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Fine-scale disturbance in an old-growth boreal forest - patterns and processes

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This is a study of the importance of fine-scale disturbance on the forest floor in a bilberry dominated old-growth Norway spruce forest in Akershus county, Norway. Propagule banks and the impacts of experimental disturbance are studied on vegetation and population levels of organization. All studies were carried out within a framework of gradients in vegetation that are interpreted ecologically, by means of three different ordination techniques and univariate statistical methods. The relative merit of the ordination techniques in summarizing structure in the present data set is discussed. The first ordination axis was interpreted as due to a complex-gradient in soil moisture (decreasing) and canopy closure (increasing). Since the performance of plant individuals (or modules) in part depends upon the abiotic environment, it is argued that an approach that integrates studies at the vegetation and population levels will be beneficial to the studies at both levels and, notably, that such an integrated approach will enhance the explanatory power of population studies. It is stressed that ordination technique must be chosen after careful consideration of data set properties.

The importance of performing experimental field studies is emphasized. Such studies are important in order to allow testing of hypotheses. Patterns, processes and rates of recovery following fine-scale disturbance are discussed. In the disturbance experiment species number rapidly (within 2-3 years) reached pre-disturbance levels or higher, while the rate of recovery was much slower for the vegetation cover, in particular of the bottom layer. The relative efficiencies of the three main revegetation processes, i.e. germination from the propagule bank, colonization, and clonal encroachment, are shown to depend on disturbance severity, areal extent and distance of dispersal. Species with numerous viable diaspores in the soil-buried propagule bank may have an advantage over other species in revegetation of disturbed patches by just being present. However, soil condition and climate constrain germination and growth, making some species microsite limited.

New insights into the pattern, processes and rate of recovery of the clonal moss *Hylocomium splendens*, have been gained from the studies of experimental disturbance. This species is demonstrated to have a remarkable ability to rapidly increase its population size through enhanced branching after fine-scale disturbance. The implication of these results is that very little can be deduced about the history of a population on the basis of a snapshot of branching rates, when the disturbance history of the site is unknown.

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CONTENTS

DISSERTATION CONTENTS

This dissertation is based on the following papers, which will be referred to by their Roman numerals:

I   Rydgren, K. 1996. Vegetation-environment relationships of old-growth spruce forest vegetation in Østmarka Nature Reserve, SE Norway, and comparison of three ordination methods. - Nord. J. Bot. 16: 421-439.

II   Rydgren, K & Hestmark, G. 1997. The soil propagule bank in a boreal old-growth spruce forest: changes with depth and relationship to aboveground vegetation. - Can. J. Bot. 75: 121-128.

III   Rydgren, K., Økland, R.H. & Økland, T. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. IV. Effects of experimental fine-scale disturbance. - (submitted).

IV   Rydgren, K., Hestmark, G. & Økland, R.H. Early revegetation following experimental disturbance in a Norwegian boreal old-growth spruce forest. - (submitted).

INTRODUCTION

INTRODUCTION

Disturbance, either natural or induced by man, affects all communities of the world to some degree, and plays an important role in determining their structure (Sousa 1984, Begon et al. 1996). The significance of disturbance in community dynamics was for a long time overlooked; notable exceptions were some studies by temperate forest ecologists (see Sousa 1984). This neglect has partly been attributed to the tendency of ecologists to concentrate on the presumed equilibrial nature of biological systems (Karr & Freemark 1985). More recently, however, disturbance has got an important role in theories of non-equilibrium systems (e.g., Pickett 1980).

Traditionally, natural disturbance was defined in terms of major catastrophic events originating in the physical environment, causing abrupt structural changes in communities and moving them away from near-equilibrium conditions (P. White 1979, Sousa 1984). Disturbance may also be initiated or promoted by the biotic component of the ecosystem, or be directly caused by the activities of organisms, e.g., by burrowing animals and by herbivory (P. White 1979, Begon et al. 1996). Those who consider biotic and physical disturbance as conceptually different terms (Dayton 1971, Sousa 1985, Paine 1994), suggest there exists an important distinction in how natural selection might be expected to act (Paine 1994). Furthermore, disturbance may be characterized with regard to causes (changes in the environment), effects (responses of populations or communities), or mechanisms (see Glenn-Lewin & van der Maarel 1992, van der Maarel 1993). Forman & Godron (1986) emphasize changes in the environment and define disturbance as "an event that causes a significant change from the normal pattern in an ecological system". Other definitions focus the responses of populations or communities to the increased availability of resources. For example, P. White & Pickett (1985) define disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." While Grime (1979) consider disturbance "to consist of the mechanisms which limit the plant biomass by causing its partial or total destruction". The importance of time scale for distinguishing mortality by disturbance from mortality caused by other causes is emphasized in Huston's (1994) definition: "Disturbance is any process or condition external to the natural physiology of living organisms that results in the sudden mortality of biomass in a community on a time scale significantly shorter (e.g., several orders of magnitude faster) than that of the accumulation of biomass."

Disturbance most often results in creation of open space, and in many cases also in enhanced resource availability through temporary reduction of resource exploitation and/or increased availability of stored resources (e.g., Denslow 1985, Schaetzl et al. 1989). Disturbance is thus linked with *succession* and may be regarded as a reset mechanism (Glenn-Lewin & van der Maarel 1992, Begon et al. 1996). In the management of natural areas, which primarily involves the manipulation of succession (Glenn-Lewin & van der Maarel 1992), an understanding of natural disturbance regimes may be crucial in order to maintain, or in many cases achieve, sustainable harvest of natural resources (Bormann et al. 1995, Chapin et al. 1996). The disturbance regime is considered to be one of the dynamic elements, or "interactive

controls", together with climate, soil resource supply and major functional groups of organisms, that must be conserved if an ecosystem is to be sustained (Chapin et al. 1996).

Characteristics of a disturbance event will influence the course of succession together with life history traits of the affected species (Sousa 1984). Three main dimensions of disturbance, which are not entirely independent of each other, are: the spatial extent, the time-scale involved and the severity (e.g., Sousa 1984, Pickett et al. 1987b, Glenn-Lewin & van der Maarel 1992, van der Maarel 1993). These dimensions must be expected to influence the relative efficiency of the different processes of recovery after disturbance. With an increase in the spatial extent of the disturbance, clonal encroachment is likely to decrease in importance relative to germination of buried seeds, rhizomes, spores or other propagules, and the importance of dispersal into the disturbed area (colonization) is likely to increase relative to clonal encroachement. The severity of a disturbance will influence the survival, and thus the potential for recovery by means of surviving rhizomes, propagules etc. capable of regeneration or germination and growth (cf. Schimmel & Granström 1996). Knowledge of the distribution of propagules in the soil is thus important for evaluating the efficiency of the different revegetation processes. Despite this, and in contrast to the voluminous literature on seed banks (see reviews by Roberts 1981, Leck et al. 1989), few studies have been made of bryophyte propagule banks (see Grime 1990, Smith 1993).

Although plant succession has been a central research topic since the 19th century with focus on pattern description and search for processes (e.g., Cowles 1899, Clements 1916, Connell & Slatyer 1977, Pickett et al. 1987a), some aspects of succession remain almost unstudied (Peet 1992): (1) the resilience of ecosystems, i.e., the degree, manner, and pace of restoration of initial structure and function in an ecosystem after disturbance (Westman 1978); (2) elasticity (i.e., rate of recovery following disturbance; one of the components of resilience); and (3) the compositional turnover along successional seres, i.e. the length of successional trajectories measured in β-diversity units. Recovery rates may be analysed by dissimilarity measures and ordination techniques (Bornkamm 1981, Westman & O'Leary 1986, Halpern 1988, Whittaker 1991, Myster & Pickett 1994). There are, however, considerable difficulties with choice of measures, techniques and statistical model (R. Økland 1990), appropriate for a particular data set (Minchin 1987, Eilertsen et al. 1990).

Despite the potential benefits of integrated approaches in ecology, plant population studies and studies of vegetation have seldom been integrated (van der Maarel 1984). Demographic parameters and other population traits have hardly at all been studied in the context of complex environmental gradients. The explanatory power of population studies is likely to be considerably improved through such an integrated approach, since the performance of the individuals (or modules) may be significantly correlated with positions along gradients. Furthermore, knowledge of plant population patterns are important for the understanding of processes behind gradient patterns.

Studies of disturbance in the boreal forest have tended to focus on the conspicuous: influence of fire (e.g., Heinselman 1973, Zackrisson 1977, Black & Bliss 1978, Johnson 1992, De Grandpré et al. 1993, Sirois 1995), windfall of trees (e.g., Sernander 1936, Liu & Hytteborn 1991), and insect attacks (e.g., Paré et al. 1993, Fleming 1996, Kneeshaw & Bergeron 1996). Our knowledge of the ecological significance of fine-scale disturbance in the forest floor is, however, very sparse. In particular, little is known of the effect of disturbance on the dynamics in bryophyte populations (but see Jonsson & Essen 1990, Jonsson 1993a, Frego 1996, R. Økland & T. Økland 1996).

AIMS

The main aim of this doctoral study is to study the effects of fine-scale disturbance in the boreal forest floor, both at the population and vegetation levels of organization, with particular reference to bryophytes an important but often ignored plant group in this ecosystem. More specifically, I intend:

(1) to evaluate the fruitfulness of an integrated approach to vegetation and population studies, and

(2) to assess patterns, processes and rates of recovery in the boreal forest following fine-scale disturbance, both at the vegetation and at the population levels of organization

THE HØGKOLLEN REFERENCE AREA

THE INVESTIGATION AREA

The northwestern part of Høgkollen in Østmarka Nature Reserve, SE Norway, 11°02′E, 59°50′N, (230-285 m a.s.l.) was selected as the investigation area used for all studies reported in this paper. In addition, data from Rausjømarka (cf. T. Økland 1990, 1996) c. 1.5 km S of
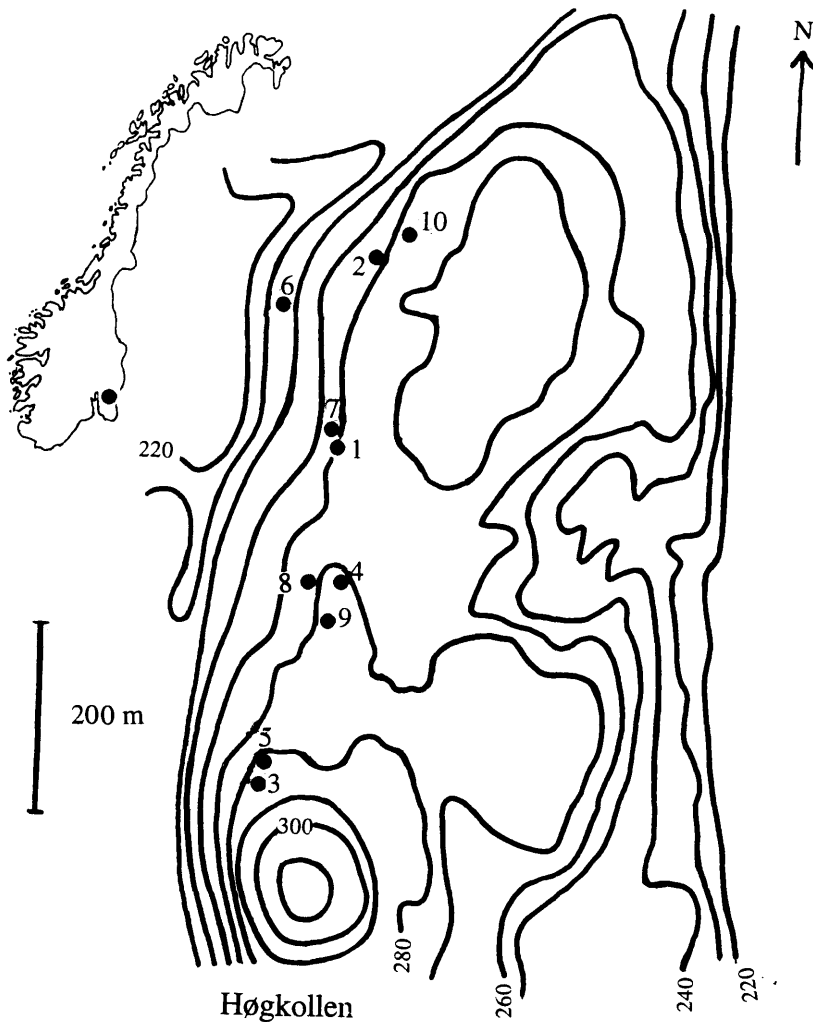

Fig. 1. Maps showing the localization of Østmarka Nature Reserve in SE Norway and positions of the ten macro sample plots (1-10) at Høgkollen.

Høgkollen are included in [III] for comparison. Only Norway spruce (*Picea abies* (L.) Karst.) forests dominated by *Vaccinium myrtillus* on poor to moderately rich submesic sites (terminology of R. Økland & Eilertsen (1993)) was included.

The bedrock consists of quartz diorite, tonalite and gneisses of Proterozoic age, and is covered by thin quaternary deposits of glaciofluvial origin (Holmsen 1951; Sigmond et al. 1984). The soil profile is of a podzol type.

The climate is slightly suboceanic with annual mean temperature of 3.9 °C, annual mean precipitation of *c.* 800 mm, and with maximum precipitation in late autumn and early winter (see papers [I, IV] for details). During the study period (1993-1996) all years were drier than normal; the summer of 1994 was particularly dry. All years except 1996 were warmer than average and all summers except 1994 were colder than average.

Aboveground (fire-scarred trees) as well as below-ground (charcoal) traces of forest fire occur at Høgkollen, but the date of the last fire is unknown. Selective logging has been performed at Høgkollen, most recently *c.* 60 years ago (B. Økland 1994).
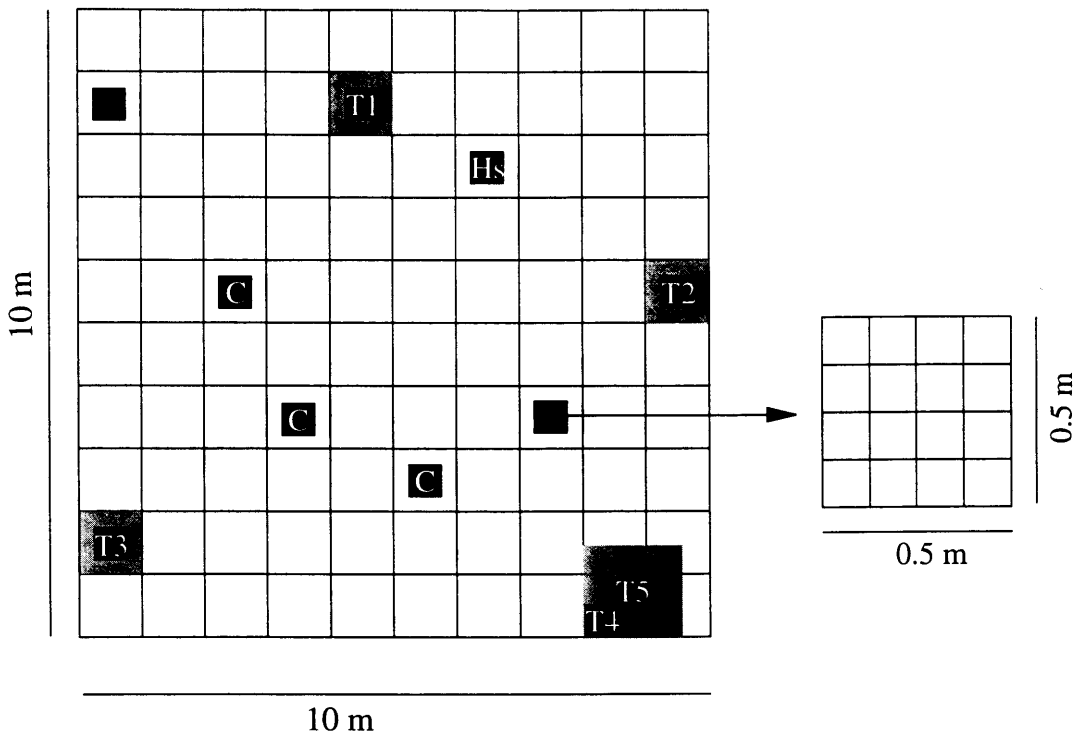
Fig. 2. An example of a macro plot with eleven randomly placed meso plots (in black). Hs - meso sample plot for experimental disturbance study of *Hylocomium splendens* [III]; T1-T5 - treatment plots (the black area constitutes the analysed plot, while the total area of black and grey constitutes the treated area) in the disturbance study of vegetation [IV]; C - control plots in the disturbance study of vegetation; without code - plots used for other demography studies.

Tab. 1. The relationship between treatment in the experimental disturbance study [IV] and soil sampling in the propagule bank study [II].

Treat-ment	Removed layers	Soil layers sampled for propagule bank study	Number of soil samples		
			Lit-ter	Peaty mor	Bleached soil
T1	Vegetation	Litter	10		
T2	Vegetation, litter	Litter	10		
T3	Vegetation, litter, peaty mor	Litter, peaty mor	10	10	
T4*	Vegetation, litter, peaty mor, bleached soil	Litter, peaty mor, bleached soil	10	10	9
T5*	Vegetation, litter, peaty mor, bleached soil	Litter, peaty mor, bleached soil	10	10	9

*Treatment 4 and 5 differ with respect to the distance of plot to intact vegetation

THE SAMPLING DESIGN

Within an area of c. 0.1 km² ten macro sample plots, each 10 × 10 m, were placed subjectively, in order to span the local environmental variation in bilberry-dominated spruce forests of the western slopes of Høgkollen (Fig. 1). Within each macro sample plot, eleven meso sample plots (each 0.5 × 0.5 m) and divided into 16 subplots, 0.0156 m² each, were placed at random; see Fig. 2 and paper [I] for details.

All except one meso plot (the experimental disturbance study of *Hylocomium splendens* [III]) from each macroplot were used for [I]. Three plots were used for demographic studies of two bryophyte species (*Hylocomium splendens*; two experimental disturbance studies of which one is reported here [III], and one descriptive demographic study of *Ptilium crista-castrensis* (K. Rydgren in prep.)). The eleven meso plots in each macro plot were randomly ordered, and the first three plots that contained 25 or more growing points (living apices) of one of the focal species were used for demographic studies. The remaining eight meso plots in each macro plot were used for the experimental disturbance study of vegetation [IV] as one of five treatments or control plots (see Tab. 1). Plots were randomly assigned to treatments. Removal of vegetation, or vegetation and soil layers, were performed in an area of 1.0 × 1.0 m in treatments T1-T3, while an area of 1.5 × 1.5 m was used in the more severe treatments (T4 and T5; see Fig. 2). Soil samples for the propagule bank study [II] were collected from all the 50 treated meso plots, and from different soil layers as described in Tab. 1. In one macro plot, the sample plots that were subjected to treatments T4 and T5 lacked mineral soil layers, and soil samples from the bleached soil layer are therefore lacking (see Tab. 1).

SUMMARY OF PAPERS

PAPER I

Paper [I] provides the gradient reference frame within which the other studies were carried out: major coenoclines and complex-gradients in the old-growth spruce forest in the study area at Høgkollen, Østmarka Nature Reserve, SE Norway are identified. Three ordination methods are compared and evaluated. The data set consisted of 100 sample plots, each 0.25 m², with 13 environmental and 5 biotic variables recorded at each plot. Parallel application of three ordination techniques, PCA, DCA and LNMDS, resulted in different sample plot configurations. PCA performed poorest due to strong influence of outliers, and circumstantial evidence indicated better performance of LNMDS than DCA. Axes 1 in DCA and LNMDS ordinations were interpreted as due to a complex-gradient with soil moisture (decreasing) and canopy closure (increasing) as the most important factors for the differentiation of vegetation. The second axes were either non-significantly correlated with the recorded variables (LNMDS) or significantly correlated with some of the variables which were significantly correlated with the first axis (DCA). Canonical correspondence analysis (CCA) was used to partition the variation in the species-sample plot matrix into strictly spatial, strictly environmental, joint spatial and environmental variation, and unexplained variation. As much as 80.9% of the variation was unexplained by the variables, probably because of small plot size and short gradient lengths (in β-diversity units). Of the 19.1% of variation explained, 54.5% was strictly environmental, and only 6.3% was joint environmental and spatial variation. This indicated that broad-scale and geographically structured environmental variation was of minor importance.

PAPER II

In this paper the soil propagule bank of bryophyte and vascular plant species was studied with respect to composition and depth distribution, applying the emergence method to 50 of the 100 sample plots used in [I]. Three different soil layers were considered: the litter layer, the peaty mor layer and the bleached soil layer.

A total of 34 taxa germinated from soil samples placed in a phytotron chamber; ferns and mosses were the most frequent. Several of the ferns in the propagule bank were lacking in the aboveground vegetation in the sample plots (i.e., *Athyrium felix-femina*, *Gymnocarpium dryopteris* and *Phegopteris connectilis*). Many of the most frequent species in the aboveground vegetation were either lacking or low-frequent in the propagule bank. Thus, the correspondence between aboveground vegetation and propagule bank was only moderately strong, and decreased with soil depth. More taxa germinated, on average, from the litter layer than from the peaty mor and bleached soil layers (7.7, 6.0 and 5.5 taxa, respectively). *Betula pubescens*, *Dicranum scoparium*, *Plagiothecium laetum* agg., and *Lophocolea heterophylla* were all more frequent in the litter layer than in the two other layers, while *Calluna vulgaris* and *Luzula pilosa* were more frequent either in peaty mor and/or in the bleached soil layer

than in the uppermost layer. Species in the deepest layers may have an advantage in revegetating the pits created by tree uprooting.

PAPER III

Effects of fine-scale experimental disturbance on the population dynamics of the perennial clonal moss *Hylocomium splendens* were studied in this paper. The performance (e.g., segment size, sporophyte production and cover) of *Hylocomium splendens* was significantly correlated with position along ordination axes (vegetation gradients interpreted in ecological terms).

Half the bryophyte cover was removed from 10 plots in a fine-scaled pattern (bryophytes were removed from every second of cells, each 2.6 cm^2). Demographic changes in this experimental population and the size of *c*. 400 mature segments (estimated from morphological field measurements) were followed from 1993 to 1995 and compared with corresponding data from a nearby unmanipulated reference population. The experimental population increased its number of *Hylocomium* growing points two-fold in two years by enhanced ramification and regeneration rates, while the reference population showed a small decrease in growing-point number. Rates of regeneration from fragments (in the gaps) and ramification were higher in the experimental population than in the unmanipulated population the first year after treatment, and rates of regeneration from intact shoot chains were higher the second year after treatment. Enhanced light penetration deeper into the moss carpet is likely to be the main cause of the observed differences between the populations, in accordance with the hypothesis forwarded by R. Økland & T. Økland (1996).

The mean size of mature segments decreased in both populations during the study, due to an extended drought period in 1994. This decrease was stronger in the experimental than in the unmanipulated population. Further size reductions are expected in the experimental population because segments produced by regeneration are smaller than a population´s average segment size. Thus, a population´s resilience after disturbance will depend on its current size structure, the frequency and severity of disturbance, and environmental conditions.

Sporophyte production was also influenced by the disturbance. In 1995 the frequency of sporophytes was more than ten times as high in the experimental population than in the unmanipulated reference population. Stimulation of fertile branch production (and gametangia) by enhanced radiation, and higher probability of successful fertilization, e.g., due to amelioration of the microclimate, may be involved. Like ramification frequency, sporophyte production in *Hylocomium splendens* was positively dependent on the size of the source segment, and a well-defined reproductive threshold, a minimum resource (size) level for successful reproduction, seems to occur.

PAPER IV

In this paper revegetation patterns were studied in three successive years in an experiment that was designed to simulate fine-scale disturbance such as uprooting. The framework of plots in

paper [I] was used; 50 of the plots were subjected to treatment and 30 were used as control plots. A disturbance severity gradient was created by varying the depth to which soil was removed. Two spatial extents of disturbance were included. The pre-disturbance number of species re-established within three years after treatment, while the total cover in the field layer, and notably in the bottom layer, re-established much more slowly. The most rapid recovery was found in the least severe treatments (removal of vegetation and removal of vegetation and the litter layer). By resprouting from intact rhizomes and clonal ingrowth, several of the vascular plants which occurred abundantly in intact forest floor vegetation (*Vaccinium myrtillus*, *V. vitis-idaea* and *Deschampsia flexuosa*), reached their initial plot frequencies within three years. Other important recovery mechanisms were germination from soil buried propagule banks (e.g., *Luzula pilosa*, *Plagiothecium laetum* agg., *Pohlia nutans* and *Polytrichum* spp.) and dispersal of propagules into the disturbed patches (e.g., *Betula pubescens* and *Picea abies*). Several species abundantly present in the soil buried propagule bank (e.g., the ferns *Athyrium filix-femina*, *Gymnocarpium dryopteris* and *Phegopteris connectilis*) but absent from disturbed patches were assumed to be microsite limited.

Disturbance severity influenced revegetation patterns, regardless whether recorded as trajectories of vegetation composition in a DCA ordination space or as change in floristic dissimilarity. The length of the successional path (in β-diversity units) increased with increasing disturbance severity, and was modified by the area of the disturbed patch, and by the distance to intact vegetation. Most trajectories moved in the same direction in all years. The estimated rate of succession differed between methods; decreasing year by year when recorded as floristical dissimilarity, while it first decreased and then increased in the ordination space.

DISCUSSION AND GENERAL CONCLUSIONS

INTEGRATION OF VEGETATION AND POPULATION BIOLOGICAL STUDIES

Vegetation and population studies may both benefit from an integrated approach (van der Maarel 1984, J. White 1985). The performance of plant individuals (or modules) is likely to depend on environmental conditions (Gottlieb 1977, Hara & Yokozawa 1994, Herben et al. 1994) and should be expected to vary according to position along complex-gradients. This is confirmed by [III], on the effects of experimental fine-scale disturbance on the population biology of the moss *Hylocomium splendens* [III]; frequency of sporophyte production, number of segments per unit area, *Hylocomium* cover and mean segment size were all significantly correlated with DCA axis 1 (the latter positively the others negatively correlated). DCA axis 1 is interpreted as due to a complex-gradient in soil moisture (decreasing) and canopy closure (increasing) [I]. The variation in module performance along environmental gradients emphasizes the importance of distributing sample plots (quadrats) in sufficient numbers along the complex-gradients of primary importance for variation in a species´ performance in order to obtain an adequate picture of the species´ population biology. There is a growing aprehension of the importance of spatio-temporal variation for demographic performance of plants (e.g., Tuljapurkar 1989). In order to avoid erroneous conclusions about factors influencing the a species´ demography, such variation should be included (Moloney 1988). However, few empirical data sets exist that cover periods longer than two years and that include environmental variation which is accounted for in a proper way (cf. Horvitz & Schemske 1995). Usually, only one or just a few sample plots are used. A strong suggestion for future plant population studies is that more plots are included and that environmental variation is appropriately quantified and included in the sample set. In fact, there is a strong need for considerations of resolution; grain and extent (cf. Wiens 1989) in population studies.

When positions of study sites along major gradients are unknown, comparisons between plant populations are burdened with considerable uncertainty because of the partial dependence of plant performance on environmental conditions. An obvious means of increasing the explanatory power of such studies is to perform them within the context of known complex-gradient, along which plot positions is (or can be) determined [I]. The explanatory power of plant population studies can also be increased by including so-called empty quadrats (Crawley 1990); quadrats where the focal species is not occurring at the start of the study. When recruitment is confined to sites other than those occupied by adult plants, a serious bias in the estimation of plant recruitment rates may occur unless empty quadrats, also including potential recruitment sites, have been included at random (Crawley 1990). Population studies performed within the framework of vegetation-environment relationships [such as provided by I] are likely to include empty quadrats, thus being well suited for both population and experimental vegetation studies [III, IV]. The potential of such a framework, with respect to inclusion of empty quadrats, is demonstrated by the recruitment of *Luzula pilosa* [IV]. *Luzula pilosa* was a low-frequency species (5%) in the original forest floor vegetation [I], but rates of recruitment after disturbance were high [IV]. The recruitment was, however, almost entirely confined to quadrats were *Luzula pilosa* was originally lacking (K. Rydgren unpubl.; see also [IV; compare figs. 4B and 5C]). Although population studies would benefit strongly from

being integrated with vegetation studies (and vice versa), empty quadrats and/or parallel analysis of vegetation-environment relationships are usually not seen in plant populations studies.

CHOICE OF ORDINATION TECHNIQUE

The performance of ordination techniques varies according to data set properties (Minchin 1987, Eilertsen et al. 1990). Proper evaluation of data set properties thus improves the probability for making a good choice. Preferentially, two principally different ordination techniques should be used in parallel in order to increase the probability that the real gradient structure has been recovered and interpretation of artifactual axes is avoided (R. Økland 1990, 1996).

The difficulties involved in choosing an appropriate ordination technique are demonstrated by several studies of succession (e.g., Facelli & D'Angela 1990, Olff et al. 1994, Olsson & Staaf 1995). Even after a long period of intensive testing of ordination techniques (e.g., Fasham 1977, Gauch et al. 1981, Kenkel & Orlóci 1986, Minchin 1987, Peet et al. 1988, R. Økland 1990), PCA is still the preferred ordination technique in such studies. PCA, which assumes a linear response of species abundances to positions along gradients (ter Braak 1987), is only potentially recommendable when gradient lengths are short (R. Økland 1990; but see [I]). This is seldom the case in succession studies (but see Brulisauer et al. 1996).

DISTURBANCE - PATTERNS, PROCESSES AND RATES OF RECOVERY

Plant ecologists have been slow to adopt an experimental attitude to their subject (Pigott 1982). In particular this applies to the study of plant communities (Gurevitch & Collins 1994). This may in part explain the lack of knowledge about different aspects of succession, for example the rate of recovery, or elasticity, following disturbance (cf. Peet 1992). A sampling design which includes experimental manipulation of disturbance, establishment of control plots, and control of initial conditions (e.g., the species composition) may serve as a framework for a study design (e.g., [III]) that may bring studies of succession from description and comparison to a stage with higher potential for inferring causality (see Pigott 1982, Gurevitch & Collins 1994). Experimental manipulation, both in population and community studies, may be the best means both of testing and rejecting hypotheses and for generating new insight (Paine 1994).

Boreal forest vegetation

A huge amount of timber, pulp, paper and other resources is harvested from trees in boreal forests. Thus, it is not surprising that the main emphasis in studies of succession following disturbance has been on tree species, with less emphasis on bryophytes and lichens (e.g.,

Carleton & Maycock 1978, Hytteborn et al. 1987, Bergeron & Dubuc 1989, Carleton & McLellan 1994). However, the processes in the different layers are closely linked (Bonan & Shugart 1989, R. Økland & Eilertsen 1993). An example is the allelopathic effect of *Empetrum hermaphroditum*, a species in the understorey, on germination of tree species from seeds (Zackrisson & Nilsson 1992), an effect that may be counteracted by presence of charcoal in the soil (Zackrisson et al. 1996). The cryptogams, bryophytes in particular, influence tree growth by their water-holding capacity and their ability to absorb nutrients (Slack 1988). The bryophyte layer may further prevent, or promote, depending upon the species, germination of the tree seeds (e.g., Ohlson & Zackrisson 1992). Patches of bare ground, for instance created by tree uprooting, may be sites of particular importance for germination of several tree species as well as many other species (e.g., Sirén 1955, Kinnaird 1974, Beatty 1984, Schaetzl et al. 1989, [IV]). Consequently, the functioning of an ecosystem is influenced by rates of recovery following disturbance, as well as successional pathways. Knowledge of these patterns and processes may be of value to basic as well as applied perspectives of ecology.

The lack of experimental disturbance studies in boreal forests with control of initial species composition makes it difficult to judge about the representativeness of rates of recovery found in my study for other areas in the boreal forest. However, circumstantial evidence suggests that species number rapidly reaches initial levels (or higher) during the first two to three years after fine-scale disturbance, but that the total cover of field and bottom layers is re-established much more slowly (5 to 30 years). Revegetation is particularly slow after (simulated) uprooting or other types of disturbance by which gaps with exposed soil are created (Jonsson & Esseen 1990, Jonsson 1993b, Jonsson & Dynesius 1993, [IV]). Disturbance severity has a great impact on the longevity of such patches, or invasion windows (cf. Gross 1980, Myster 1993), which are available for recruitment. The least severely disturbed patches are likely to have the shortest life span [IV]. At a regional scale, climate probably has a relatively larger impact on the rates of recovery of the bottom layer than it has on the field layer; recovery rates in the bottom layer are slower in areas with a drier climate (compare Jonsson 1993a, 1993b and [IV]), as most cryptogamic species grow only in periods when they are moist while otherwise being inactive (Stålfelt 1937, Busby & Whitfield 1978, R. Økland 1997).

The pattern and rate of recovery following fine-scale disturbance are dependent on species-specific traits. The three main processes involved in revegetation of a patch are: (1) germination of buried seeds, rhizomes, spores or other propagules; (2) dispersal of propagules into the disturbed patches (colonization); (3) clonal encroachment. Their relative efficiencies depend on disturbance severity, areal extent of the disturbance and distance of dispersal (Schimmel & Granström 1996, Frego 1996, [IV]). In very small disturbed patches in the forest floor (1-10 cm in diameter), clonal encroachment seems to be the main recovery strategy for bryophytes (Frego 1996, [III]). With increasing patch size, germination from the propagule bank and dispersal from outside increase in importance (Jonsson 1993a, 1993b, [IV]). Disturbance severity influences the species survival probability both in the aboveground vegetation and in the soil-buried propagule bank (Schimmel & Granström 1996, [IV]) and also affects the conditions for germination of the propagule bank [II]. Climate and site conditions play important roles in constraining germination and growth. Presence of species with high abundance in the soil as viable propagules (such as ferns [II]) is no guarantee for successful revegetation (Jonsson 1993a, [IV]).

Hylocomium splendens: *a boreal forest bryophyte*

Field experiments are more commonly used in plant population studies than in studies of plant communities (Gurevitch & Collins 1994), but even very simple and potentially interesting experiments like sowing of extra seeds are seldom performed (Crawley 1990). The lack of knowledge of bryophyte population biology is also much a result of the difficulty involved in non-destructive tagging of shoots (R. Økland 1995, During & Lloret 1996). However, the coloured-ring tagging technique introduced by R. Økland (1995) opens possibilities for progress, at least for larger species.

Hylocomium splendens is one of the largest, most widespread, and most thoroughly studied boreal forest bryophytes (e.g., Tamm 1953, Busby et al. 1978, Busby and Whitfield 1978, Callaghan et al. 1978, Skre & Oechel 1981, Sonesson et al. 1992, R. Økland 1995, 1997, Potter et al. 1995). However, the frequent occurrence of dense carpets of the species (cf. Callaghan et al. 1978, 1996) has been difficult to explain, because long-term population studies and experimental studies of the response of the species to fine-scale disturbance have both been lacking. It is now clear that disturbance influences the population dynamics of this species considerably [III]. Subjected to fine-scale disturbance, a *Hylocomium splendens* population may increase its number of modules two-fold in two years [III] through enhanced ramification and regeneration, and even sporophyte production seems to increase. There is, however, still no indication of germination from spores, at least in established vegetation [III]. The implication of these results is that very little can be deduced about the history of a population on the basis of a snapshot of branching rates, when the disturbance history of the site is unknown. Low branching rates may imply that the cryptogamic mat is dense, but may also be an effect of low mean segment size (see Callaghan et al. 1996).

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