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Slow recovery of bryophyte assemblages in middle-aged boreal forests regrown after clear-cutting



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ABSTRACT

Clear-cutting followed by even-aged forestry is transforming forests around the globe. There is growing concern that considerable parts of the native forest biodiversity will not be able to re-colonize these new stands before the next clear-cutting. The development of species assemblages during the full forestry rotation period must be understood in order to assess the need for management adaptations and to get a basis for their design. Knowledge is accumulating from studies of permanent plots before and shortly after clear-cutting, but for later stages only comparative studies have been published (space-for-time substitutions). In this study, I combined this comparative approach with direct monitoring of the pace of assemblage recovery in boreal stands regrown after clear-cutting half a century ago (treatment stands). I found little re-colonization in assemblages of mosses and liverworts between an initial survey to a resurvey 15 years later in 0.1-ha permanent plots of upland and stream-side forest. The assemblages of the treatment stands were still significantly different from those in matched old control forests that had never been clear-cut. The treatment stands had significantly fewer species of liverworts and of the substrate-based species subgroup "wood or bark", and the six most negatively affected species were liverworts more or less specialized to this substrate. The only significant recovery recorded over the 15 years was for the "rocks or boulders" subgroup in upland stands, probably related to a shadier and moister climate resulting from canopy development. During the inter-survey period, some of the upland treatment stands were thinned. All disfavored subgroups recovered less in thinned than in not thinned upland stands, most likely as a result of a return to lighter and drier microclimates and direct mechanical disturbance. The incomplete and slow recovery halfway into the forestry rotation period calls for action. Adaptation of thinning for conservation has rarely been implemented in boreal forest management, but has a large potential. To facilitate re-colonization by disfavored liverworts and mosses growing on wood or bark and/or under shaded and moist conditions, I suggest retention of unlogged patches during thinning and addition of coarse deadwood on the ground in these patches. Such measures would also favor re-colonization of other late-successional species.

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1. Introduction

Globally, complete canopy removal affected 2.3 million square kilometers of forests from 2000 to 2012 (Hansen et al., 2013), equaling an annual area almost the size of Great Britain. Much of this area is then managed as even-aged secondary stands. Because of the large and increasing area covered by such stands, their ability to sustain biodiversity must be better understood. There is growing concern that some components of the native forest biodiversity will not be able to recolonize the new stands before the next clear-cutting, not even when native trees dominate (Kuuluvainen et al., 2012). Measures to reduce these negative impacts on biodiversity are therefore taken, mainly at final felling (Gustafsson et al., 2012; Johansson et al., 2013).

The boreal forest is one of the world's largest terrestrial biomes. The dominating management regime is even-aged forestry, including clear-

* Tel.: +46 907865535, +46 702756840 (cellphone). *E-mail address:* mats.dynesius@emg.umu.se. cutting and frequently also active regeneration measures and thinning before the next clear-cutting (Kuuluvainen et al., 2012). Since World War II, large parts of the biome have in this way been converted. In Sweden, for example, about 1% of the forest land is clear-cut each year (Anonymous, 2014) and native or introduced tree species are then established and managed in even-aged stands. There are therefore abundant opportunities to study how the biodiversity of more natural forests is represented in this new boreal forest type, also relatively long after clear-cutting. Such studies have recently started to emerge, and the dominant approach has been space-for-time substitution, inferring effects from differences among stands with different histories and ages (Ross-Davis and Frego, 2002; Similä et al., 2002; Botting and Fredeen, 2006; Dynesius et al., 2009; Hilmo et al., 2009; Schmalholz and Hylander, 2009; Widenfalk and Weslien, 2009; Baldwin and Bradfield, 2010; Stenbacka et al., 2010; Rudolphi and Gustafsson, 2011; Ylisirniö et al., 2012). Such studies are useful because they rapidly provide information on long-term processes, but the approach is more appropriate for some communities and community characteristics

than for others (Walker et al., 2010). In addition, the matching of plots in the different stand classes compared is never perfect and the controls used, consisting of areas less affected by forestry, are often not representative of the landscape and may have suffered extinctions because they are small and isolated (Lindbladh et al., 2013). Longitudinal studies using permanent plots provide stronger evidence on effects of clearcutting and on the pace of the subsequent assemblage recovery, but are difficult to conduct due to the long time periods involved. Thus, the longitudinal studies available focus on immediate changes caused by the clear-cutting disturbance itself and the subsequent early colonization/extinction dynamics (e.g. Jalonen and Vanha-Majamaa, 2001; Nelson and Halpern, 2005; Hylander and Weibull, 2012). The longitudinal study in this article covers assemblage development much longer after clear-cutting of two distinct boreal forest habitats (stream-side and upland). Two organism groups are assessed, mosses and liverworts (bryophytes), which both have high boreal species numbers (Dynesius and Zinko, 2006) and respond strongly to clear-cutting (e.g. Newmaster and Bell. 2002).

Clear-cutting has been shown to disturb bryophytes mechanically and climatically and to cause species extirpation and colonization (e.g. Fenton et al., 2003), followed by a rapid recovery over the first decade, at least in boreal stream-side forest (Hylander and Weibull, 2012). Using a comparative approach, Dynesius and Hylander (2007) found some further recovery of boreal stream-side bryophyte assemblages during the following few decades. However, 30-50 years after clearcutting, boreal bryophyte assemblages still differed between regrown treatment stands and matched control stands of the type that were originally logged (old stands that had not previously been clear-cut; Dynesius et al., 2009). The difference was larger in upland than in stream-side sites. The most negatively affected groups in this, as in many other studies (e.g. Halpern et al., 2014), were liverworts and species growing mainly on tree-related substrates (mostly decomposing wood, but also bark of tree bases and of trunks of broadleaved trees). In upland forests also bryophytes living on the ground and on rocks and boulders had lower numbers of species in the treatment stands (Dynesius et al., 2009). Little is known about how bryophyte assemblages develop even later in the forestry rotation. However, in a south-boreal area with a relatively impoverished forest bryophyte flora, a study using a chronosequence of regrown and managed upland stands dominated by spruce suggested that assemblages do not change between 30 and 100 years after clear-felling (Schmalholz and Hylander, 2009). This inferred lack of change remains, however, to be validated in direct studies of permanent plots, involving a wider range of boreal forest habitats and in less impoverished regions.

In this article, I present the first study to combine a comparative and longitudinal approach half-way into the clear-cutting forestry rotation. The study builds on the already mentioned study by Dynesius et al. (2009) of bryophytes in stands 30–50 years after clear-cutting, which was completed in 1996–1997 and covers much of Northern Sweden. The same 0.1 ha plots and their corresponding controls were resurveyed 14–15 years later, in both stream-side and upland sites. This resurvey simultaneously provides (i) an assessment of the differences in bryophyte assemblages between regrown treatment stands 45–60 years after clear-cutting and old more natural forests and (ii) evidence on the pace of recovery at this critical stage of stand development.

A 15-year period is approximately one sixth of the recommended period between two clear-cuttings in north Swedish forestry and thus represents a significant part of the time available for assemblage recolonization. The time period is long enough for the bryophyte environment (e.g. microclimate and tree substrates) in the treatment stands to change considerably towards old-forest conditions due to tree growth, understory vascular plant succession etc. Also, at the time of the initial survey there most likely were immigration credits among species intolerant to clear-cutting and extinction debts among species favored by this disturbance, and these should at least partly have been realized by the time of the re-survey. I therefore expected the assemblages in treatment stands to have changed. I tested this prediction by comparing the temporal changes in species numbers between treatment and control, thereby eliminating pseudo-changes caused by the survey method. I did so for a number of phylogenetic and functional bryophyte subgroups in both upland and stream-side sites.

In addition, I expected the recovery to be smaller in treatment stands that were thinned during the period, because thinning introduces mechanical disturbance and microclimatic change that make the environment more similar to clear-cuts. I therefore made analyses comparing the changes in thinned and not thinned stands.

I hypothesized that species turnover (appearances and disappearances of species in individual 0.1 ha plots) between surveys should be higher in (i) stream-side than in upland stands, because they are exposed to frequent disturbance caused by fluvial erosion and deposition, and (ii) in treatment than in control stands, because their environment are in a state of more rapid directional change and may also be subjected to logging (thinning). Temporal turnover should also be higher for species specialized to short-lived substrates with low cover, because by chance such substrates intermittently disappear from relatively large areas. I evaluated these hypotheses by comparing stand types and species groups concerning their relative between-survey species turnover.

2. Methods

2.1. Study area and design

The study was conducted over a large region in the Middle and North Boreal Zones of northern Sweden (Ahti et al., 1968) between 62°08′ and 66°16′ N at altitudes ranging between 95 and 600 m above sea level. The natural stand-replacing disturbance in the region was forest fire, which occurred at widely varying frequencies over the study region (Drobyshev et al., 2015). Dominant native trees are the shade tolerant Norway spruce (*Picea abies*), and the pioneers Scots pine (*Pinus sylvestris*) and birch (*Betula pubescens* and *Betula pendula*). The forests in this region have been increasingly logged during the past two centuries and since the 1950s clear-cutting forestry has dominated totally. From c. 1970, the non-native lodgepole pine (*Pinus contorta*) has been widely planted.

In the original study (Dynesius et al., 2009) 18 study sites were used. In each study site two pairs of 0.1-ha plots ($20 \text{ m} \times 50 \text{ m}$ rectangles) were surveyed, one pair in upland and one in stream-side locations. The plots in a pair were located to be as similar as possible except for stand history; one had been clear-cut sometime between the mid-1940s to the mid-1960s (treatment) and one was an old forest that had never been clear-cut (control). The majority of the upland controls appeared to have originated after fires long ago, although no data on fire history was collected. The origins of stream-side control stands were less obvious, although traces of fires were sometimes found. About two thirds of the control plots had stumps from selective logging long ago, whereas the others seemed unlogged.

The original plot number was 72 (18 sites \times 4 plots). For the resurvey, one remote site, located in the far west of the study area, was removed for budget reasons. In another site, the upland control plot had been struck by a forest fire and was therefore not resurveyed. This left 67 plots in the resurveyed data set, i.e. 17 pairs of stream-side plots, 16 pairs of upland plots, and a single upland treatment plot. The latter plot is excluded from all analyses except a comparison between thinned and not thinned upland treatments, where it was included in the thinned group. The details of the plot selection procedure and the geographical site locations are found in Dynesius et al. (2009).

2.2. Habitat properties

Data collected in the first study showed that glacial till, often including large boulders, was the dominant mineral soil type in the study plots. In parts of some plots, the till was covered by peat or sandy to Download English Version:

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