



Short-term effects of alternative thinning treatments on the richness, abundance and composition of epixylic bryophytes, lichens, and vascular plants in conifer plantations at microhabitat and stand scales

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ABSTRACT

Epixylic (log-dwelling) flora contribute much to forest biodiversity, but have been shown to decline with intensive management, perhaps through the reduced supply of coarse woody debris, their preferred substrate, and the altered mesoclimate of the understory. Such declines might be ameliorated through modifying the plantation management practices. This study examined the response of epixylic flora to commercial thinning treatments in 6 mid-rotation conifer plantations of northwestern New Brunswick, Canada. Treatments included an unthinned control, and thinning with: moderate debris, moderate debris with added snags, or no-debris. Epixylic flora were surveyed in the first and third year after thinning, on 30 logs in each of the 4 treatments, using both 10 × 20 cm quadrats (%-cover) and a presence-absence census of whole-logs. Treatments were evaluated at log and stand scales, based on the putative disturbance-sensitivity of different epixylic functional groups. Analyses included indicator species analysis, ANOVA of functional group richness and cover, NMS ordination, and PERMANOVA. Thinning with no-debris or moderate-debris reduced species richness at the stand scale, and increased cover at the log-scale. Composition shifted towards chlorolichens, vascular plants, and forest floor or asexually-reproducing bryophytes in thinned treatments, whereas liverworts and bryophytes with desiccation-sensitivity or those lacking asexual reproduction showed slight declines; most bryophyte groups showed no change. Moderate debris with snags and unthinned treatments showed the fewest compositional differences, and maintained many of the same sensitive groups, but all thinned treatments showed similar trajectories of compositional change. Additional monitoring is required to determine whether thinning with moderate debris and snags offers effective conservation of epixylic species, but debris removal (e.g., for biomass harvest) should be discouraged.

1. Introduction

1.1. Impacts of plantations and importance of epixylics

Woody debris is a particularly species-rich and functionally important component of forest ecosystems, but its abundance and diversity are negatively impacted by intensive management (e.g., plantation silviculture). In addition to impacting nutrient cycling (Hafner et al., 2005; Kappes et al., 2007), modifying understory water balance (Unsworth et al., 2004), and providing critical travel corridors and shelter for wildlife (Bunnell et al., 2002; Lisgo et al., 2002), coarse woody debris (CWD) hosts more species (including many sensitive bryophytes and lichens) than most other substrates in boreal and sub-boreal systems (Cole et al., 2008; Crites and Dale, 1998). Consequently, the negative ecological impacts of forest management can be significantly exacerbated by practices such as stump or slash (tree-tops and branches) harvesting, which explicitly seek to improve fiscal returns by

minimizing residual woody debris (Berch et al., 2011; Berger et al., 2013; Walmsley and Godbold, 2010). Such reduction in CWD reduces the frequency of those species that depend upon it, due either to a simple species-area relationship (Botting and DeLong, 2009) or to a density-dependent relationship between local abundance and dispersal probability (Sillett et al., 2000).

Intensive forest management also impacts biodiversity in other ways relative to minimal management approaches (Carnus et al., 2006; Ross-Davis and Frego, 2002). Studies in which CWD is not explicitly altered, but the canopy has been thinned or removed, have shown large declines among epixylic species (Caners et al., 2013b; Crites and Dale, 1998; Halpern et al., 2014). Given that reducing canopy cover is known to increase the mean and variability in understory temperatures while reducing humidity (Brooks and Kyker-Snowman, 2008; Von Arx et al., 2012), and that most bryophytes and lichens are poikilohydric (Green et al., 2008; Proctor, 2009), some have suggested that intensive management disproportionately affects epixylic species because they are

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more sensitive to evaporative stresses than those that occupy forest floor or mineral soil substrates (Andersson and Hytteborn, 1991; Arseneault et al., 2012; Rambo and Muir, 1998a; Söderström, 1988). In contrast, most epixylic vascular plants would be expected to benefit from increased temperatures and light, since they are homeohydric.

The short rotations that are typical of plantation forests may also reduce the likelihood of successful dispersal or colonization among rare or infrequent species (Battles et al., 2001; McAlpine et al., 2014; Pykälä, 2004; Ranius and Roberge, 2011). This is because, especially for species that have continuous reproduction over many years, the probability of successful dispersal is not simply a function of the amount of suitable habitat and proximity of source populations, but of the longevity of both source populations and potentially suitable habitat. In addition, old-forest associated species may require many years to reach reproductive maturity, such that intensively managed forests would be unlikely to ever develop viable source populations (e.g., Öckinger and Nilsson, 2010). Finally, metapopulation theory suggests that species which rely primarily on sexually, vs. asexually produced propagules, may be more effective at dispersing over long distances, but are less effective at establishing large populations in suitable habitat (Löbel et al., 2006; Löbel and Rydin, 2010). This increases their reliance upon a smaller number of reproductive individuals for population growth, and likewise their susceptibility to extinction (Fedrowitz et al., 2012). There is, however, considerable variability in life-history strategies (e.g., substrate generalist vs. obligate specialist), and consequently, the most disturbance-sensitive species are likely those with both specialized habitat requirements and reproductive or dispersal limitations (Löbel et al., 2006)

1.2. Modifications that could conserve species

Several modified silvicultural prescriptions hold promise for improving biodiversity conservation of epixylic flora. Obviously it is necessary to ensure that existing CWD is minimally disturbed, and that CWD recruitment can occur over time; understanding how much CWD is required, and of what types, have been partially considered elsewhere (Müller and Büttler, 2010; Villard and Jonsson, 2009), and is beyond the scope of this study. For poikilohydric species that are sensitive to disturbance due to the accompanying microclimatic changes, increasing canopy tree or fine woody debris retention may improve conservation outcomes by providing microclimatic buffering (Dynesius et al., 2008; Pharo and Lindenmayer, 2009; Rudolphi and Gustafsson, 2011). Some success in conserving herbaceous species has been shown by using structural complexity treatments in naturally-regenerated forests; these focus on retaining large proportions of the canopy while increasing standing and fallen dead wood in small gaps (Smith et al., 2008). In plantations, however, a balance must be struck between minimizing disturbance frequency, for the sake of dispersal-limited species, and improving canopy or habitat heterogeneity; forgoing mid-rotation thinning may be an appropriate low-cost strategy to maintain habitats for shade-tolerant species, but may come at the expense of CWD recruitment, for example.

1.3. Objectives & hypotheses

The objectives of this study were to (1) evaluate the early responses of the epixylic community to several alternative silvicultural prescriptions (treatments), and thereby be able to recommend one or more treatments to improve biodiversity conservation in plantations, and (2) to use the responses of functional groups within these plantations to better understand whether the impacts are primarily mediated through habitat modification or metapopulation processes. If the negative impacts of management on epixylic communities are primarily mediated via the loss or reduction of substrates, then any reductions in richness or abundance should be limited to groups with slower growth or primarily sexual reproduction on CWD that has been relatively undisturbed after

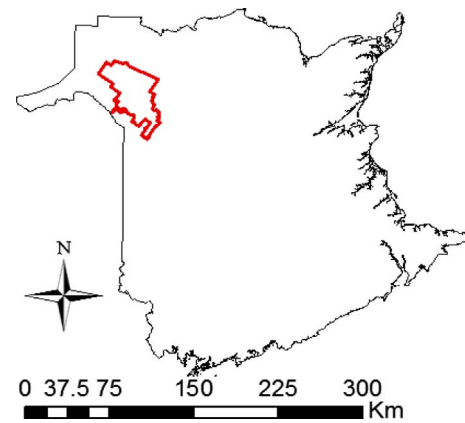


Fig. 1. Map of New Brunswick showing study area (in red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

moderate thinning, regardless of debris retention levels. Alternatively, if the negative impacts of management on epixylic communities are primarily mediated via the changes in desiccation stress, significant reductions in richness or abundance should result, particularly for those functional groups with low desiccation resistance.

2. Methods

2.1. Study area(s)

This study took place in the 220,000 ha Black Brook experimental forest in northwestern New Brunswick (Fig. 1). This silvicultural land-base is privately owned by J.D. Irving, Limited, and primarily dedicated to white spruce (*Picea glauca*) plantations. This area was historically covered with coniferous forests, which were dominated by balsam fir, white spruce, or red spruce, and mixedwood forests, which were dominated by shade-tolerant hardwoods (e.g., *Acer rubrum*) with lesser components of balsam fir, white spruce, or red spruce (Province of New Brunswick, 2007). Soils are mostly thick and loamy in low-lying terrain, and more coarse-textured in uplands (Province of New Brunswick 2007). Seasons are distinct, with cool winters (mean December–February temp. = -11.2°C), and warm summers (mean June–August temp. = 16.5°C ; Environment Canada 2015).

Monthly temperature and precipitation data from the nearest weather station (St. Leonard Airport), showed that temperatures during the study period were generally above the 1981–2010 climate normals, especially in the summer: August of 2011 had minimum and mean temperatures of 1–2 degrees greater than normal, while August of 2012 showed 2–3 degrees of increase over climate normals (Environment Canada, 2015). Spring and summer of 2011 were also somewhat wetter than the 30-year climate normals (the mean of the same measures from 1981 to 2010), whereas, July, August, and September of 2012 were notably drier than normal (Environment Canada, 2015).

Six 25-year old, 20–40 ha, softwood plantations (henceforth, ‘plantations’) were selected as part of a larger collaborative study (NSERC CRDPJ 373858 – 08; MacLean et al. 2015). Canopy trees ranged from 10 to 18 cm in diameter at breast height (DBH), with stocking densities of approximately 2700 stems/ha. Coarse woody debris averaged $33\text{ m}^3\text{-ha}$ (range from 10 to $100\text{ m}^3\text{-ha}$), and was mostly < 20 cm in diameter, well-decayed, and hardwood-dominated (mostly white- or yellow birch) when it could be identified; properties did not differ significantly among treatments (tested with 1-way ANOVA). Although some CWD was recently blown down, much of it resulted from two periods of disturbance in the stands’ histories: a spruce budworm outbreak in the late 1950s, and site preparation activities in the early 1980s (G. Pelletier, personal communication, 2011). Additional

analysis of relationships between CWD properties and epixylic communities will be presented in a subsequent paper. Dominant (planted) canopy species included white spruce, balsam fir (*Abies balsamea*), and black spruce (*Picea mariana*), with their relative abundance varying among plantations. All plantations had some natural regeneration of *Acer rubrum*, *Acer saccharum*, *Populus tremuloides*, *Betula papyrifera*, *Betula alleghaniensis*, or *Prunus virginiana* either in the understory or sub-canopy strata, and were chosen for similar site fertility, slope, and drainage attributes. Common understory species include *Cornus canadensis*, *Coptis trifolia*, *Dryopteris intermedia*, *Oclemena acuminata*, and *Rubus pubescens*. More extensive site descriptions can be found in (Haughian and Frego, 2016).

Each plantation was divided into four treatments of approximately equal size. Three treatments from each plantation were thinned in autumn or winter of 2010 by removing approximately 40% of trees (by basal area), and the fourth was left untreated as a control (CO). Thinned blocks were randomly assigned a debris-treatment alternative: (1) no-debris (ND), tree tops and brush were removed to simulate a biomass harvest; (2) moderate-debris (MD), tree tops and brush were retained as per current practice in Black Brook; or (3) moderate debris with snags (MD+), tree tops and brush were retained as in the MD, and clumps of trees were killed by girdling to simulate natural mortality and create snags. Mechanized thinning was applied in series of parallel strip-cuts (23 m apart) that were perpendicular to the access road. Each strip-cut left a 3.5 m-wide cutting trail along which all vegetation was removed, but soil may have been disturbed up to 6 m from the edge of each cutting trail, leaving retention strips of 11 m without ground-layer disturbance. Thinning preferentially removed of small trees over large ones.

2.2. Field data collection

An effect size of 12% (or 1 standard deviation) in richness or cover was chosen for this study, because this was the maximum inter-year change observed in understory vegetation from unharvested forests in recent studies near the study area (Fenton et al., 2003; Roberts and Zhu, 2002), suggesting that this size of a change could occur due to the combination of observer error and natural fluctuations over time. Given the constraints of plantation replication ($n = 6$), and letting $\alpha = \beta$, because there was no clear priority of minimizing one error over the other (Underwood, 1997), this change was expected to be detectable at $\alpha = 0.09$ in a 2-factor ANOVA-design. Similar criteria have also been used by others to set critical effect sizes in environmental monitoring (Munkittrick et al., 2009). For consistency, these error levels were applied to all subsequent tests. Power calculations were performed using G*Power v 3.1.5 (Faul et al., 2007).

Thirty horizontal pieces of CWD (diameter ≥ 10 cm and length ≥ 1 m) were selected, using a random-clustered approach, from those present in each treatment for bryophyte sampling and monitoring. Three logs were chosen within each of 10 randomly located clusters in each treatment (stand). Logs were selected randomly, provided that they were at least 5 m apart from each other (to avoid spatial autocorrelation – as per preliminary tests), and that they did not appear to be from the same tree. Logs were considered the sample unit for data collection, while the experimental sample unit was the treatment-block (i.e. stand). If logs > 10 cm in diameter could not be found within 5–8 m of each other, observers sampled logs as small as 7.5 cm in diameter that fell within this distance, then used the nearest logs > 10 cm beyond it.

Bryophyte (moss and liverwort), lichen, and vascular plant cover on logs was assessed using both abundance-quadrats and whole-log presence-absence surveys. Quadrats were 10×20 cm, and vegetation cover was recorded to the nearest percentage, using visual cover estimates for each detected species (or, when identification was not possible, each morphotype). Quadrats were positioned on the zenith of the log at the mid-point of the long axis, and marked with galvanized nails.

To increase species-capture rates, each log was also censused for epixylic species throughout its entire surface. Species were identified *in situ* when possible, and in the laboratory when necessary. The two surveys were conducted between May 11th and July 20th, 2011, and between May 20th and July 20th 2013.

Several other variables were recorded on site. Non-living components of the 10×20 cm quadrats were visually estimated; these surface coverings included exposed wood, bark, litter (leaves, needles and other small organic materials), fine woody debris (FWD – dead wood between 0.5 and 7.5 cm), humus, mineral soil (particles < 2 mm), and gravel (0.2–8 cm). To quantify variability in light, canopy photos were taken above the center of each quadrat using a digital camera (Sony Cybershot 5.1 megapixel) equipped with a hemispherical (180°) photo lens (Japan Optics HD MK II DSLR 0.18X). The camera was placed on a bubble-leveled platform that straddled the log with the top of the hemispherical lens 10–15 cm above the surface of the quadrat. Photos were analyzed using Gap Light Analyzer software (version 2.0, Frazer et al., 1999), and summarized as canopy openness (cf. Baldwin and Bradfield, 2010).

2.3. Identification and nomenclature

Mosses were identified according to Ireland (1982). Several challenging moss taxa (*Amblystegium*, *Brachythecium*, *Hyprnum*, and *Sciurohypnum*) were identified according to the Bryophyte Editorial Committee (2014, 2007). Liverworts were identified according to (Faubert, 2012; Schuster, 1992, 1980, 1974, 1966). Lichens were identified according to Hinds and Hinds (2007), while vascular plants were identified according to (Hinds, 2000). Nomenclature followed more recently published sources (Barkley et al., 2006; Bryophyte Editorial Committee, 2014, 2007; Faubert, 2012; Hinds, 2000; Hinds and Hinds, 2007). When bryophyte or lichen specimens lacked the requisite features for identification, they were assigned to the most frequent or morphologically similar species from the same genus.

All field and laboratory identifications from the plantations were done by the author. Voucher specimens were verified by local experts and deposited in the herbarium at the New Brunswick Museum (NBM). Bryophyte and vascular plant vouchers were verified by Bruce Bagnell and Gart Bishop, respectively, (both Research Associates with the New Brunswick Museum and B&B Botanical), while lichen vouchers were verified by Dr. Stephen Clayden (Research Curator of Botany and Mycology, New Brunswick Museum).

2.4. Analytical methods

Analyses were conducted using a three-tiered approach: whole community, functional groups, and individual species. The whole community was evaluated using (a) 2-factor ANOVA to compare overall cover and richness of epixylic flora among plantation treatments for the two survey years, and (b) Nonmetric Multidimensional Scaling (NMS) ordination, using the same criteria as above, but summarizing species as stand-scale totals using presence-absence data from whole-log censuses, coupled with permutation-based multivariate analysis of variance (PERMANOVA), using both quadrat and whole-log censuses to compare community composition between survey years and among treatments. Significant results were followed by a Tukey's multiple comparison test (or the randomization equivalent for PERMANOVA), and evaluated for significance at $\alpha = 0.09$. All ANOVA tests were conducted in SPSS v 21 (SPSS 2015), and all PERMANOVA tests were conducted in Primer v 6 (Clarke and Gorley, 2006). Because PERMANOVA is distribution-free, whole log-scale data could be used as replicates in a blocked design for evaluating compositional differences, with plantation as a random effect. (Using individual logs as the replicates was not feasible for parametric statistical tests or ordinations, because the high zero-inflation and large inter-log differences caused substantial deviation from distributional normality, heterogeneity of variances, and result-

instability.) Indicator species analysis (ISA) was used to better understand associations between species and plantation treatments. Although ISA is robust to differences in group sizes (Legendre and Legendre, 2012), there is no correction for accommodating repeated measures; consequently, only 2013 quadrat data were used for the ISA.

Data were summarized in as richness or %-cover before ANOVA tests. Shannon's and Simpson's diversity indices (Shannon, 1948; Simpson, 1949), and Pielou's evenness (Pielou, 1966) were considered, but preliminary analyses with these added little new information to analyses of richness and %-cover. Species richness and cover were first calculated from the 10 × 20 cm quadrats. For richness, both quadrat-scale mean values (the geometric mean of richness from all quadrats in a treatment-block), and stand-scale totals (the total species list for a treatment), were calculated. Cover was summarized only as the mean cover from all quadrats in a treatment block, because unlike species richness, cover did not differ based on using total or mean values. Next, species richness was calculated using presence-absence censuses of whole-logs, at the whole log-scale (the geometric mean number of species per log in a plantation-treatment) and stand-scale total (the total species list for each plantation-treatment) values.

Functional groups were chosen on the basis of previously demonstrated utility (Baldwin and Bradfield, 2005; During, 1979; Fenton and Bergeron, 2008; Lang et al., 2009; Oishi, 2009; Rambo and Muir, 1998a) and logical consideration of shared taxonomic, morphological or anatomical characteristics that may influence their response to disturbance (Hedderon and Longton, 1996; Hedenäs, 2001; Oishi, 2009). Taxonomic functional groups were lichens, liverworts, mosses, and vascular plants. Finer levels of taxonomic resolution (e.g., *Sphagnum* spp., chlorolichens vs. cyanolichens) were used for ordination overlays, but excluded from other analyses, due to distributional abnormalities created by the low frequencies of these sub-groups.

The second functional group classification focused on bryophytes, and was a hierarchical reflection of the low frequency and high environmental tolerance of non-specialists growing on logs, and the possible limiting mechanisms for epixylic specialists (Fig. 2). Both literature sources and exploratory analyses of species traits (not included), suggested that hierarchical groupings based on habitat features at large-scales (e.g., Arseneault et al., 2012; Baldwin and Bradfield, 2007), and colony or species attributes at smaller scales (e.g., Baldwin and

Bradfield, 2007; Hedenäs and Hedenäs, 2001; Oishi, 2009), would meet these criteria. The first division separated forest vs. disturbed-area associates, while the second separated substrate generalists from emergent- (trees or woody debris) substrate forest-associates. Disturbed area associates were infrequent, and forest floor generalists mostly adhered to a weft or cushion growth form, so they were not further subdivided. Emergent substrate specialists were subdivided into groups based on colony structure: dense and overlapping or woven (e.g., most *Brachythecium* species, *Dicranum fuscescens*), vs. loosely tangled in a single layer against the substrate. This division was regarded as relevant to desiccation-resistance, and therefore to disturbance responses. Loosely tangled species were further differentiated as: (1) predominantly sexual (e.g., *Amblystegium serpens*) vs. predominantly asexual (e.g., *Leskeella nervosa*) propagation, and (2) colony structure loose but mostly contiguous (e.g., *Barbilophozia attenuata*), vs. largely isolated shoots, here termed 'sidekick' species (e.g., *Anastrophyllum hellerianum*; Haughian and Frego, 2017). The first trait emphasized the possible role of asexual reproduction in facilitating post-disturbance colony expansion (Kimmerer, 1994; Laaka-Lindberg et al., 2006), while the second further-emphasized the role of colony structure to desiccation-resistance.

The effects of treatment and survey year on the richness (at stand and quadrat scales) and %-cover (quadrat scale), and on the richness (at stand and log scales using whole-log data) of taxonomic and habitat & life-form functional groups were evaluated using 2-factor ANOVA, followed by Tukey's tests. All variables were tested for homogeneity of variance and normal error distributions before analyses; although several variables violated these assumptions, the violations were minor, and reanalysis after log- or arcsine-square-root transformation yielded the same results (i.e., significant vs. non-significant), so the original tests were retained.

3. Results

At least 213 species (see Supplement 1) were detected growing on logs in the plantations, including 22 lichens, 35 liverworts, 71 mosses, and 85 vascular plants. Only 208 taxonomic entities are used in this report, because sterile forms of 4 moss and 1 liverwort species could not be identified; however, their presence in the study area was verified by occasional fertile specimens. The actual number of lichen and vascular

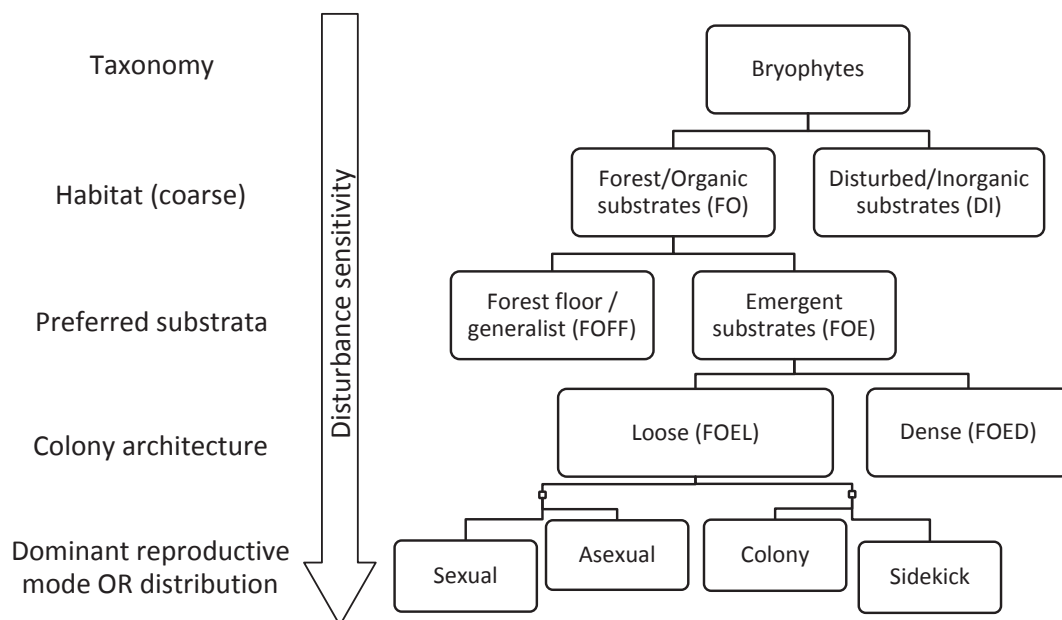


Fig. 2. Bryophyte habitat and life-form functional groups, based on a nested hierarchy of traits that presumably correlates with disturbance-sensitivity. Habitat and substrate associations, as well as colony architecture, reproductive mode, and independence were largely derived from descriptions in published flora (Faubert, 2012; Ireland, 1982), but were modified for several species based on the authors' observations of prevailing features in the study area; species assignments to particular functional groups are provided in Supplement 1.

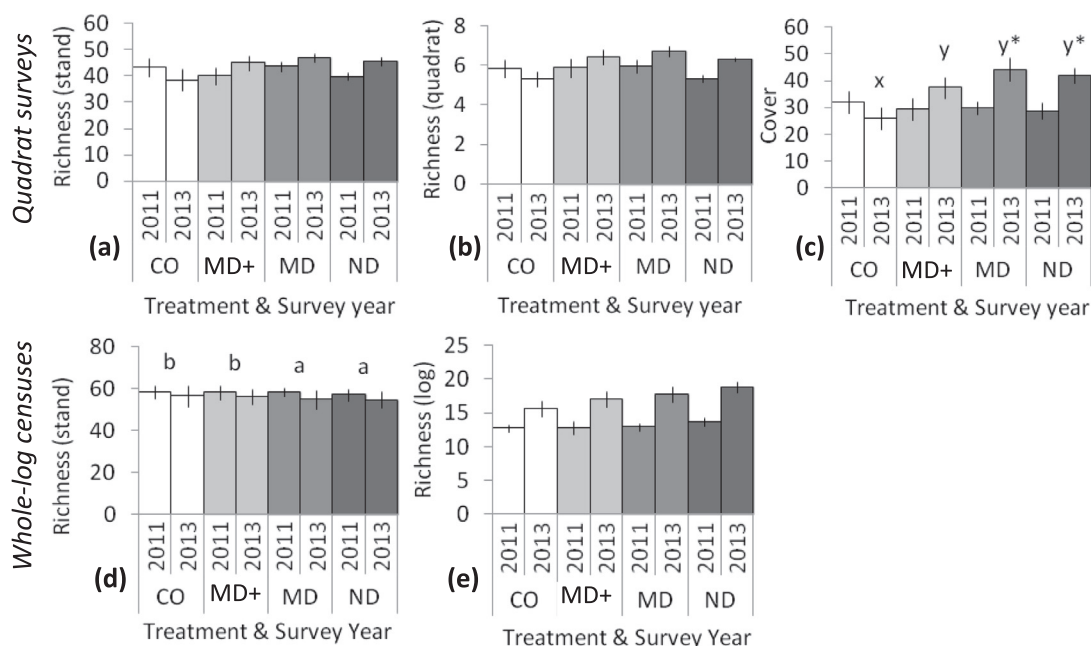


Fig. 3. Mean (\pm SE) species richness and cover of epixylic flora, by treatment and survey year. Results shown from quadrat-based surveys (top row) and whole-log censuses (bottom row). From left to right is shown stand-scale total richness, log or quadrat-scale mean richness, and quadrat-scale cover. Lower case letters indicate homogeneous subsets ($\alpha = 0.09$) from post-hoc (Tukey's HSD) treatment comparisons within years, while asterisks indicate treatments that experienced significant changes between years. CO = control, MD+ = moderate debris with snags, MD = moderate debris, and ND = no debris.

taxa is also conservative, because underdeveloped specimens were combined into sub-genus level morphological groups.

3.1. Whole community analysis

3.1.1. Overall richness and cover

Epixylic richness from quadrats increased significantly between 2011 and 2013 at the quadrat scale ($P_{\text{year}} = 0.070$, $F = 3.476$, $df = 1,47$, Fig. 3b), but changes were small (mean change of 0.5–1 species per quadrat), and treatment and interaction effects were not significant. Epixylic richness from quadrats summarized as stand-scale totals showed similar patterns but differences were not significant (Fig. 3a). Epixylic cover increased significantly between survey years in MD and ND treatments ($P_{\text{year} \times \text{treatment}} = 0.028$, $F = 3.371$, $df = 3,47$; Fig. 3c), with an average increase of 14.4 and 13.2%, respectively.

Based upon whole-log censuses, at the log-scale, epixylic richness increased between surveys ($P_{\text{year}} = < 0.001$, $F = 43.597$, $df = 1,47$) but showed no treatment effects or interactions (Fig. 3e). In contrast, epixylic richness at the stand scale declined between survey years ($P_{\text{year}} = < 0.001$, $F = 49.037$, $df = 1,47$), and was significantly greater in CO and MD+ treatments than MD or ND treatments ($P_{\text{treatment}} = 0.073$, $F = 2.505$, $df = 3,47$; Fig. 3d).

3.1.2. Composition

Ordination of whole-log data (stand-scale totals) created a stable (instability = 0.00001, stress = 10.50078), 3-dimensional solution after 500 iterations. The three NMS axes captured approximately 95% of the variance in the data. Axis 1 captured 47.1% of the variance, and primarily represented pre-existing compositional differences among plantations (treatment means are clustered in the center, whereas plantation means are spread across the axis; Fig. 4). It was positively correlated with richness of *Sphagnum* spp., *Cladonia* spp., and the liverwort *Ptilidium pulcherrimum*, and negatively correlated with the richness of mosses (especially generalist epixylics such as *Callicladium haldeanum* and *Brachythecium* spp.) and cyanolichens (mostly *Peltigera* spp.; Fig. 4). Axis 2 captured 30.0% of the variance, again primarily differentiating among plantations, but also between the ND (no debris)

treatment and other treatments (Fig. 4a and b). The axis represented a gradient from high richness of *Sphagnum* spp., *Cladonia* spp., forest floor mosses (e.g., *Pleurozium schreberi*), and the liverwort *Ptilidium pulcherrimum*, to cyanolichens, generalist epixylic mosses (e.g., *Callicladium haldeanum*, *Brachythecium* spp.), and the liverwort *Lophocolea heterophylla*. Axis 3 represented only 9.6% of the variance, and emphasized the change between survey years, with changes in treatment scores appearing to correspond with treatment intensity (Fig. 4c and d). Compositionally, axis 3 most strongly represented a gradient from high to low richness of vascular plants (e.g., *Maianthemum canadensis*, *Abies balsamifera*), and to a lesser extent, of mosses and chlorolichens (e.g., *Dicranum scoparium*, *Cladonia ochrochlora*). In terms of non-living cover classes, litter was positively correlated with axes 2 and 3, bark with axis 2, and bare wood with axis 1.

PERMANOVA of both quadrat and whole-log data (both at the log-scale) confirmed that community composition was significantly related to both treatment ($P_{\text{quadrats}} = 0.009$; $P_{\text{whole-logs}} = 0.030$) and survey year ($P_{\text{quadrats}} = 0.025$; $P_{\text{whole-logs}} = 0.002$), but interaction effects were also present in both (quadrats: $P = 0.003$; whole-logs: $P = 0.026$). Multiple comparison tests confirmed that differences at the quadrat scale were significant between CO and MD, CO and ND, and MD+ and ND within each survey year, and that all treatments changed significantly between years. Whole-log composition differed significantly between CO and all other treatments, and between MD+ and ND treatments, only in 2013, but all treatments still differed significantly between years. Analyses of whole-log data explained almost twice as much variance as those based on quadrat data (total $\eta^2_{\text{quadrat}} = 0.1123$ vs. total $\eta^2_{\text{whole-log}} = 0.2102$).

3.2. Taxonomic groups

3.2.1. Quadrat surveys

Significant richness and cover differences among taxonomic groups were more frequently found at the quadrat-scale than the stand-scale (summary of results in Table 1; full results of functional group ANOVAs are presented in Supplement 2). Mosses were the most abundant and species-rich group; moss richness was significantly affected by both

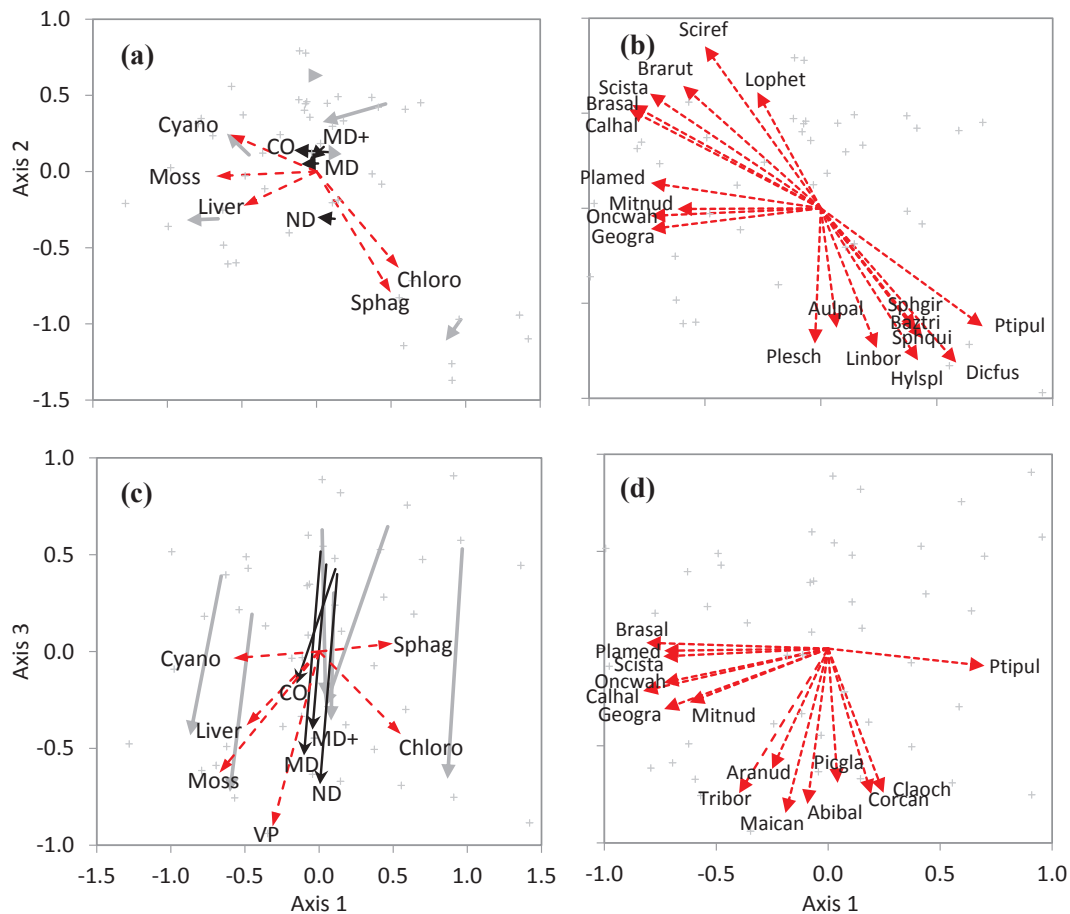


Fig. 4. NMS ordination of stands in species space, using stand-scale frequency of occurrence values for each plantation-treatment-year (gray plus-signs); (a, c) mean scores for plantations (gray arrows) and treatments (black arrows and 2-letter codes) for each survey year (origin of arrow is 2011, point is 2013; CO = control, MD+ = moderate debris with snags, MD = moderate-debris, ND = no-debris); taxonomic functional group (a, c) and individual species (b, d) correlations shown in dashed and solid lines, respectively; the strength and direction of correlations is shown for groups with $r > 0.48$; species names are abbreviated using the first three letters of the genus and specific epithet.

survey year and treatment, but only at the quadrat-scale (Table 1); it increased significantly between survey years, and was significantly greater in MD than control treatments. Moss cover was significantly influenced by the year \times treatment interaction; cover was greater in 2013 than 2011, but post-hoc tests showed that increases in cover were significant only in thinned treatments (Table 1). Liverwort richness and cover appeared to decline with greater disturbance intensity (i.e., from CO to ND) at both quadrat and stand scales, but treatment effects were significant only for cover (Table 1). Post-hoc tests confirmed that liverwort cover was significantly lower in MD and ND treatments than controls (Table 1); survey year and interactions were not significant.

Lichens and vascular plants showed similar trends. Lichen cover did not differ significantly among treatments or survey years, and no effects on richness were detected at the stand-scale (Table 1). At the quadrat scale, lichen richness increased significantly between survey years (Table 1). There appeared to be a weak year \times treatment interaction, with lichen richness increasing in thinned vs. decreasing in control treatments, but it was not significant (Table 1). Vascular plant richness increased significantly between survey years at both scales, with a trend towards larger changes in thinned treatments, but interaction terms were not significant (Table 1). Vascular plant cover appeared to increase between years in thinned treatments, and not in controls, but differences were non-significant (Table 1).

3.2.2. Whole-log surveys

Liverwort richness differed among treatments at only the stand-scale; MD+ treatments were significantly less rich than controls, although the mean response trajectories suggested this difference would

be short-lived (Table 1). Liverwort richness was not significantly impacted by survey year or interaction effects at either scale. Moss richness at the log scale increased between survey years, but was not significantly affected by treatment or interactions; at the stand-scale, moss richness showed no response to main effects or their interaction (Table 1).

Lichen richness (at both stand and log-scales) was significantly greater in ND treatments than in controls, with other treatments intermediate (Table 1). Neither survey year nor interactions significantly affected lichen richness. Vascular plant richness increased significantly between survey years at both log and stand-scales; they were also significantly affected by treatment, but only at the stand scale; MD treatments were richer than controls, with other treatments intermediate (Table 1).

The indicator species analysis yielded few significant indicators, with only 7 out of over 200 possible taxa being selected. The only indicator from control treatments was *Radula complanata* ($P = 0.041$), a species that is most commonly epiphytic on Angiosperm trees. The only vascular plant selected as an indicator was *Dryopteris carthusiana* ($P = 0.086$), a medium-sized wood fern, which was associated with MD treatments. No debris treatments showed the strongest associates, including the common forest floor species *Cladonia crispata* ($P = 0.048$), *Cladonia cristatella* ($P = 0.012$), and *Cladonia chlorophaea* ($P = 0.003$), and *Dicranum polysetum* ($P = 0.006$).

Table 1

Functional group ANOVA results (mean richness/cover value for each treatment-year combination; italics indicate statistical significance at $P \leq 0.09$); homogeneous groups from Tukey's multiple comparison tests shown by superscript letters (differences between treatments) or bold font (differences between years). S.U. = sample unit.

S.U.	Variable	Group	Log-scale (mean)								Stand-scale (total)							
			CO		MD+		MD		ND		CO		MD+		MD		ND	
			'11	'13	'11	'13	'11	'13	'11	'13	'11	'13	'11	'13	'11	'13	'11	'13
Quadrats	Cover	Lichen	1.3	0.7	1.6	1.6	1.5	2.0	1.0	1.7	N/A							
		Liverwort	2.8 ^b	1.9 ^b	2.1 ^{ab}	2.0 ^{ab}	1.3 ^{ab}	1.7 ^{ab}	1.1 ^a	1.6 ^a	N/A							
		Moss	26.1 ^a	21.4 ^a	23.6 ^b	30.2^b	25.2 ^b	35.2^b	23.6 ^b	33.3^b	N/A							
		Vascular Plant	1.9	1.9	2.2	3.7	1.9	5.5	3.1	5.5	N/A							
		DI	0.2 ^a	0.1 ^a	0.8 ^{ab}	0.3 ^{ab}	0.3 ^b	0.7 ^b	0.1 ^a	0.2 ^a	N/A							
		FOFF	16.9	14.8	13.5	18.6	15.4	24.8	17.0	25.6	N/A							
		FFOED	6.3 ^{ab}	4.8 ^{ab}	6.8 ^b	7.1 ^b	6.9 ^b	6.9 ^b	3.9 ^a	4.4 ^a	N/A							
		FOELasexual	1.6	1.0	1.9	3.0	1.3	1.8	1.8	2.6	N/A							
		FOELsexual	3.4	2.4	2.7	2.5	2.3	2.2	1.6	1.8	N/A							
		FOELcolony	4.1	2.8	4.2	5.1	3.3	3.8	3.0	3.9	N/A							
	FOELsidekick	0.9 ^b	0.6 ^b	0.5 ^b	0.4 ^b	0.3 ^a	0.2 ^a	0.4 ^{ab}	0.5 ^{ab}	N/A								
	Richness	Lichen	0.4	0.3	0.4	0.5	0.4	0.6	0.3	0.5	3.8	2.8	3.7	3.0	4.0	5.3	3.5	4.0
		Liverwort	1.3	1.0	1.2	1.1	1.1	1.0	1.0	1.0	10.7	9.0	8.3	9.5	8.7	8.2	8.8	8.8
		Moss	3.8	3.6	3.9	4.3	4.0	4.5	3.6	4.1	24.2	20.7	21.5	23.2	23.8	24.5	21.8	22.3
		Vascular Plant	0.3	0.3	0.5	0.6	0.4	0.7	0.4	0.7	4.7	6.0	6.5	9.3	7.2	9.0	5.7	10.5
		DI	0.3 ^a	0.2 ^a	0.3 ^a	0.3 ^a	0.4 ^b	0.4 ^b	0.2 ^a	0.3 ^a	2.8 ^b	3.7 ^b	2.7 ^a	1.7 ^a	1.5 ^a	1.8 ^a	2.2 ^a	1.8 ^a
		FOFF	1.7	1.6	1.5	1.7	1.7	2.0	1.8	2.0	8.7	9.0	8.2	7.5	8.7	8.5	9.2	9.8
		FFOED	1.1 ^b	1.2 ^b	1.2 ^b	1.3 ^b	1.2 ^b	1.2 ^b	0.9 ^a	1.0 ^a	7.2	7.2	7.5	7.2	6.7	7.7	5.8	6.7
		FOELasexual	0.6	0.6	0.6	0.8	0.5	0.7	0.6	0.8	4.0 ^{ab}	3.7 ^{ab}	4.5 ^b	3.7 ^b	3.0 ^{ab}	4.7^{ab}	3.7 ^a	3.8 ^a
		FOELsexual	1.4	1.1	1.4	1.3	1.3	1.1	1.1	1.0	9.8	9.2	12.0	9.7	10.0	10.0	9.8	9.0
FOELcolony		1.4	1.1	1.4	1.3	1.3	1.2	1.1	1.0	9.7	8.3	11.2	8.8	9.2	10.0	9.5	8.7	
FOELsidekick	0.5 ^b	0.4 ^b	0.3 ^{ab}	0.3 ^{ab}	0.2 ^a	0.2 ^a	0.3 ^{ab}	0.3 ^{ab}	4.2	4.5	5.3	4.5	3.8	4.7	4.0	4.2		
Whole-logs	Richness	Lichen	0.9 ^a	0.8 ^a	0.8 ^{ab}	1.0 ^{ab}	1.0 ^{bc}	1.1 ^{bc}	1.0 ^c	1.4 ^c	6.7 ^a	4.2 ^a	6.0 ^{ab}	6.0 ^{ab}	6.7 ^{ab}	7.8 ^{ab}	7.3 ^b	8.5 ^b
		Liverwort	2.9	3.2	2.8	3.2	2.7	3.1	3.2	3.7	16.0 ^b	15.5 ^b	12.0 ^a	14.3 ^a	14.0 ^{ab}	13.2 ^{ab}	13.7 ^{ab}	15.2 ^{ab}
		Moss	8.6	9.6	8.7	10.2	8.8	10.4	9.0	10.2	30.5	33.2	30.0	31.2	32.5	33.3	33.0	34.5
		Vascular Plant	0.4	2.1	0.5	2.7	0.5	3.1	0.5	3.5	5.3 ^a	17.5^a	6.8 ^{ab}	21.3^{ab}	7.7 ^b	26.7^b	6.3 ^{ab}	24.3^{ab}
		DI	0.4 ^a	0.3^a	0.3 ^a	0.5^a	0.5 ^b	0.7^b	0.5 ^b	0.7^b	3.3 ^a	3.7^a	2.7 ^a	3.7^a	5.0 ^b	5.2^b	3.5 ^{ab}	4.8^{ab}
		FOFF	3.4	3.7	3.3	3.8	3.5	3.9	4.0	4.1	10.7 ^a	11.3 ^a	10.3 ^a	10.8 ^a	12.0 ^{ab}	11.3 ^{ab}	13.3 ^b	13.2 ^b
		FFOED	3.2	3.6	3.4	3.7	3.3	3.6	2.9	3.2	9.3	11.3	9.3	9.5	8.7	9.0	9.2	9.3
		FOELasexual	1.8 ^a	2.1^a	1.7 ^{ab}	2.4^{ab}	1.7 ^a	2.2^a	1.9 ^b	2.6^b	5.7	5.3	5.0	6.0 [*]	6.0	5.5	5.3	6.8 [*]
		FOELsexual	3.3	3.5	3.3	4.0	3.2	3.8	3.7	4.4	17.5 ^b	17.0 ^b	14.7 ^a	15.5 ^a	14.8 ^a	15.5 ^a	15.3 ^{ab}	15.5 ^{ab}
		FOELcolony	2.8	3.0	2.7	3.0	2.5	3.0	3.0	3.4	17.0	16.5	15.3	16.0	16.0	15.0	16.0	16.8
		FOELsidekick	1.2	1.6	1.0	1.4	1.0	1.4	1.2	1.6	6.2	5.8	4.3	5.5	4.8	6.0	4.7	5.5

3.3. Habitat/life-form functional groups

3.3.1. Quadrat surveys

Richness of disturbed area/inorganic substrate (DI) bryophytes differed among treatments at both scales (Table 1), but the stand-scale effects were larger ($\eta^2 = 0.29$ vs. $\eta^2 = 0.20$). The direction of these differences changed between scales: at the quadrat scale, richness was greater in MD treatments than others, while at the stand scale, it was greatest in controls (Table 1). DI bryophyte cover was significantly impacted by treatment, survey year, and their interaction (Table 1). Cover was significantly greater in MD and MD+ treatments than controls, but only in 2013, and only MD treatments showed a significant increase between years (Table 1). Richness of forest floor-dwelling (FOFF) bryophytes was not impacted by treatment, survey year, or interaction terms at either scale; their cover increased significantly between survey years, but no treatment or interaction effects were significant (Table 1). Among emergent substrate bryophytes, richness and cover of those with dense colonies (FOED) differed among treatments only at the quadrat scale (Table 1). Post-hoc tests affirmed that ND treatments had significantly lower FOED bryophyte cover and richness than other thinned treatments, and significantly lower richness than controls (Table 1).

Loosely-colonial, emergent-substrate bryophytes (FOELColony) showed neither significant main effects nor interactions on cover and richness, at either scale (Table 1). Emergent-substrate bryophytes with isolated shoots (FOELSidekick) showed significant treatment effects on cover and richness at the quadrat scale (Table 1); post-hoc tests confirmed that cover was greater in controls than in thinned treatments,

whereas richness was only greater in controls than MD treatments, with others intermediate (Table 1).

Richness and cover of FOEL bryophytes with predominantly sexual reproduction (FOELSexual) were not impacted by main effects or their interaction, at either scale (Table 1). Cover of FOEL bryophytes with predominantly asexual reproduction (FOELAsexual) was not significantly impacted by survey year or treatment, regardless of scale (Table 1). Richness of FOELAsexual bryophytes increased significantly (Table 1) between survey years at the quadrat scale (Table 1). At the stand-scale, FOELAsexual bryophytes increased between survey years only in MD treatments; MD+ treatments were richer than MD treatments in 2011, but did not differ in 2013 (Table 1).

3.3.2. Whole log censuses

The richness of disturbed-habitat/inorganic substrate (DI) bryophytes was significantly impacted by both treatment and survey year (Table 1); richness increased between survey years, and was significantly greater in MD and ND treatments than MD+ or control treatments at the log scale, and greater in MD treatments than CO or MD+ treatments at the stand scale (Table 1). Forest floor bryophytes differed significantly among treatments only at the stand-scale, with ND treatments being significantly richer than MD+ treatments and controls (Table 1).

Among emergent-substrate bryophytes, only FOELSexual showed significant effects at the stand scale with controls significantly richer than MD+ and MD treatments (Table 1). At the log scale, FOELAsexual, FOELcolony, and FOELSidekick bryophytes showed significantly increased richness between survey years (Table 1). Richness of

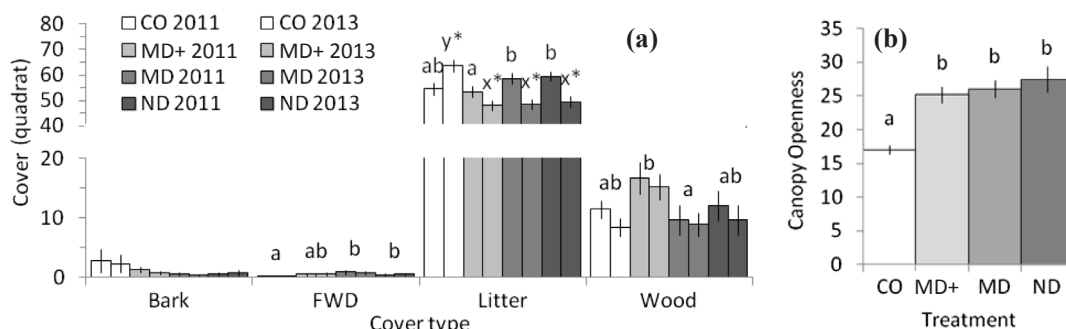


Fig. 5. Mean (\pm SE) non-living cover classes (a) and canopy openness (b), by treatment and year (2012 only for canopy openness), based upon quadrat-scale mean values; letters indicate homogeneous subsets ($\alpha = 0.09$) from post-hoc (HSD) treatment comparisons within each survey year. CO = control, MD+ = moderate debris with snags, MD = moderate debris, and ND = no debris.

FOELAsexual bryophytes was significantly higher in ND treatments than controls, with other treatments intermediate.

3.4. Individual species associations

The indicator species analysis from plantations yielded far fewer significant indicators than expected, with only 7 out of over 200 possible taxa being selected. The only indicator from control treatments was *Radula complanata*, a species that is most commonly epiphytic on hardwood trees in the area. The only vascular plant selected as an indicator was *Dryopteris carthusiana*, a medium-sized wood-fern, which was associated with moderate-debris treatments. The strongest indicators were three cup-bearing *Cladonia* species and a common forest floor moss (*Dicranum polysetum*), all of which associated with the no-debris treatments.

3.5. Plantation environment and non-plant cover

In terms of non-living cover classes, bark coverage was greatest in control treatments, and least in MD and ND treatments, but these differences were non-significant (Fig. 5a). Fine woody debris was significantly more abundant in thinned than control treatments, while litter was greater in controls than thinned treatments, and increased between years in controls, but decreased in thinned treatments (Fig. 5a). Exposed wood was affected by treatment, being significantly greater in MD+ than in MD treatments (Fig. 5a). Only one set of post-thinning canopy measurements were available to be compared among treatments. Canopy openness ($P < 0.0001$, $df = 3, 23$) was significantly (8–10%) greater in thinned than control treatments, but thinned treatments did not differ from each other (Fig. 5b).

4. Discussion

Overall, the epixylic community became more like the upper surfaces of logs because of thinning; generalist species increased across logs in response to thinning, but a small number of infrequent species may have been reduced. These inferences are drawn from the fact that thinning caused increased cover but no significant changes in species richness, at either quadrat or stand scales, for communities assessed with quadrats, but significantly reduced richness (particularly in MD and ND) at the stand scale, for the whole-log censuses. Moreover, NMS and PERMANOVA showed that epixylic communities on log tops (from quadrats) differed in both survey years, suggesting a fast response to treatments, whereas communities from whole log-censuses differed only in 2013, suggesting a slower response. The differences seen between whole-log and quadrat surveys suggest that species which avoid the tops of logs are more likely to be lost after thinning than those that favour the tops of logs; this may be because log sides provide a more sheltered habitat, thereby harbouring more desiccation-sensitive species. Species favouring more open-canopied conditions (e.g., lichens

and vascular plants) responded positively to thinning in whole-log censuses, but not in quadrat surveys, further reinforcing the idea that log sides were the key areas of community change. This result agrees with several other studies; in general, substrate-specialists and liverworts are negatively impacted with increasing intensity of silvicultural disturbance, whereas generalists are positively impacted by it (Arseneault et al., 2012; Caners et al., 2013b, 2010), and that this change is likely mediated by the accompanying change in understory humidity (Caners et al., 2010; Heithecker and Halpern, 2006).

Thinning and debris removal negatively impacted the richness of putatively disturbance-sensitive groups (e.g., liverworts, FOELAsexual bryophytes and FOELsidekick bryophytes). Given that the plantations were only 25 years old and relatively dominated by disturbance-resistant life-forms, this finding should be considered conservative. Similar compositional effects of disturbance have been detected in other studies of epixylic communities, and may represent a generalized response to disturbance. For example, Arseneault et al. (2012) found that generalist species performed better than epixylic specialists in response to stand thinning, and Baldwin and Bradfield (2007) found that epixylic species were less abundant, and disturbance-associated epigeic species were more abundant, in small retention patches as compared to larger ones. Likewise, Åström et al. (2005) showed that vascular plants and inorganic-substrate bryophytes were not affected by slash-harvest, whereas liverworts and organic-substrate bryophytes declined.

The increases in epixylic richness between survey years, regardless of treatment effects, may have been caused by above-average growing season weather conditions, or may simply be part of the natural community development as these forests age and the CWD decays. This trend was notable mainly at fine spatial scales (log or quadrat), but involved most functional groups (e.g., lichens, mosses, and vascular plants, and the more robust life-forms). Many have shown that bryophyte and macrolichen richness increase as forests age (Caruso and Rudolphi, 2009; Crites and Dale, 1998; Newmaster et al., 2003), and while much of this has been attributed to increasing habitat complexity (Fenton and Bergeron, 2008; Löbel et al., 2006; Ohlson et al., 1997), it may also result from a naturally slow increase in dispersal-limited, infrequent species (Sillett et al., 2000; Söderström and Doring, 2005). In the present study, however, such an explanation seems unlikely, given the lack of coinciding increases in species richness at the stand scale. Rather, the increased richness at fine scales is more likely the result of increasing detectability, via expansion of species that were already common, without significant losses of infrequent species.

Those functional groups that increased in response to thinning treatments, and also to debris removal in one case, were primarily groups that are not of conservation concern (i.e., DI and FOFF bryophytes, *Cladonia* spp., and vascular plants). The declines in richness and cover of DI bryophytes in control treatments at the quadrat scale may even indicate shade-intolerance, although this effect was alleviated at the treatment block scale. Although shade intolerance has little importance for conservation in intensively-managed forests, it has not

been widely documented among bryophytes, and should be further investigated as an uncommon strategy in a predominantly shade-adapted group (Marschall and Proctor, 2004). More generally, the increased light and heat that likely accompanied thinning (Chen et al., 1993; Fenton and Frego, 2005) may have enhanced the decay rate of the woody debris (Wu et al., 2010), making it more like the forest floor, and thereby increasing the suitability of conditions for germination and growth of what are normally epigeic (living on soil or humus) species (Collins et al., 1985). For bryophytes, the increased light itself may benefit some species, as other researchers have shown positive growth responses to partial canopy disturbance (Cleavitt et al., 2008; Muir et al., 2006), or positive associations with reduced canopy cover (Botting and Fredeen, 2006; Root and McCune, 2010). Similar increases in richness and abundance have been shown for chlorophyte-associated macrolichens after canopy disturbances, such as many *Cladonia* species (Botting and Fredeen, 2006; Bunnell et al., 2008; Lesica et al., 1991), and generalist vascular plants of the forest floor, such as *Cornus Canadensis* and *Linnaea borealis* (Ares et al., 2010; Macdonald and Fenniak, 2007; Ramovs and Roberts, 2003; Roberts and Zhu, 2002). Although other species of vascular plants and lichens have been shown to respond negatively to canopy disturbance (e.g., *Erythronium americanum*; Haughian and Frego, 2016; Ramovs and Roberts, 2005), these species were not common on CWD in the present study.

Metapopulation processes and reproductive strategies appeared to have played a small role in the responses of different functional groups to thinning and debris removal. Substantial investment in asexual reproduction may be adaptive as a disturbance response strategy in bryophytes, lichens, and vascular plants (Aikens et al., 2007; Kimmerer, 1994; Laaka-Lindberg et al., 2003; Webb, 1998), because it ensures rapid reproduction, greater reestablishment success, and often faster growth (Laaka-Lindberg et al., 2003). In contrast, sexual reproduction requires a greater long-term investment, meaning a more stable habitat is needed, but such reproduction extends the dispersal area due to the smaller propagule size and greater probability of becoming airborne (Löbel et al., 2006; Söderström and Doring, 2005). While low abundances meant that few lichens and vascular plants were subdivided by reproductive strategy, both groups were most frequently represented by asexually-reproducing species: *Cladonia* spp. dominated the lichen group, and rhizomatous herbs (e.g., *Cornus canadensis*, *Coptis trifolia*, *Dryopteris* spp., *Rubus pubescens*) dominated the vascular plant group. It seems likely that the positive response these groups showed to thinning and debris removal in this study is at least partly because of their ability to reproduce quickly and copiously via vegetative means. In contrast, putatively disturbance-sensitive bryophytes (loosely colonial or non-colonial epixylic specialists) showed small differences in their response based upon whether they were classified as primarily sexual or asexual reproducers. FOELsexual bryophytes combined sexual reproduction with a desiccation sensitive life-form, and were less species rich at both stand and logs scales. Such groups may be difficult to conserve without simultaneously increasing stand rotation times and improving habitat quality because they require both continued microclimatic stability (Caners et al., 2013a) and high substrate frequency to persist (Pohjamo et al., 2006).

Several analyses showed different effects of treatments using log-scale means than using stand scale totals, reinforcing recent criticisms of the ‘scalability’ assumption in traditional silvicultural experimental designs; even intensively managed forests have some level of heterogeneity, such that the average condition of small survey plots is unlikely to reflect trends at larger scales (Metlen and Fiedler, 2006; Puettmann et al., 2009). This study cannot comment on whether the mean losses or gains in species richness are equivalent to ‘natural dynamics’, since equivalent mature stands were not sampled. Nevertheless, conservation objectives are generally aimed at large- rather than small-scale targets; log-frequency (mean) reductions may simply indicate reduced abundance or frequency of a population due to the initial shock of altered habitat. Recovery to pre-disturbance levels will likely be more rapid when

impacts are small, rather than large-scale (due to the reduced proximity of propagule sources in the latter).

Several groups showed different effects of treatments from quadrat surveys than from whole-log censuses; these were likely the result of small-scale niche-differentiation among epixylic species leading to quadrat surveys being biased towards a particular subset of the community. Such results could also arise from differences in the total amount of surveyed habitat, or the type of data (continuous vs. binomial) that were generated. Yet, given that (1) a large number of logs were surveyed in each stand, (2) many more species were recovered (both on average and in total) from whole-log censuses than quadrats, and (3) whole-log censuses included all species from quadrat surveys, but not vice-versa, it is reasonable to attribute many of the differences in treatment responses (between the different sample units) to the wider range of microhabitat conditions, and accompanying niche-specializations, that exists across entire logs compared with only the tops. Previous studies have shown that bryophyte species may preferentially occupy different parts of logs (Botting and DeLong, 2009; Kimmerer and Young, 1996; Rambo and Muir, 1998b), but with the exception of Kimmerer and Young’s (1996) “regeneration niche”, no attempts have yet been made to generalize particular micro-niches with functional traits.

This study had several limitations. First, it was limited in its ability to test whether thinning impacts are mediated through habitat modification or metapopulation processes for most epixylic taxa, due to the unequal distribution of sexual vs. asexually reproducing species in different substrate and life-form groups, but there is some evidence that sexual strategy impacts the degree of disturbance-intolerance for species that are sensitive to changes in habitat. Indeed, it may be the combination of niche (e.g., microclimate) and neutral (e.g., dispersal) mechanisms that creates the greatest sensitivity to disturbance (Löbel and Rydin, 2010) especially for leafy liverworts and loosely colonial bryophytes. Another limitation stems from the large number of statistical tests that were performed. While the multi-scale, multi-sample unit, and multi-taxon approach is a strength of this study, it necessitated a large number of statistical tests, which necessarily corresponds with a higher rate of error. Because many of the patterns shown here correspond with trends across the literature, and because several of these patterns were confirmed using multiple analytical methods, readers can be reassured of the validity of certain results, but additional experimentation is required to confirm or refute the patterns described here, particularly with respect to the changes in richness and abundance of specific functional groups.

4.1. Synthesis and recommendations

This study demonstrated that the most substantial changes in mid-rotation management were related to thinning, and less to reductions in woody debris. Removal of 40% of the standing basal area results in considerable reductions in canopy cover, and probably changes the understory climate, thereby leading to increased cover and richness of lichens, mosses, and the epixylic community as a whole. On the other hand, thinning and debris removal were detrimental for certain epixylic liverworts and loose or non-colonial epixylic bryophytes. Whether retaining 60% of trees (as in the present study) is appropriate for plantations is uncertain, but studies of thinning in naturally-regenerated stands may provide some guidance: in general, retaining $\geq 75\%$ of trees can make stands comparable to unthinned stands, whereas retaining less than 50% results in measurable changes, including a loss of sensitive species (e.g., Caners et al., 2013b, 2010; Dovčiak et al., 2006). Testing additional retention levels for plantations would be advantageous in resolving this uncertainty. Biomass harvesting appears to conflict with conserving sensitive epixylic species even in the short-term, and given the lack of newly created (coarse and fine) woody debris, these negative impacts will likely increase over time. While these same treatments appeared to be the most beneficial for improving

lichen richness, they were not significantly more so than other thinned treatments which retained debris on-site. Of all plantation treatments, a mixture of the ‘no management’ (CO) and the ‘low-intensity management’ (MD/MD+) options may be the most effective for simultaneously conserving sensitive epixylics while promoting less sensitive groups, at least in the short-term. Whether mid-rotation creation of snags (MD+ treatment) leads to increased CWD, and therefore, increased epixylic diversity and abundance in the long-term, requires additional study.

Regarding whether these changes are brought about primarily via habitat modification or metapopulation processes, the combination of functional group responses suggests that both play a role. Among the putatively sensitive bryophytes (i.e., loosely colonial epixylics), those with asexual reproduction seem to cope with more intense disturbance (i.e., biomass removal) more effectively than those with primarily sexual reproduction when viewed at the stand scale; this suggests that metapopulation processes are responsible for changes. On the other hand, when these putatively sensitive bryophytes are divided by colonial vs. non-colonial growth forms, the non-colonial forms show clear reductions in mean cover and richness on the tops of logs, but no change or a slight increase in richness at the stand scale or in surveys of whole logs; this suggests a negative impact of altered habitat conditions on species with the least desiccation resistance. Ultimately, additional monitoring is required to determine whether initial differences in the responses of such sensitive groups translate into longer-lasting, or larger-scale, changes that warrant corrective management actions. In the interim, additional experimentation with epixylic leafy liverworts (e.g., *Cephalozia* spp.) and sparsely or non-colonial mosses (e.g., *Platydictya subtilis*), especially those that reproduce only sexually, and under varying canopy conditions and levels of disturbance, could yield additional insights as to optimal configurations of plantations for biodiversity conservation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.02.019>.

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