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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