maturity (or time since major disturbance) and how this differs in forests of different productivity and with different management regimes.

Today, clear-felling, is the main type of whole stand disturbance in managed forest landscapes. Wildfires, the main large scale disturbance reducing canopy cover in natural forests, are rare in modern production forests (Parviainen, 1996; Engelmark, 1999), as a result of improved fire prevention. Stormfellings and insect outbreaks occur infrequently but timber is salvaged and hence the result is similar to a clear-felling operation. Even if clear-felling in several ways resembles natural large scale disturbances, for example with regard to light conditions, there are also important differences. It is rare that all trees die after natural disturbance, which results in a structural diversity in the new stand. The young stands established in the clear-cut are often homogenous and dense compared to naturally regenerating forests. It has also been shown that young forests have become denser in resent years due to decreased thinning activity (Anon, 2002). Hence, the positive effects of disturbance on species richness in early or intermediate stages of succession may possibly be impaired. This highlights the importance of studying the effect of thinning on plant diversity, together with stand succession, in managed forests.

In the present study, we examine how disturbance, in the form of cutting and thinning, affects plant communities in boreal forests. The analysis is based on survey data covering most of northern and central Sweden; a data set that contains variables such as forest maturity, thinning regimes and fertility as well as an inventory of the field layer plant community.

More specifically our study is based on four predictions. First, we examine how the number of plant species per unit area changes during the succession following clear-cutting. Our prediction is that (1) plant species richness will be highest at stages following cutting, i.e. during the cutting or young forest stages. In terms of species composition, we predict that (2) the increase in species richness will be the result of colonization of early seral plants in sites dominated by a few shade tolerant species in mature forest stages. Moreover, we examine how thinning operations, as a small scale disturbance, affect plant communities in both the young and pre-mature forest classes. We predict that (3) plant species richness will be higher, and hence the effect of cutting sustained, when stands are thinned. We also relate the effects of both cutting and thinning to site fertility. We predict that (4) both the number of species and the increase in species richness due to disturbance is highest on fertile sites. Finally we close the paper with a discussion of the results with respect to the preservation of forest diversity. We discuss how management could be developed to create more favorable disturbance regimes for plant diversity in managed boreal forests.

2. Materials and methods

2.1. Forest and plant data

This study is based on data from the National Forest Inventory (NFI) and National Survey of Forest Soils and Vegetation (NSFV) of Sweden. These surveys cover the whole forested area of Sweden and have been conducted, in their present form, since 1983. Initially the objective of the survey was to assess forest productivity and relate this to variables such as vegetation, soil type and slope. In the last decade, the purpose of the survey has broadened to be more suitable for environmental monitoring, and more variables and plant species have been included (Odell and Ståhl, 1998). The database, rather unique with respect to its duration and the area covered, has until recently not been used for ecological issues (Bergstedt and Milberg, 2001).

The surveys are designed so that sampling plots are located along the sides of quadrates (side length: 1200 m in northern and 1000 in central parts of Sweden) which are evenly distributed in a grid system covering the whole of Sweden. One quadrate contains eight plots, one in each corner and one on the middle of each side. Further details of the survey design are given in Ranneby et al. (1987).

A subset of permanent plots (20 379 plots) was the subject of a vegetation and soil inventory under the auspices of the NSFV. This survey included a detailed inventory of the bottom layer bryophytes and field layer plants as well as the shrubs present. Sample plots for the forest variables were circular with a radius of 10 or 20 m. The vegetation plots had the same centre point as the forest plots, with an area of 100 m^2, i.e. a radius of 5.64 m.

The NSFV vegetation inventory of vascular plants consisted of presence/absence data for 201 plant species or species groups. The 201 plant species are:

- Species common over a large part of Sweden or common in large regions.
- Species typical for a broad range of forest habitats including grazed forests, marshes and forested rocky outcrops.
- Species easy to identify over a whole season (May–October), including non-flowering and vegetative stages.

Data for grasses and sedges in the database were limited to only a few species and these were included in form of four general groups defined by the NSFV on both ecological and morphological as well as methodological grounds. Poaceae were grouped into two categories—broadleaved (Dominated by *Poa nemoralis*, *Melica nutans*, *Deschampsia cespitosa*, *Agrostis capillaris*, *Calamagrostis arundinacea*, *Milium effusum* and *Phragmites australis*) and narrowed leaved (dominated by *Deschampsia flexuosa*). Sedges were divided into the categories ‘sedges on moist ground’ and ‘sedges on non-moist ground’ (Appendix 1). Species nomenclature follows Karlsson (2004).

2.2. Study design

The study was restricted to the northern and central parts of boreal Sweden (Fig. 1). This area constitutes a large part of the Swedish forested land but is still rather homogenous with respect

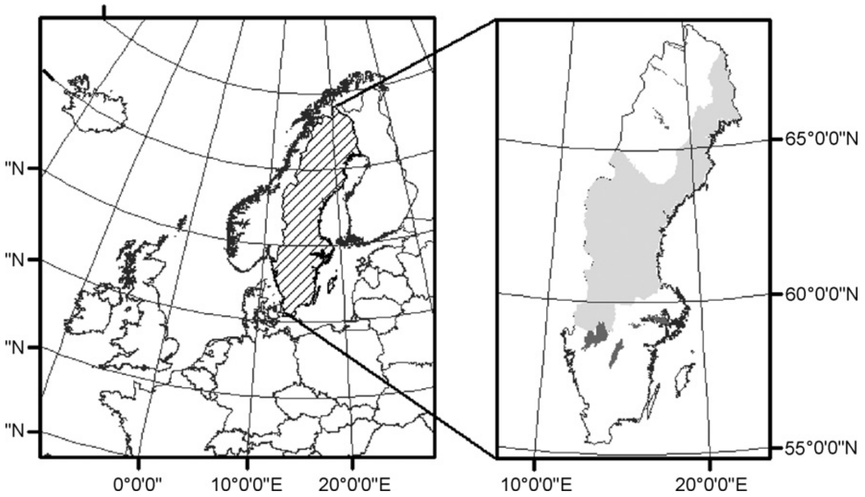

Fig. 1. The area of north-eastern and central Sweden (grey area in right panel) from which survey data in the study were collected. Number of plots = 4465.

to climate and forest type (Kempe et al., 1992). Moreover, the study was restricted to include only pine (*Pinus sylvestris* L.) dominated and spruce (*Picea abies* (L.) H. Karst.) dominated stands (>70% crown cover). In the full data set, pine and spruce stands were by far the most common types, and the only stand types which had sufficient observations in each category to allow statistical analyses of the effect of maturity class, productivity and thinning. In addition to these two selection criteria, the study included only standard sized, non-divided plots representing a single forest type; the aim was to optimize the species richness comparisons. These restrictions resulted in 4465 plots; 2927 pine dominated and 1538 spruce dominated.

For pine and spruce, respectively, the plots were divided into eight classes: four maturity classes within each of two fertility classes. The maturity classes were based on the maturity classes defined in the field instructions for the NFI (Anon, 1983–2003). The first class "cutting" was defined as stands with trees shorter than 1.3 m (maturity class B1 in NFI). The second class "young" was defined as stands with a mean tree height of more than 1.3 m but with a diameter less then 100 mm (B2–B3). The third class "pre-mature" (C1–C3) was defined as stands containing trees with a diameter larger than 100 mm. The fourth class "mature" (C4, D1–D2) included stands which had reached the age and maturity appropriate for final cutting. The median age of mature stands, both pine and spruce, was 115 years. Of the spruce stands, 90% were older than 85 and younger than 155 years. Of the pine stands, 90% were older than 85 and younger than 145 years. We chose to use maturity classes rather than age classes because disturbance effects over time on field layer plants, such as for example light conditions, are related to stand structure rather than simply to the stand age. Time is however highly correlated with maturity class in the present study.

The fertility classes were "rich" and "poor" indicating, respectively, sites above and below the median fertility. The median fertility was 4 m^3/ha and year for pine and 5 m^3/ha and year for spruce and reflects mean production potential over one rotation (i.e. not current production at the time for measurement). Fertility was estimated in the field and was based on three factors: temperature climate, water and nutrient availability. For each factor there are several indicators (see Hägglund and Lundmark, 1981).

Thinning of forest stands during the rotation period is essential in order to produce high quality timber. Early in the rotation, cut trees are still too small to have any commercial value. This kind of thinning is known as "pre-commercial". As the forests grow, the trees cut during thinning operations become more valuable. Thinning of marketable wood is usually referred to as "commercial". The two types of thinning are recorded separately in the NFI. Pre-commercial thinning is recorded up to 25 years after the operation has been undertaken. Thus pre-commercial thinning, which is carried out almost exclusively in the "young" maturity class, may be recorded in the "pre-mature" class.

2.3. Data analysis

Species richness, i.e. the number of species per plot, was used as the response variable in the analyses. Prior to statistical analysis, these data were natural logarithm transformed to compensate for their skewed distribution. For ease of interpretation, species numbers are presented untransformed.

The effect of productivity and maturity class (successional stage) on species richness was tested using a full factor ANOVA, with productivity (two levels) and maturity class (four levels) as well as their interaction used to explain the variance in log number of species. The effects of thinning were analyzed in the same way, comparing the difference in log species number in thinned and unthinned stands, and with two levels of site fertility. All analyses were performed with type 3 sum of squares, since the data set was not balanced with respect to the variables tested.

Changes in species composition with stand maturity were described using correspondence analysis. This multivariate technique is appropriate because the data are represented by presence/absence (Legendre and Legendre, 1998). Species observed in fewer than ten plots were excluded from the analysis. Ordinations of species according to maturity class and site fertility are presented in biplots, representing the two first correspondence analysis axes.

For species with a mean cover of more than 10% in any of the maturity classes, changes in cover were also examined using an ANOVA with maturity class as the explanatory variable. For species with lower cover values, the measure of change probably involves too much uncertainty (Ringvall et al., 2005). The cover was estimated visually as a continuous measure.

To identify species which are strongly coupled to particular age classes an indicator species analysis was performed (Dufrêne and Legendre, 1997). The analysis calculates indicator values for all species by multiplying the proportional abundance of a species in a site type with the proportional frequency of a species in the same site type. The significance of values was tested using a Monte Carlo permutation test with 1000 runs. ANOVAs were performed using the GLM procedure and correspondence analyses using the

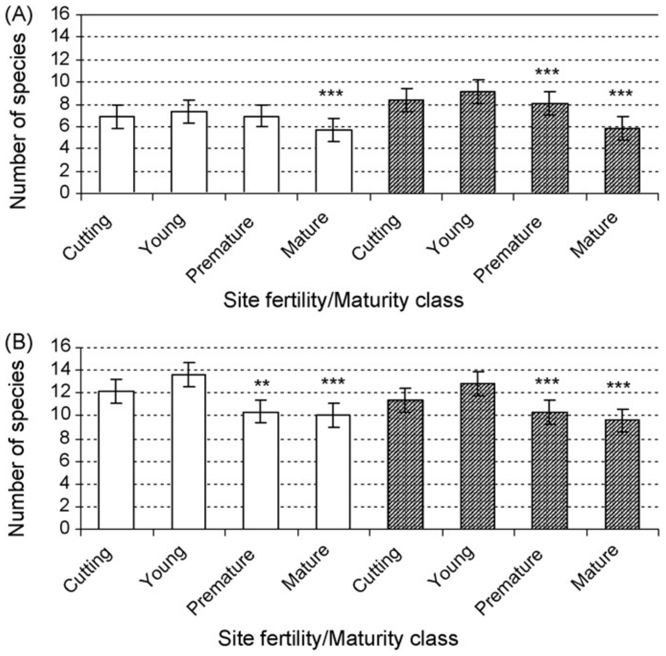

Fig. 2. Difference in the mean number of species between fertility and maturity classes. (A) Pine stands. (B) Spruce stands. Dark bars—"rich" sites. Significant differences from the "young" forest stage in an ANOVA of log number of species, with Tukey-Kramer adjustment for multiple comparisons (see Table 1) are indicated, *-$p < 0.05$, **-$p > 0.01$, ***-$p > 0.001$.

CORRESP procedure, in the SAS software (version 9.1). Indicator species analysis was performed using the PC-ORD (Version 4) statistical package.

3. Results

In both pine and spruce forests, the mean number of species per plot was significantly higher in the early successional stages than in mature forests (Fig. 2, Table 1). Species richness was consistently highest in the "young" maturity class (Fig. 2), even when the differences between "cutting" and "young" maturity classes were not significant at the 5% level.

In the pine stands species richness was also affected by productivity. Species richness was higher on fertile sites (Table 1), but there was also an interaction effect with forest maturity class (Table 1). The difference in species richness between "young" and "mature" was greater on "rich" than on "poor" sites (Fig. 2, Table 1). Hence, species numbers in the mature stages were rather similar at rich and poor sites, whereas in the young forests, species number was higher at the rich sites. In spruce stands productivity had no effect (Fig. 2, Table 1).

Table 1
Summary statistics of a factorial ANOVA examining the effects of fertility and maturity class on species richness (log number of species). (A) Pine stands, $p < 0.0001$, $n = 2927$, $R^2 = 0.12$. (B) Spruce stands, $p < 0.0001$, $n = 1538$, $R^2 = 0.04$.

Source of variation	DF	*F* value	*P*
A			
Fertility	1	59.92	<.0001
Maturity class	3	99.21	<.0001
Fertility*maturity class	3	7.93	<.0001
B			
Fertility	1	0.16	0.692
Maturity class	3	11.11	<.0001
Fertility*maturity class	3	0.46	0.7094

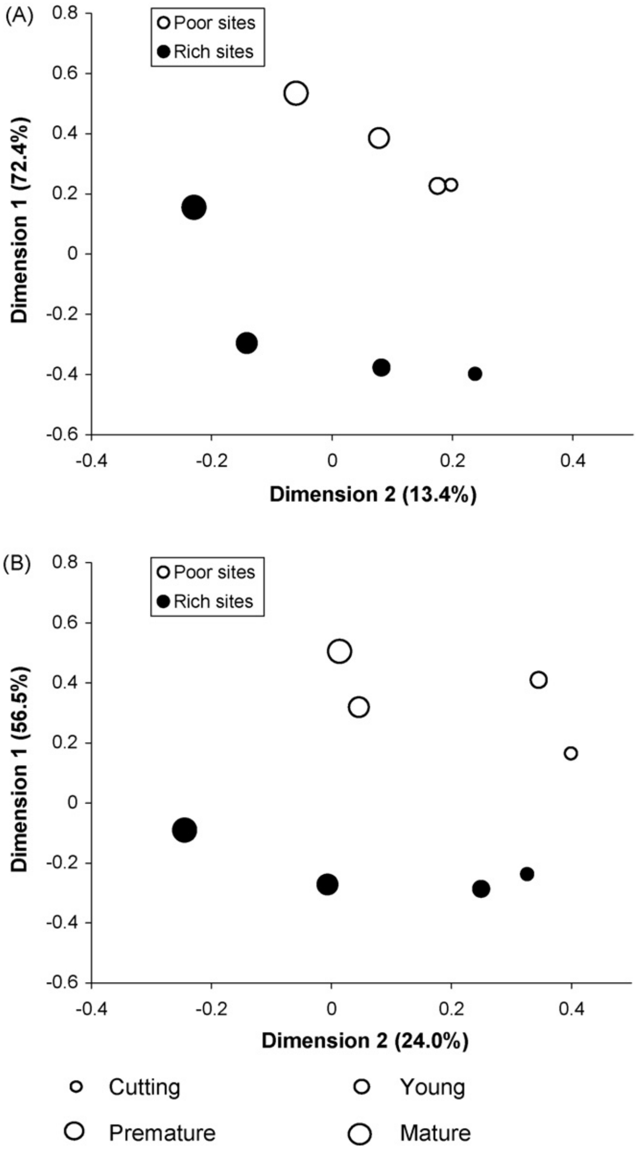

Fig. 3. Ordination diagram for maturity and fertility classes with respect to the first two dimensions of a correspondence analysis examining the frequency of plant species. Species with less than ten observations were excluded from the analysis. (A) Pine stands. (B) Spruce stands.

The variation in species richness was accompanied by a variation in species composition with both maturity and fertility class (Fig. 3, Table 2). The first two axes in the correspondence analysis of species composition explain more than 80% of the variability in species composition for both pine and spruce stands. Fig. 3 shows that axis 1 describes much of the variation due to productivity whereas axis 2 describes much of the variation due to stand maturity. The correspondence analysis shows a typical successional change with maturity class, with the "young" and "pre-mature" classes as intermediates between the "cutting" and "mature" classes (Fig. 3.). On "poor" sites, especially pine dominated ones, there is less variation in species composition among maturity classes than on the "rich" sites (Fig. 3).

Several species were also identified with affinities to particular maturity classes, in the indicator species analysis (Table 2). All maturity classes, except pre-mature spruce forests, had at least one significant indicator. Typical disturbance species such as *Oxalis acetosella* (Oxalidaceae) (Spruce forests), *Epilobium angustifolium* (Onagraceae), were typical for the "cutting" class. Species such as

Table 2

Significant indicator values >10, based on indicator species analysis, for species in different maturity classes. (A) Pine stands and (B) spruce stands.

Maturity class	Species	Indicator value	*P*-value
A			
Cutting	Epilobium angustifolium L.	29.2	0.001
Young	Stellaria longifolia Muhl. ex Willd.	11.8	0.001
	Melampyrum pratense L.	18.6	0.001
	Narrowleaved Poaceae	24.3	0.001
	Solidago virgaurea L.	12.0	0.001
	Sedges on non-moist ground	17.3	0.001
Pre-mature	Linnaea borealis L.	14.1	0.001
Mature	Vaccinium myrtillus L.	25.0	0.014
	Empetrum nigrum L.	19.5	0.001
	Calluna vulgaris (L.) Hull	18.4	0.002
B			
Cutting	Epilobium angustifolium L.	35.4	0.001
	Sedges on moist ground	12.8	0.001
	Sedges on non-moist ground	20.9	0.002
	Oxalis acetosella L.	10.7	0.047
Young	Stellaria longifolia Muhl. ex Willd.	22.9	0.001
	Melampyrum pratense L.	22.8	0.001
	Maianthemum bifolium (L.) F. W. Schmidt	17.9	0.036
	Broad leaved Poaceae	24.3	0.001
	Solidago virgaurea L.	18.3	0.001
	Dryopteris carthusiana (Vill.) H. P. Fuchs	10.3	0.026
Pre-mature			
Mature	Lycopodium annotinum	14.5	0.001
	Linnaea borealis L.	23.5	0.001
	Listera cordata (L.) R. Br.	10.7	0.001
	Orthilia secunda (L.) House	11.0	0.003
	Vaccinium myrtillus L.	25.6	0.013
	Vaccinium vitis-idaea L.	24.6	0.036

Table 4

Summary statistics of a factorial ANOVA examining the effects of pre-commercial thinning and fertility on species richness (log number of species) in pine forests. (A) Maturity class “young”, $p < 0.0001$, $n = 943$, $R^2 = 0.06$. (B) Maturity class “pre-mature”, $p < 0.0001$, $n = 1026$, $R^2 = 0.04$. Comment: The pre-commercial thinnings were only carried out in stands of the “young” maturity class but were recorded up to 25 years later. Thus pre-commercial thinning was also recorded in the “pre-mature” class.

Source of variation	DF	*F* value	*P*
A			
Fertility	1	27.92	<.0001
Thinning	1	5.24	0.0223
Fertility*Thinning	1	4.39	0.0364
B			
Fertility	1	17.94	<.0001
Thinning	1	11.2	0.0008
Fertility*Thinning	1	1.19	0.2748

Table 5

Summary statistics of a factorial ANOVA examining the effects of productivity and pre-commercial thinning on species richness (log number of species) in spruce forests. (A) Maturity class “young”, $p = 0.0861$, $n = 236$, $R^2 = 0.03$. (B) Maturity class “pre-mature”, $p = 0.0022$, $n = 295$, $R^2 = 0.05$. Comment: The pre-commercial thinnings were only carried out in stands of the “young” maturity class but were recorded up to 25 years later. Thus pre-commercial thinning was also recorded in the “pre-mature” class.

Source of variation	DF	*F* value	*P*
A			
Fertility	1	0.02	0.8896
Thinning	1	2.3	0.1306
Fertility*Thinning	1	5.86	0.0162
B			
Fertility	1	1.04	0.309
Thinning	1	9.3	0.0025
Fertility*Thinning	1	0.22	0.6366

Stellaria longifolia (Caryophyllaceae) and *Melampyrum pratense* (Orobanchaceae) were typical for the “young” maturity classes (Table 2). The “mature” class was characterized by two types of species. First, the “mature” class was characterized by field layer dominating Ericaceae species such as *Vaccinium myrtillus* and *Empetrum nigrum*. Second, the “mature” class was also characterized by less common mycoheterotrophic species such as *Listera cordata* (Orchidaceae) and *Orthilia secunda* (Pyrolaceae), first and foremost in spruce forests (Table 2). Another orchid *Goodyera repens* was also a significant indicator of mature stands but with indicator values far below 10 (1.2 and 2.5 for pine and spruce stands respectively).

Only three species, *V. myrtillus*, *V. vitis-idaea* and the narrow leaved Poaceae, had a mean cover of at least 10% in any of the maturity classes. The cover of *V. myrtillus* was significantly lower in the “cutting” and “young” forest stages than in the “pre-mature” and “mature” forest stages, in both pine and spruce forests (Table 3A and B). The cover of *V. vitis-idaea* was significantly lower in the “young” and “cutting” stages than in the “pre-mature” and “mature” stages, in pine forests (Table 3A). There was a much greater cover of the narrow leaved Poaceae in the “cutting” and “young” forest stages than in the “pre-mature” and “mature” stages in both pine and spruce forests (Table 3A and B).

Pre-commercial thinning also affects species richness. In “young” forests of both pine and spruce there was a significantly higher species richness in stands were pre-commercial thinning had been undertaken than in other stands (Tables 4 and 5, Figs. 4 and 5). The effect of pre-commercial thinning (actually performed during the “young” stage) was most pronounced in the “pre-mature” maturity class (Tables 4B–5B, Figs. 4B and 5B). In the “young” maturity class, but not the “pre-mature” one, there was also a significant interaction effect between thinning and

Table 3

Difference in mean cover between maturity classes for the three most common species. (A) Pine stands. (B) Spruce stands. Significant differences from the mature forest stage in an ANOVA with Tukey-Kramer adjustment for multiple comparisons are indicated, *-$p < 0.05$, **-$p > 0.01$, ***-$p > 0.001$.

	Vaccinium vitis-idaea	P	Vaccinium myrtillus	P	Narrow leaved Poaceae	P
A						
Cutting stage	7.79	***	8.00	***	11.58	***
Young forest	9.75	***	9.72	***	8.36	***
Pre-mature forest	12.95	ns	16.84	ns	4.68	***
Mature forest	14.82		20.91		0.76	
B						
Cutting stage	4.62	ns	6.23	***	22.11	***
Young forest	7.42	ns	12.24	***	10.46	***
Pre-mature forest	7.83	ns	15.94	***	3.21	ns
Mature forest	8.26		21.77		0.68	

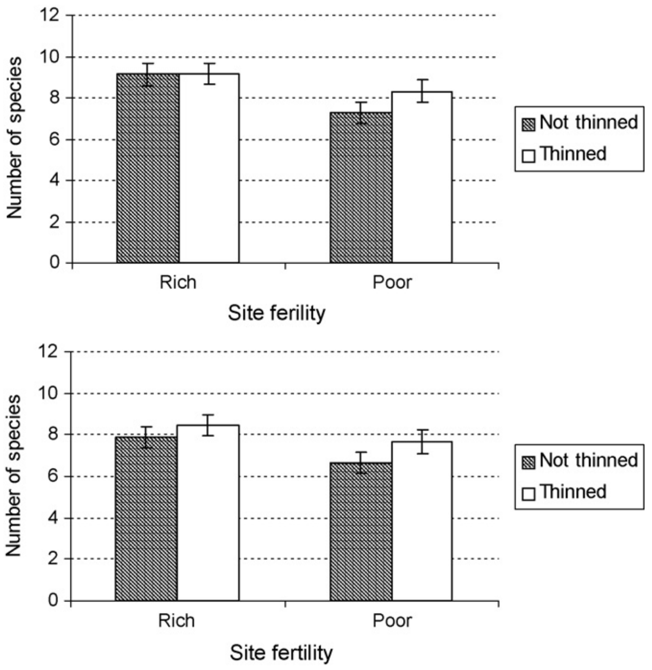

Fig. 4. Difference in the mean number of species between pine stands previously subjected to pre-commercial thinning and pine stands not subjected to pre-commercial thinning. (A) Maturity class "young" and (B) maturity class "pre-mature".

productivity for both pine and spruce (Tables 4A and 5A). However, in contrast to the effect of clearfelling, the effects of thinning were stronger on "poor" than on "rich" sites. For commercial thinning in pre-mature stands, we were unable to detect any effect on plant diversity, either in pine stands (ANOVA, $p = 0.124$, $n = 977$) or in spruce stands (ANOVA, $p = 0.756$, $n = 387$).

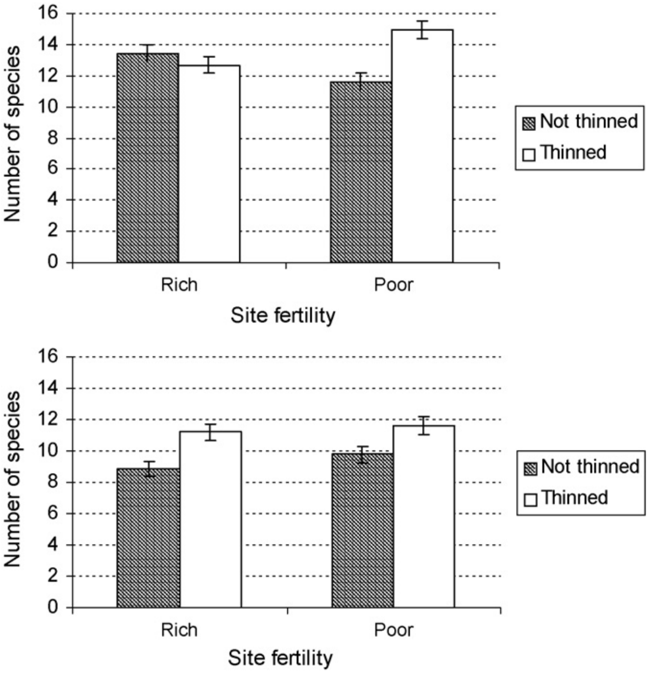

Fig. 5. Difference in the mean number of species between spruce stands previously subjected to pre-commercial thinning and spruce stands not subjected to pre-commercial thinning. (A) Maturity class "young" and (B) maturity class "pre-mature".

4. Discussion

This study is a large scale analysis of the disturbance dynamics of plant communities in relation to disturbance caused by forestry operations. The analysis made use of stand and plant species data from a large and representative area of Swedish forests. This contrasts with much hypothesis testing in ecology, which is often undertaken in controlled experiments over small areas. Despite many factors being uncontrolled in the large survey data set, the study shows that there is a significant variation in diversity related to management disturbance; this follows the main predictions of plant ecological theory and may have important implications for forest management.

4.1. Cutting and succession

In this study species richness increased after cutting and peaked after some time of stand development, i.e. in the young forest stage (Fig. 2). With respect to the increased species richness in the young forest stage, our results are in line with the intermediate disturbance hypothesis (Connell, 1978; Cordonnier et al., 2006; Hart and Chen, 2008). Young forests (20–30 years old) are intermediate in terms of light, nutrient and ground conditions, and even if forests can grow for more than 150 years these factors are rather unaffected by the clear-cutting event after 50 years.

One mechanism to explain the intermediate disturbance hypothesis is that disturbance adversely affects superior competitors but not eradicate them entirely, and facilitates colonization by less competitive species, which result in more species co-existing. Although this study does not explicitly examine the mechanisms behind disturbance—species richness relationships, it shows that much of the change in overall species composition in the habitat studied is related to *Vaccinium* dominance. Disturbance by cutting decreases the occurrence, as well as the cover, of the most frequent *Vaccinium* species (Tables 2 and 3). This creates opportunities for pioneer species, such as *Epilobium* and *Solidago*, to colonize and establish (Table 2). The peak in species number in the "young" maturity class probably results from a maximum overlap between early and late successional plants.

When extrapolating from a snapshot sample of stands of different maturities, there is a risk that we are examining historical trends in management regimes rather than succession. However, decreased dominance of Ericaceous species after cutting has been shown in time series data for Scandinavian boreal forests (Bråkenhielm and Liu, 1998). In pine forests, for example, cutting resulted in a substantial decrease in *Calluna vulgaris* (Bråkenhielm and Liu, 1998). The same pattern, in terms of occurrence, is observed in this study (Table 2A). The colonization of plant species such as *Epilobium* in early successional stages is also a well known pattern. Few studies have, however, related these successional patterns to changes in species richness within the framework of disturbance-based theories. However, a peak in species richness of vascular plants in young stands has previously been demonstrated in Canadian boreal forests (Hart and Chen, 2008). Furthermore, Haeussler et al. (2002) found a peak in species richness at intermediate stages of disturbance intensity (in contrast to time since disturbance) in managed boreal forests. This underlines the fact that many types of disturbance, both in terms of intensity and time since its occurrence, affect plant species richness (Shea et al., 2004).

Although species richness is at its peak in young forests, several less common species associated with late successional stages disappear after cutting; these include light sensitive mycoheterotrophic species in the families Orchidaceae and Pyrolaceae (Table 2). This pattern has also been observed in other boreal plant systems (Haeussler et al., 2002).

The species list used in the national inventory includes virtually all common forest plant species (201 species). The fact that very rare species are not included and that grasses and sedges are grouped might be regarded as a flaw. This will underestimate the total number of species in the different site types. However the focus of this paper is on local species richness, or species density, which is the mean number of species per unit area in different site types (Maturity classes and thinning regimes). This is an appropriate measure to use when analyzing the effect of disturbance on species co-existence and species richness. It is worthwhile noticing that of the 201 "common" species on the present list, 40 occur in less than 10 plots and 59 are not found at all, in the analyzed plots. Thus if "rare" species had been added to the list it would have resulted in very few hits with little, if any, effect on the mean values or our main findings. The lumping of species of grasses and sedges into species groups probably has a larger effect on species richness in this study. However, since both grasses (narrow leaved poace) and sedges are more common in cutting and young maturity classes (Table 2), the identification of separate species in these groups are likely to increase rather then decrease the peak in species richness after cutting disturbance. A strength in this study is that we can calculate mean species richness in different site types from a large sample, 4465 plots, covering a large part of boreal Sweden. Including all or most of the plant species of northern Sweden would render such an effort impracticable.

When the effects of cutting and succession are related to site fertility the patterns are more complex. In pine, but not in spruce, stands species richness increased with site fertility, but fertile sites exhibited a higher species richness after cutting (disturbance) than poor sites (Fig. 2, Table 1). The effect of the fertility × cutting interaction on species richness is in line with Grime's (1979) theory. This states that fewer species are adapted to stressed environments and that the potential increase in species richness after disturbance is limited. Dry and nutrient-poor pine stands are indeed stressful environments, with only a few species such as *Vaccinium vitis-idaea*, *Calluna vulgaris* present. One possible reason why a fertility × cutting interaction is found for pine stands, and not spruce stands, is that spruce stands are, on average, somewhat more mesic and fertile (median = 5 m^3/year) than pine stands (median = 4 m^3/year); only pine sites have very poor and dry conditions. The correspondence analysis shows that species composition changes with both site fertility and succession in pine and spruce forests (Fig. 3). As much as 80% of the variation in species composition is explained by the first two axes. Moreover, the variation in species composition with succession in both types of forests seems to be greater on fertile than on poor sites (Fig. 3). Hence the response to disturbance and fertility seems to be expressed more strongly in terms of composition than species richness. This may, however, be partly explained by a relatively low overall variation in species composition in the data set.

4.2. Thinning

Pre-commercial thinning affects species richness in both "young" and "pre-mature" forests (Tables 4 and 5, Figs. 4 and 5). The results indicate that the peak in species richness in young forests may be further increased if pre-commercial thinning is undertaken. Moreover, the "decrease" in species richness in "pre-mature" stands seems to be lower in stands subjected to pre-commercial thinning during the "young" forest stage (Figs. 4 and 5). In other words, the development into a species poor, late successional stage may be faster if young forests are not thinned. This process does not seem to be compensated for by commercial thinning in the pre-mature stage: this operation has no significant positive effect on species richness. Disturbance in the form of commercial thinning is probably too weak to have any marked effects on the plant community at that stage of succession.

Due to limitations in the data set, neither the thinning intensity nor the time since thinning could be considered in our study. Thinned stands may have been thinned as long as 25 years before the survey date. This probably leaves us with a rather large variation in the actual forest structure, which is one explanation for the observed effects being relatively small (a mean difference in the order of one or two species), and why there is a large amount of unexplained variance. The thinning variable used prevented us from examining the effect of disturbance intensity or occasion (such as the IDH), in the same way we were able to do for cutting. However, the results of this study highlight the importance of interactions between succession (after a large scale disturbance in the form of cutting) and small scale disturbance (thinning) for plant diversity. Relatively few studies have related thinning to plant diversity. Lindgren et al. (2006), however, demonstrated that thinning increases the species richness of plants in Canadian boreal forests.

In contrast to the interaction effects between maturity and productivity (Table 1), the effect of pre-commercial thinning on species richness was more positive on poor sites than on rich ones (Tables 4 and 5, Figs. 4 and 5). One possible explanation is that gaps in the canopy cover after thinning last longer at poor sites than at rich sites.

4.3. Conclusions and management implications

Our study demonstrates that disturbance to the crown cover, by clear-felling, may result in a peak in plant species richness as stands reach the "young" forest stage. This pattern is in line with processes predicted by ecological theory and data from natural communities under natural disturbance regimes. Time series data on stem densities show that young forests in Sweden have become much denser during the last decade, due to a decrease in thinning intensity (Anon, 2002). This leads to a fast closure of the canopy cover and a rapid reduction in light available to the field layer vegetation. If young forests become too dense some of the positive effects of disturbance to the crown cover are probably lost. The present study indicates that ordinary pre-commercial thinning in young forests can, at least to some extent, counteract this effect, something that later (commercial) thinning cannot. Hence we point out that early thinning of young stands, especially fertile and lush ones, is important for plant diversity in managed forests. We also suggest that pre-commercial thinning could be further developed to favor plant diversity. The creation of larger gaps and retaining groups of deciduous trees are examples of thinning strategies that may favor plant diversity.

It is important to point out that the positive effects of disturbance on plant diversity does not mean that forestry could be intensified for example by shortened stand rotation time, without negative effects on plant diversity. Several plant species are restricted to old and mature forests and the increased species richness observed in young forests cannot compensate for the loss of such species and habitats. The point in this paper is that knowledge of the relationship between disturbance, succession and plant species richness in managed forests may help us to identify relatively moderate adjustments to management regimes which may improve the prerequisites for plant diversity over the whole forest cycle and over a relatively large area.

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Appendix A. Plant species and plant species groups in the analysis

Frequency	Species (or species group)	Family
4263	Vaccinium myrtillus L.	Ericaceae
4251	Vaccinium vitis-idaea L.	Ericaceae
3374	narrowleaved Poaceae	Poaceae
2281	Melampyrum pratense L.	Orobanchaceae
2081	Empetrum nigrum L.	Ericaceae
2019	non-mesic Cyperaceae	Cyperaceae
1961	Linnaea borealis L.	Linnaeaceae
1795	Calluna vulgaris (L.) Hull	Ericaceae
1773	Stellaria longifolia Muhl. ex Willd.	Caryophyllaceae
1460	Epilobium angustifolium L.	Onagraceae
1440	Maianthemum bifolium (L.) F. W. Schmidt	Convallariaceae
1318	Solidago virgaurea L.	Asteraceae
1267	broadleaved Poaceae	Poaceae
967	Gymnocarpium dryopteris (L.) Newman	Woodsiaceae
899	Vaccinium uliginosum L.	Ericaceae
844	Lycopodium annotinum L.	Lycopodiaceae
681	Equisetum sylvaticum L.	Equisetaceae
559	Oxalis acetosella L.	Oxalidaceae
520	Dryopteris carthusiana (Vill.) H. P. Fuchs	Dryopteridaceae
505	Orthilia secunda (L.) House	Ericaceae
502	Geranium sylvaticum L.	Geraniaceae
476	Melampyrum sylvaticum L.	Orobanchaceae
465	Other Cyperaceae	Cyperaceae
434	Rubus saxatilisL.	Rosaceae
364	Rubus chamaemorus L.	Rosaceae
346	Rhododendron tomentosum Harmaja	Ericaceae
293	Potentilla erecta (L.) Raeusch.	Rosaceae
256	Anemone nemorosa L.	Ranunculaceae
198	Phegopteris connectilis (Michx.) Watt	Thelypteridaceae
194	Vaccinium oxycoccos L.	Ericaceae
194	Athyrium filix-femina (L.)/distentifolium	Athyriaceae
171	Andromeda polifolia L.	Ericaceae
167	Viola palustrisL.	Violaceae
159	Viola riviniana Rchb.	Violaceae
154	Cornus suecicaL.	Cornaceae
143	Diphasiastrum complanatum (L.) Holub	Lycopodiaceae
137	Listera cordata (L.) R. Br.	Orchidaceae
136	Fragaria vescaL.	Rosaceae
128	Filipendula ulmaria (L.) Maxim.	Rosaceae
107	Ranunculus acris L.	Ranunculaceae
107	Veronica officinalis L.	Scrophulariaceae
106	Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae
99	Dactylorhiza maculataL.	Orchidaceae
99	Cicerbita alpina (L.) Wallr.	Asteraceae
87	Geumrivale L.	Rosaceae
82	Equisetum palustre L.	Equisetaceae
75	Equisetum pratense Ehrh.	Equisetaceae
73	Paris quadrifolia L.	Trilliaceae
72	Cirsium helenioides (L.) Hill	Asteraceae
72	Taraxacum spp.	Asteraceae
72	Crepis paludosa (L.) Moench	Asteraceae
67	Equisetum arvense L.	Equisetaceae
59	Lycopodium clavatum L.	Lycopodiaceae
57	Comarum palustre L.	Rosaceae
57	Angelica sylvestris L.	Apiaceae
56	Convallaria majalis L.	Convallariaceae
53	Rumex acetosaL.	Polygonaceae
53	Goody era repens (L.) R. Br.	Orchidaceae
48	Galeopsis spp.	Lamiaceae
47	Alchemilla spp.	Rosaceae
45	Rubus arcticusL.	Rosaceae
43	Vicia spp	Fabaceae
38	Veronica chamaedrys L.	Scrophulariaceae
38	Cirsium palustre (L.) Scop.	Asteraceae
37	CalthapalustrisL.	Ranunculaceae
36	Hepatica nobilis Schreb.	Ranunculaceae
36	Eriophorum angustifolium Honck.	Cyperaceae
36	Tussilago farfara L.	Asteraceae
35	Valeriana spp.	Valerianaceae
35	Bistorta vivipara (L.) Delarbre	Polygonaceae
35	Antennaria dioica (L.) Gaertn.	Asteraceae
33	Gnaphalium spp.	Asteraceae
30	Achillea millefolium L.	Asteraceae
30	Moneses uniflora (L.) A. Gray	Ericaceae
28	Lathyrus linifolius (Reichard) Bässler	Fabaceae
28	Saussurea alpina (L.) DC.	Asteraceae
28	Rumex acetosella L.	Polygonaceae
28	Arctostaphylos uva-ursi (L.) Spreng.	Ericaceae
22	Anthriscus sylvestris (L.) Hoffm.	Apiaceae
22	Campanula spp.	Campanulaceae
22	Epilobium collinum/montanum L.	Onagraceae
22	Dryopteris filix-mas (L.) Schott	Dryopteridaceae
21	Aconitum lycoctonum L.	Ranunculaceae
19	Hypericum spp. L.	Clusiaceae
17	Equisetum fluviatile L.	Equisetaceae
16	Urtica dioica L.	Urticaceae
16	Selaginella selaginoides (L.) P. Beauv. ex Schrank & Mart.	Selaginellaceae
16	Huperzia selago (L.) Bernh. ex Schrank & Mart.	Lycopodiaceae
15	Menyanthes trifoliata L.	Menyanthaceae
15	Stellaria graminea L.	Caryophyllaceae
15	Parnassia palustris L.	Parnassiaceae
13	GaliumborealeL.	Rubiaceae
12	Polypodium vulgare L.	Polypodiaceae
12	Polygonatum spp.	Liliaceae
11	Petasites frigidus (L.) Fr.	Asteraceae
9	Silene dioica (L.) Clairv.	Caryophyllaceae
9	Corallorhiza trifida Châtel.	Orchidaceae
9	Platanthera bifolia (L.) Rich.	Orchidaceae
9	Trifolium repens L.	Fabaceae
8	Succisa pratensis Moench	Dipsacaceae
8	Achillea ptarmica L.	Asteraceae
8	Leucanthemum vulgare Lam.	Asteraceae
8	Cirsium arvense (L.) Scop.	Asteraceae
7	Trifolium pratense L.	Fabaceae
6	Pinguicula vulgaris L.	Lentibulariacea
6	Senecio vulgaris L.	Asteraceae
5	Lysimachia thyrsiflora L.	Myrsinaceae
5	Euphrasia spp.	Scrophulariaceae
5	Listera ovata (L.) R. Br.	Orchidaceae
4	Peucedanum palustre (L.) Moench	Apiaceae
4	Lysimachia vulgaris L.	Myrsinaceae
3	Actaea spicataL.	Ranunculaceae
3	Chrysosplenium alternifolium L.	Saxifragaceae
3	Lotus corniculatus L.	Fab ace ae
3	Cirsium vulgare (Savi) Ten.	Asteraceae
3	Matteuccia struthiopteris (L.) Tod.	Woodsiaceae
2	Viola mirabilisL.	Violaceae
2	Rumex spp.	Polygonaceae
2	Moehringia trinervia (L.) Clairv.	Caryophyllaceae
2	Plantago major L.	Plantaginaceae
2	Trollius europaeus L.	Ranunculaceae
2	Equisetum hyemale L.	Equisetaceae
2	Stellaria nemorum L.	Caryophyllaceae
2	Thelypteris palustris Schott	Thelypteridaceae
2	Viola tricolor L.	Violaceae
2	Trifolium medium L.	Fab ace ae
1	Stachys sylvatica L.	Lamiaceae
1	Galium verumL.	Rubiaceae
1	Drosera spp.	Droseraceae
1	Aegopodium podagraria L.	Apiaceae
1	Scrophularia nodosa L.	Scrophulariaceae
1	Pedicularis palustris L.	Orobanchaceae
1	Scheuchzeria palustris L.	Scheuchzeriaceae
1	Artemisia vulgaris L.	Asteraceae
1	Tripleurospermum perforatum (Mérat) Laínz	Asteraceae

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