DISTURBANCE SEVERITY AND COMMUNITY RESILIENCE IN A BOREAL FOREST

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Abstract. We studied the resilience of southeastern Norwegian old-growth *Picea abies* forest floor vegetation to experimental disturbance. Five treatments, differing in depth of removal of vegetation and soil layers and making up a gradient in disturbance severity, and three controls, were replicated 10 times. The experiment was analyzed with respect to the full species composition before and for seven years after treatment. The soil-buried propagule bank and local environmental conditions were recorded before treatment. Total cover of vascular plants and bryophytes and lichens increased slowly after treatment and was still below pre-disturbance levels after seven years. The rate of succession, measured as change in floristic dissimilarity between recordings made in successive years, declined with time for all treatments. The magnitude of vegetation change was strongly influenced by disturbance severity. DCA ordination revealed a main gradient in species composition from undisturbed forest floor to severely disturbed vegetation three years after disturbance, while in the fourth year, the direction of vegetation change turned in the direction of pre-disturbance positions. The turning point represented the maximum abundance of pioneer species (e.g., *Luzula pilosa* and *Pohlia nutans*) relative to dominant species before the disturbance (e.g., *Dicranum majus* and *Hylocomium splendens*). The return to pre-disturbance positions from the fourth year was, however, slow and will probably take 5–25 more years to be completed if current trends continue. DCA ordination revealed two additional, interpretable, gradients in vegetation; one related to pulses of regeneration from the soil-buried propagule bank; the other represented a gradient in pre-disturbance environmental conditions. We demonstrate that one vegetation gradient related to time after disturbance is insufficient to account for the full complexity of revegetation processes following disturbance.

Key words: boreal forest; disturbance; gap; propagule bank; recruitment; resilience; succession.

INTRODUCTION

Disturbance occurs on a variety of scales, potentially affects all levels of biological organization, and therefore plays important roles in the structuring of populations, communities, and ecosystems (White 1979, Pickett et al. 1989). Biotic responses to disturbance are a key factor for understanding ecosystem dynamics, and therefore for management (Malanson and Trubaud 1987, Chapin et al. 1996, Gibson et al. 2000). Disturbance typically creates open spaces and releases resources (Connell and Slatyer 1977, Schaetzl et al. 1989). Depending on the characteristic, i.e., extent, time, and magnitude (Glenn-Lewin and van der Maarel 1992), of a disturbance, the vegetation may show a response varying from resistance, via recovery with more or less complete return to the initial state, to irreversible changes (Connell and Slatyer 1977, Cat-

telino et al. 1979, Collins et al. 2000, van de Koppel and Rietkerk 2000).

Disturbance and succession are inextricably linked because disturbance may act as a reset mechanism for succession (Glenn-Lewin and van der Maarel 1992). The resilience, i.e., the speed of return to the initial state (the reciprocal of the return time; Pimm 1991) is an important characteristic of the successional process. Quantified by the rate of change in species composition (Malanson and Trubaud 1987, Whittaker 1991, Myster and Pickett 1994, Foster and Tilman 2000), resilience may be compared among disturbances of different types and intensities, in different sites and ecosystems (Shugart and Hett 1973, Rydgren et al. 1998). Successional rates can be measured in various ways, emphasizing different aspects of vegetation change (Shugart and Hett 1973, Bornkamm 1981, Malanson and Trabaud 1987, Myster and Pickett 1994). The most commonly used are measurement of floristic dissimilarity, and measurement of coordinated vegetation change along gradients using ordination techniques (Myster and Pickett 1994, Donnegan and Rebertus 1999, Collins 2000).

The boreal forest is a disturbance-prone ecosystem, affected by disturbances with extent varying from kilometers (e.g., wildfires) to meters (e.g., single-tree uprooting by strong winds) or less (e.g., animal activity) (Jonsson and Esseen 1990, Johnson 1992, Rydgren et al. 1998). Disturbance cause and severity, and the areal extent of each disturbed patch, influence vegetation resilience and successional patterns after fine-scale disturbance, but the mechanisms involved and the patterns they cause are poorly known (Schimmel and Granström 1996, Jonsson and Esseen 1998, Rydgren et al. 1998). Other factors with largely unknown influence on successional patterns are the initial, pre-disturbance, environmental conditions and species composition of the aboveground vegetation and the soil-buried propagule bank. Furthermore, the speed, and variation in speed, of regrowth dynamics after disturbance of the boreal forest floor remains unknown. These and other aspects of disturbance-initiated vegetation dynamics can be assessed in an experiment in which treated sites are monitored before and for a long time after treatment (Connell and Sousa 1983, Gurevitch and Collins 1994, Collins 2000). Plant ecological time-series data that meet these requirements and cover a time span of four or more years are exceptional (Gurevitch and Collins 1994).

In 1993 we began an experimental disturbance study in a boreal old-growth forest in southeastern Norway, that complies with the specifications given above (Rydgren 1997, Rydgren et al. 1998). As parts of this study, we analyzed vegetation–environment relationships (Rydgren 1996) and determined the species composition of the soil-buried propagule bank (Rydgren and Hestmark 1997) prior to experimental fine-scale disturbance treatment. Patterns of recovery for the first three years after the disturbance event were analyzed by Rydgren et al. (1998), without reference to initial conditions. The first three, often chaotic, years represent a very short time period in recovery and longer time series are needed to generalize about patterns. We predict that the successional rate decreases with time as a result of declining availability of open microsites and intensification of interspecific interactions (Shugart and Hett 1973, Bazzaz 1979, Lepš 1987, Foster and Tilman 2000). We also predict return of the species composition towards the pre-disturbance situation but at rates that vary according to disturbance severity (longer return time with increasing severity).

In the present study, we use data on initial conditions and seven years of recovery after experimental fine-scale disturbance to quantify successional rates. Disturbance treatments mimic the effects of roe-deer and elk, making heat and rut hollows, and tree uprooting that causes mineral soil to be exposed. Our main aim is to assess the importance of disturbance severity and initial conditions for the revegetation process after fine-scale disturbance.

MATERIALS AND METHODS

Study area and disturbance experiment

The study was carried out in Østmarka Nature Reserve, southeastern Norway (11°02′ E, 59°50′ N), 230–285 m above sea level, at Høgkollen, in *Picea abies* forests with understory dominance by *Vaccinium myrtillus*. The climate is slightly suboceanic with annual precipitation of ~800 mm and annual mean temperature of 3.9°C (see Rydgren [1996, 1997] for a thorough description of the study area).

Ten 10×10 m macro plots (blocks) were selected, within which eight 0.50×0.50 m vegetation plots were randomly placed (five subjected to different treatments, three controls). Treatment was performed manually with a small spade 23–25 August 1993. Roots in a given layer were removed by hand. Three treatments were applied to areas of 1.0×1.0 m centered upon the plots: T_V, removal of vegetation; T_L, removal of vegetation and the litter layer; T_M, removal of vegetation, the litter, and the mor soil layers. Two other treatments (T_{B1} and T_{B2}, removal of vegetation, the litter, and the mor and bleached soil layers) were applied to areas of 1.5×1.5 m: T_{B1} plots in one corner of the treated area, bordering onto intact vegetation on two sides, and T_{B2} in the center of the treated area. These five treatments represent a disturbance severity gradient that varies in the depth to which soil was removed (T_V, T_L, T_M, T_{B1}, and T_{B2}). T_{B2} is considered a more severe disturbance than T_{B1} because of the longer distance to intact vegetation. The sampling design was treated as balanced, with 30 control plots and 10 replicates for each of the five treatments.

Vegetation was recorded in each plot between 20 June and 2 July every year 1993–2000 (80 plots in each of eight years = 640 observations). Species abundances were recorded as frequency in 16 subplots; in each of which presence or absence of all species was recorded. A species was recorded as present when covering any part of the subplot. In 1994, nine plots were empty (no species recorded). Our species $\times$ observation matrix thus consisted of 63 species and 631 observations. In addition, the total cover (in percentage) of each of vascular plant and cryptogam (bryophyte and lichen) layers were recorded.

Initial conditions

Relationships between (undisturbed) vegetation and the environment (13 recorded variables: slope, aspect favourability, heat index, soil depth [minimum, median, and maximum], convexity on three different scales, canopy density index, soil moisture, loss on ignition, and pH) before treatment in 1993 were studied by Rydgren (1996, 1997), using a set of 100 0.25-m² plots (two extra plots from each block in addition to the eight experimental plots). One main gradient in species composition was found, as corroborated by close similarity of the first axes of LNMDS (local non-

metric multidimensional scaling by DECODA, version 2.01 [Minchin 1990]: species abundances standardized by division with species maximum; dimensionality = 2; dissimilarity measure = percentage dissimilarity) and DCA (detrended correspondence analysis [Hill 1979]; standard options with detrending by segments and nonlinear rescaling, except that species with frequency in the whole data set less than the median frequency were down-weighted [Eilertsen et al. 1990]). This main gradient was interpreted by analysis of correlations with environmental variables as a complex gradient with soil moisture (decreasing) and canopy closure (increasing) as prominent factors (Rydgren 1996). Statistical analyses of relationships between initial conditions and successional trajectories were based upon plot scores along the first LNMDS axis, as this axis was generally slightly more strongly correlated with environmental variables (Rydgren 1996) and thus considered a better index for relative positions of the 50 treated plots along the main gradient.

Soil samples for determination of the species composition of the propagule bank were collected separately from all soil layers removed by disturbance treatment (the depths of the different layers were: litter 0–5 cm, mor 5–10 cm, and bleached layer 10–15 cm) in all treated plots. An auger with a diameter of 3.5 cm was used. Each soil sample was represented by two parallels, and a total of 196 soil samples were set to cultivation in a phytotron chamber (for further details see Rydgren and Hestmark 1997). The species composition was found by the emergence method (Roberts 1981), and the emergent species from the different layers from the same plot were pooled in the present analyses. Emergent *Sphagnum* and *Polytrichum* specimens were included whenever possible to determine to species.

Statistical analysis

The Bray-Curtis (BC; Legendre and Legendre 1998) compositional dissimilarity index (percent dissimilarity/100) was calculated for each plot between the initial year (1993) and each other year, and between successive years after disturbance. The successional rate (Helle and Mönkkönen 1985) was estimated as BC for successive years.

The full species × observations matrix was subjected to DCA ordination (options as in *Methods*: *Initial conditions*) using CANOCO (version 4.0, ter Braak and Šmilauer 1998). The mean resultant displacement of plots from each treatment from year to year was displayed by vector diagrams where vector lengths represent successional rates in ordination space (Whittaker 1991).

The species composition of the soil-buried propagule bank in the 50 treated plots was related to gradients in the full data set by passively fitting, i.e., they are not included in the process of axis extraction but are fit into the ordination after the axes are defined, the observations of presence or absence in the 50 propagule bank samples into the DCA ordination.

Univariate (ANOVA) and multivariate (MANOVA) tests, as implemented in the Profile analysis module in SAS (SAS Institute 1992), procedure ANOVA for balanced design (von Ende 1993), were used to test for statistically significant effects of treatments and years since treatment on: (1) cover transformed to $\log_2(x + 1)$, (2) BC dissimilarity between repeated analyses of aboveground vegetation compared with species composition before disturbance, and (3) successional rates calculated as the BC dissimilarity of species composition between successive years. In the repeated measures analysis of variance (SAS Institute 1992) contrast variables were analyzed between successive time periods. One-way ANOVA was used to test for differences in successional rate among years within treatments. In case of significant effects ($P < 0.05$) in univariate ANOVA, a multiple comparisons test (Scheffé's test) was used to test treatment pairs for differences between means.

Wilcoxon signed rank tests were used to test if plot positions along DCA ordination axes were significantly displaced away from previous year's position. Kendall's rank correlation coefficients (τ) were calculated between the maximum absolute displacement of each plot away from its pretreatment position along DCA ordination axes and treatment severity (given on an ordinal scale, controls = 0, treatments $T_V - T_{B2} = 1–5$ in accordance with a priori assumptions of treatment severity as corroborated by Rydgren et al. [1998]). Kendall's τ was also calculated for the 50 treated plots between positions along the main initial gradient (LNMDS 1) and positions along the DCA ordination axes of the full data set.

RESULTS

Vegetation cover

Vascular plant cover has increased slowly but significantly after disturbance (Fig. 1A; $F = 58.3$, df = 6, 270, $P < 0.001$), and at rates not significantly different between treatments (time × treatment; $F = 1.42$, df = 24, 270, $P = 0.098$). Seven years after disturbance, cover was still below pre-disturbance levels.

Bryophyte and lichen cover has also increased significantly ($F = 201.1$, df = 6, 270, $P < 0.001$), but more slowly than vascular plants (Fig. 1B) and at rates that differed among treatments (time × treatment; $F = 4.22$, df = 24, 270, $P < 0.001$). After the third year after disturbance, the least severe treatment, T_V (removal of vegetation) had significantly higher bryophyte and lichen cover than other treatments (comparison within single years; Scheffé's test).

Species composition

Floristic dissimilarity.—Regardless of treatment, the species composition of treated plots became more sim-
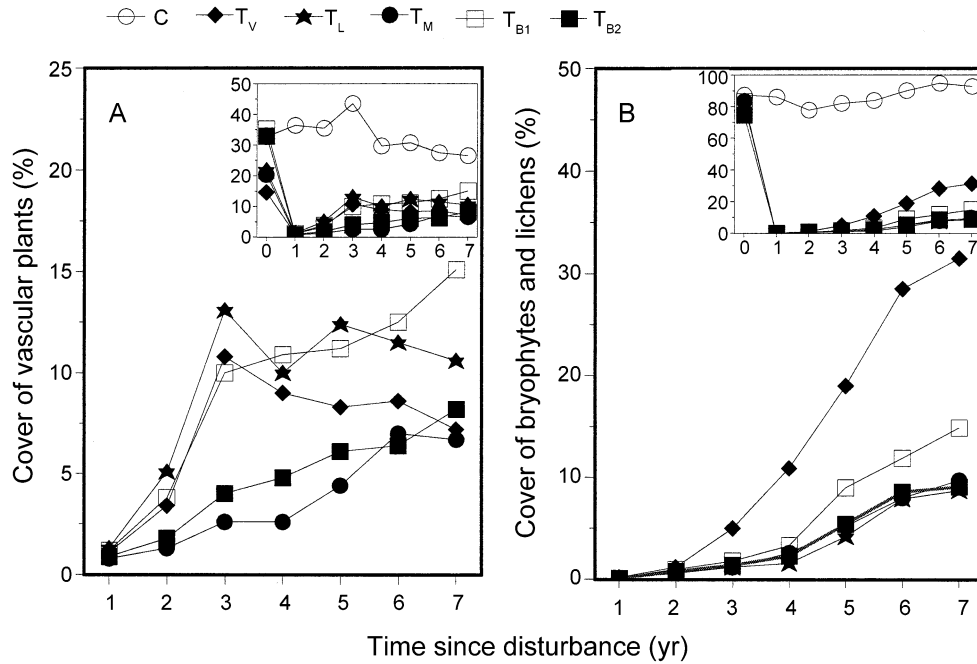
FIG. 1. Mean percent cover before (insets) and for seven successive years after the experimental disturbance treatment, (A) for vascular plants, and (B) for bryophytes and lichens. Treatments: C, control; T_V, removal of vegetation; T_L, removal of vegetation and litter; T_M, removal of vegetation, litter, and the mor soil layers; T_{B1} and T_{B2}, removal of vegetation, litter, and the mor and bleached soil layers. T_{B2} differs from T_{B1} with respect to the distance to intact vegetation.

ilar to the pre-disturbance composition year by year after treatment ($F = 163.0$, df = 6, 270, $P < 0.001$; Fig. 2A); although patterns of decrease in Bray-Curtis (BC) floristic dissimilarity differed among treatments (time × treatment; $F = 3.11$, df = 24, 270, $P < 0.001$).

Rates of succession, measured as BC between plots in successive years, declined significantly with time ($F = 242.1$, df = 6, 270, $P < 0.001$) and was in the last one-year period only slightly higher than in the control

(Fig. 2B). Successional rates differed among treatments (time × treatment; $F = 1.98$, df = 24, 270, $P = 0.005$).

DCA axis 1, a gradient in prominence of pioneer species.—The main gradient in species composition as revealed by DCA ordination (total inertia 2.73, eigenvalue 0.39, gradient length 3.28 SD units) ran from the undisturbed forest floor to severely disturbed plots, three years after treatment. Significant plot displacements along DCA axis 1 away from initial and previous
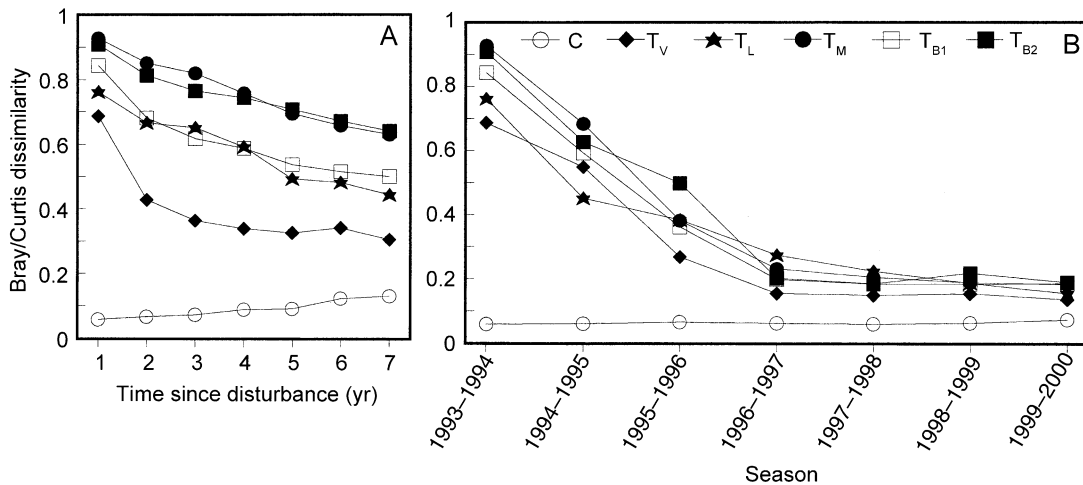

FIG. 2. Mean Bray-Curtis compositional dissimilarity among treatments: C, control; T_V–T_{B2}, disturbances of different kinds (see Fig. 1 legend). (A) Comparison with species composition before disturbance; (B) successional rate, i.e., the percentage dissimilarity between successive years.
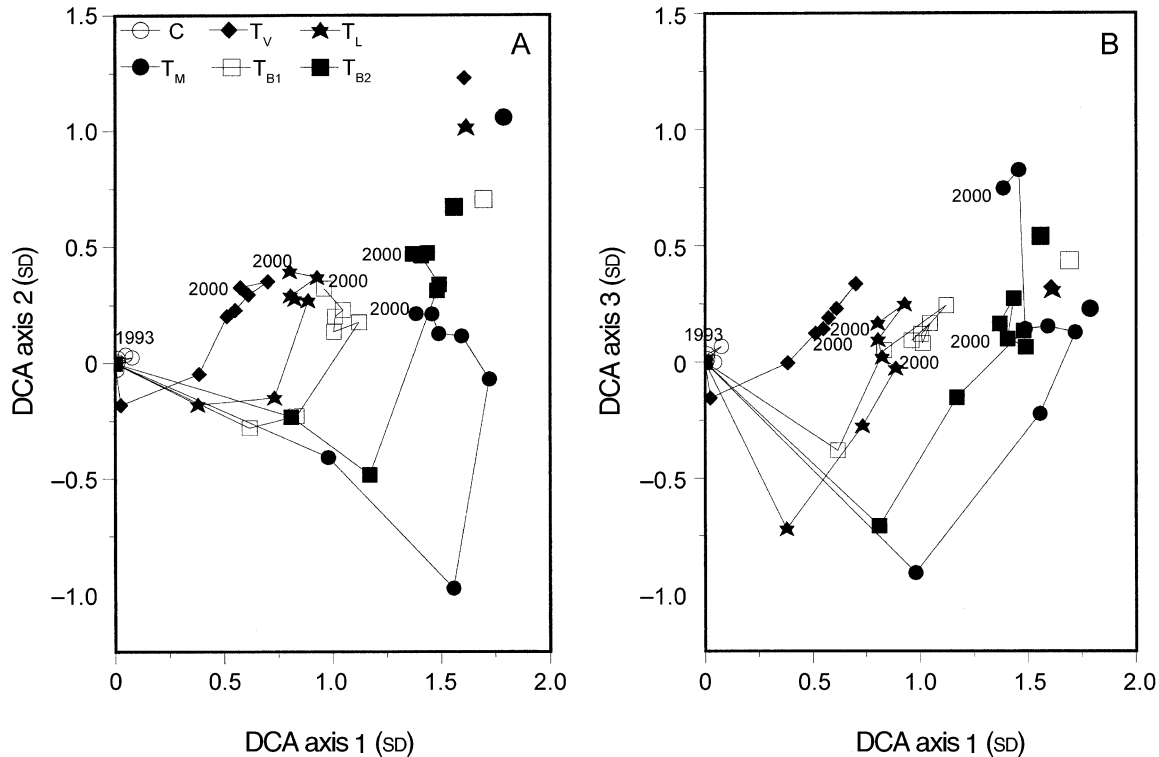
FIG. 3. Displacement vectors in DCA ordination space obtained for the full data set (631 plots × 63 species), for (A) axes 1 and 2 and (B) axes 1 and 3. The mean resultant displacement of each treatment × year since disturbance combination is shown. Different years for the same treatment are connected by lines. Unconnected symbols represent means of DCA scores, 10 for each treatment, of the propagule bank as passively fit into the DCA ordination of the full data set. T_V–T_{B2} represent disturbances of different kinds (see Fig. 1 legend), subjected after census in 1993.

years' positions (Wilcoxon signed rank test, $P <$ 0.0001 for all tests) were observed for all one-year periods after treatment until 1996 (Fig. 3). In 1996–1997, displacement ceased. Reversed displacement was observed thereafter, slight and insignificant 1997–1998 and 1998–1999 (Wilcoxon's signed rank tests, $P >$ 0.06), and significant 1999–2000 (Wilcoxon signed rank test, $P <$ 0.0001). DCA axis 1 represented a gradient in the relative abundance of pioneer species such as *Betula pubescens*, *Calluna vulgaris*, *Luzula pilosa*, *Plagiothecium laetum*, *Pohlia nutans*, and *Polytrichum formosum* that were absent from or rare in the undisturbed understory vegetation vs. dominants in the undisturbed forest floor, such as *Maianthemum bifolium*, *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis* (Fig. 4). The turning point, three years after treatment, represented the maximum abundance of pioneer species (the abundance of which thereafter leveled off or declined slightly) relative to dominant species before the disturbance (e.g., *Dicranum majus* and *Hylocomium splendens*) that gradually reestablished. Maximum plot displacement, from initial observations to the turning point along DCA axis 1, was greatest for T_M, larger for T_{B2} than for T_{B1} (differing by distance to intact vegetation), and least for T_V and T_L (Fig. 3). The significant correlation of maximum

displacement with the disturbance severity index ($\tau =$ 0.399, $P <$ 0.001, $n = 50$) was brought about by the higher abundance of pioneer species and slower reestablishment of pre-disturbance dominants in more severely disturbed plots. This main gradient in species composition was nonlinearly related to time since disturbance as well as disturbance severity (Fig. 3A).

DCA axis 2, a gradient in regeneration pulses from the soil-buried propagule bank.—The second most important gradient in species composition (eigenvalue 0.18, gradient length 3.20 SD units) mainly separated the 1995 and 1996 observations (Fig. 3; Wilcoxon signed rank test, $P <$ 0.0001), implying a strong displacement of plots in direction of the species composition of the propagule bank (Fig. 3A). Small and mostly insignificant displacements (in the same direction) occurred in subsequent years. High scores (estimated optima) along DCA axis 2 (see the Appendix) were obtained by pioneer species that rapidly became abundant in 1996, e.g., *Betula pubescens*, *Calluna vulgaris*, and *Plagiothecium laetum*, *Pohlia nutans*, and *Polytrichum formosum* (Fig. 4), and that have remained abundant thereafter. These species were among the most frequent in the propagule bank. Low scores were obtained by pioneer species that became abundant in 1995, e.g., *Luzula pilosa*, that were less frequent in the propagule bank (see the Appendix).
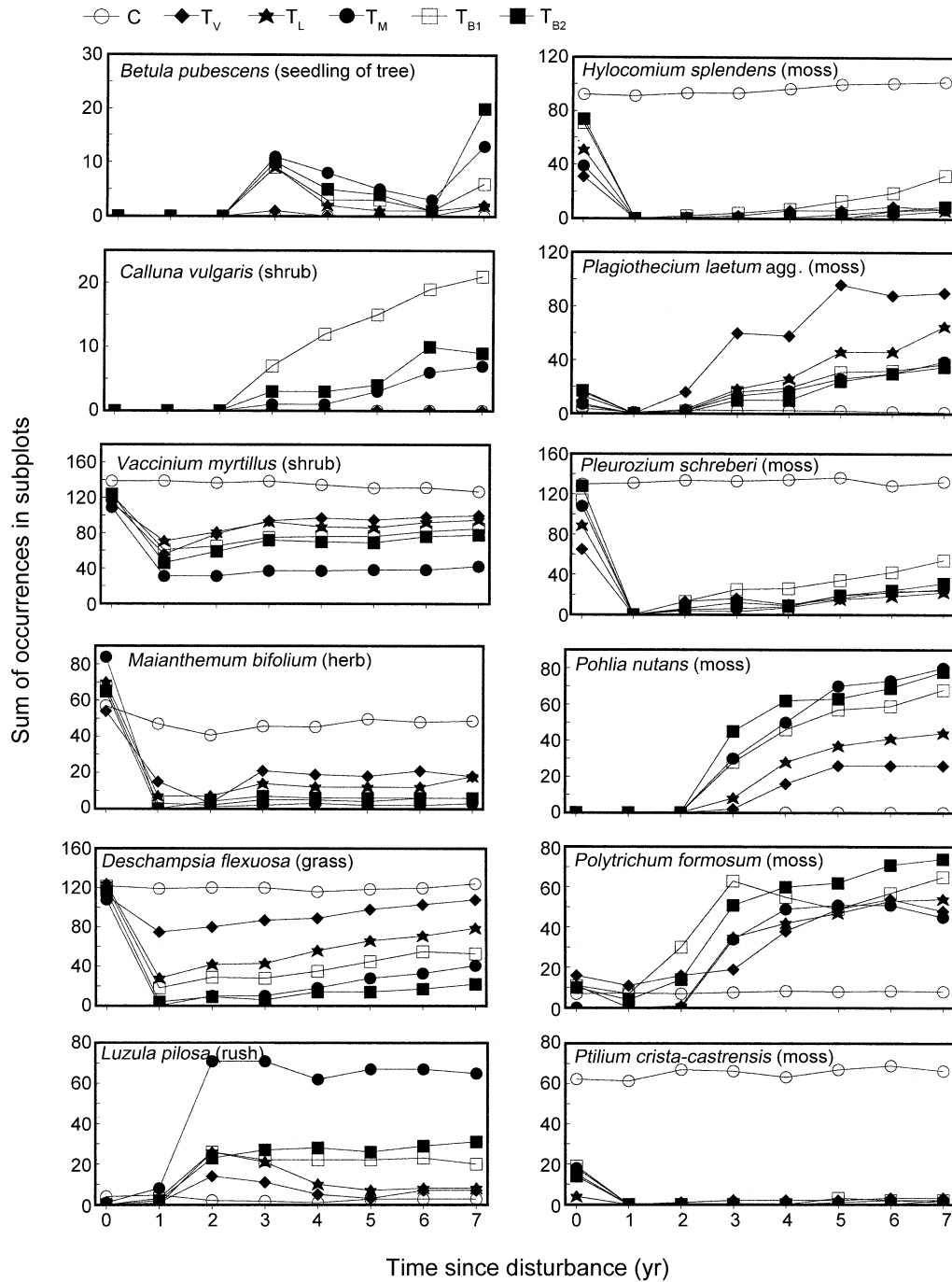
FIG. 4. Species abundances measured as the sum of subplot occurrences before and for seven successive years after disturbance treatments. Key to treatments: C, control; T_V, removal of vegetation; T_L, removal of vegetation and litter; T_M, removal of vegetation, litter, and the mor soil layers; T_{B1} and T_{B2}, removal of vegetation, litter, and the mor and bleached soil layers. T_{B2} differs from T_{B1} with respect to the distance to intact vegetation.

Maximum plot displacement along DCA axis 2 was significantly correlated with the disturbance severity index ($\tau = 0.242$, $P = 0.022$, $n = 50$). Plots subjected to the most severe treatment (T_{B2}; naked mineral soil without opportunities for ingrowth from the margins) were placed closest to their propagule-bank counterparts while the converse was true for the mildest treatment T_V (Fig. 3). DCA axis 2 reflected a gradient in relative abundance of pioneer species, with high and low abundance in the soil-buried propagule bank, respectively.
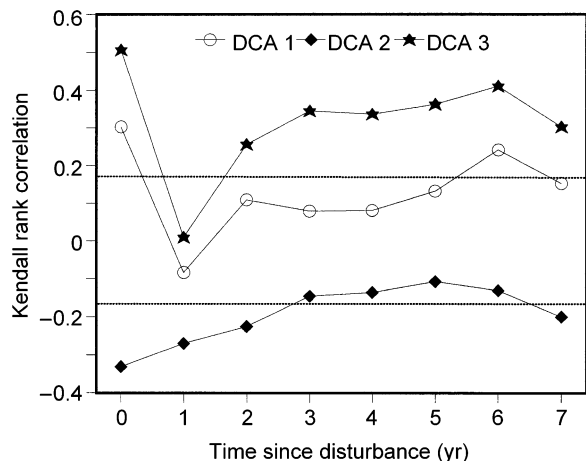
FIG. 5. Kendall rank correlations (τ) between DCA ordination scores obtained for the full data set (631 plots × 63 species) between the plots that were disturbed in 1993 and initial conditions (soil moisture and increasing canopy closure) expressed as LNMDS (local nonmetric multidimensional scaling) axis 1 scores for the same plots. The horizontal dotted lines indicates ~95% confidence envelopes for τ. Sample size (n) is 50, except for the first year after disturbance when n = 41.

Note that the relative positions along DCA axis 2 of plots that differ in DCA axis 1 score are fixed by the detrending procedure, which inevitably produces a tongue-shaped point configuration in cases where there is little variation along a second axis near one end and large variation near the other end of a previous axis. Thus, the strong displacements along an independent axis (DCA axis 2) in the third year after disturbance can be validly inferred, while the displacement of severely treated plots (towards lower DCA axis 2 scores) in the first and second years after treatment may be artifactual.

DCA axis 3, a gradient related to pre-disturbance environmental conditions.—Significant year-to-year plot displacements, in oscillating directions were observed in five of the seven one-year periods (Fig. 3B; Wilcoxon signed rank tests, all *P* < 0.0001). DCA axis 3 (eigenvalue 0.15, gradient length 2.56 SD units) was therefore not related to revegetation after treatment and maximum plot displacements along this axis were uncorrelated with the disturbance severity index (τ = 0.141, *P* = 0.182). Contrary to DCA axes 1 and 2, DCA axis 3 was correlated with positions along the (main) gradient in undisturbed forest related to decreasing soil moisture and increasing canopy closure (Fig. 5). High scores (estimated optima) along DCA axis 3 (Appendix) were obtained by species typically occurring in dry sites under closed canopies, e.g., *Dicranum majus* and *Goodyera repens*, while low scores were obtained by species typical of open habitats, e.g., *Calluna vulgaris*, and *Polytrichum juniperinum*. DCA axis 3 thus indicated a long-lasting role of the initial environmental conditions in determining the direction

of successional changes after the chaotic first phase (of duration one year) that follows fine-scale disturbance.

DISCUSSION

Succession

We demonstrate that from three years after disturbance succession rates decline, both measured as displacement in the ordination space and as floristic dissimilarity between plots in successive one-year periods. Such a decrease in succession rate with time is common in many herbaceous communities (Shugart and Hett 1973, Prach et al. 1993, Myster and Pickett 1994, Foster and Tilman 2000). At the same time our results show that the revegetation succession does not follow a simple path, but is related to three independent gradients. The main gradient in species composition (DCA axis 1) runs from the undisturbed forest floor to severely disturbed vegetation three years after disturbance and reflects the relative importance of pioneer species favored by severe disturbance vs. species of the undisturbed forest floor. The second gradient differentiates between pioneer species that have high and low abundance in the soil-buried propagule bank, and differ with respect to the timing of reestablishment: some species establish immediately after disturbance (e.g., *Luzula pilosa*) while other species establish three years after disturbance (e.g., *Betula pubescens*, *Calluna vulgaris*, and *Pohlia nutans*). This differentiation reflects differences in species' traits such as recolonization efficiency, which is strongly influenced by the climate (the extremely dry summer of 1994 can explain the difference in our case) and recolonization strategy (Rydgren et al. 1998).The third gradient is related to initial environmental conditions. Three phases in the revegetation succession can be discerned. In the first phase, lasting for two years, pioneer species increase in importance relative to undisturbed forest-floor species. In the second phase, the third year after treatment, the increase of pioneer species continues while, at the same time and apparently independently, displacement along a new gradient is brought about by a strong pulse of regeneration from the soil-buried propagule bank. The third phase, still not completed seven years after treatment, is characterized by slow vegetation change in favor of species well represented in the soil-buried propagule bank (DCA axis 2) and/or typical of the undisturbed forest floor (reversal of displacement along DCA axis 1). The reversal along the main gradient occurs first in severely treated plots, with highest prominence of pioneer species.

An estimate of the time still needed for treated plots to return to the initial species composition, based upon the present rate of vegetation change (i.e., the length of the vector between the two last years for the different treatments in Fig. 3) is 5–25 years, depending on disturbance severity. Most likely, however, the rate of change will continue to slow down because the closing

of invasion windows (cf. Gross 1980) for bryophytes and lichens appears to be a slow process, and because several of the abundant pioneer species (e.g., *Pohlia nutans* and *Polytrichum* spp.) may be persistent for many decades after a disturbance event (Jonsson and Esseen 1990). There are, however, considerable uncertainty with respect to the speed of the revegetation process in later phases. There are indications that bryophyte cover increase may follow an sigmoidal curve with rapid increase in the intermediate phase in which conditions for bryophyte growth are rapidly enhanced (Busby et al. 1978, Økland and Økland 1996, Rydgren et al. 2001) and leveling off in the late phase when density has become so high that negative density effects on growth occur (Økland 2000, Pedersen et al. 2001).

Disturbance: severity and size

Disturbance severity strongly influences revegetation patterns, as shown by the significant correlations between the magnitude of the maximum displacement of plot positions along the two main revegetation gradients (DCA axes 1 and 2) and depth of removal of soil layers as well as the size of the disturbed patch. Disturbance extent and severity impacts revegetation patterns by the vertical structure of the propagule bank and belowground structures such as roots and rhizomes (Granström 1982, Schimmel and Granström 1996, Rydgren and Hestmark 1997), by qualitative differences between the exposed soil layers (with respect to organic matter and nutrient content, etc.), and by the size of the area exposed and thus the distance to intact vegetation. Depth of soil removal influences survival of belowground structures such as roots and rhizomes, important sources for recovery after disturbance (Flinn and Wein 1977, Schimmel and Granström 1996, Rydgren et al. 1998). We find better recovery of species that regenerate mainly from underground structures, and with rhizomes and roots mainly confined to the upper part of the mor layer, e.g., *Vaccinium myrtillus* and *Deschampsia flexuosa* (Schimmel and Granström 1996), in less strongly disturbed patches (Hautala et al. 2001). In contrast, species that colonize by seed germination and that have an abundant soil-buried seed bank (e.g., *Calluna vulgaris* and *Luzula pilosa*), show better recovery in the more severe disturbed patches, probably because of higher abundance of fertile seeds in deeper soil layers (Rydgren and Hestmark 1997), which may reflect historical changes in species abundance as a result of succession (McGraw 1987).

Because many boreal forest species rely on clonal growth for recruitment, the size of a patch laid open by disturbance is an important determinant of the recolonizing success of different species (Økland 1995*a*, Frego 1996, Jonsson and Esseen 1998). Thus the opportunity for clonal ingrowth in T_{B1} plots but not in T_{B2} explains the better recovery of pre-disturbance dominants such as the grass *Deschampsia flexuosa* in the former, and means that T_{B1} treatment plots are situated closer to pre-disturbance plots than T_{B2} plots in the ordination. Clonal ingrowth is particularly important for the bryophytes *Hylocomium splendens* and *Pleurozium schreberi*, which lack a soil-buried propagule bank (Jonsson 1993, Rydgren and Hestmark 1997) and for which germination from spores is likely to play a minor ecological role (Jonsson and Esseen 1998, Rydgren and Økland 2002; but see Cronberg 2002).

Initial conditions

The correlation between the third DCA ordination axis and the main vegetation gradient in undisturbed vegetation (LNMDS axis 1), related to variation in canopy cover and soil moisture conditions (Rydgren 1996), persistent for seven years after disturbance treatment, shows that revegetation patterns are also influenced by fundamental ecological conditions. A plausible mechanism is that the availability of diaspores after disturbance depends on presence of a species before disturbance, which varies along the initial gradient (Rydgren 1996). Most notably, this is expected to be the case for species such as *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Hylocomium splendens*, and *Ptilium crista-castrensis*, which depend on rhizomes or surviving roots, a soil buried propagule bank, clonal encroachment of surrounding vegetative shoots, and/or establishment from inblown or extant clonal fragments (Jonsson 1993, Økland 1995*b*, Jonsson and Esseen 1998, Rydgren et al. 1998), for successful reestablishment. Soil moisture and/or canopy cover may also directly influence regeneration success. While soil moisture supply and radiation at forest-floor level are not likely to have been much altered by our treatment, the increased radiation in treefall gaps enhances germination and establishment of many forest species (Schaetzl et al. 1989, Gray and Spies 1996). Initial conditions are likely to be of less importance for revegetation patterns the more strongly the environment is changed in by the disturbance, although they may still influence successional trajectories to some extent (Halpern 1988). Although the influence of initial conditions on the course of succession has been recognized in previous studies (Dyrness 1973, Connell and Sousa 1983, Halpern 1988), empirical corroboration of such initial effects is sparse (Myster and Pickett 1990). More studies in which species composition and environmental conditions are recorded both before and after (experimental) disturbance are therefore needed for general patterns in the relative importance of initial conditions and disturbance characteristics for revegetation patterns to emerge.

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APPENDIX

A table showing constancy percentage (for species with occurrence at least 3.0% in the total data set consisting of 640 samples) in control plots over all years (1993–2000), along with species percentages, in treated plots in 1993 before disturbance, in the different years after disturbance (1994–2000), and within treatments over all years after disturbance, as well as species optima for the three first axes in a DCA ordination and species composition of the propagule bank of the treated plots before treatment in 1993 is available in ESA's Electronic Data Archive: *Ecological Archives* E085-054-A1.