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Linking the biological traits of boreal bryophytes to forest habitat change after partial harvesting

Richard T. Caners [a,*], S. Ellen Macdonald [b], René J. Belland [c]

[a] Alberta Biodiversity Monitoring Institute, Royal Alberta Museum, Edmonton, Alberta, Canada
[b] Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada
[c] Department of Renewable Resources/Devonian Botanic Garden, University of Alberta, Edmonton, Alberta, Canada

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ABSTRACT

Biological traits are potentially important for understanding mechanisms of plant species responses to alteration of local habitat conditions through natural and anthropogenic disturbance. Forest harvesting is a prominent disturbance in the circumpolar boreal biome, influencing stand- and landscape-scale patterns of forest structure and biodiversity. We examined a range of variable retention harvesting intensities (10%, 50%, and 75% dispersed green-tree retention harvesting and unharvested controls) in terms of their effectiveness for maintaining mosses and liverworts with differing biological traits. Bryophytes were sampled in 20 m radius plots 5–6 years post-harvest in 24 forest stands (each 10 ha) of two forest types (broadleaf-coniferous mixedwood, coniferous-dominated). We first examined the environmental factors that were the strongest predictors of species composition across the forest types and retention levels. We then used fourth-corner analysis to relate differences in the forest environment to species traits. Selected traits included bryophyte group, life form, habitat requirements, and reproductive and dispersal characteristics. The strongest predictors of species composition were ground-level moisture (estimated using growth of the moss *Hylocomium splendens*) and degree of canopy cover. Fourth-corner analysis showed that forest type, retention level, and their associated moisture conditions were closely related to the abundances of species characterized by different biological traits. Species with rare sporophyte production, larger spores, dioicous sexuality, or that require greater moisture or shade, were affiliated with higher retention and forest moisture. Reduced abundances of species with these traits after harvesting may detrimentally affect their capacity to disperse and re-establish, and suggests that moisture limitation is an important environmental filter that may restrict their representation at harvested sites. Coniferous-dominated forests supported higher abundances of several species types compared to mixed forests, including liverworts, acrocarpous mosses, and species that have greater moisture requirements, dioicous sexuality, or infrequent sporophyte production. This conveys the importance of coniferous forests as bryophyte habitat in mixedwood landscapes and the influence of canopy composition on regional species distributions. Understanding the tolerances of species exhibiting particular traits after harvesting may improve predictions about species extirpation risk and inform approaches to ensure their continued survival.

1. Introduction

Local and regional patterns of species diversity are structured by both the biological requirements of species and how these are influenced by underlying environmental gradients (Whittaker, 1956; Whittaker and Levin, 1975; Huston, 1979, 1994). Species differ in biological attributes (traits) that are evolutionarily adapted to a range of conditions (Levins, 1968; Kassen, 2002) and these characterize the species' capacity to reproduce, disperse, become established, and to persist in a habitat. Alteration of habitat conditions (e.g., microclimate) may detrimentally affect the persistence of a species at a location, if the changed environment is beyond the range of tolerance for a species' traits to successfully perform (Lynch and Gabriel, 1987; Chapin et al., 1993). Thus, species with different traits might respond in dissimilar ways to habitat modification and this can influence local biodiversity (Keddy, 1992; Lavorel and Garnier, 2002; Hewitt et al., 2005). Biological traits of species are, therefore, potentially meaningful indicators of species' persistence and recovery following habitat change or disturbance.

Forest harvesting is a prevalent form of disturbance in the circumpolar boreal biome. Although boreal forests are adapted to

* Corresponding author. Address: Alberta Biodiversity Monitoring Institute, Royal Alberta Museum, 12845-102 Avenue, Edmonton, Alberta, Canada T5N 0M6. Tel.: +1 780 453 9104; fax: +1 780 454 6629.
E-mail address: Richard.Caners@gov.ab.ca (R.T. Caners).

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recurrent natural disturbances, including fire, insect outbreaks, and canopy gap-formation processes, harvesting disturbance is substantially different from these (Niemelä, 1999; Haeussler and Kneeshaw, 2003). Recent studies have documented the effects of forest management practices on landscape scale patterns of forest structure and composition (Bergeron et al., 1998; Cyr et al., 2009) and associated impacts on biodiversity (Kuuluvainen, 2009). This has been accompanied by growing interest in the development of forest harvesting practices that retain structural features characteristic of unmanaged forests (Lindenmayer et al., 2006). Variable retention harvest systems are increasingly being used to moderate growing conditions and preserve elements of forest structure (biological legacies) in the hopes of maintaining ecosystem processes and enhancing species survival or recovery in the harvested matrix (Lindenmayer and Franklin, 2002; Lindenmayer et al., 2006). However, we are just beginning to understand the effects of variable retention harvesting on different forest biota (Lindenmayer et al., 2006; Rosenvald and Lõhmus, 2008; Kuuluvainen, 2009).

The biological traits of species may better explain the effects and consequences of harvesting than by examining species identity alone, yet traits have rarely been used for this purpose. Species may become locally extirpated if habitat conditions are unsuitable after forest harvesting, and re-establishment will be limited for species that have ineffective reproduction and/or dispersal capacities, or if inhospitable conditions in the forest matrix impede species colonization (Hylander, 2009). Diaspore size, fecundity, and dispersal vectors can influence recruitment (McEuen and Curran, 2004), and life form is often associated with environmental conditions to which a species is adapted (Raunkiaer, 1934; Bates, 1998). The unique physiology and habitat requirements of boreal mosses and liverworts make them well suited to study the effects of habitat change on species. Bryophytes can attain high abundance on the forest floor and influence several ecosystem processes (e.g., Chapin et al., 1987; Nilsson and Wardle, 2005). The internal moisture content of forest bryophytes is at equilibrium with their surroundings, and some species are negatively affected by desiccation and exposure following forest harvesting (e.g., Hylander et al., 2005; Dynesius et al., 2009). Bryophytes stand to benefit from the retained forest structure, canopy cover, and habitat heterogeneity provided by variable retention harvesting, yet the mechanisms influencing bryophyte response to forest harvesting are poorly understood. Examination of relationships between species' biological traits and their response to retained forest structure can provide insights into the effects of disturbance and species' propensity for post-disturbance recovery.

Our objective was to determine whether the biological traits of bryophyte species could explain changes in species abundance across a range of partial harvesting intensities in boreal mixedwood forests. This study expands on previous research (Caners et al., 2010, 2013) that examined changes in bryophyte assemblages after partial harvesting. We selected a limited number of traits describing bryophyte group, life form, habitat requirements, and reproductive and dispersal characteristics, all of which are considered to be important determinants of species persistence in forests (e.g., Bates, 1998; Laaka-Lindberg et al., 2000; Söderström and During, 2005). Differences in the abundances of species with particular traits after harvesting may reflect species' sensitivities to altered habitat. We hypothesized the following: (i) species with life forms that are characterized by loosely arranged shoots (e.g., rough mats, solitary creeping) will be more sensitive to harvesting and may decline in abundance at lower retention in contrast to species with more densely arranged shoots (e.g., cushions, turfs); (ii) species that require greater moisture and lower illumination under natural conditions will exhibit reduced abundances after harvesting compared to species adapted to the opposite conditions; and (iii) species with the following reproductive and dispersal traits may decline in abundance at lower retention: perennial as opposed to annual phenology; dioicous as compared to monoicous sexuality; and rare in contrast to frequent sporophyte production.

2. Methods

2.1. Study area

Research was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site in northwestern Alberta, Canada (56°46′N, 118°22′W). The site is situated in the Lower Boreal Highlands Natural Subregion of the Boreal Forest Natural Region in Alberta (Natural Regions Committee, 2006). Regional climate is continental with a mean daily temperature of 1.2 °C and mean total annual precipitation of 402 mm, with 294 mm falling as rain (Environment Canada, 2013). Forests are dominated by varying amounts of broadleaf (primarily *Populus tremuloides* Michx. and *Populus balsamifera* L.) and coniferous (primarily *Picea glauca* [Moench] Voss) canopy cover, with lower abundances of *Abies balsamea* (L.) Mill., *Betula papyrifera* Marsh., *Picea mariana* (Mill.) B.S.P., and *Pinus contorta* Dougl. ex Loud. Topography is undulating with moderate relief and elevation ranges from 677 to 880 m above seal-level.

2.2. Study design

We examined the influence of forest canopy composition and retention level on bryophytes using a factorial design with replication at the forest stand level. During the winter of 1998/1999, harvesting treatments were randomly applied to forest stands (each approximately 10 ha in size) in two different forest types: mixed broadleaf-coniferous (“mixed”, 35–65% broadleaf canopy cover) and coniferous-dominated (“coniferous”, >70% coniferous canopy cover) composition. Harvesting treatments consisted of 10%, 50%, and 75% dispersed green-tree retention with unharvested stands as controls. Harvesting was conducted using a modified shelterwood pattern in which machine traffic was restricted to 5-m-wide corridors that alternated with 15-m-wide retention strips, minimizing disturbance to forest floor organic substrates. Trees were first removed from machine corridors, resulting in 75% canopy retention in a stand. To achieve other retention levels, retention strips were partially harvested by systematic removal of trees >5 cm diameter, while accounting for the timber already removed from the corridors (Spence et al., 1999; Work et al., 2004; http://www.emendproject.org).

Bryophytes and forest structure were sampled during the 2004–2005 growing seasons in three replicate stands per harvesting treatment per forest type, for a total of 24 sampled stands. Prior to harvesting, stands were unmanaged and had established after fire approximately a century ago. Replicates of each forest type were similar in ecological site classification, understory vegetation, and age (Spence et al., 1999; Work et al., 2004).

2.3. Forest structure measurements

Within each stand we randomly established six sampling points. Each point was then repositioned by the shortest distance required to fall on the centerline of a retention strip. A 3.98 m radius (50 m^2) circular plot was centered on each sampling point and the following measures of forest structure were obtained: crown cover (assessed at 1 m height by convex spherical densiometer); cover of trees and shrubs <2 m height, graminoids, forbs, bryophytes, forest floor substrates, and exposed mineral soil, using visual estimates; depth of the forest floor litter-fermented humus