Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation

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ABSTRACT

Six intensively managed white spruce (*Picea glauca* (Moench) Voss) plantations located in three general landscape contexts (plantation dominated, hardwood dominated, and mixed hardwood and plantation) in northern New Brunswick underwent alternative commercial thinning (CT) treatments: 1) an unthinned control; and three 40% basal area CT removals, with 2) slash and tops remaining on site (*status quo* CT), 3) branches and tops extracted from the site (biomass removal CT), and 4) clumps of unthinned trees left, and one-half girdled to create snags (enhanced structure CT). We examined responses of taxa that have a clear connection to deadwood and thinning response: beetles and bird species that are directly dependent upon deadwood, ground vegetation species sensitive to disturbance, and small mammals that have been observed to have low density in planted stands. Results three years post-thinning showed that crown width and tree growth responded positively to CT, and herbaceous vegetation diverged from reference stands and unthinned treatments with CT, but greatest compositional change was associated with biomass removal CT. Beetles responded positively to CT, small mammal species responded both positively (red-backed voles) and negatively (woodland jumping mice) to CT, but areas dominated by plantations had negative effects on voles. Effects of CT on songbirds were unclear and their quantification would require larger treated blocks, but maintenance of habitat at the landscape level is essential for the conservation of bird species that require deadwood. The experimental biomass removal CT was least similar to both unthinned and older unmanaged stands, and may therefore be detrimental to biodiversity conservation efforts. These results are only the initial three years after treatment but set the study up to permit a long-term legacy of determining long-term responses of taxa over stand development.

Keywords: commercial thinning, beetles, songbirds, small mammals, ground vegetation, deadwood, tree growth response, plantation habitat

RÉSUMÉ

Six plantations d’épinette blanche (*Picea glauca* (Moench) Voss) aménagées de façon intensive, et situées dans trois paysages forestiers différents (prédominance de plantation, prédominance de feuillus et mélange de feuillus et de plantation) dans le nord du Nouveau-Brunswick ont fait l’objet de traitements d’éclaircie alternatifs (ÉC) : 1) témoin non éclairci; et trois éclaircies commerciales à 40 % de la surface terrière avec 2) abandon des branches et des houppiers sur le parterre de coupe (ÉC *statu quo*), 3) enlèvement des branches et des houppiers de sur le parterre de coupe (ÉC avec prélèvement de la biomasse), et 4) maintien de groupes d’arbres non éclaircis et annelés à moitié pour créer des chicots (ÉC avec structure améliorée). Nous avons étudié les taxons qui ont un lien étroit avec le bois mort ainsi que leur réaction à l’éclaircie : les coléoptères et les oiseaux qui ont absolument besoin de bois mort, les espèces vivant dans la végétation du sol, sensibles aux perturbations, ainsi que les petits mammifères connus pour leur faible densité dans les plantations. Trois ans après l’éclaircie, les résultats montrent que la largeur de la cime et la croissance des arbres ont réagi positivement à l’ÉC, et que la végétation herbacée différait de celle des peuplements de référence et non soumis à une ÉC, mais c’est dans l’ÉC avec prélèvement de la biomasse qu’on observait le plus grand changement de composition. Les coléoptères ont réagi positivement à l’ÉC alors que les petits mammifères ont réagi à la fois positivement (campagnol à dos roux) et négativement (souris sauteuse des bois) au traitement, mais les étendues dominées par la plantation ont eu un effet négatif sur les campagnols. L’ÉC ne semble pas avoir eu d’effet clair sur les oiseaux chanteurs et il aurait fallu des blocs plus étendus pour être en mesure de les quantifier; cependant, il est essentiel de préserver leur habitat à l’échelle du paysage pour assurer la conservation des espèces d’oiseaux qui ont besoin de bois mort dans leur milieu. C’est l’ÉC expérimentale avec prélèvement de la biomasse qui montrait le plus de différence avec les peuplements non éclaircis et les peuplements plus âgés non aménagés; elle pourrait donc nuire aux efforts pour maintenir la biodiversité. Ces résultats tracent un premier portrait, trois ans seulement après le traitement, mais positionnent l’étude comme un legs durable pour évaluer la réaction à long terme des taxons tout au long de la vie du peuplement.

Mots-clés : éclaircie commerciale, coléoptères, oiseaux chanteurs, petits mammifères, végétation du sol, bois mort, réaction des arbres, habitat de plantation.

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Introduction

At least part of Canada's forest will continue the intensification of forest management over the next decades through plantation forestry. A key criticism of plantations is that planted stands are 'sanitized', which reduces structural diversity, species diversity, and volumes of downed and standing deadwood. Concerns are typically most focused on paucity of deadwood and reduced species diversity in the overstory. This research determined the influence of key habitat structures, early in the rotation of planted stands, on animal and plant taxa, and how their improved management can be better incorporated into the overall forest management strategy. We focussed on taxa that have strong connections to deadwood and thinning response, namely invertebrates and birds that are dependent upon deadwood, ground vegetation sensitive to disturbance, and small mammals that have low densities in planted stands (Ramovs and Roberts 2003, 2005). We experimentally manipulated habitat structure during commercial thinning (CT) treatments in six white spruce (*Picea glauca* (Moench) Voss) plantations, and determined influence and effects of landscape context around sample plantations on selected taxa.

White spruce is an ecologically and economically important species with over 114 000 ha planted in Canada in 2012 (Canadian Council of Forest Ministers 2014). CT of plantations occurs when size of thinned trees permits conversion to useable wood products to increase commercial productivity (Nyland 2002, Pelletier and Pitt 2008). To contribute to biodiversity conservation while procuring renewable timber (Vincent *et al.* 2009), traditional silvicultural practices which focus primarily on wood production may need to be modified.

The ecological contribution of plantations to biodiversity objectives at the landscape scale is not well understood, but is an important topic as forest management intensification occurs. J.D. Irving, Limited, in New Brunswick, has been establishing spruce plantations for over 50 years, and owns one of the most intensively managed forests in Canada. The Irving landscape provides a good test case of effects of plantations on biodiversity.

Intensive forest management may negatively impact biodiversity through (*i*) direct effects of tree removal and site preparation (Freedman *et al.* 1993, Ross-Davis and Frego 2002), (*ii*) indirect environmental changes that stem from homogenizing and simplifying stand structure (Ramovs and Roberts 2003), and (*iii*) reduction of source populations and propagules that may reduce the probability of re-colonization after timber harvesting (Zobel *et al.* 2006). In particular, intensive management that includes whole-tree or 'biomass' harvesting (using unmerchantable wood as fuel) could increase negative impacts of plantations on biodiversity because it reduces forest structure to a greater extent than conventional harvesting (Freedman *et al.* 1996, Rudolphi and Gustafsson 2005). Nonetheless, the one-third greater yield of plantations above conventional forestry in New Brunswick (Erdle and Ward 2008) has led to increased plantations (Hartley 2002, Loo and Ives 2003). If plantations continue to expand and to intensify, it will become increasingly challenging to maintain current levels of biodiversity. Yet, managed forests may have some biodiversity value.

Forest managers may be able to partially compensate for negative impacts of plantations at the landscape scale by integrating principles of natural disturbance emulation management at the stand scale (Hartley 2002, French *et al.* 2008). In some cases, appropriate plantations can be regarded as ecosystem restoration, for example, planting white spruce and red spruce (*Picea rubens* Sarg.) and white pine (*Pinus strobus* L.) in areas where these species have been reduced. As afforestation, reforestation, and forest restoration are key strategies to mitigate climate change, plantation establishment will likely be an important tool in maintaining forest resilience in the face of climate change (e.g., Pawson *et al.* 2013).

We examined the consequences of changing stand structures on selected taxa during regularly scheduled CT management entries in six 22 to 30-year-old white spruce plantations. Four treatments included (*i*) an unthinned control, and three 40% basal area removal thinning treatments, with (*ii*) slash and tops remaining on site (*status quo* CT), (*iii*) branches and tops extracted from the site (biomass removal CT), and (*iv*) clumps of unthinned trees left, and one-half girdled to create snags (enhanced structure CT).

In addition to tracking species composition, tree growth, and dead wood response to CT, we evaluated response of four selected groups of taxa for the following reasons: (*i*) *forest floor vascular plants* can be sensitive to anthropogenic disturbance, often showing increased diversity after a disturbance takes place (Paillet *et al.* 2010) and some species require coarse woody debris (CWD) as substrate (Simard *et al.* 1998); *(ii) saproxylic invertebrates* are associated with dead and dying wood (Speight 1989), and have been shown to decline in richness in response to thinning in naturally regenerated forest (Klimaszewski *et al.* 2003) and with practices that reduce deadwood, but we suspected that they may benefit from coarse and fine woody debris (FWD) produced by CT due to the paucity of this resource in plantations; (*iii*) *small mammals* have lower abundance in intensive spruce plantations than in naturally regenerated softwood (Bowman *et al.* 2001a, Fuller *et al.* 2004, Keppie *et al.* 2005), and large contiguous patches of plantations have been characterized with reduced small mammal abundance (Bowman *et al.* 2001a); and (*iv*) *forest birds* are tightly linked to stand structure and deadwood, with up to 40% of North American forest birds using cavities for nesting (McComb and Lindenmayer 1999), and many of those species depend on deadwood as a source of food (e.g., Bütler *et al.* 2004).

Specific Objectives and Hypotheses

Herbaceous vegetation: We predicted that the herbaceous vascular plant community in the unthinned control (CO) would be the most similar to that of older, naturally regenerated forests (NAT), whereas that of biomass removal CT (BR) would be least similar as a result of more intense and more recent disturbance (canopy and soil).

Beetles: Recent studies (reviewed in Grove 2002 and Langor *et al.* 2008) have shown considerable influence of forest practices on invertebrate communities. We tested the hypothesis that increases in woody debris and canopy openness associated with CT temporarily increase beetle abundance across feeding guilds. For specific guilds, we hypothesized that: (*i*) plant feeder species will rapidly increase in abundance following CT because of increased accessibility and growth of understory vegetation; (*ii*) inner and outer bark saproxylic beetles, which directly depend on woody debris (Speight 1989), will increase in abundance according to the gradient of dead wood available for one to three years because FWD decays rapidly (Hammond *et al.* 2001, 2004); and (*iii*) predatory species will increase in abundance as their prey increases following CT. Because outer bark beetles depend on dead wood preconditioning by inner bark beetles (Hammond *et al.* 2001, Stokland *et al.* 2012), they should increase in abundance after inner bark beetles. Because the successive arrival of the beetle guilds can occur over a short period, beetle response to the treatments will be examined within and between seasons.

Small mammals: We hypothesized that red-backed voles (*Myodes gapperi* Vigors) and woodland jumping mice (*Napaeozapus insignis* Miller), being conifer stand specialists (Bondrup-Nielson 1987, Boonstra and Krebs 2012), are directly affected by plantation management. We predict CT to enhance small mammal abundance via increasing plantation structural diversity (Carey and Wilson 2001) and the addition of CWD and FWD accessible to small rodents (Sullivan *et al.* 2011). We hypothesized that *status quo* CT would increase and biomass removal CT would decrease small mammal density, and assessed plantations in three surrounding landscape contexts: plantation dominated, hardwood dominated, and mixed hardwood and plantation.

Songbirds: We hypothesized that creating deadwood (both standing and fallen) through alternative CT would increase avian biodiversity by providing foraging substrates. We mapped breeding territories and predicted that species responding positively to thinning treatments would show higher densities within enhanced structure (snags) blocks, whereas species that are not responding to the treatments would establish territories randomly among treatments.

Methods

Study area

Black Brook District is a 220 000 ha landbase in northern New Brunswick owned by J.D. Irving, Limited. It includes arguably the most intensively managed forest in Canada, with over 50 000 ha of primarily spruce plantations, as well as high-value shade tolerant hardwood stands managed for sawlogs and veneer logs by single-tree selection and patch cuts. At Black Brook, clearcuts are generally replanted within one year of the final harvest, and since the 1990s, J.D. Irving, Limited has adopted a variable retention approach where islands of mature trees and clumps of advanced regeneration are maintained to provide structural diversity. Following harvest, mechanical site preparation is used to create favourable seedling microsites and herbicide is often aerially applied to control competing vegetation. About one-half of planted stands are cleaned between ages 10 and 15 years to release the best crop trees and maintain optimum density. CT is generally prescribed at ages from 20 to 40 years to remove lower quality stems and focus the volume on fewer stems. Planted stands are eligible for final harvest between 35 to 55 years of age.

Plot measurements

The study design consisted of six >20 ha white spruce plantations, 22–30 years old, which underwent CT treatments for this study in fall 2010 or winter 2011. Two plantations were located in each of three general landscape contexts: plantation dominated, hardwood dominated, and mixed hardwood and plantation. Effects of landscape context were only analyzed for small mammals in this paper. Plantations were selected on the basis of similar stand characteristics, divided into four ~ 5 ha blocks, with each block subjected to one of four treatments: (*i*) an unthinned control; and three 40% basal area removal thinning treatments, with (*ii*) slash and tops remaining on site (*status quo* CT), (*iii*) branches and tops extracted from the site (biomass removal CT), and (*iv*) 11-12 clumps of unthinned trees (10 trees per clump) left, and one-half girdled to create snags (enhanced structure CT). Five 0.04 ha circular permanent sample plots (PSPs) were randomly located in each treatment block (total = 6 plantations × 4 blocks × 5 PSPs = 120 PSPs), measured before and after thinning treatments, and measured three years later.

In each PSP, all trees were tagged and DBH and tree density were measured before (in 2010), immediately after CT (2011), and three years after CT (2013). Height, height to crown base, and crown radius in four cardinal directions of each tree were measured after the CT. Three years after thinning, a sample of five to 45 trees per plot (calculated based on variability using coefficient of variation from an initial sample and 20% error) was measured for height and crown width.

Herbaceous vegetation

Six plots (10 m × 16.67 m) were randomly distributed throughout each treatment block in each experimental plantation (6 × 4 × 6 = 244 plots). In the summers of 2011 and 2012, percent cover of each herbaceous layer species (< 0.5 m tall) was visually assessed in three 1 × 1 m quadrats per plot and then abundance estimates were pooled by plot. Additional species noted during a systematic search were assigned plot-level abundance of 0.1%.

For comparison with older, more contiguous stands, herbaceous vegetation data were obtained from nearby spruce-dominated stands (M. Roberts and K. Frego, unpublished data) initiated by clearcut logging in the mid-1960s. These reference stands, (*i*) naturally regenerated (NAT), (*ii*) planted but unthinned (UT), and (*iii*) planted and thinned twice (CT2), were surveyed in 2006 as above (n = 3, 2, 2 stands respectively, each with 40 quadrats but no additional systematic search). Taxonomic resolution was made commensurate by pooling some taxa to form 119 genus- or family-level ecologically similar units (*Amelanchier*, *Aster*, excluding *A. acuminata* and *A. macrophylla*, *Betula*, *Carex*, *Dryopteris*, *Hieracium*, Poaceae, *Prunus*, *Pyrola*, *Ribes*, *Salix*, *Solidago*, and *Viola*).

Beetle sampling

We sampled beetles using flight intercept traps made of two clear acrylic sheets, 30.5 cm × 61 cm, perpendicularly nested one inside the other. A funnel supporting a plastic glass filled with a solution of 70% ethanol and 2% soap was attached at the base of the sheets. The top of the trap was covered with a circular piece of styrene to reduce input of debris and rain. In each treatment block, traps were placed along a transect parallel to the thinning trails (when present), perpendicular to an extraction road, and at least 200 m from other block edges. On each transect, a trap was set 5, 15, 30, 60, and 120 m (i.e., approximately at treatment block centre) away from the road. The traps were suspended between two trees ~1.6 m above the ground. One hundred and thirty-five traps were installed, 20 in each of the six plantations and five in each of three coniferous forests, at least 380 ha left unmanaged for decades. The first year (2011), traps were deployed from June 22–July 5 until August 22–24. In 2012 and 2013, traps were deployed from June 3–6 to August 26–28. Trap content was collected biweekly, and identification was conducted using current systematic literature. All species were assigned to a feeding guild following Dollin *et al.* (2008). Greater details about traps, their arrangement, and species identification are provided in Nadeau *et al.* (2015a).

Small mammals

We trapped small mammals in unthinned, biomass removal CT, and *status quo* CT treatment blocks during mid-spring and mid to late summer in 2011 and 2012 for five consecutive days. We used a single, square 100-trap grid and medium-sized (7.5 cm × 8.75 cm × 22.5 cm) Sherman galvanized folding live traps spaced 10 m apart to maximize recapture likelihood (Bergeron and Jodoin 1989, Jorgensen 2004). Traps were checked twice daily at dawn and late afternoon. Unsalted peanuts were used as bait, and a 25 cm^2 rectangle of cotton was provided during spring and autumn to reduce cold temperature mortality of captured animals. The enhanced structure CT was excluded because trees were girdled in 2011, too late to affect rodent populations noticeably within the study period.

Captured mice and voles were identified to species and uniquely tagged with a small, numbered Monel ear tag applied to one ear for identification. Animal handling followed guidelines set forth by the American Society of Mammalogists (Gannon and Sikes 2007) and the University of New Brunswick Animal Care Committee (2011).

We used *Density 4.4* (Efford 2012) software to calculate density as it assumes that the more an animal moves, the more likely it will be captured (Efford 2004). This software spatially maps trap locations and records which individuals were caught in which traps and how much each individual moved, which is used to build potential home range size (Efford 2004). Home range size was used to calculate capture probability as a decreasing function moving away from home range centre, which was then used to calculate population density (Efford 2004).

Songbirds

We surveyed songbirds using spot mapping (Bibby *et al.* 2000) where observers walk transects and map bird locations to the nearest 12.5 m. We mapped the territories of eight species (Table 1) in treatment blocks in five plantations. The Paget Brook plantation was omitted due to poor accessibility for early morning surveys. Each plot was surveyed eight times during the breeding season and a territory drawn (Bibby *et al.* 2000) based on clusters of at least two detections separated by a minimum of 10 days, counter-singing individuals, and territory size estimated from the literature (Table 1).

In the same study area, Guénette and Villard (2005) reported large variation in forest bird tolerance to forest management intensity. Thus, to accurately determine effects of increasing dead wood on birds, we focussed on eight focal species associated with dead wood for foraging, nesting, or both (Table 1). Also, because girdling trees to increase deadwood could decrease the density of nesting or foraging substrates for species that require high densities of live trees, we also included species associated with this structural component. Information about the eight focal species, by category, is summarized in Table 1.

Treatment blocks within plantations were (*i*) relatively small (~ 5 ha) compared to the territories of many songbird (e.g., boreal chickadee (*Poecile hudsonicus* Forester) > 5 ha, Ficken *et al.* 1996) and woodpecker species (e.g., black-backed woodpecker (*Picoides arcticus* Swainson) 150 ha, Tremblay *et al.* 2009) and (*ii*) spatially adjacent. Therefore, no statistical tests were conducted as territories overlapped treatment blocks. Instead, species maps are presented and patterns of distribution are discussed.

Data analyses

Mean DBH and density, as well as basal area and diameter distribution were calculated for each PSP and treatment block before and after thinning. Mean crown width and live crown ratios were also calculated per PSP and treatment block three years post-thinning. Periodic annual increment (PAI) in DBH and basal area increment for each treatment were calculated before (2010) and after (2013) thinning. Statistical comparisons were made for the above stand structural attributes between plantations and treatments using a nested ANOVA with treatment as a fixed factor, plantation as a random factor and plot as a random factor nested in plantation. Where residuals of the data had non-normal distribution or unequal variance, Box-Cox transformations were applied. All significant differences were assessed at $p < 0.05$.

Herbaceous vegetation composition was compared between years and among thinning treatments relative to the reference stands using non-metric multidimensional scaling (NMS) ordination on Bray-Curtis distances and taxa with frequency >1. The optimal number of axes and the stability of resulting axis configurations were achieved from a random starting configuration; the ordination was constructed using a maximum of 50 runs with real data and 250 iterations (randomizations) to evaluate the optimal configuration (*PCORD v5.0,* McCune and Mefford 2006). The differences in species composition between years and among treatments were compared for experimental plantations using permutation-based analysis of variance (PERMANOVA), with time and treatment as fixed effects and plantation as a random effect in *Primer v6.0* (Clark and Gorley 2006). PERMANOVA was applied using Bray-Curtis distances, with 9999 permutations and type III sum of squares; it was followed by permutation-based, pairwise multiple comparison tests (Clark and Gorley 2006).

Hypotheses about the effects of landscape context, treatments, and their interaction on small mammal densities were tested using repeated-measures ANOVAs (Delaney and Maxwell 1981). One-way ANOVAs, Shapiro-Wilks tests, or both, were used for *post-hoc* testing of significant differences. Beetle abundance was analyzed as a function of sampling date and treatment using regression analysis, comparing slopes and intercepts using *R version 2.15.2* (R Core Team 2012). Values of mean beetle abundance per trap per site per sampling event received a common logarithmic transformation. To account for curvilinear effects, models included a quadratic term. Assumptions regarding normality, linearity and homoscedasticity were met.

Table 1. Summary of pertinent information and predictions for eight focal songbird species, representing four categories of deadwood/forest type use that were assessed in each treatment block in five plantations.

Species		Prediction
Species associated with fine woody material		
1. White-Throated Sparrow	(*Zonotrichia albicollis*) mainly forages in dense undergrowth or brush piles (Falls and Kopachena 1994). Territories range from 0.4-1.3 ha (Lowther and Falls 1968).	Positive response to thinning treatments creating piles of fine woody debris.
Species associated with coarse woody debris		
2. Winter Wren	(*Troglodytes troglodytes*) may nest in natural cavities, decaying stumps or uprooted trees. Territory size is estimated at 1.2-2.8 ha (Freemark *et al.* 1995).	May respond positively to treatments that create piles of woody debris.
Species associated with standing dead wood		
3. Brown Creeper	(*Certhia americana*) is associated with old forests (Hejl *et al.* 2002, Poulin *et al.* 2013) and in particular with large-diameter, live trees for foraging (Poulin *et al.* 2008) and snags for nesting (Poulin *et al.* 2013). There is a threshold of 66 large stems/ha (>30 cm) in the occurrence of this species, whose breeding territory ranges from 2.3-9.4 ha (Poulin *et al.* 2013).	No response to enhanced treatment because tree girdling is too recent. Other treatments do not produce preferred nesting/foraging substrates.
4. Boreal Chickadee	(*Poecile hudsonicus*) nests in well-decayed snags, stumps, or in old woodpecker holes (Ficken *et al.* 1996) and require at least 5 ha for nesting territories (McLaren 1975). Tree girdling may provide nesting substrates for this species but this operation was too recent at the time of surveys to allow excavation by this species.	Given large area requirements relative to body size, territories would overlap several different treatments.
5. Red-breasted Nuthatch	(*Sitta canadensis*) typically nests in tall, well-decayed snags (DeGraaf and Yamasaki 2001). It often uses old woodpecker cavities. Territory size in this species is highly variable (from less than 1 ha to ~ 10 ha, Sabo 1980), and so is its annual density (MacKay *et al.* 2014).	Tree girdling could increase occurrence, but decomposition of girdled trees would be insufficient at the time of our surveys.
6. Black-backed Woodpecker	(*Picoides arcticus*) is a specialist of old conifer forests requiring recently dead snags for foraging and relatively large snags for nesting (Tremblay *et al.* 2010, Craig *et al.* in review). This species is often associated with recently burned stands but fires are uncommon in New Brunswick. In unburned forests of northern Québec, Black-backed Woodpecker territories contained a density of at least 35 m^3/ha of spruce snags (Tremblay *et al.* 2010). The Black-backed Woodpecker has by far the largest home range (~ 150 ha; Tremblay *et al.* 2009) of the eight focal species.	We predicted that this species would be essentially absent from the 20-25 year old plantations.
Species associated with closed spruce-dominated canopy		
7. Cape May Warbler	(*Dendroica tigrina*) feeds on insects in coniferous foliage (MacArthur 1958). Cape May Warblers have small territories (0.5 ha; Kendeigh 1947).	Expected to be negatively affected by thinning treatments but establish territories primarily in unthinned plots.
8. Bay-breasted Warbler	(*Dendroica castanea*) also forages on insects of coniferous foliage. Bay-breasted Warbler territories are ~ 1.5 ha (Sabo 1980). Both Cape May and Bay-breasted Warblers are strongly associated with spruce budworm (*Choristoneura fumiferana*) outbreaks and are present at much lower abundance between outbreaks (Kendeigh 1947, Venier *et al.* 2009).	Expected to occur more often in unthinned plots.

Results and Discussion

Tree species composition

Softwood species in the six plantations were primarily planted white spruce, some planted black spruce (*Picea mariana* (Mill) BSP), and naturally regenerated balsam fir (*Abies balsamea* L.). Hardwood species were all naturally regenerated and included trembling aspen (*Populus tremuloides* Michx.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white birch (*Betula papyrifera* Marsh), and yellow birch (*Betula alleghaniensis* Britt.). Pin cherry (*Prunus pensylvanica* L.) and willow (*Salix spp*.) made up 0.8-1.2% of stem density and contributed little to the overstory so were excluded from the species composition analysis (Fig. 1).

Prior to CT, white spruce constituted 65-96% of the basal area in each treatment block in the six plantations, except in one plantation where white spruce comprised 38-43% and black spruce up to 49% (Fig. 1a). For all six plantations combined, hardwood species made up <1% of the basal area, ranging from sugar and red maple with a mean of 0.2 m^2/ha (0.8%) to yellow and white birch with 0.03 m^2/ha (0.1%). The experimental sites were specifically selected to be conifer-dominated and uniform, so low amounts of hardwood are not surprising.

Three years after CT, species composition was similar to that observed prior to thinning (Fig. 1b). White spruce composed 70-97% of the basal area for treatment blocks in all

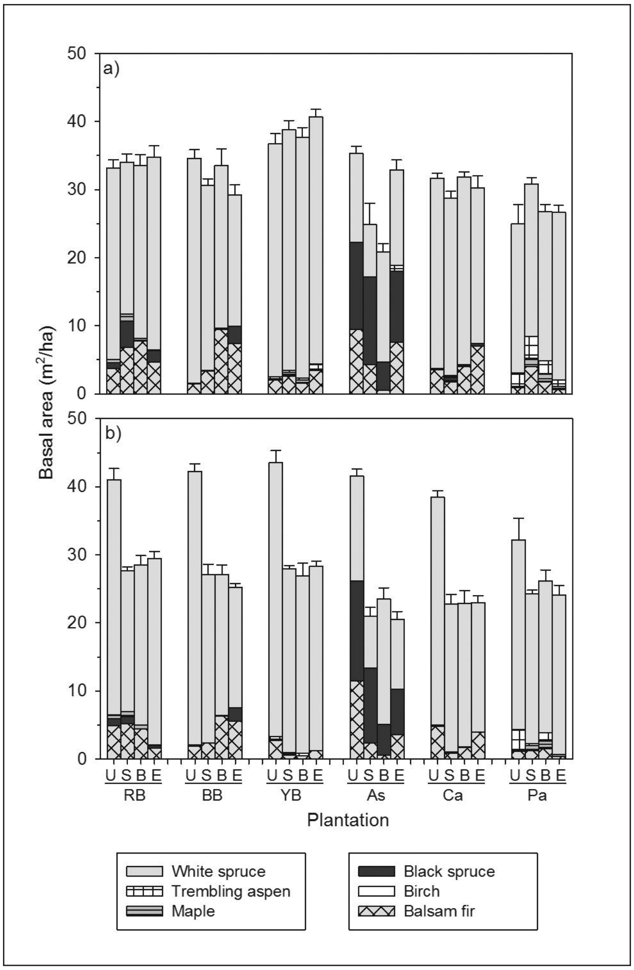

Fig. 1. Basal area by species in each of four treatments in six spruce plantations **(a)** before and **(b)** after thinning. Abbreviations: U: unthinned, S: *status quo* commercial thinning (CT), B: biomass removal CT, and E: enhanced structure CT treatments; RB Roussel Brook, BB Brown Brook, YB Yellow Brook, As Airstrip, Ca Canton, and Pa Paget plantations.

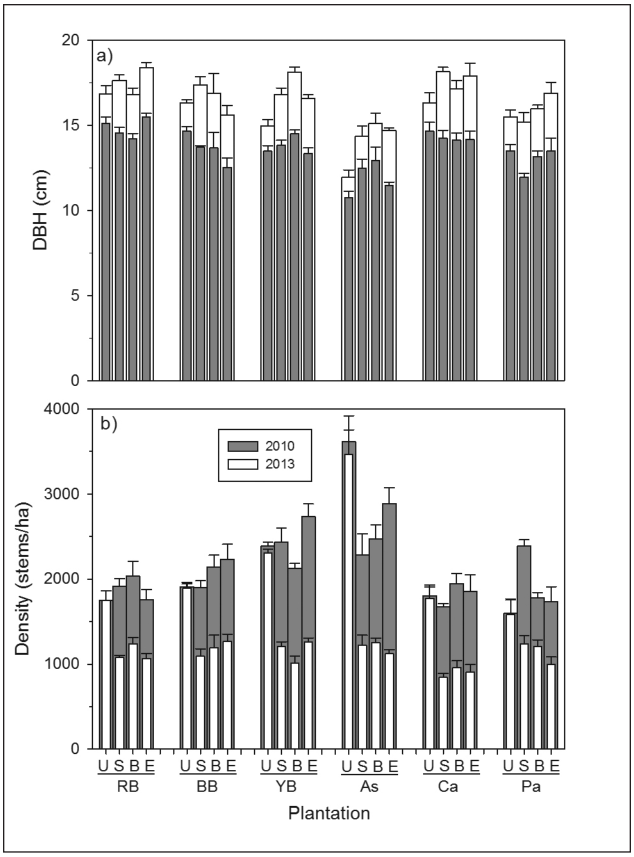

Fig. 2. Mean **(a)** diameter at breast height (DBH) and **(b)** tree density in each treatment for six spruce plantations before (2010) and after (2013) thinning. U, S, B, and E represent unthinned, *status quo* commercial thinning (CT), biomass removal CT, and enhanced structure CT treatments, respectively. RB, BB, YB, As, Ca and Pa represent Roussel Brook, Brown Brook, Yellow Brook, Airstrip, Canton and Paget plantations, respectively.

plantations except for one which included both white and black spruce. White spruce basal area ranged from 13 m^2/ha to 30 m^2/ha in the plantations, and balsam fir averaged 11% (4 m^2/ha) in the unthinned and 8-11% (2 m^2/ha to 3 m^2/ha) in the CT treatments. Three years after CT, basal area was 35-37% (14 m^2/ha to 15 m^2/ha) lower than in unthinned, while it increased by 15-39% (5 m^2/ha to 9 m^2/ha) in unthinned plots (Fig. 1b). This was expected, as CT creates the growing space to maximize individual tree growth rates.

Tree and stand responses to CT

Prior to CT, there were no differences in mean DBH between treatments. Three years after thinning, trees in all CT treatments had larger mean DBH (16.6-16.7 cm) compared to the unthinned treatment (15.3 cm) (Fig. 2a). Three years post-thinning, DBH differed between plantations, and mean DBH increment differed between plantations and among treatments; unthinned (mean 0.51 cm/tree/yr) was less than all CT treatments: biomass removal CT (0.61 cm/tree/year), enhanced structure CT (0.68 cm/tree/year), and *status quo* CT (0.67 cm/tree/year).

Although thinning debris can increase the pool of mineralizable nutrients and potentially influence nutrient supply to the remaining trees (Carlyle 1995), three years post-thinning, CWD resulting from CT showed little to intermediate signs of decay (Omari and MacLean 2015). Three years post-thinning, CWD volume increased by 14-27% in the *status quo* and enhanced structure treatments, by 6% after the biomass removal treatment versus 0.1% in unthinned (Omari and MacLean 2015). Mean snag volume changed little, less than 1 m^3/ha among treatments, and girdled trees in the enhanced structure added only 0.7 m^3/ha of snags (Omari and MacLean 2015). Mean volume of cut stumps was similar among treatments, averaging 4.7 m^3/ha in the biomass removal and 4.6-4.9 m^3/ha in the *status quo* and enhanced structure CT. Total deadwood volume (CWD plus snags) differed among plantations but not between treatments.

As expected, following CT, density and basal area differed between the unthinned and CT treatments, ranging from 1100-1140 stems/ha for CT versus 2130 stems/ha in unthinned plots (Fig. 2b). In all plantations, most trees had DBH of 10-15 cm prior to thinning versus 15-20 cm three years after thinning. Basal area averaged 40 m^2/ha in the unthinned treatment three years post-thinning compared to 25-26 m^2/ha in the CT treatments (Figs. 1b, 3a). Mean basal

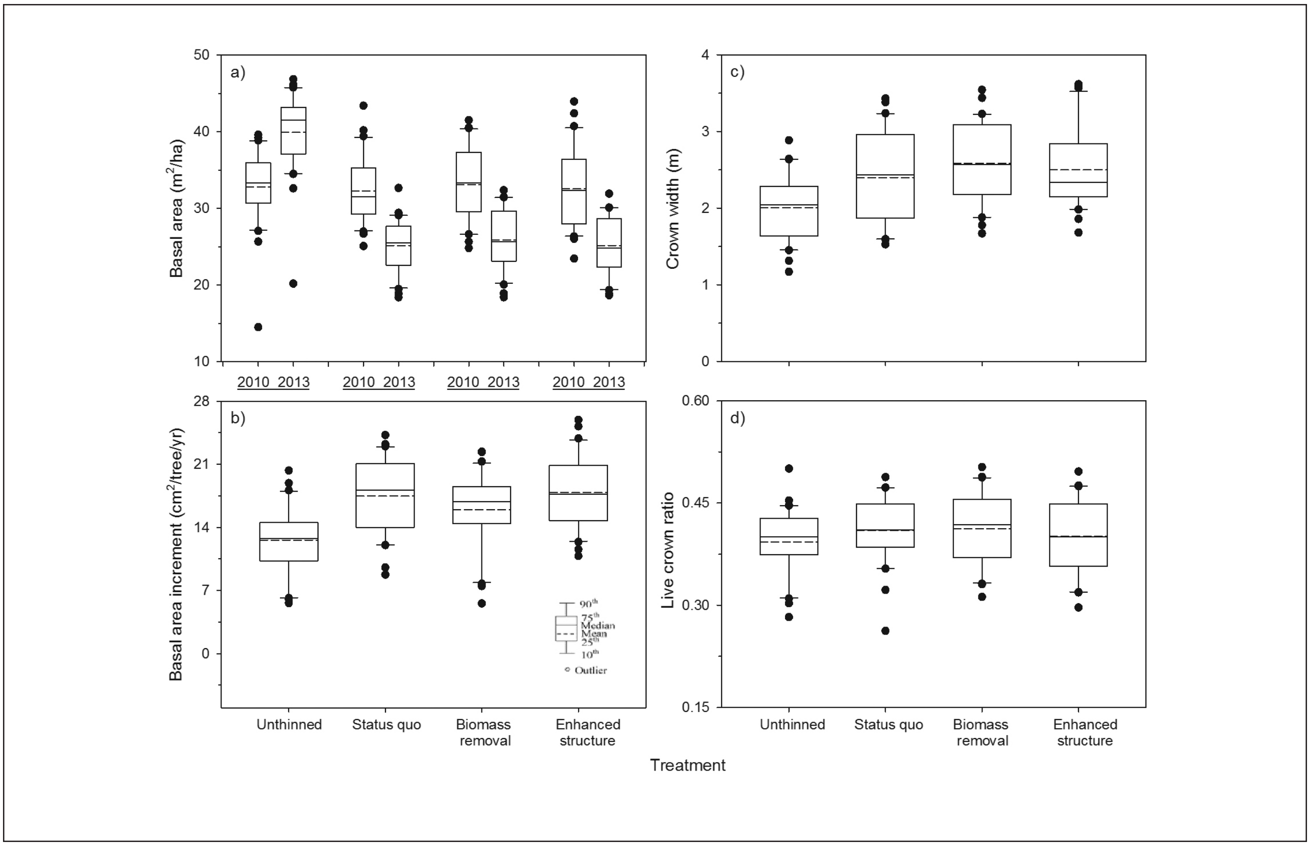

Fig. 3. Basal area **(a)**, **(b)** basal area increment, **(c)** crown width, and **(d)** live crown ratio in 30 plots in each of unthinned and three commercial thinning treatments for six spruce plantations, three years after thinning.

area increment (Fig. 3b) differed between plantations, and was lower in the unthinned treatments (12.6 cm^2/tree/yr) compared to all CT treatments (16.0-17.9 cm^2/tree/yr). Although three years post-thinning trees in CT treatments had higher mean DBH and basal area increment than those in the unthinned, higher tree density resulted in higher basal area in the unthinned treatment. There was a clear growth response to CT. Mean crown width differed between plantations and treatments three years after thinning, averaging 2.0 m in unthinned versus 2.4-2.6 m in CT (Fig. 3c). Live crown ratio three years post-thinning differed between plantations but not between treatments, ranging from 39-41% among CT treatments (Fig. 3d). Crown length was also not significantly different among treatments, averaging 4.6 m in unthinned versus 4.7-4.8 m in the thinned treatments. Following thinning, crown expansion occurs over both the short- and long-term by about 80% in thinned pine and spruce, 200% in aspen, and over 100% in ash and oak (*Quercus robur* L.) (Peterson *et al.* 1997, Juodvalkis *et al.* 2005). As a result, light interception and the amount of photosynthetic active radiation absorbed by trees in CT stands increase, and this contributes to increased tree growth. In the current study, crown widths differed between unthinned and all CT treatments, but live crown ratio did not, so CT may increase growth by its positive effect on crown width more so than crown depth.

Herbaceous vegetation

Over 200 herbaceous vascular species were detected from older reference forests (100 taxa) and the two survey years in experimental plantations (179 taxa in 2011, 183 in 2012).

The optimal NMS configuration, reached after 171 iterations, was three-dimensional, with stress = 14.051, instability < 0.00001, and similar variance captured on each of the three axes (r^2 = 0.235, 0.255 and 0.279 respectively). Axis 3 (Fig. 4a) primarily captured the variation in species composition among plantations, and between reference and experimental stands (PERMANOVA $P_{plantation}$ = 0.0001, df = 5); a major contributor to Axis 3 appeared to be the presence of a well-developed shrub layer in reference stands (e.g., *Viburnum spp*.). Axes 1 and 2 (Fig. 4b) were more relevant in their combined capture of the variation related to treatment effects. Based on the positions of the reference stands, they represent a gradient of increasing disturbance frequency and intensity from lower left to upper right. The experimentally thinned treatments experienced a parallel shift in composition (as shown by vectors) on these axes, away from the compositions of the older naturally regenerated and unthinned reference stands ($P_{treatment}$ = 0.0589, df = 3), however, the magnitude of their changes differed ($P_{plant×treatment}$ = 0.0001, df = 15). Multiple comparison tests confirmed that between-year changes within biomass removal and enhanced structure treatments were significant ($P < 0.03$, df = 5). This shift was positively correlated ($r > 0.38$ on Axes 1 or 2; Fig 4c) with increasing abundance of rhizomatous forest herbs, wood ferns, regenerating hardwoods and ruderal taxa.

Three trends are worthy of note. First, all young experimental plantations lacked the mid-sized shrub layer (e.g., *Viburnum nudum* L.) that was present in older reference stands; this may be expected to develop with time. Second, plant composition in unthinned experimental treatments

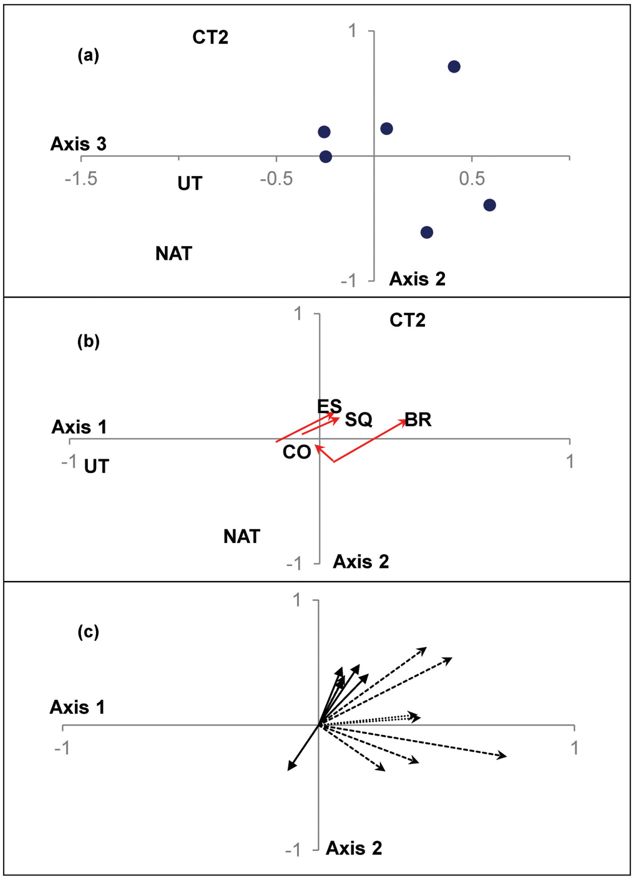

Fig. 4. (a) Reference treatment (codes) and experimental plantation (circles) centroids plotted on Axes 2 and 3 of NMS ordination to show range of compositional variation; **(b)** Reference treatment (codes) and experimental treatment (vectors from 2001 to 2012 centroid) plotted on Axes 1 and 2 of NMS ordination, and **(c)** selected species-correlations on Axes 1 and 2 presented as vectors from origin (length of vector = strength of correlation); solid lines = shrubs and regenerating hardwoods (e.g., *Acer* spp., *Populus tremuloides* Michx.) dashed lines = rhizomatous forest herbs (e.g., *Cornus canadensis* L., *Maianthemum canadense* (Desf.) Greene) and ferns (e.g., *Dryopteris* spp.), and dotted lines = ruderal species (Poaceae, *Chamerion angustifolium* (L.) Holub).

(controls) did not change significantly between years and their species composition was the most similar to naturally regenerated and unthinned older stands. Lastly, in spite of the initial compositional differences among experimental plantations, the ground flora of all thinned treatments diverged from that of naturally regenerated and unthinned older stands and the control treatment, with the greatest change in the biomass removal CT treatments.

Although the primary difference between *status quo* (SQ) and enhanced structure (ES) treatments versus biomass removal (BR) treatments was the removal of logging debris, the shift in species composition in the latter treatment was likely also related to increased soil disturbance or reduced soil protection. Aikens *et al.* (2007) found that the degree of change in understory plant communities was greater with both canopy opening and soil disturbance than canopy opening alone. As in our study, this change was characterized by expansion of pre-existing forest herbs and ferns, and invasion of ruderal species. Burke *et al.* (2008) found the same pattern with higher-intensity thinning treatments that exposed soil. It is likely that the provision of woody debris (or the lack thereof) as a substrate for vascular plants may be less important to forest floor vegetation composition than disruption of the general substrate (Pyle and Brown 2002). Although it is too early to evaluate the relative merits of thinning with moderate levels of debris creation or retention, removal of woody debris (biomass for pulp or fuel) initially results in a compositional shift away from that found in mature, naturally regenerated forests, and therefore is incompatible with biodiversity conservation objectives; its long-term effects on rare or sensitive species require further study.

Effects of treatments on beetle feeding guilds

We collected 76 212 individual beetles. The list of species recovered in 2011 and 2012 is provided in Nadeau *et al.* (2015a). Beetle abundance in each feeding guild usually declined throughout the sampling seasons (Fig. 5). Generally, the number of beetles per feeding guild was similar between CT plantations and old forests, while unthinned plantations supported 5–6 times fewer beetles than old forests and CT plantations (Fig. 5). The slopes and intercepts of the relationships between beetle abundance and time often differed between treatments but these differences usually faded as the time since thinning increased (Fig. 5; Table 2). Trends were similar between the various CT treatments (Fig. 5).

For plant feeder beetles, slopes and intercepts of relationships between beetle abundance and time differed in 2011 because CT plantations exhibited a steeper decline in abundance and supported more beetles than unthinned plantations (Fig. 5a; Table 2). In 2012, a difference in intercept occurred stemming from higher initial abundance in CT than unthinned plantations (Fig. 5a; Table 2). In 2013 no differences between treatments were detected (Table 2). For inner bark beetles, intercepts differed in 2011 because unthinned plantations initially supported fewer beetles than CT plantations (Fig. 5b; Table 2). In 2012, slopes and intercepts differed (Table 2), due to a steeper decline in beetle abundance in old forests than in plantations (Fig. 5b), as well as to higher initial numbers in old forests (Fig. 5b). In 2013, slopes and intercepts differed (Table 2) because of steeper declines in beetle abundance in old forests than in plantations and in CT than in unthinned plantations (Fig. 5b). Unthinned plantations initially supported fewer beetles than CT plantations, and plantations initially supported fewer beetles than old forests (Fig. 5b). For outer bark beetles, no differences in slope occurred but differences in intercept of relationships between beetle abundance and time occurred in all three sampling years (Table 2) because initial outer bark beetle densities were higher in CT than unthinned stands (Fig. 5c). For predatory beetles, intercepts differed between treatments in 2011 (Table 1) because early in the season, unthinned plantations supported fewer beetles than CT and biomass removal CT plantations supported fewer beetles than *status quo* CT plantations (Fig. 5d). Intercept also differed in 2012 (Table 2), stemming from a higher initial density being recorded in CT than unthinned plantations (Fig. 5d). No differences between treatments were detected in 2013 (Table 2).

These results support the general hypothesis that changes in woody debris and canopy openness associated with CT of plantations can increase beetle abundance across feeding

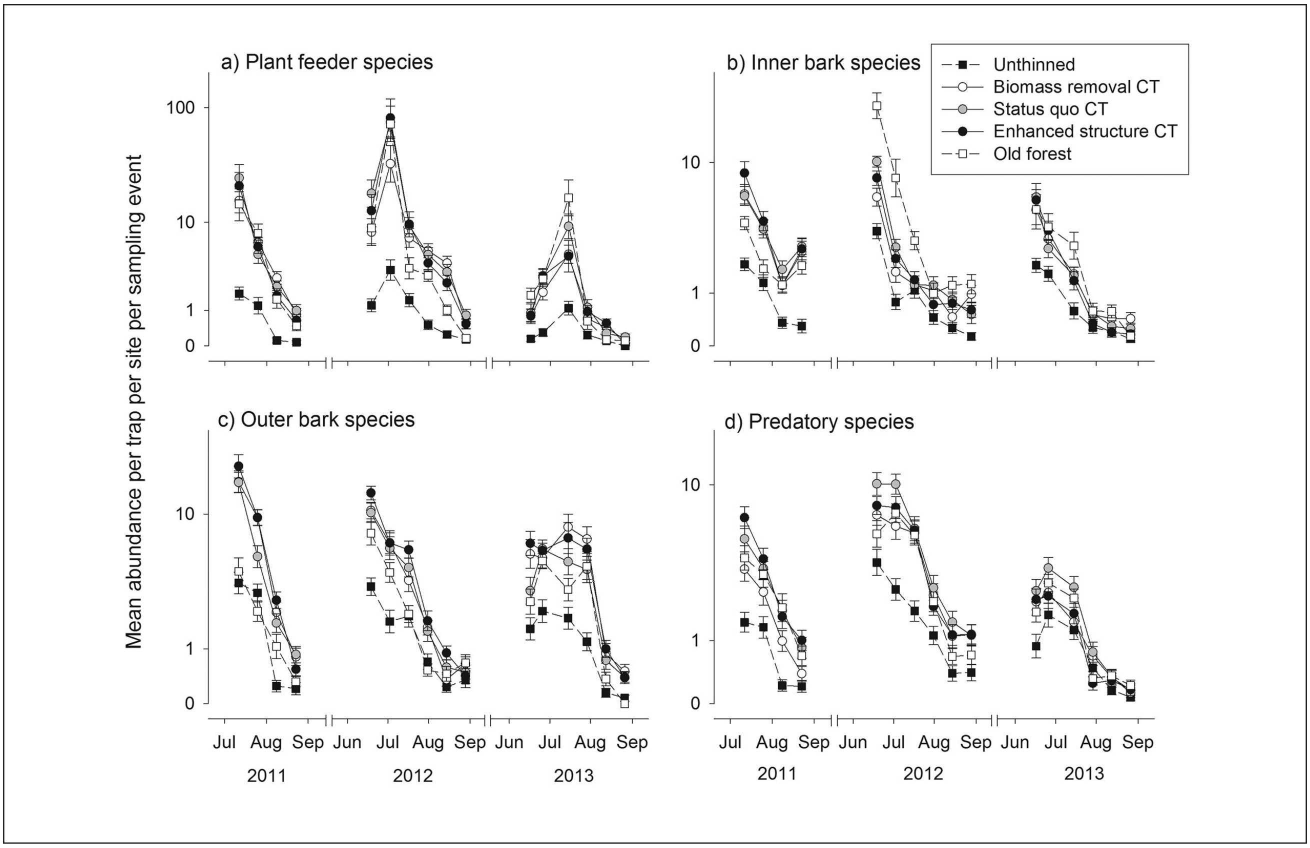

Fig. 5. Mean beetle abundance (± SEM) per trap per two weeks in unthinned and three commercial thinned (CT) treatments as a function of the sampling date for **a)** plant feeder beetles (i.e., species consuming leafy vegetation, pollen, nectar, roots and/or decomposing plant material), **b)** inner bark beetles (i.e., species feeding on xylem, phloem and/or sap), **c)** outer bark beetles (i.e., species grazing on fungal fruiting bodies, fungal hyphae and/or slime molds), and **d)** predatory beetles (i.e., species consuming invertebrates and/or decomposing animal material).

guilds. Beetle abundance in CT plantations was comparable to that of older naturally regenerated forests in the same area, and was considerably higher than abundance in unthinned plantations. Conversely, our hypotheses for specific feeding guilds were poorly supported because beetle response to the treatments was strong and similar across guilds. Changes in chemical and structural components of dead wood occur over time and should promote beetle species succession (reviewed in Nadeau *et al.* 2015b), with inner bark species colonizing woody debris first but declining in abundance rapidly because dead wood is only fresh for a short period (Hammond *et al.* 2001, 2004), and outer bark species colonizing later (Esseen *et al.* 1992, Vanderwel *et al.* 2006). However, inner bark species were still abundant in CT areas in 2013, even if they declined from 2012 to 2013. In addition, there was no delay between the increase in abundance of inner and outer bark beetles, both within or between seasons, possibly because outer bark species recovered in this study feed on early succession fungi (Vanderwel *et al.* 2006). The expected effect on saproxylic beetles of the woody debris gradient produced by the treatments was not observed, in part because girdled trees took two summers to die, suggesting that canopy openness had a greater effect on beetles than the amount of residual wood, which is consistent with another study of the effect of biomass removal on leaf litter invertebrates (Work *et al.* 2014). Our hypothesis that plant feeder and predatory species should reach higher abundances in CT plantations because of higher vegetation (Ranius and Jansson 2000) and prey content (Wermelinger *et al.* 2002) was supported, as well as our hypothesis that the increase in abundance of predatory species would be delayed. However, the decline of both plant feeder and predatory species in 2013 was not expected as crown closure has not occurred yet.

We conclude that CT can promote occurrence of beetles across different guilds during the first three summers following thinning, but additional sampling seasons will be necessary to determine how long these effects on beetle communities last.

Effects of treatments on small mammals

We completed 36 367 trap nights over 2011 and 2012 totaling 4064 captures. Short-tailed shrews (*Blarina brevicauda* Say) were the most common (8.4/100 trap nights), red-backed voles second (0.91/100 trap nights), woodland jumping mice third (0.84/100 trap nights), and deer mice (*Peromyscus maniculatus* Wager) fourth (0.49/100 trap nights). All other mammal species captured (≤0.13/100 trap nights) were too irregular to track abundance.

Deer mice and short-tailed shrews were not affected by either surrounding landscape composition (two plantations each in plantation-dominated, hardwood-dominated, or mixed plantation-hardwood landscapes) or CT or interac-

Table 2. Regression analyses fitted to the longitudinal beetle abundances per year, treatment, and feeding guild (Fig. 5). The degrees of freedom are 4,9 for 2011 and 4,19 for 2012–2013. A significant effect indicates that at least one of the slope or intercept values differed from the others. Polynomial contrasts by regression, in italics, were carried out to identify the source of differences.

	2011		2012		2013	
	Slope	**Intercept**	**Slope**	**Intercept**	**Slope**	**Intercept**
Plant feeder beetles	4.266*	17.059**	1.157	4.551**	0.459	1.865
Old forests vs. Plantations	*0.609*	*0.450*	–	*0.037*	–	–
Commercial thinned vs. Unthinned	*13.120***	*67.180***	–	*24.876***	–	–
Status quo vs. Biomass removal	*1.437*	*0.569*	–	*0.137*	–	–
Status quo vs. Enhanced structure	*0.003*	*1.757*	–	*0.011*	–	–
Inner bark beetles	0.553	10.651**	5.640**	24.237**	7.004**	14.107**
Old forests vs. Plantations	–	*0.336*	*11.860***	*41.990***	*6.105**	*12.379***
Commercial thinned vs. Unthinned	–	*41.728***	*0.432*	*28.818***	*19.640***	*40.029***
STATUS QUO VS. BIOMASS REMOVAL	–	*0.078*	*1.836*	*1.374*	*0.198*	*0.327*
Status quo vs. Enhanced structure	–	*0.329*	*0.071*	*1.233*	*0.312*	*0.345*
Outer bark beetles	2.495	13.364**	2.216	7.454**	0.236	8.073**
Old forests vs. Plantations	–	*2.606*	–	*1.424*	–	*0.985*
Commercial thinned vs. Unthinned	–	*46.082***	–	*35.108***	–	*33.217***
Status quo vs. Biomass removal	–	*1.450*	–	*0.064*	–	*1.737*
Status quo vs. Enhanced structure	–	*2.342*	–	*1.211*	–	*1.132*
Predatory beetles	0.654	17.756**	0.615	10.915**	0.431	1.685
Old forests vs. Plantations	–	*0.817*	–	*0.105*	–	–
Commercial thinned vs. Unthinned	–	*30.665***	–	*46.245***	–	–
Status quo vs. Biomass removal	–	*17.289**	–	*2.460*	–	–
Status quo vs. Enhanced structure	–	*2.063*	–	*2.063*	–	–

* $0.05 \geq P \geq 0.01$ ** $P < 0.01$

tions (Table 3). Woodland jumping mice were not affected by landscape composition, but did express an aversion to CT (Table 3). Woodland jumping mice density averaged 5-6 fold greater in unthinned (13.8/ha) than in CT (2.1/ha). Red-backed voles were affected by both landscape and treatment, but there was no interaction (Table 3). Voles were more abundant in *status quo* CT with debris retained than either unthinned or biomass removal CT. Effect of landscape composition was not significant.

Generally, short-tailed shrews and deer mice do not appear to be affected by CT nor by landscape context; therefore, they likely do not require special management considerations. We found woodland jumping mouse density to be inordinately high in mid-rotation, non-CT plantations within a hardwood dominated landscape when compared to densities within other stand types (Morris 1955, Bowman *et al.* 2001a, Fuller *et al.* 2004, Keppie *et al.* 2005). Therefore, we advise maintaining some plantations over 25 years of age in a non-CT state and maintaining hardwood stands if present. Further, as hibernation is a significant bottle neck for jumping mice survival, planted non-CT sites with optimal hibernation locations—well-drained or sloped terrain—need to be maintained across the landscape (Ovaska and Herman 1988). As jumping mice home ranges span 0.4-5.0 ha in these Black Brook plantations (Dracup 2013), and their linear movements have been reported up to over 600 m (Bowman *et al.* 2001b), it is likely that if a sloped or well-drained, mid-rotation, non-CT plantation, or mature softwood stand ≥ 5 ha is within 600 m of another such site, jumping mice should be able to move to and populate the adjacent site. Further, riparian buffers facilitate dispersal and residency, so buffer presence may enhance jumping mice movement through a landscape (Ovaska and Herman 1988).

Vole capture rates in *status quo* CT within hardwood and mixed hardwood-plantation landscapes were similar to previous results in natural softwood stands (0-13.5/100 trap nights (Morris 1955, Bowman *et al.* 2001a, Fuller *et al.* 2004, Keppie *et al.* 2005). Therefore, plantation CT in hardwood and mixed hardwood-plantation landscapes can improve plantation structure for red-backed voles if debris is retained (i.e., *status quo* CT). However, our results concur with Bowman *et al.* (2001a) that large areas of plantations are detrimental to red-backed voles.

As vole density was depressed within plantation-dominated landscapes, special care must be taken when designing these areas so as not to inhibit dispersal. We recommend that large contiguous areas of plantations be broken up by islands of naturally regenerated forest. Voles have been recorded to move up to a maximum of 494 m (Bowman *et al.* 2001b), and maintain home ranges averaging 0.2-0.5 ha in Black Brook plantations (Dracup 2013). Patches of untreated forest ≥ 1.0 ha in size are able to maintain internal structural integrity (de Graaf 2008), and would be able to maintain at least two breeding female voles (Bondrup-Nielson 1987). Red-backed voles should be able to disperse to and out of these patches if placed ≤ 252 m apart, and maintaining these small patches within plantation-dominated landscapes should allow small populations to establish and enhance colonization of surrounding, less desirable forest space.

Table 3. Mean (n=2) density/ha ± SEM of deer mouse, red-backed vole, woodland jumping mouse, and short-tailed shrew per commercial thinning (CT) treatment per landscape (plantation dominated, hardwood dominated, or mixed) averaged over spring and summer 2011 through 2012 with RM-ANOVA results, in the Black Brook District, northwest New Brunswick.

Species and Landscape	Density/ha (±SEM) per Treatment			RM-ANOVA Landscape			Treatment			Landscape x Treatment		
	Unthinned	Biomass Removal CT	Status Quo CT	df	F	p	df	F	p	df	F	p
Deer mouse												
Hardwood	3.8±1.8	6.7±2.5	5.4±2.2	2	4.07	0.06	2	0.51	0.62	4	1.46	0.29
Mixed	5.8±2.8	3.1±0.9	4.3±1.5	–	–	–	–	–	–	–	–	–
Plantation	4.1±2.8	0.6±0.5	1.0±0.5	–	–	–	–	–	–	–	–	–
Woodland jumping mouse												
Hardwood	13.8±4.6	3.6±1.8	2.4±1.2	2	1.09	0.38	2	5.00	0.04	4	0.43	0.79
Mixed	6.1±2.2	2.1±0.9	2.3±1.0	–	–	–	–	–	–	–	–	–
Plantation	7.4±3.3	1.5±1.0	0.8±0.5	–	–	–	–	–	–	–	–	–
Red-backed vole												
Hardwood	1.1±0.6	2.6±1.1	7.2±2.3	2	5.18	0.03	2	6.70	0.02	4	0.75	0.58
Mixed	4.2±1.1	3.4±1.6	7.1±1.8	–	–	–	–	–	–	–	–	–
Plantation	1.2±0.8	0.3±0.2	2.7±1.5	–	–	–	–	–	–	–	–	–
Short-tailed shrew												
Hardwood	12.3±4.7	5.6±3.4	5.5±3.2	2	0.82	0.47	2	2.77	0.12	4	0.48	0.75
Mixed	12.0±5.3	8.4±4.6	10.1±4.6	–	–	–	–	–	–	–	–	–
Plantation	9.0±4.2	5.6±3.8	6.3±3.1	–	–	–	–	–	–	–	–	–

Effects of treatments on songbirds

Territory maps for two plantations illustrate the typical patterns observed among plantations and species (Fig. 6). Detections of White-throated Sparrow (*Zonotrichia albicolis* Gmelin) were mostly concentrated along plantation edges. It is unclear whether this species responded positively to the addition of FWD because occurrence of sparrows in the enhanced and *status quo* CT blocks was inconsistent between plantations (Fig. 6a).

As predicted, the Black-backed Woodpecker and Brown Creeper (*Certhia americana* Bonaparte) were virtually undetected. A Black-backed Woodpecker did respond to a playback in one plantation during a single count in the biomass removal CT block that borders a mature spruce forest. The plantation was revisited and repeated playback trials were conducted, but did not produce a second sighting in the plantations. Red-breasted Nuthatch (*Sitta canadensis* L.) and Cape May Warbler (*Setophaga tigrina* Gmelin) were represented only by scattered, mostly peripheral detections and Winter Wren (*Troglodytes hiemalis* Viellot) was absent from all but two sites. Maps were not produced for the Black-backed Woodpecker, Red-breasted Nuthatch or Cape May Warbler due to their scarcity in the plantations. Boreal Chickadee (*Poecile hudsonicus* Forester) territories broadly overlapped treatment blocks, showing no avoidance or preference for any treatment *per se* (Fig. 6b).

The Bay-breasted Warbler (*Setophaga castanea* Wilson) reached higher occurrences than expected, given the fact that this was not a spruce budworm outbreak year (Fig. 6d). It showed no detectable preference for a given treatment and instead appeared to be avoiding roads and areas directly adjacent to deciduous plots (e.g., Fig. 6d, Roussel Brook plantation).

We detected little evidence for a response to CT by focal bird species. However, the experimental design was not optimal for testing treatment effects on forest birds for three reasons. First, the area of treatment blocks was small relative to the territory size of many bird species, including those most likely to respond negatively to intensive plantation silviculture, e.g., woodpeckers and Brown Creeper (MacKay *et al.* 2014). This was obvious when examining territory maps. For instance, it was unclear whether the Boreal Chickadee was using the plantations as its main breeding territory or an extension thereof. High area requirements made these species susceptible to respond to habitat surrounding the plantation sites. Second, treatment blocks were generally adjacent to one another, making it more difficult to detect effects because individuals may nest in one block and forage in another or establish a territory overlapping two treatments. Third, responses by species at the plantation level (e.g., Winter Wren and Bay-breasted Warbler) may confound the detection of eventual responses to treatments within plantations.

Despite obtaining descriptive results with regard to songbirds, we have reason to believe that increasing deadwood through thinning treatments in 22–30 year-old plantations could influence their use over time by bird species dependent on deadwood. Indeed, in the same study site, we compared bird assemblages of commercially mature (40-50 year-old) CT treatment blocks (n = 60) with various amounts of deadwood, with bird assemblages of naturally-regenerated, mature conifer stands (n = 42), and found that stand structure and snag density were important predictors of species assemblage (MacKay *et al.* 2014). Therefore, benefits of CT treatments that increase deadwood in plantations for songbirds may only become apparent as stands mature.

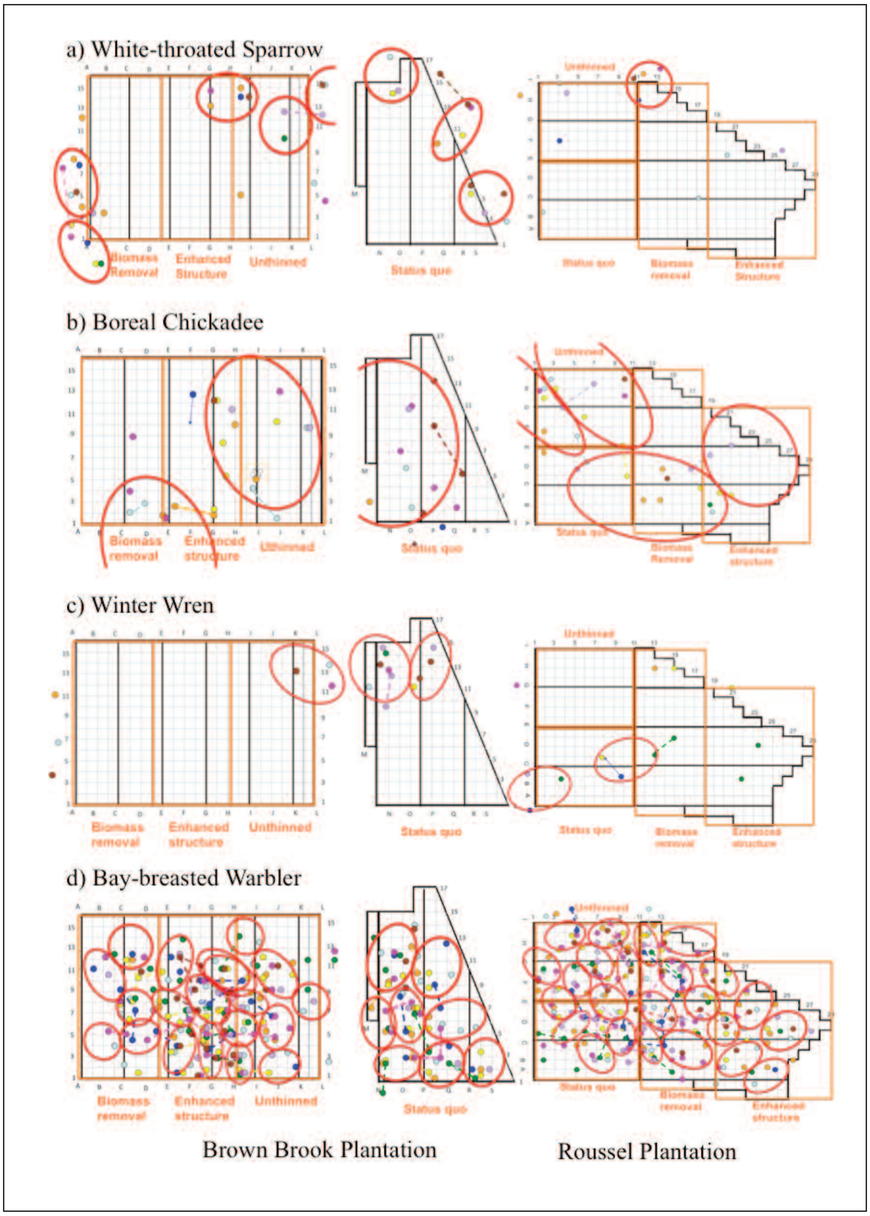

Fig. 6. Detections of White-throated Sparrow, Boreal Chickadee, Winter Wren, and Bay-breasted Warbler (coloured dots, with colours representing eight survey dates from May-June 2011), and estimated territories (red ellipses) in two 25 year old spruce plantations. Treatment blocks that are not separated by roads are delineated by orange rectangles.

Conclusions

Our original predicted magnitude of response (high, medium, low; increase or decrease) and speed of response (fast, moderate, slow) are summarized along with the three-year study results by treatment in Table 4. Overall results by taxa were as follows:

1. Tree growth: Three years after CT, tree DBH increment was 20-33% greater in the three CT treatments than in the unthinned plots. Mean crown width was lower in unthinned than in CT plots by 0.4-0.6 m per tree. Live crown ratio did not differ between unthinned and CT, indicating that CT increased basal area growth by its effect on crown width.

2. Herbaceous vegetation: Composition in unthinned plots changed little between years and remained the most compositionally similar to the older reference stands. The biomass removal CT treatment showed both the greatest magnitude of change and the least similarity to reference and unthinned stands. For herbaceous plants, the conservation merits of all thinning treatments require more time to assess, but in the short-term, biomass removal appears to be detrimental.

3. Beetles: CT promoted occurrence of beetles across different guilds during the first three summers following thinning. Our results support the general hypothesis that changes in woody debris and canopy openness associated with CT of plantations increase beetle abundance across all feeding guilds. Beetle abundance in CT plantations was comparable to that of older naturally regenerated forests in the same area and was considerably higher than in unthinned plantations. Hypotheses that specifically considered each feeding guild were poorly supported because beetle response to the treatments was strong and similar across guilds.

4. Small mammals: Short-tailed shrews and deer mice were not affected by either surrounding landscape or CT. Woodland jumping mice were not affected by landscape but averaged 5-6 fold less in CT than unthinned. Red-backed voles were affected by both landscape and treatment, being more abundant in *status quo* CT with debris retained than in unthinned or biomass removal CT and less dense in plantation dominated than in either hardwood or mixed landscapes. Recommendations include: (*i*) maintain some plantations > 25 years-old in a non-CT state for woodland jumping mice; (*ii*) leave unharvested retention patches to benefit voles; and, (*iii*) diversify large planted areas through multiple age class, retention, and regeneration strategies.

5. Songbirds: There was little evidence for a response to CT by eight focal bird species. However, the experimental design was not optimal for testing treatment effects on forest birds because the treatment block area (~5 ha) was small relative to territory size for many bird species, including those most likely to respond negatively to intensive plantation silviculture. Surveys were conducted too soon after tree girdling in the enhanced structure CT plots because girdled trees had not yet decayed sufficiently to be excavated.

Table 4. Predicted magnitude and speed of response of beetle, plant, small mammal, and bird taxa to three commercial thinning (CT) treatments, relative to the unthinned: status quo thinning, biomass removal thinning, and enhanced structure (unthinned clumps and girdled trees). 'Predict' columns are original predicted response, and 'Results' columns include observed year 3 results. Arrows indicate direction of response (increase or decrease); numbers refer to the three CT treatments.

	1. Unthinned	2. Status quo CT		3. Biomass removal CT		4. Enhanced structure CT	
Taxa		**Predict**	**Results**	**Predict**	**Results**	**Predict**	**Results**
Magnitude of response							
Beetles							
Plant feeder beetles	–	High↑	High↑	> 2	= 2	= 2	= 2
Inner bark beetles	–	High↑	High↑	< 2	= 2	> 2	= 2
Outer bark beetles	–	High↑	High↑	< 2	= 2	> 2	= 2
Predatory beetles	–	High↑	High↑	= 2	= 2	≥ 2	= 2
Plants							
Vascular (cover)	–	High↑	Mod.↑	High↑	High↑	High↑	Mod.↑
Vascular (richness)	–	Mod.↑	Low↑	Low↑	Low↑	Mod.↑	Low↑
Small mammals							
Red Back Voles	–	High↑	High↑	Low↓	High↓	Unknown	No effect
Deer Mice	–	High↑	Low	Low↓	Low	Unknown	No effect
Jumping Mice	–	High↑	High	Low↓	High↓	Unknown	No effect
Birds	–	Mod.↑	No effect	Low↓	No effect	High↑	No effect
Speed of response							
Beetles							
Plant feeder beetles	–	Fast	Fast	Fast	Fast	–	–
Inner bark beetles	–	Fast	Fast	Fast	Fast	Fast	–
Outer bark beetles	–	Moderate	Fast	Moderate	Fast	Moderate	–
Predatory beetles	–	Moderate	Moderate	Moderate	Moderate	–	–
Plants							
Vascular	–	Moderate	Moderate	Fast	Fast	Slow	Moderate
Small mammals							
Red Back Voles	–	Fast	Fast	Moderate	Fast	Slow	Absent
Deer Mice	–	Fast	Unknown	Moderate	Unknown	Slow	Absent
Jumping Mice	–	Fast	Fast	Moderate	Fast	Slow	Absent
Birds	–	Slow	Slow	Slow	Slow	Moderate	Slow

Overall, results showed that crown width and tree growth responded positively to CT; herbaceous vegetation was affected little by *status quo* CT but was negatively affected by the experimental biomass removal CT; beetles responded positively to CT; small mammal species responded both positively (red-backed voles) and negatively (woodland jumping mice) to CT, but large landscape areas of plantations had negative effects; and the effects of CT on songbirds were unclear and requires larger treated blocks, but deadwood-requiring species require forest patches with high densities of dead wood at the landscape scale. These early results demonstrate the complexity of assessing biodiversity within ecosystems, even within a limited range of sites and treatments. Results from the initial three years after treatment of the experimental study sites really set the study up to permit a long-term legacy of responses of taxa over stand development.

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