<http://www.diva-portal.org>

This is the published version of a paper published in *Ecology*.

Citation for the original published paper (version of record):

Åström, M., Dynesius, M., Hylander, K., Nilsson, C. (2007)

Slope aspect modifies community responses to clear-cutting in boreal forests.

Ecology, 88(3): 749-758

<http://dx.doi.org/10.1890/06-0613>

Access to the published version may require subscription.

N.B. When citing this work, cite the original published paper.

Permanent link to this version:

<http://urn.kb.se/resolve?urn=urn:nbn:se:umu:diva-12424>

SLOPE ASPECT MODIFIES COMMUNITY RESPONSES TO CLEAR-CUTTING IN BOREAL FORESTS

MARCUS ÅSTRÖM,¹ MATS DYNESIUS,^{1,3} KRISTOFFER HYLANDER,² AND CHRISTER NILSSON¹

¹Landscape Ecology Group, Department of Ecology and Environmental Science, Umeå University, SE-901 87, Umeå, Sweden

²Plant Ecology, Department of Botany, Stockholm University, SE-106 91, Stockholm, Sweden

Abstract. Slope aspect modifies microclimate and influences ecological processes and spatial distribution of species across forest landscapes, but the impact of slope aspect on community responses to disturbance is poorly understood. Such insight is necessary to understand landscape community dynamics and resilience. We compared bryophyte (liverworts and mosses) communities in matched 0.02-ha plots of four boreal stand types in central Sweden: recently clear-felled and mature stands dominated by Norway spruce in south-facing and north-facing slopes. Differences between forests and clear-cuts were interpreted as effects of clear-cutting, and differences between south- and north-facing slopes as effects of aspect. In response to clear-cutting, bryophyte cover and composition changed more in south-facing slopes. Only one out of ten significantly declining species in south-facing slopes also declined significantly in north-facing slopes. North-facing slopes lost fewer bryophyte species, and among those, fewer forest species and fewer species associated with wood and bark. In north-facing slopes, the average proportions of mosses and liverworts shared between the forest and the clear-cut plot were 88% and 74%, respectively. Corresponding numbers for south-facing slopes were 79% and 33%. In addition, more bryophyte species were added in north- than south-facing slopes after clear-cutting, somewhat reducing the difference in compositional change between aspects. South- and north-facing mature forests differed in species composition, mostly due to higher richness of mosses in south-facing slopes. The smaller changes in bryophyte communities on north-facing slopes in response to clear-cutting have implications for ecosystem dynamics and management as high local survival may enhance landscape-level resilience.

Key words: clear-cutting; disturbance; forest; habitat quality; liverworts; mosses; resilience; slope; species composition; stability.

INTRODUCTION

Disturbance occurs at a variety of spatial and temporal scales and affects ecosystem function and structure (Pickett et al. 1989). Knowledge on biotic responses to disturbance is essential for understanding ecosystem stability and dynamics and hence management (Pimm 1991, Chapin et al. 1996). Resistance (i.e., the degree of change) and resilience (i.e., the rate, manner or degree of return to initial conditions) are linked to the intensity and spatial extent of disturbance (Halpern 1988, Pimm 1991, Jonsson and Esseen 1998) but are also affected by environmental heterogeneity at both local and landscape scales (Bengtsson 2002, Bengtsson et al. 2003). Landscape topography contributes to habitat heterogeneity by influencing microclimate, ground-water flow, and ecological processes such as fire regime, biomass decomposition, soil formation and production (Geiger 1965, Verbyla and Fischer 1989, Mudrick et al. 1994, Mermoz et al. 2005, Zinko et al.

2005). In the northern hemisphere, north-facing slopes are darker, moister, and colder because they receive less solar radiation than otherwise similar south-facing slopes (Holland and Steyn 1975). Previous studies have shown that aspect, through its impact on microclimate, influences the spatial distribution of vascular plants (e.g., Cantlon 1953, Bale et al. 1998, Olivero and Hix 1998). However, the effects on bryophytes have received less attention and earlier studies have been restricted to few sites or small plots (Cantlon 1953, Söderström 1981, Økland et al. 2003). Site sparsity reduces the generality of results and small grain size only allows studies of a fraction of the local species pool. Furthermore, results from small study plots may suggest that many species with low abundance are locally absent.

The effects of aspect on microclimate may differ between clear-felled and forested slopes (cf. MacHattie and McCormack 1961). Olivero and Hix (1998) and Økland et al. (2003) proposed that slope aspect may influence succession after stand-replacing disturbances such as clear-cutting. For example, it is likely that canopy removal causes an increase in radiation to levels exceeding the tolerance of more forest organisms in south- than in north-facing slopes. However, to our knowledge, no study has specifically addressed how slope

Manuscript received 12 April 2006; revised 16 August 2006; accepted 5 September 2006. Corresponding Editor: N. C. Kenkel.

³ Corresponding author.

E-mail: mats.dynesius@emg.umu.se

aspect influences biotic responses to clear-cutting. We address this question using understory boreal forest bryophytes (liverworts and mosses) as model organisms.

Bryophytes are strongly affected by microclimate (Busby et al. 1978, Hylander 2005), making them particularly well suited for studies on effects of slope aspect and canopy disturbance. Overstory canopies buffer understory microclimate (Chen et al. 1999) and clear-cutting changes wind, light, and temperature patterns, generally reducing bryophyte cover and affecting composition and richness (Fenton and Frego 2005, Hylander et al. 2005). Late-successional species are negatively affected while pioneers are favored (Rydgren et al. 2004, Hylander et al. 2005, Uotila and Kuoki 2005). Moreover, many bryophytes depend on sustained humidity during establishment (Schofield 1985) and therefore colonization after clear-cutting may vary with moisture conditions. Mosses and liverworts may respond differently because most moss species are less shade adapted and drought sensitive than the majority of liverworts (Marschall and Proctor 2004). Hence, moss richness is less affected by exposure (Fenton et al. 2003, Åström et al. 2005, Hylander et al. 2005). Furthermore, forest species, and species associated with convex substrates such as logs, stumps, and tree bases, are more prone to local extinction following clear-cutting (Hylander et al. 2005).

We explored the influence of slope aspect on the response of understory bryophytes to forest clear-cutting and on bryophyte communities in general by testing the following five hypotheses: (1) south-facing slopes experience a larger reduction in bryophyte cover after clear-cutting; (2) south-facing slopes encounter greater losses of liverworts and species associated with forests and wood and bark substrates; (3) species recruitment in response to clear-cutting is higher on (moister) north-facing than on (drier) south-facing slopes; (4) in mature forests, south-facing slopes harbor fewer liverworts and species associated with wood and bark substrates, but instead more mosses and species linked to exposed habitats; (5) the imprint of aspect on bryophyte richness and composition is larger in clear-cuts than in forests. These hypotheses were analyzed by comparing the bryophyte flora of matched 0.02-ha plots of four stand types: century-old mature stands and 3–22 year-old clear-cuts on north- and south-facing slopes. We interpreted differences between forests and clear-cuts as effects of clear-cutting and differences between north- and south-facing slopes as effects of slope aspect.

METHODS

Study area

The study area was situated in the middle boreal zone (Ahti et al. 1968) in the province of Ångermanland, Sweden, between latitudes 63°35' and 64°05' N. The area is characterized by thick delta sediments forming terraces intersected by ancient gully systems with scarps, ridges, and ravines up to 50 m high. The soil material

consists of sandy-loamy-silty sediment and soils are podzolics. Till or bedrock of mostly acidic gneiss or granite is underlying the sediments. The mature forests are dominated by Norway spruce (*Picea abies* L. Karst) and Scots pine (*Pinus sylvestris* L.) with scattered broadleaves (*Betula pubescens* Ehrh., *B. pendula* Roth, and *Populus tremula* L.). The forests are intensively managed and clear-cutting has been the main mode of timber extraction for the last 60 years (Wastenson and Nilsson 1995). Mean annual precipitation is ~750 mm and mean temperature for January and July is –9°C and +15°C, respectively (Raab and Vedin 1995). By using aerial photos, topographic maps, and field visits, we identified 10 sites where an ancient gully system was present within a spruce-dominated forest stand and a nearby clear-felled stand formerly dominated by spruce. In each of the 10 sites, we selected a south- and a north-facing slope located in the forest and a south- and a north-facing slope located in the clear-cut. All four slopes at each site were similar with respect to slope inclination and slope length. In each of the four slopes we randomly located a plot midpoint. In each site, the midpoints were then relocated vertically to become matched (among the four stand types) in relation to the valley bottoms and the ridge tops. Around the midpoints, a 0.02-ha (10 × 20 m) sample plot was placed with the long side perpendicular to the slope contours. No surface rocks, boulders or stones were present in the plots and the sediment texture was similar within each site. Plot midpoints were located at least 25 m from the nearest stand edge and sites were between 0.75 and 40 km apart. Plot altitudes ranged from 120 to 190 m above sea level, which is below the highest postglacial coastline.

Habitat properties

We recorded slope inclination, distances from plot midpoint to ridge top, valley bottom, and stand edges, and slope aspect using an inclinometer, a measuring tape, a GPS and a 360° compass (90° = E), respectively. Latitude and elevation for each plot were retrieved from maps. Using slope inclination, aspect, and latitude as input variables, we applied Eq. 2 of McCune and Keon (2002) to estimate potential annual direct incident radiation (PAR; MJ·cm⁻²·yr⁻¹) in each plot. Stand ages of mature forests and years since clear-cutting were provided by landowners and the local Forestry Board, or determined by extracting increment cores from two dominant trees in each plot (forests only). We visually estimated cover (m²) of coarse woody debris (CWD; mid-bole diameter >10 cm), fine woody debris (FWD; diameter 1–10 cm), and bare ground (exposed litter, humus, and mineral soil). All tree stems >10 cm at stump height were counted. We measured basal area at breast height of living trees using a relascope. Tree canopy cover was estimated visually for spruce, pine, and broadleaves separately. All data (including bryophyte data) were collected in July–August 2004.

South- and north-facing slopes were oriented between 120° and 230° (180° = S) and 325° and 64° (360°/0° = N), respectively (Appendix A). Slopes were generally steep with inclinations ranging 20–43° and PAR was roughly three times higher in south-facing than in north-facing slopes. The 10 forest stands were on average 107 years old (range 80–134 years) and the 10 clear-cut stands were harvested on average 11 years before the study (range 3–22 years). There were some differences in forest structure between south- and north-facing slopes in both forests and clear-cuts. For example, south-facing forests had more broadleaved trees, mainly aspen (*Populus tremula* L.) and covers of CWD, FWD, and bare ground were higher in south-facing slopes and in clear-cuts (Appendix A).

Bryophyte data collection and ecological classification of species

Each 200-m² plot was divided into five 40-m² (4 × 10 m) subplots in which we recorded presence of all moss and liverwort species and visually estimated total cover (m²) of bryophytes. From the subplot records we calculated the number of species present and the bryophyte cover in each 200-m² plot. Species were divided into three mutually exclusive substrate groups (wood and bark, undisturbed ground, and exposed mineral soil), and two habitat groups (forest and open habitats) based on Hallingbäck (1996) and personal experience from the region. Wood and bark species are those mainly associated with woody debris and tree-bases (up to 2 m). The “open habitats” group includes species mainly inhabiting treeless habitats such as roadsides, riverbanks, open mires, and rocky outcrops. Taxonomy and nomenclature follow Söderström and Hedenäs (1998), except for the recently described *Lophozia ciliata* (Söderström et al. 2000). A few species groups were treated as a single aggregate species because they could not always be distinguished: *Brachythecium oedipodium* and *B. rutabulum*; *B. reflexum* and *B. starkei*; *Bryum* sp.; *Dicranum fuscescens* and *D. flexicaule*; *Plagiothecium laetum* and *P. curvifolium*; *Calypogeia* spp., *Cephaloziella* spp., *Cephalozia lunilifolia*, and *C. affinis*; *Lophozia silvicola* and *L. ventricosa*; and *Pellia* spp.

Data analysis

Pairwise comparisons of plots of opposite aspect were made within the same clear-cuts and forest stands, controlling for the variation in stand age. For each pair of forest and clear-cut plots, we calculated the number of species “lost” and “added” in response to clear-cutting. Lost species were those found only in the forest plot and added species those found only in the clear-cut plot. In a comparative study like this, these estimates do not only include turnover caused by clear-cutting, but also spatial turnover unrelated to clear-cutting. However, this does not bias the results since the magnitude of spatial turnover was similar in south- and north-facing forests (0.64 and 0.60, respectively [Jaccard’s index of

similarity where every forest plot was compared with all other of the same aspect and then averaged]). The frequency of individual species was calculated as the number of subplots where a species was present (up to five subplots per 200-m² plot), whereas occupancy was the number of 200-m² plots of each kind where a species was found (up to 10 plots for each of the four stand types).

We used the blocked multiresponse permutation procedure (MRBP; PC-ORD; McCune and Mefford 1999) to analyze differences in bryophyte composition among the four stand types. The subplot frequencies (1–5) of all species present were used as input data (Appendix B). We also used MRBP to analyze differences between aspects in the magnitude of compositional change in response to clear-cutting, as well as differences between forests and clear-cuts in the magnitude of compositional change in response to aspect. In these analyses we used the pairwise differences in frequencies between forests and clear-cuts or between aspects. We applied site as the blocking variable and aspect (south or north) or stand type (forest or clear-cut) as grouping variables. Euclidean distance was used as the distance measure. We used Monte Carlo permutation tests (with 1000 permutations) to test for significant differences in composition. The effect size (represented by *A*) ranges from 1 (identical within-group agreement) to 0 (agreement expected by chance [McCune and Grace 2002]).

To illustrate the variation in species composition we plotted site and species scores from a non-metric multidimensional scaling ordination (NMS or NMDS), which is a robust method for exploring ecological data (McCune and Mefford 1999). We used Euclidean distance and default settings (global NMS, a stability criterion of 0.005, number of iterations with real data 10, maximum number of iterations 100) in PC-ORD version 4 (McCune and Mefford 1999). We report a two-dimensional solution because stress was considerably reduced compared to a one-dimensional solution (from 32.8 to 17.8). Three axes further reduced stress (to 10.3) but because stress values of <20 are considered sufficient (McCune and Grace 2002) and for the sake of simplicity we did not introduce a third axis. We rotated the ordination diagram 45°, which increased the interpretability of the axes in relation to the measured environmental variables (McCune and Mefford 1999).

The relationship between environmental variables (except slope inclination and aspect as those are synthesized in PAR) and site scores were explored using Spearman rank correlations due to non-normality in some cases. In each stand type, we also tested the effect of CWD on richness of bryophytes associated with bark and wood using linear least-square regression. The effect of FWD was not analyzed because of the positive correlation between FWD and CWD and because more bryophyte species occur on CWD than on FWD. For all other comparisons we used the Wilcoxon’s signed rank

FIG. 1. NMS ordination plots summarizing differences in (a) site scores and (b) species scores between south- and north-facing forests and clear-cuts (200-m² plots). In (a), circles are forests, and triangles are clear-cuts. Solid symbols are north-facing slopes. Labels denote site number. In (b), 26 species were excluded because they were found in fewer than three of the 40 plots. Solid symbols are liverworts. Species name abbreviations are explained in Appendix B.

test, except for plot occupancy of individual species, for which the sign test was used. Although testing of occupancy and frequency for every single species result in very high experiment-wise error, these analyses were mainly exploratory. Therefore, no correction of *P* values was made. Normality was tested using the Kolmogorov-Smirnov's test. SPSS for Windows Version 13.0.1 was used for all statistical analyses (SPSS 2004), except for species composition.

RESULTS

Altogether, we found 47 moss and 27 liverwort species in the 40 plots together encompassing 0.8 ha (Appendix B). Bryophyte cover in south-facing plots was lower than in north-facing plots (200 m²), both in forests (143 ± 11 m² vs. 182 ± 6 m² [mean $\pm$ SE]; $P = 0.007$) and in clear-cuts (61 ± 14 m² vs. 152 ± 12 m²; $P = 0.005$). The difference in cover between aspects was greater in clear-cuts than forests ($P = 0.037$).

Species composition in south- and north-facing slopes

Bryophyte species composition differed between south- and north-facing forests ($A = 0.136$; $P = 0.0020$; MRBP) as well as between clear-cuts of opposite aspects ($A = 0.244$, $P = 0.0008$). The difference in composition between aspects was greater in clear-cuts than forests ($A = 0.122$, $P = 0.0013$). PAR correlated strongly ($r = 0.74$, $P < 0.0001$) with the site scores of axis 2 (Appendix A). Also FWD, bare soil cover and distance to ridge top correlated positively with axis 2 (and covaried with PAR; Appendix A).

In forests, south-facing slopes were richer in mosses, but the richness of the six other groupings of species was not affected by aspect (Fig. 2a). Six mosses were more frequent (had a higher occupancy and/or frequency) in south-facing forests whereas two moss and two liverwort species were more frequent in north-facing forests (Table 1). Richness of species associated with bark and wood were positively related to cover of CWD in north-facing ($P = 0.009$, $R^2_{\text{adj}} = 0.54$), but not in south-facing forests ($P = 0.699$).

Richness of mosses did not differ between clear-cuts of opposite aspects whereas richness of liverworts and species associated with wood and bark, undisturbed ground, and forests were higher in north-facing clear-cuts (Fig. 2b). Only two moss species were more frequent in south-facing clear-cuts, whereas six moss and four liverwort species were more frequent in north-facing clear-cuts (Table 1). Cover of CWD had no significant effect on richness of species associated with bark and wood in neither north-facing ($P = 0.248$) nor south-facing clear-cuts ($P = 0.912$).

Response to clear-cutting

Clear-cutting reduced bryophyte cover ($P = 0.005$ in both south- and north-facing slopes). However, the reduction by 82 m² (55%) in south-facing slopes was greater than the 30-m² (18%) decline in north-facing slopes ($P = 0.037$). Clear-cuts differed in species composition from their forest counterparts ($A = 0.215$, $P = 0.0008$ and $A = 0.112$, $P = 0.0011$, for south- and north-facing slopes respectively; MRBP). However, this difference was greater in south- than north-facing slopes ($A = 0.122$, $P = 0.0013$). This is also illustrated by the NMS ordination where the south-facing clear-cuts are separated from the forests along the first axis, while the north-facing clear-cuts overlap broadly with the forests (Fig. 1a). This axis correlated with stand age, tree basal area, stem number and canopy cover (Appendix A).

In south-facing slopes clear-cutting reduced species richness of liverworts (−3 species; $P = 0.017$), forest species (−7 species; $P = 0.005$), and species associated with wood and bark (−4 species; $P = 0.005$), but raised richness of species associated with open habitats (+3 species; $P = 0.027$). In contrast, clear-cutting caused no reduction in any group in north-facing slopes but increased richness of mosses (+3 species; $P = 0.024$) and species associated with mineral soil (+2 species; $P =$

FIG. 2. Comparison of species richness (mean $\pm$ SE) in south-facing (open bars) and north-facing (gray bars) slopes for phylogenetic, substrate-, and habitat-based bryophyte groups in (a) forests and (b) clear-cuts. Differences in richness between opposite aspects were tested using Wilcoxon's signed rank tests. *P* values < 0.05 are shown in boldface type; *N* = 10 plots of 200 m² each.

0.020) and open habitats (+3 species; *P* = 0.011). Clear-cutting removed the difference between aspects found for mosses in forests, but instead introduced differences for liverworts and species associated with wood and bark, undisturbed ground, and forests (Fig. 2a, b). North-facing slopes lost fewer species of mosses, liverworts, species associated with wood and bark, and species associated with forests (Fig. 3). Furthermore, more species of four bryophyte groups (liverworts, forest species, wood/bark species, and undisturbed ground species) were added in north-facing slopes (Fig. 3). The average number of moss species shared between forest and clear-cut plots in a site did not differ between aspects (15.1 and 14.3 species in south- and north-facing slopes, respectively; *P* = 0.227). On average, this accounted for 79% (south-facing slopes) and 88% (north-facing slopes) of the mosses found in a forest plot. In contrast, the number of shared liverwort species was substantially lower in south-facing (1.9 species or 33%) than in north-facing slopes (5.6 species or 74%; *P* = 0.005).

In south-facing slopes clear-cutting reduced occupancy and/or subplot frequency of ten species associated with wood and bark or undisturbed ground in forests.

Only one of these species decreased also in north-facing slopes (Table 2). Five species of the open habitat group increased in response to clear-cutting. Two forest species increased in north-facing clear-cuts (Table 2).

DISCUSSION

Aspect and the bryophyte community

In accordance with our hypothesis 5, we found a larger impact of aspect on the bryophyte community in clear-cuts than in forests in terms of cover, richness (Fig. 2a, b) and composition. There were, however, important differences between aspects also in forests (e.g., Fig. 1a). The NMS axis 1 represents structural differences between clear-cuts and forests whereas along axis 2 the north- and south-facing slopes are clearly separated (Fig. 1a, Appendix A). Most of the variation in the other measured habitat properties can be explained by the variation in PAR and stand age. However, the relatively strong correlation between distance to ridge top (*r* = 0.54) and axis 2 of the NMS reflects that the south-facing plots were located somewhat further from ridge top and hence plots were less exposed (Appendix A).

TABLE 1. Species with significant affinities to south- or north-facing slopes in either forests or clear-cuts.

Species	N	Forests					
		Occupancy			Frequency		
		South	North	P	South	North	P
More frequent in south-facing slopes							
<i>Brachytecium oedipodium/rutabulum</i>	10	10	8	0.500	4.2 (0.4)	2.7 (0.6)	0.033
<i>Brachytecium reflexum/starkei</i>	10	10	8	0.500	4.5 (0.3)	2.8 (0.6)	0.042
<i>Brachytecium salebrosum</i>	9	9	1	0.008	3.8 (0.2)	0.6 (0.6)	0.010
<i>Ceratodon purpureus</i>	1	1	0	...	1.0 (0.0)	0.0 (0.0)	...
<i>Dicranum polysetum</i>	10	10	7	0.250	4.2 (0.6)	2.9 (0.7)	0.048
<i>Dicranum scoparium</i>	10	10	10	1.000	4.7 (0.2)	3.9 (0.3)	0.038
<i>Rhodobryum roseum</i>	7	7	1	0.031	1.4 (0.2)	0.3 (0.3)	0.023
More frequent in north-facing slopes							
<i>Aulacomnium palustre</i>	1	1	0	...	1.0 (0.0)	0.0 (0.0)	...
<i>Barbilophozia lycopodioides</i> (L)	7	6	7	0.219	2.3 (0.7)	4.1 (0.4)	0.111
<i>Calypogeia</i> sp. (L)	10	6	10	0.125	1.8 (0.6)	3.7 (0.4)	0.035
<i>Dicranum majus</i>	10	10	10	1.000	4.0 (0.3)	4.8 (0.2)	0.114
<i>Hylocomium splendens</i>	10	10	10	1.000	4.9 (0.1)	5.0 (0.0)	0.317
<i>Lophozia obtusa</i> (L)	6	0	6	0.031	0.0 (0.0)	1.3 (0.3)	0.020
<i>Lophozia silvicola/ventricosa</i> (L)	10	7	9	0.625	1.5 (0.4)	2.5 (0.6)	0.169
<i>Polytrichum commune</i>	10	10	10	1.000	3.7 (0.5)	4.9 (0.1)	0.042
<i>Ptilium crista-castrensis</i>	10	10	10	1.000	4.4 (0.3)	5.0 (0.0)	0.109
<i>Sphagnum capillifolium</i>	5	0	5	0.063	0.0 (0.0)	2.2 (0.6)	0.042
<i>Tetraphis pellucida</i>	10	10	10	1.000	2.3 (0.5)	3.0 (0.5)	0.347

Notes: Data for occupancy are totals (0–10), and frequencies are means (with SE in parentheses). N is the number of plot pairs where a species was found in at least one of the plots. Frequencies are calculated on the basis of these plot pairs only, i.e., plot pairs where the species is absent are not included. “(L)” denotes liverwort species. Plot size is 200 m². P values were derived from sign tests (plot occupancy) or Wilcoxon’s signed rank tests (frequency). P values < 0.05 are shown in boldface type. For habitat and substrate affinity of each species, refer to Appendix B.

Thus the differences between the opposite aspects might be slightly underestimated.

As predicted by hypothesis 4, south-facing forests were richer in mosses, probably as a result of higher cover of broadleaved trees (mainly relatively base-rich aspen), CWD, FWD, bare ground (Appendix A), and herbs (M. Åström, unpublished data). Woody debris (e.g., Kruys and Jonsson 1999), disturbed mineral soil (Jonsson and Esseen 1990), and through-fall from base-rich broadleaved trees (Weibull and Rydin 2005) have been shown to raise moss diversity in spruce forests. Moreover, herb litter stimulates species preferring eutrophic conditions, such as *Rhodobryum roseum* (Koponen 1966). One could argue that competition and litter-fall from vascular plants reduce moss cover in south-facing forests (Bergamini et al. 2001), implying reduced richness. However, north-facing forests had higher cover of ground-living bryophytes, covering most of the FWD and mineral soil, which most likely reduced numbers of bryophyte species specifically associated with these substrates.

The moister microclimate in north-facing forests favored moisture dependent species (e.g., the moss *Sphagnum girgensohnii*; Fig. 1b). However, in contrast to our hypothesis 4 and to Söderström (1981), we did not find greater richness of liverworts and species associated with wood and bark in north-facing forests. This may be an effect of our studied forests being managed and poor in convex substrates such as CWD,

structures that are vital for boreal forest liverworts and wood inhabiting species (e.g., Hylander et al. 2005). Consequentially, richness of these groups was low compared to that of old-growth forests also in our north-facing forests. However, high humidity stimulates colonization and raises richness of bryophytes on dead wood (Lindström 2003). Accordingly, only north-facing forests displayed a positive relationship between CWD cover and richness of species associated with wood and bark. It is therefore likely that CWD-rich forests would show larger differences between south- and north-facing slopes in the richness of this species group.

Aspect and response to clear-cutting

The larger differences in bryophyte communities between clear-cuts and forests in south-facing slopes (Fig. 1a) demonstrate that the effects of clear-cutting may vary considerably within hilly landscapes. As predicted (hypotheses 1 and 2), bryophyte cover was less reduced, and fewer liverworts and species associated with forest and wood/bark were lost (Fig. 3) or declined in north-facing clear-cuts (Table 2). In addition to our hypothesized differences in response, fewer moss species were lost in north-facing slopes. PAR was three times higher in south-facing forests whereas tree densities were similar to densities in north-facing forests (Appendix A). Therefore, the tree layer absorbs and reflects more radiation in south-facing slopes. Consequently, clear-cutting in south-facing slopes results in a higher

TABLE 1. Extended.

N	Clear-cuts					
	Occupancy			Frequency		
	South	North	P	South	North	P
10	10	10	1.000	3.2 (0.5)	3.4 (0.4)	0.490
10	10	10	1.000	3.3 (0.4)	3.0 (0.4)	0.854
9	7	6	1.000	1.9 (0.5)	1.6 (0.5)	0.631
10	10	7	0.250	3.4 (0.8)	1.5 (0.4)	0.012
10	10	9	1.000	4.2 (0.4)	2.9 (0.5)	0.040
10	10	10	1.000	4.8 (0.2)	4.8 (0.1)	1.000
2	1	1	1.000	0.5 (0.5)	2.0 (2.0)	0.655
8	1	8	0.016	0.1 (0.1)	1.6 (0.4)	0.014
10	2	10	0.008	0.2 (0.1)	3.6 (0.3)	0.005
10	1	10	0.004	0.1 (0.1)	2.6 (0.3)	0.004
10	8	10	0.500	1.6 (0.4)	4.4 (0.3)	0.005
10	10	10	1.000	4.1 (0.4)	5.0 (0.0)	0.038
7	0	7	0.016	0.0 (0.0)	2.0 (0.4)	0.017
10	1	10	0.004	0.1 (0.1)	3.2 (0.3)	0.004
10	10	10	1.000	3.7 (0.4)	4.8 (0.1)	0.015
10	9	10	1.000	1.8 (0.4)	5.0 (0.0)	0.007
1	0	1		0.0 (0.0)	4.0 (0.0)	
10	5	10	0.063	0.8 (0.3)	2.9 (0.2)	0.007

radiation increase at ground level which may cause greater microclimatic challenges for forest organisms. The smaller change in north-facing slopes was probably caused by their clear-cuts being considerably shadier and hence moister than south-facing clear-cuts. These findings parallel the results of previous studies of species

resistance to clear-cutting, showing higher survival in shady and moist microhabitats, e.g. patches of remnant canopies (Fenton and Frego 2005, Hylander et al. 2005). However, patches of relatively sheltered microhabitats within transformed environments are not likely to support the most disturbance-intolerant species. We studied managed forests with intolerant species, but one taxon (the relatively vulnerable *Calypogeia* spp. [Hylander et al. 2002]) declined significantly also in north-facing clear-cuts (Table 2).

The comparatively smaller range in site scores of south-facing clear-cuts along both axes (Fig. 1a) suggests that their communities are homogenized. One reason for this may be that stumps and logs were deprived of most of their bryophyte vegetation in south-facing clear-cuts (M. Åström, *personal observation*), removing variation in CWD cover as a cause of variation in species composition (recall the lack of correlation between CWD cover and richness of wood- and bark-species).

Our results suggest that aspect also modifies post-disturbance colonization of bryophytes (Fig. 3 and Table 2). In accordance with our hypothesis 3, more species colonized in north-facing slopes in response to clear-cutting (Fig. 3) and all colonizers were native species. However, colonization of moss species and species growing on mineral soil and in exposed habitats (e.g., *Ceratodon purpureus* and *Polytrichum juniperinum*) did not differ between aspects (Fig. 3 and Table 2). Such

FIG. 3. Comparison between south-facing (open bars) and north-facing (gray bars) slopes for the number of bryophyte species lost and added in response to clear-cutting. Lost species are species that were present only in the forest plot of a matched plot pair, whereas added species only appeared in the clear-cut plot. Other details are as described in the Fig. 2 legend.

TABLE 2. Species with a significant response to clear-cutting in south- and/or north-facing slopes.

Species	N	South-facing slopes					
		Occupancy			Frequency		
		Forest	Clear-cut	P	Forest	Clear-cut	P
Negative response to clear-cutting							
<i>Calypogeia</i> sp. (L)	6	6	1	0.063	3.0 (0.6)	0.2 (0.2)	0.027
<i>Chiloscyphus profundus</i> (L)	10	9	4	0.125	2.6 (0.5)	0.5 (0.2)	0.015
<i>Dicranum majus</i>	10	10	8	0.500	4.0 (0.3)	1.6 (0.4)	0.007
<i>Hylocomium splendens</i>	10	10	10	1.000	4.9 (0.1)	4.1 (0.4)	0.039
<i>Lophozia silvicola/ventricosa</i> (L)	7	7	1	0.031	2.1 (0.4)	0.1 (0.1)	0.017
<i>Plagiothecium laetum/curvifolium</i>	10	10	10	1.000	4.9 (0.1)	4.2 (0.2)	0.038
<i>Ptilium crista-castrensis</i>	10	10	9	1.000	4.4 (0.3)	1.8 (0.4)	0.014
<i>Rhodobryum roseum</i>	7	7	1	0.031	1.4 (0.2)	0.1 (0.1)	0.014
<i>Sanionia uncinata</i>	10	10	10	1.000	4.5 (0.2)	2.7 (0.4)	0.011
<i>Tetraphis pellucida</i>	10	10	5	0.063	2.3 (0.5)	0.8 (0.3)	0.019
Positive response to clear-cutting							
<i>Aulacomnium palustre</i>	2	1	1	1.000	0.5 (0.5)	0.5 (0.5)	1.000
<i>Brachytecium salebrosum</i>	10	9	7	0.625	3.4 (0.4)	1.7 (0.5)	0.072
<i>Ceratodon purpureus</i>	10	1	10	0.004	0.1 (0.1)	3.4 (0.4)	0.007
<i>Dicranum scoparium</i>	10	10	10	1.000	4.7 (0.2)	4.8 (0.2)	0.705
<i>Jungermannia caespiticia</i> (L)	4	0	4	0.125	0.0 (0.0)	1.0 (0.0)	0.046
<i>Pohlia nutans</i>	10	10	10	1.000	3.2 (0.4)	4.7 (0.2)	0.026
<i>Polytrichum juniperinum</i>	10	5	10	0.063	1.5 (0.5)	4.2 (0.3)	0.008

Note: For details and definitions, see Table 1.

species often colonize or increase in abundance after disturbance (Rydgren et al. 2004, Hylander et al. 2005, Uotila and Kuoki 2005) and our results indicate that they can find suitable microsites for establishment also in the drier south-facing clear-cuts.

The age range of clear-cuts was quite wide (3–22 years) and one could expect differences in species composition between the young and the old clear-cuts. However, differences were rather small (M. Åström, *unpublished data*) probably because most changes in composition and richness of forest bryophytes in response to clear-cutting are immediate and remain for at least 30–50 years (Dynesius and Hylander 2007). However, pioneer species that are stimulated by disturbance disappear rather quickly as succession proceeds (Dynesius and Hylander 2007). It is likely that such a development is occurring in our clear-cut plots and would have been possible to detect in a larger data set.

Synthesis

This study provides evidence that slope aspect influences bryophyte composition in forests and modifies biotic responses to clear-cutting. North-facing slopes retain more forest species at least through the first decade after clear-cutting, and allow coexistence of early and late successional species. These surviving populations may facilitate recolonization through generally shorter dispersal distances and a denser propagule rain in the landscape (Bengtsson 2002). This is especially important for species with poor dispersal abilities. For example, several boreal forest bryophytes mainly reproduce clonally, lack a soil propagule bank, and seldom produce spores (Jonsson 1993, Rydgren and Hestmark 1997). Jonsson and Esseen (1998) showed that the size of

a disturbed patch influences recovery rates of such species. Because of the smaller change in north-facing slopes one might argue that these communities are more resistant and enjoy a greater potential for high local resilience. However, we suggest that clear-cutting causes a larger microclimatic changes (a larger “disturbance”) in south- than in north-facing slopes, and that this is the main determinant of the differences in response rather than initial differences in community composition. This parallels studies reporting more intense disturbance by fires on (drier) western or southwestern aspect (e.g., Kushla and Ripple 1997) and may be experimentally tested by evaluating biotic response to various combinations of aspect and canopy thinning.

The interaction between slope aspect and canopy disturbance is likely to have important ecological effects at the landscape scale. Hilly landscapes are richer in species than level landscapes, presumably because they host more habitats. Assuming that level landscapes show a response that is intermediate to that of the south- and north-facing slopes, our results suggest that hilly landscapes are rich in species also because north-facing slopes serve as refugia after canopy disturbance. Ecosystem capacity to reorganize after disturbance is partly determined by species survival and their spatial distribution (Bengtsson et al. 2003) and therefore north-facing slopes may enhance landscape scale resilience.

The importance of the interactions between slope aspect and canopy cover on microclimate will differ depending on the environmental demands of the focal organisms and geographical location. For example, the insolation contrast between north- and south-facing slopes is greatest at mid-latitudes (45°) and diminishes toward the equator and the poles (Holland and Steyn

TABLE 2. Extended.

North-facing slopes						
N	Occupancy			Frequency		
	Forest	Clear-cut	P	Forest	Clear-cut	P
10	10	10	1.000	3.7 (0.4)	2.6 (0.3)	0.020
6	5	5	1.000	2.0 (0.8)	2.0 (0.7)	0.739
10	10	10	1.000	4.8 (0.2)	4.4 (0.3)	0.157
10	10	10	1.000	5.0 (0.0)	5.0 (0.0)	1.000
10	9	10	1.000	2.5 (0.6)	3.2 (0.3)	0.254
10	10	10	1.000	5.0 (0.0)	4.9 (0.1)	0.317
10	10	10	1.000	5.0 (0.0)	5.0 (0.0)	1.000
2	1	1	1.000	1.0 (1.0)	2.0 (2.0)	0.655
10	10	10	1.000	3.4 (0.5)	2.6 (0.5)	0.066
10	10	10	1.000	3.0 (0.5)	2.9 (0.2)	0.887
8	0	8	0.008	0.0 (0.0)	1.6 (0.4)	0.008
6	1	6	0.063	0.8 (0.8)	2.3 (0.6)	0.034
7	0	7	0.016	0.0 (0.0)	2.1 (0.4)	0.017
10	10	10	1.000	3.9 (0.3)	4.8 (0.1)	0.041
3	0	3	0.250	0.0 (0.0)	1.3 (0.3)	0.102
10	9	10	1.000	2.3 (0.4)	4.9 (0.1)	0.004
9	4	8	0.219	0.7 (0.3)	3.3 (0.6)	0.029

1975). Therefore, we hypothesize that the interaction between slope aspect and canopy removal could be even more important in, for example, southern Europe. Including a latitudinal gradient in the experiment proposed above could test this hypothesis. However, many other factors influence the climatic contrast between aspects, for example clouds, wind, and precipitation.

We found several examples of species being more abundant in south-facing slopes in forests that after clear-cutting increased only in north-facing slopes (e.g., *Brachytecium salebrosum*, *Dicranum scoparium*; Tables 1 and 2). This suggests that species may migrate between stands with different slope aspect in response to changes in canopy cover. Such “aspect migration” may also promote successful habitat tracking of species in response to climate change, similarly to the well-known altitudinal migrations. To conclude, several unexplored “aspects of aspect” deserve further attention, both as a venue for improving ecological theory and as a basis for wise management of forest landscapes.

ACKNOWLEDGMENTS

Holmen Skog, The Church of Sweden, SCA Skog, The Swedish Forestry Board, and several private landowners provided stand data and field sites. We thank Sandra Karlsson, Roland Jansson, and Ola Lindroos for valuable help. Three anonymous reviewers provided helpful comments on an earlier version of this paper. The study was financially supported by the Björkman Fund (to M. Åström) and the Swedish Energy Agency (to C. Nilsson).

LITERATURE CITED

Ahti, T., L. Hämet-Ahti, and J. Jalas. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5:169–211.

- Åström, M., M. Dynesius, K. Hylander, and C. Nilsson. 2005. Effects of slash harvest on bryophytes and vascular plants in southern boreal clear-cuts. *Journal of Applied Ecology* 42: 1194–1202.
- Bale, C. L., J. B. Williams, and J. L. Charley. 1998. The impact of aspect on forest structure and floristics in some eastern Australian sites. *Forest Ecology and Management* 110:363–377.
- Bengtsson, J. 2002. Disturbance and resilience in soil animal communities. *European Journal of Soil Biology* 38:119–125.
- Bengtsson, J., P. Angelstam, T. Elmqvist, U. Emanuelsson, C. Folke, M. Ihse, and M. Nyström. 2003. Reserves, resilience and dynamic landscapes. *Ambio* 32:389–396.
- Bergamini, A., D. Pauli, M. Peintinger, and B. Schmid. 2001. Relationships between productivity, number of shoots and number of species in bryophytes and vascular plants. *Journal of Applied Ecology* 89:920–929.
- Busby, J. R., L. C. Bliss, and C. D. Hamilton. 1978. Microclimate control of growth rates and habitats of boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecological Monographs* 48:95–110.
- Cantlon, J. E. 1953. Vegetation and microclimates on north and south slopes of Cushtunk Mountain, New Jersey. *Ecological Monographs* 23:241–270.
- Chapin, F. S., M. S. Torn, and M. Tatenno. 1996. Principles of ecosystem sustainability. *American Naturalist* 148:1016–1037.
- Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brososke, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49:288–297.
- Dynesius, M., and K. Hylander. 2007. Resilience of bryophyte communities to clear-cutting of boreal stream-side forests. *Biological Conservation*, *in press*.
- Fenton, N. J., and K. A. Frego. 2005. Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests. *Biological Conservation* 122:417–430.
- Fenton, N. J., K. A. Frego, and M. R. Sims. 2003. Changes in forest floor bryophyte (moss and liverwort) communities four years after forest harvest. *Canadian Journal of Botany* 81: 714–731.
- Geiger, R. 1965. The climate near ground. Harvard University Press, Cambridge, Massachusetts, USA.
- Hallingbäck, T. 1996. Ekologisk katalog över mossor. [The bryophytes of Sweden and their ecology.] Swedish Species Information Centre, Uppsala, Sweden.
- Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69: 1703–1715.
- Holland, P. G., and D. G. Steyn. 1975. Vegetation responses to latitudinal variations in slope angle and aspect. *Journal of Biogeography* 2:179–183.
- Hylander, K. 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology* 42:518–525.
- Hylander, K., M. Dynesius, B. G. Jonsson, and C. Nilsson. 2005. Substrate form determines the fate of bryophytes in riparian buffer strips. *Ecological Applications* 15:674–688.
- Hylander, K., B. G. Jonsson, and C. Nilsson. 2002. Evaluating buffer strips along boreal streams using bryophytes as indicators. *Ecological Applications* 12:796–806.
- Jonsson, B. G. 1993. The bryophyte diaspore bank and its role after small-scale disturbance in boreal forests. *Journal of Vegetation Science* 4:819–826.
- Jonsson, B. G., and P.-A. Esseen. 1990. Treefall disturbance maintains high bryophyte diversity in boreal spruce forests. *Journal of Ecology* 78:924–936.
- Jonsson, B. G., and P.-A. Esseen. 1998. Plant colonization in small forest-floor patches: importance of plant group and disturbance traits. *Ecography* 21:518–526.

- Koponen, T. 1966. Distribution of *Rhodobryum roseum* in Finland in the light of line survey and frequency maps. *Annales Botanici Fennici* 3:399–405.
- Kruys, N., and B. G. Jonsson. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests in northern Sweden. *Canadian Journal of Forest Research* 29:1295–1299.
- Kushla, J. D., and W. J. Ripple. 1997. The role of terrain in a fire mosaic of a temperate coniferous forest. *Forest Ecology and Management* 95:97–107.
- Lindström, K. 2003. Wood-living bryophyte species diversity and distribution: differences between small-stream and upland spruce forests. Master's Thesis. Department of Ecology and Environmental Science, Umeå University, Sweden.
- MacHattie, L. B., and R. J. McCormack. 1961. Forest microclimate: a topographic study in Ontario. *Journal of Ecology* 49:301–323.
- Marschall, M., and M. C. F. Proctor. 2004. Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll *a*, chlorophyll *b* and total carotenoids. *Annals of Botany* 94:593–603.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM Software Design, Gleneden Beach, Oregon, USA.
- McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13:603–606.
- McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data. MJM Software Design, Gleneden Beach, Oregon, USA.
- Mermoz, M., T. Kitzberger, and T. T. Veblen. 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. *Ecology* 86:2705–2715.
- Mudrick, D. A., M. Hoosein, R. R. Hicks, and E. C. Townsend. 1994. Decomposition of leaf litter in an Appalachian forest: effects of leaf species, aspect, slope position and time. *Forest Ecology and Management* 68:231–250.
- Økland, T., K. Rydgren, R. Halvorsen Økland, K. O. Storaunet, and J. Rolstad. 2003. Variation in environmental conditions, understorey species number, abundance and composition among natural and managed *Picea abies* forest stands. *Forest Ecology and Management* 177:17–37.
- Olivero, A. M., and D. M. Hix. 1998. Influence of aspect and stand age on ground flora of southeastern Ohio forest ecosystems. *Plant Ecology* 139:177–187.
- Pickett, S. T. A., J. Kolasa, J. J. Armesto, and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* 54:129–136.
- Pimm, S. L. 1991. The balance of nature? Ecological issues in the conservation of species and communities. Chicago University Press, Chicago, Illinois, USA.
- Raab, B., and H. Vedin, editors. 1995. National atlas of Sweden: climate, lakes and rivers. SNA Publisher, Stockholm, Sweden.
- Rydgren, K., and G. Hestmark. 1997. The soil propagule bank in a boreal old-growth spruce forest: changes with depth and relationship to aboveground vegetation. *Canadian Journal of Botany* 75:121–128.
- Rydgren, K., R. H. Økland, and G. Hestmark. 2004. Disturbance severity and community resilience in a boreal forest. *Ecology* 85:1906–1915.
- Schofield, W. B. 1985. Introduction to bryology. First edition. Blackburn Press, Caldwell, New Jersey, USA.
- Söderström, L. 1981. Distribution of bryophytes in spruce forests on hill slopes in central Sweden. *Wahlenbergia* 7:141–143.
- Söderström, L., and L. Hedenäs. 1998. Checklista över Sveriges mossor. [A checklist to the bryophytes of Sweden.] *Myrnia* 8: 58–90.
- Söderström, L., L. Hedenäs, and K. Damsholt. 2000. A new species of *Lophozia* (subgen. *Protolophozia*) from Fennoscandia. *Lindbergia* 25:3–5.
- SPSS. 2004. SPSS for Windows. Version 13.0.1. SPSS, Chicago, Illinois, USA.
- Uotila, A., and J. Kouki. 2005. Understorey vegetation in spruce-dominated forests in eastern Finland and Russian Karelia: successional patterns after anthropogenic and natural disturbances. *Forest Ecology and Management* 215: 113–137.
- Verbyla, D. L., and R. F. Fischer. 1989. Effects of aspect on ponderosa pine height and diameter growth. *Forest Ecology and Management* 27:93–98.
- Wastenson, L., and N.-E. Nilsson, editors. 1995. National atlas of Sweden: the forests. National Board of Forestry, Jönköping, Sweden.
- Weibull, H., and H. Rydin. 2005. Bryophyte species richness on boulders: relationship to area, habitat diversity and canopy tree species. *Biological Conservation* 122:71–79.
- Zinko, U., J. Seibert, M. Dynesius, and C. Nilsson. 2005. Plant species numbers predicted by a topography based ground-water-flow index. *Ecosystems* 8:430–441.

APPENDIX A

A table of habitat properties of forests and clear-cuts in south- and north-facing slopes and their correlations with NMS site scores and potential annual direct radiation (*Ecological Archives* E088-048-A1).

APPENDIX B

A table of taxonomic, substrate, and habitat groups and plot occupancy and frequency of all 74 bryophyte species (*Ecological Archives* E088-048-A2).