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Influence of harvesting on understory vegetation along a boreal riparian-upland gradient

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ABSTRACT

Management of riparian forests, and how they respond to disturbance, continues to be a focus of interest in the literature. Earlier studies on riparian plant community assembly following harvesting in the boreal forest have focused merely on highly contrasting microhabitats within a landscape, for example, stream-bank riparian habitat or upland habitat. Sustaining biodiversity and evaluating the success of riparian management requires an understanding of plant community assembly following overstory harvesting across the landscapes, e.g., along the entire riparian-upland gradient, and how they recover over time. Using pre- and post-harvest data, we quantified how riparian harvesting along a disturbance gradient affects understory plant species diversity, abundance, turnover, and composition. We also asked how these disturbance–response relationships vary from stream edge to uplands. We expect changes in the plant community will be greater and recovery to be slower with increased disturbance severity. Based on the ecology of riparian versus upland, we also expect harvesting to exert a stronger control with increasing distance from the stream channel through the colonization of early successional species and extirpation of extant species. We found that disturbance severity (i.e., from cut-to-shore) from harvesting exerted strong controls on the dynamics of understory vegetation in boreal riparian forests, which was still evident seven years after the disturbance event. However, the dynamic responses strongly differed with the distance from the stream channel. Specifically, streamside communities harvested with or without a 30 m riparian buffer, were maintained to a condition similar to uncut forests. However, upland communities were less resistant to overstory harvest and subsequently colonized by early successional species present in pre-harvest riparian plots. Furthermore, vascular and non-vascular plants exhibited contrasting responses in their richness, abundance, turnover, and composition. Our results indicate that streamside understory vegetation is inherently more resistant to stand-replacing disturbance than upland assemblages.

1. Introduction

Managing ecological services provided by riparian ecosystems continue to be a focus of interest and debate. Inclusion of riparian buffers in forest management plans is a standard practice across North America, albeit with variations among provinces, states, and agencies. Although riparian buffers were devised initially to protect aquatic organisms and habitat, they have more recently been included as an element in terrestrial conservation initiatives. The application of riparian buffers have created artificial, linear patterns of mature forests along lakes, rivers and streams (Buttle, 2002; Kreutzweiser et al., 2012; Sibley et al., 2012), which has led to concerns about the lack of heterogeneity across the landscape and its effect on biodiversity. This concept has stimulated research into the use of disturbance (e.g., harvesting) in riparian habitats as a management tool (Sibley et al., 2012; Zenner et al., 2012). Earlier studies on riparian plant community assembly following harvesting in the boreal forest (e.g., Lamb et al., 2003; Biswas and Mallik, 2010; Braithwaite and Mallik, 2011) have focused merely on highly contrasting microhabitats within a landscape, for example, stream-bank riparian habitat or upland habitat. If a goal of riparian management is to sustain biodiversity, then understanding responses of understory plant community to overstory harvesting across the landscapes, e.g., along the entire riparian-upland gradient, is paramount to evaluating the long-term success of riparian management with respect to conservation.

Hydrological disturbance events (i.e., erosion of the soil surface and abrasion by suspended sediment and debris) and the ability of fluvial systems to act as conduits for the dispersal of propagules, structure streamside communities in space and time (Naiman

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and Décamps, 1997). Laterally, frequency and severity of flood disturbance typically decline with increased distance from the active channel, paralleled by an increase in ground-water depth. Along the same gradient, understory light availability generally decreases as tree density increases (Nierenberg and Hibbs, 2000; Lamb and Mallik, 2003; Palik et al., 2003). In sum, the overall effect of disturbance, resource quantity and quality of streamside habitats—which generally shape the structure and functioning of understory plant communities—may not be uniform across the stream-bank riparian – upland gradient. Thus, it is very likely that understory plant communities in stream-bank riparian forests may not respond to logging in the same manner as those in upland forests.

Overstory harvesting and associated ground disturbance alters understory plant communities directly through increasing mortality of individuals, propagules sources, local populations or groups of species, or indirectly by varying microclimatic conditions, habitat heterogeneity, and resource availability (Halpern and Spies, 1995; Roberts and Gilliam, 1995; Bergeron and Harvey, 1997; Scheller and Mladenoff, 2002). Both direct and indirect processes result in directional shifts in the plant community affecting both species diversity and composition. As a reflection of increased resource quantity, vascular species diversity often increases following canopy removal, whereas intolerant non-vascular species decrease (e.g., Halpern, 1988; Reich et al., 2001; Hart and Chen, 2008). In the boreal forest, understory streamside communities are usually highly productive and comprised of a variety of species and functional groups, including generalist plant species, specialized species adapted to streamside habitats (riparian obligates), and early successional species occurring in productive habitats at the trade-off of being less competitive in resource stressed environments (Lamb et al., 2003; Dynesius et al., 2009; Biswas and Mallik, 2010). In contrast, boreal upland understory communities are primarily driven by light availability and thus dominated by shade tolerant species that are unable to compete in early successional environments, such as ericaceous shrubs (e.g., *Rhododendron groenlandicum*, *Vitis* spp., and *Gaultheria hispidula*) and feathermoss (e.g., *Pleurozium schreberi*, *Hylocomnium splendens*, and *Ptilium crisa-castrensis*) (Nilsson and Wardle, 2005; Hart and Chen, 2008). Since vascular and non-vascular richness and cover is expected to increase and decrease, respectively, we predict that changes in the understory community will be more marked with increasing distance from the stream channel.

Community assembly following disturbance occurs within a temporal scale, and is a reflection of biotic (e.g., regional species pool) and abiotic (nutrient availability) processes. As such, time since disturbance is a critical factor when evaluating the effects of forest management on biodiversity and community composition (Roberts and Gilliam, 1995). A few studies have reported on the early impacts on understory vegetation to harvesting disturbance following partial harvesting (i.e., gap creation) (Zenner et al., 2012; Mallik et al., 2013), and adjacent clear-cutting (i.e., buffer strips) (Lamb et al., 2003; Biswas and Mallik, 2010). Yet, to our knowledge, there are no studies that have followed riparian plant communities through a disturbance event, although the need for these data is recognized (Mallik et al., 2013). Based on shifts in the life-history strategies of the extant plant community along the stream bank riparian-upland gradient, we expect recovery to be slower with increasing distance from the stream channel as changes in more upland communities are more likely to be sustained through the colonization of early successional species and extirpation of extant species.

Through a controlled field experiment using pre- and post-harvest data, we quantify how harvesting treatments (i.e., cut-to-shore, riparian buffers and uncut) affect understory species diversity, composition, and turnover over seven years. We also test if the treatment effects shift with distance from the stream channel (i.e., along a stream edge to upland gradient).

2. Materials and methods

2.1. Study area

The study is located in the Lower Foothills sub-region of the Boreal Plain, approximately 20 km northwest of Whitecourt, Alberta. The climate is sub-humid with a mean annual precipitation of 577 mm recorded at a weather station at Whitecourt (elevation 782 m) (Environment Canada, 2010). Rolling topography is a common feature of the study area. Soils originated from moderately fine to fine-textured till or glaciolacustrine parent material. The characteristic canopy is dominated by lodgepole pine (*Pinus contorta*Dougl. ex Loud. var. latifolia Engelm), white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx) and balsam poplar (*Populus balsamifera* L.) in well-drained sites, and black spruce (*Picea mariana* (Mill.) BSP) and tamarack (*Larixlaricina (DuRoi*) K. Koch) in poorly drained sites.

2.2. Experimental design and data collection

Headwater stream sites, ranging in 0.5–1 m in width, were randomly selected in the study region to receive the following treatments listed in order of increasing disturbance severity; uncut (reference), riparian buffer, and cut-to-shore, each with four replicates, for a total of 12 sites. All selected sites originated from stand replacing fire in 1940. Uncut sites were undisturbed (i.e., no forestry activity in the adjacent upland). Buffer sites were clearcut with a 30 m wide un-harvested forest strip adjacent to the stream channel. Cut-to-shore sites were clearcut to the edge of the stream channel. Tree-length harvesting, i.e., trees were felled, topped, and delimbed at the stump before being dragged to roadside, was conducted during January to March 2004.

At each site, three randomly located, 30-m long transects were established running perpendicular from the stream to the upland. Along each transect, two 1-m^2 understory vegetation plots were randomly located within each of the following distance ranges from the stream bank: 0–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m and 25–30 m, for a total of 12 plots per transect and 36 plots per site. Percent cover (0–100%) of each vascular and non-vascular plant species in each plot was estimated by eye (Mueller-Dombois and Ellenberg, 1974). All plants were identified to species with an exception of a few that were identified to genus, since it was not feasible to identify them to species in the field without flowers or fruits (e.g., *Carex* spp., *Salix* spp. and *Viola* spp.). Vegetation sampling was conducted during the periods of peak vegetation cover in the summer (July through August) prior to treatment, i.e., Yr 0 (2003) and the summers of Yrs 1 (2004), 5 (2008) and 7 (2010) after treatment. Within each site, species cover data of the 6 plots at each distance range were averaged to derive a mean.

2.3. Statistical analyses

2.3.1. Species richness, abundance and turnover

Species richness (*S*) was used as a measurement of diversity, which is the total number of species in each sample plot. Species richness is related to sampling area (Rosenzweig, 1995). We used a species accumulation curve (SAC) to assess adequacy of sampling efforts and to compare richness among treatments. The mean SAC and its standard deviation are computed from random permutations of the data (Gotelli and Colwell, 2001). SAC was carried out using specaccum function in the vegan package (Oksanen et al., 2013) using R version 3.0.1 (R core team, 2013). Abundance was

quantified through a summation of total species percent cover in each sample plot. To quantify species dynamics among multiple measurements, a species turnover rate index (T) for each sampling plot that includes both colonization and local extirpation from two successive measurements was calculated as Bakker et al. (2003):

$$T = 1 - (\text{number of species present at both } t \text{ and } t + 1)/[(S_t + S_{t+1})/2] \quad (1)$$

where S_t and S_{t+1} are species richness at time t (Yr 0) and $t + 1$ (Yrs 1, 5 and 7), respectively. T can range from 0 to 1, indicative of no species turnover to a complete change in community composition, between two successive measurements.

To test the effects of harvesting and distance from stream on total, vascular and non-vascular species richness, abundance and turnover, we used the following repeated measures general linear models (rGLM):

$$Y_{ijklm} = \mu + H_i + D_j + H \times D_{ij} + \varepsilon_{(ij)k} + T_l + H \times T_{il} + D \times T_{jl} + H \times D \times T_{ijl} + \varepsilon_{(ijl)m} \quad (2)$$

where Y_{ijklm} is species richness, total abundance or turnover; μ is the overall mean; H_i (i = 1–3) is the effect of harvesting, D_j is the continuous factor, distance from stream; $\varepsilon_{(ij)k}$ is the error term associated with between-subjects; T_l is the effect of the sampling year; $\varepsilon_{(ijkl)m}$ is the error term associated with within-subjects. For each rGLM, in addition to testing data normality and homogeneity of variances, we assessed the sphericity (i.e., symmetry of the covariance matrix) with Mauchly's criterion test and applied the Huynh-Feldt correction to the results if the assumption was violated at P = 0.05 (Huynh and Feldt, 1976). The effect size (η^2) was calculated to estimate the proportion of the total variance attributed to an effect (Tabachnick and Fidell, 1989).

2.3.2. Species composition

Trends in successional pathways of understory vegetation, following the harvesting treatments, were evaluated using non-metric multidimensional scaling (NMS) ordination with Sørenson's distance measure. NMS was carried out using PC-ORD version 5 (McCune and Grace, 2002; McCune and Mefford, 2005) set to the slow and thorough auto-pilot mode to select the optimal solution (i.e., dimensionality). NMS is suited for community data because it uses non-metric rank ordering to perceptually map data and avoids assumptions of the underlying structure of the data (i.e., normality and homogeneity of variance) made by traditional ordination techniques (McCune and Grace, 2002).The criterion for success is the measure of "stress", which is an inverse measure of fit to the data (McCune and Grace, 2002), a lower stress value represents a better fit. An acceptable stress value for community ecology data is generally between 10 and 20 (Clarke, 1993). Data were first relativized by species maximum, to lessen, but not to eliminate the influence of dominant species on the patterns and trends identified by NMS ordination. This procedure reduces the skew and overall coefficient of variation of the data, and lessens sampling error in ocular estimations (McCune and Grace, 2002). All plant species were used in the ordination analysis, with the exception of species occurring in <5% of sampling units (McCune and Grace, 2002). Successional vectors were created to connect sites through time.

Multiple Response Permutation Procedure (MRPP) with Sørenson's distance measure (Bray and Curtis, 1957) was used to test for differences in species composition among treatments and distance ranges. Pairwise comparison was used to assess differences among harvesting treatments. Separate MRPPs were ran for Yrs 1, 0, 5 and 7 to examine if compositional differences among treatments were detected at each sampling period. MRPP is a non-parametric analog to discriminant function analysis and is thus not limited by assumptions of normally-distributed data or homogenous variances (Mielke and Berry, 2001; McCune and Grace, 2002). The procedure produces a P value as well as an agreement statistic (A) value. The latter describes within-group homogeneity compared to random expectation and has a range of −1 to 1. If all samples in a group are identical, A = 1. When agreement within group equals expectation by chance, A = 0. If there is more within-group heterogeneity than expected by chance, then A < 0 (McCune and Grace, 2002).

Finally, indicator species analysis (ISA) with an extension that allows for the combination of site groups (De Caceres and Legendre, 2009; De Caceres et al., 2010) was used to assess habitat associations (i.e., distance from the stream channel and harvesting treatment) of understory species and how these associations vary with time. We chose this extension method rather than the original ISA procedure because the latter fails at detecting species related to conditions prevailing in two or more *a priori* groups of sites and it is likely that species' habitat requirements are met in more than one group or treatment. Where the original ISA method looked for the group that the species was maximally associated, the extension method retains the combination of groups showing the strongest association with the target species (De Caceres and Legendre, 2009; De Caceres et al., 2010). The point-biserial correlation coefficient (r_{pb}) association index was chosen, which is the Pearson correlation between species abundance data (quantitative variable) and site membership to a site-group combination (binary variable) (see De Caceres and Legendre, 2009 for details). Statistical significance of the association was evaluated with a permutation test of 1000 iterations. We grouped sites by riparian (0–10 m), transition (10–20 m) and upland (20–30 m) communities and harvesting treatment (uncut, buffer, cut-to-shore). Species occurring at less than two sites were removed from the analyses to not confuse statistical artifact with a meaningful biological response. MRPP and ISA were run with R version 3.0.1 (R core team, 2013) with packages vegan 2.0–7 (Oksanen et al., 2013) and indicspecies (De Caceres et al., 2010). For MRPP and ISA, P-values were corrected with the Holm test for multiple comparisons.

3. Results

3.1. Species richness, abundance and turnover

One hundred and five vascular and non-vascular species were identified throughout this study. The responses of species richness of total, vascular and non-vascular understory plants to treatment differed significantly among the distance ranges to stream and with year of measurement (Table 1). Total species richness decreased with distance to stream in Yrs 0, 1, and 5, but this overall trend changed for cut-to-shore treatment in Yr 7 where species richness increased (Fig. 1). Furthermore, total species richness was higher for cut-to-shore treatment than uncut and buffer treatments on transition and upland sites at Yr 7, but not for other years or streamside sample plots (Fig. 1). Vascular species richness tracked similarly to total species richness across the distance ranges and over time (Table 1). In Yr 1, non-vascular species richness decreased in all distance ranges, except for the streamside plots, following both buffer and cut-to-shore treatments. In Yr 5, non-vascular richness was still lower in cut-to-shore treatments relative to Yr 0, but was similar in buffer and uncut treatments at all distance ranges. Finally, non-vascular richness did not differ with treatment in Yr 7. Distance related variables accounted for 57%, 58%, and 35% of the variation in total, vascular and non-vascular species richness (Table 1), respectively. For all treatment classes, species accumulation curves (SAC) relating species richness to number of sampling plots (Fig. 2), demonstrated that community species richness was sufficiently captured within the

Table 1
Repeated measures general linear model relating species richness (m^{-2}) of total, vascular and non-vascular understory vegetation to harvesting treatment and distance from stream over time in Central Alberta, Canada.

Source	*d.f.*	Total			Vascular			Non-vascular		
		F	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2
Between subjects										
Harvest (H_i)	2	0.14	0.87	0.01	0.61	0.55	0.02	2.28	0.11	0.08
Distance (D_j)	5	**2.99**	**0.02**	**0.22**	2.60	**0.04**	**0.19**	0.67	0.65	0.06
Harvest × distance (HD_{ij})	10	0.27	0.99	0.05	0.28	0.98	0.05	0.17	0.99	0.03
Error ($\varepsilon_{k(ij)}$)	54									
Within subjects[a]										
Year (T_l)	3	**21.03**	**<0.001**	**0.28**	18.22	**<0.001**	**0.25**	7.71	**<0.001**	**0.13**
Year × harvest (HT_{il})	6	**8.64**	**<0.001**	**0.24**	7.11	**<0.001**	**0.21**	11.03	**<0.001**	**0.29**
Year × distance (DT_{jl})	15	**1.91**	**0.03**	**0.15**	2.00	**0.04**	**0.16**	1.42	0.14	0.12
Year × harvest × distance (HDT_{ijl})	30		0.13	0.20	1.66	**0.05**	**0.23**	1.08	0.37	0.17
Error ($\varepsilon_{m(ijkl)}$)	162									

[a] Huynh–Feldt epsilon was applied to correct for sphericity. Significant effects are shown in boldface type.

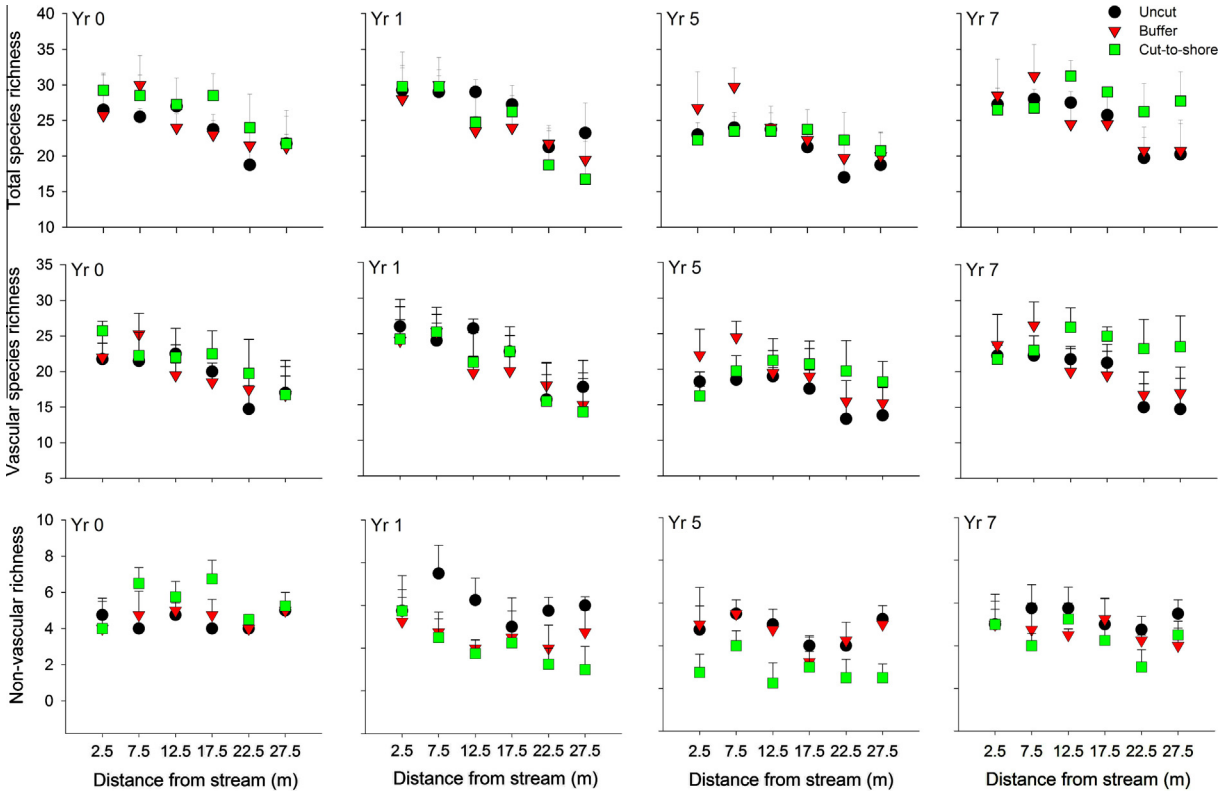

Fig. 1. Mean (+1 Standard Error) species richness (m^{-2}) of total, vascular and non-vascular understory plant species over a seven year sampling period in relation to distance from stream in uncut, buffer, and cut-to-shore boreal watersheds.

experimental design, and are therefore a good estimator for community richness.

Percent cover of total understory vegetation, which accounted for 66% of its variation explained by our rGLM model, strongly differed with sampling year, treatment and distance from stream (Table 2). At all distance ranges, total understory cover strongly decreased at Yr 1 from Yr 0 for both buffer and cut-to-shore treatments, but not for the uncut treatment (Fig. 3). Among treatments, cut-to-shore had the lowest total cover at Yr 1; buffer had the highest total cover at Yr 5, whereas at Yr 7, total cover was higher for cut-to-shore on uplands (Fig. 3). Vascular species percent cover had similar patterns to those of total understory cover except a more pronounced difference among treatments at Yr 5 (Fig. 3). By contrast, non-vascular species cover was generally lower after cut-to-shore treatment; but the difference among treatments was far less in the streamside plots relative to further upland where the changes were more pronounced (Fig. 3).

Total, vascular and non-vascular species turnover was strongly related to harvesting treatments across all distance ranges and sampling years (Table 3). Total species turnover was generally highest in the cut-to-shore sites, whereas species turnover in the uncut and buffer sites was similar at all distance ranges along the riparian-upland gradient (Fig. 4). Vascular species turnover more or less followed the patterns in total species turnover, but the turnover did not differ among treatments in the riparian and transition plots (Fig. 4). Non-vascular species turnover was considerably higher in the cut-to-shore treatment than uncut and buffer, particularly in Yrs 5 and 7.

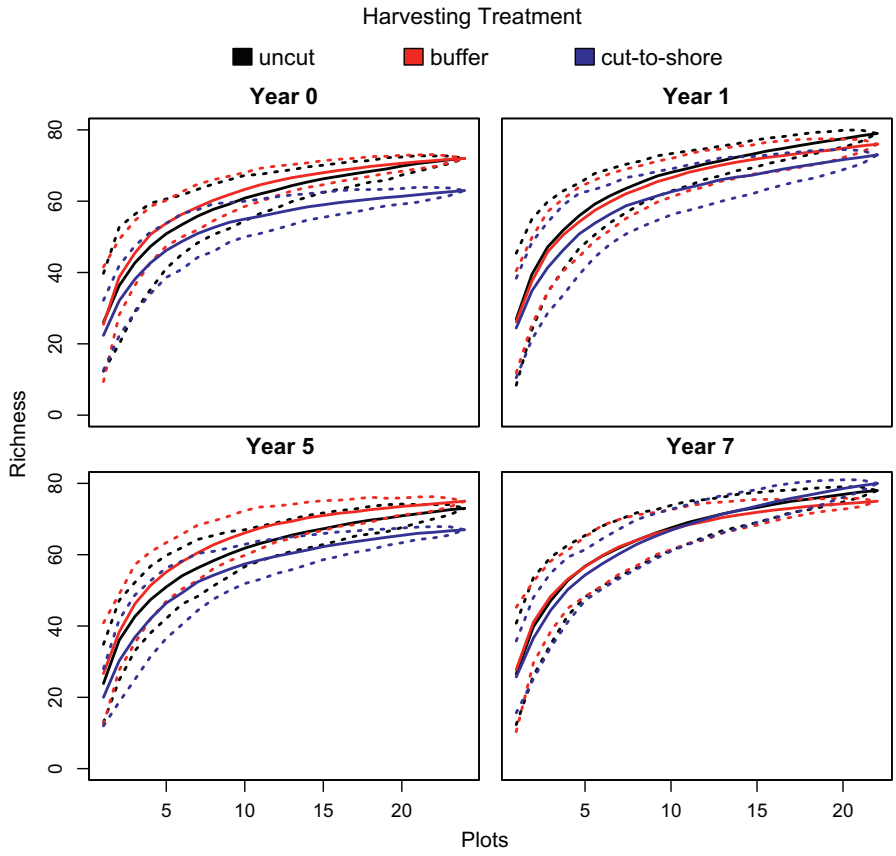

Fig. 2. Species accumulation curves (SAC) relating total species richness to boreal understory sampling plots in uncut, buffer, and cut to shore treatments. The solid line represents the SAC and the dashed line represents one standard deviation.

Table 2
Repeated measures general linear model relating abundance (i.e., percent cover) of total, vascular and non-vascular understory vegetation to riparian harvesting treatment and distance from stream over time in Central Alberta, Canada.

Source	*d.f.*	Total			Vascular			Non-vascular[b]		
		F	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2
Between subjects										
Harvest (H_i)	2	**4.85**	**0.01**	**0.15**	2.56	0.09	0.09	**4.52**	**0.01**	**0.16**
Distance (D_j)	5	1.85	0.12	0.15	**4.99**	**0.001**	**0.32**	1.66	0.16	0.11
Harvest × distance (HD_{ij})	10	0.93	0.52	0.15	0.52	0.87	0.09	0.24	0.99	0.03
Error ($\varepsilon_{k(ij)}$)	54									
Within subjects[a]										
Year (T_l)	3	**103.82**	**<0.001**	**0.66**	**101.60**	**<0.001**	**0.65**	**29.84**	**<0.001**	**0.38**
Year × harvest (HT_{il})	6	**9.63**	**<0.001**	**0.26**	**11.66**	**<0.001**	**0.30**	**7.22**	**<0.001**	**0.27**
Year × distance (DT_{jl})	15	0.90	0.53	0.08	0.88	0.57	0.08	**2.71**	**0.003**	**0.18**
Year × harvest × distance (HDT_{ijl})	30	0.59	0.91	0.10	0.39	0.99	0.07	1.05	0.61	0.14
Error ($\varepsilon_{m(ijkl)}$)	162									

[a] Huynh–Feldt epsilon was applied to correct for sphericity. Significant effects are shown in boldface type.
[b] Variable was square-root transformed.

3.2. Species composition

NMS ordination identified a 3-dimensional solution with a final stress of 8.45. Although only one ordination was performed, sites were separated by treatment to aid interpretation (Fig. 5). Axes 1, 2, and 3 corresponds to 39%, 39%, and 17% of understory floristic variation, respectively (Fig. 4). Axis 1 represented a gradient of common boreal riparian species (e.g., the leafy mosses *Plagiomnium cuspidatum* and *Climacium dendroides*) to common upland species (e.g., the ericaceous shrubs *Vaccinium myrtilloides* and *Rhododendron groenlandicum,* and the feather mosses *Ptilium crista-castrensis* and *Pleurozium schreberi*). Axis 2 represented a gradient of shade-tolerant feather mosses (*P. crista-castrensis*, *P. schreberi*, and *Hylocomnium splendens*) to shade-intolerant vascular species (e.g., *Calamagrostis canadensis* and *Salix* spp.). Axis 3 was positively correlated to tall shrubs (e.g., *Alnus rugosa* and *Vibernum edule*). Study sites lined up along Axis 1 according to distance from stream, but compositionally shifted over time depending on harvesting treatment. Uncut sites remained relatively stable in each sampling year, particularly in the 20–30 m from shore range (Fig. 5a). The buffer treatment underwent moderate changes with the upland shifting towards a riparian community (Fig. 5b). Upland sites in the cut-to-shore treatment experienced the most drastic changes in position in the ordination space relative to Yr 0, through

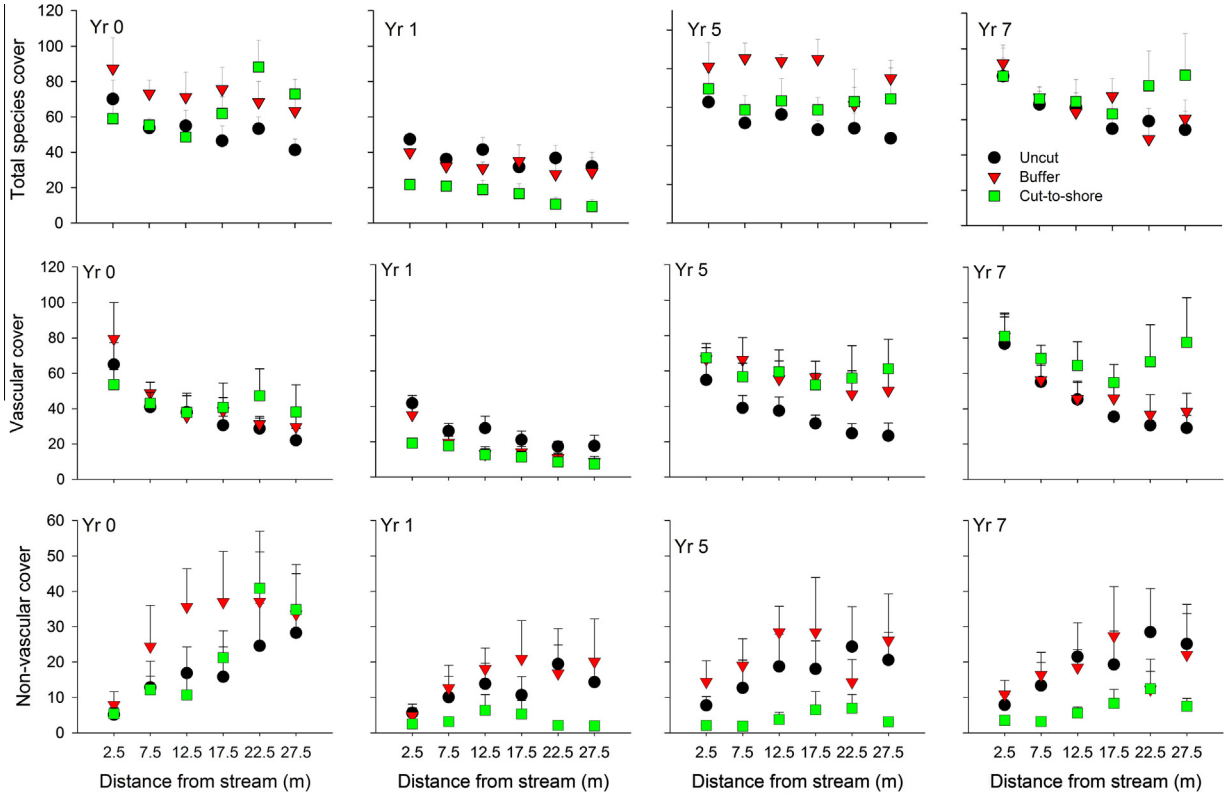

Fig. 3. Mean (+1 Standard Error) abundance (i.e., percent cover) of total, vascular and non-vascular understory plant species over a seven year sampling period in relation to distance from stream in uncut, buffer, and cut-to-shore boreal watersheds.

Table 3
Repeated measures general linear model relating species turnover (i.e., colonization and extirpation) of total, vascular and non-vascular understory vegetation to riparian harvesting treatment and distance from stream over time in Central Alberta, Canada.

Source	*d.f.*	Total			Vascular			Non-vascular[b]		
		F	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2
Between subjects										
Harvest (H_i)	2	**15.84**	**<0.001**	**0.37**	**8.96**	**<0.001**	**0.25**	**21.29**	**<0.001**	**0.44**
Distance (D_j)	5	1.67	0.16	0.13	1.89	0.11	0.15	0.77	0.58	0.07
Harvest × distance (HD_{ij})	10	0.90	0.54	0.14	1.43	0.19	0.21	0.34	0.97	0.06
Error ($\varepsilon_{k(ij)}$)	54									
Within subjects[a]										
Year (T_l)	3	**69.61**	**<0.001**	**0.56**	**32.49**	**<0.001**	**0.38**	**10.17**	**<0.001**	**0.16**
Year × harvest (HT_{il})	6	**8.54**	**<0.001**	**0.24**	**4.58**	**0.002**	**0.15**	**4.81**	0.001	0.15
Year × distance (DT_{jl})	15	1.02	0.43	0.09	0.45	0.88	0.04	1.58	0.12	0.13
Year × harvest × distance (HDT_{ijl})	30	1.55	0.09	0.22	0.97	0.51	0.15	1.00	0.47	0.16
Error ($\varepsilon_{m(ijkl)}$)	162									

[a] Huynh–Feldt epsilon was applied to correct for sphericity. Significant effects are shown in boldface type.
[b] Variables were ln-transformed.

an increase in typical riparian species such as grasses, forbs and willows, and decrease in feathermoss (Fig. 5c).

As expected, compositional differences among harvesting treatments were not detected using MRPP for Yr 0 at any of the distance ranges (Table 4). At streamside (0–5 m), composition only differed between uncut and cut-to-shore treatment at Yr 1, but it became similar for all treatments at Yrs 5 and 7. At the distance range of 5–10 m, composition was similar among all treatments during each sampling period. Composition consistently differed between uncut and cut-to-shore treatments at Yrs 1, 5, and 7 for uplands (20–25 m and 25–30 m), whereas this difference was only observed at Yrs 5 and 7 for the transitional zone (10–20 m).

Forty-six indicator species (IS) were identified as having an affinity for one or more habitat group in at least one sampling year (See Supplementary data Table S.1). Twenty-two IS were identified in Yr 0, of which two-thirds were associated with riparian (0–10 m) habitat. Many of these riparian species (i.e., *Calamagrostis canadensis*, *Equisetum* spp., *Galium triflorum*, *Lonicera involucrata*, *Mitella nuda*, *Plagiomnium* spp, and *Rubus pubescens*) had fidelity for the riparian habitat regardless of the sampling year or treatment. However, all IS associated with upland (20–30 m) communities in Yr 0 (i.e., *Cornus canadensis*, *Lathyrus ochroleucus*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Vaccinium vitis-ideae*) were no longer associated with the cut-to-shore treatment in Yrs 1, 5

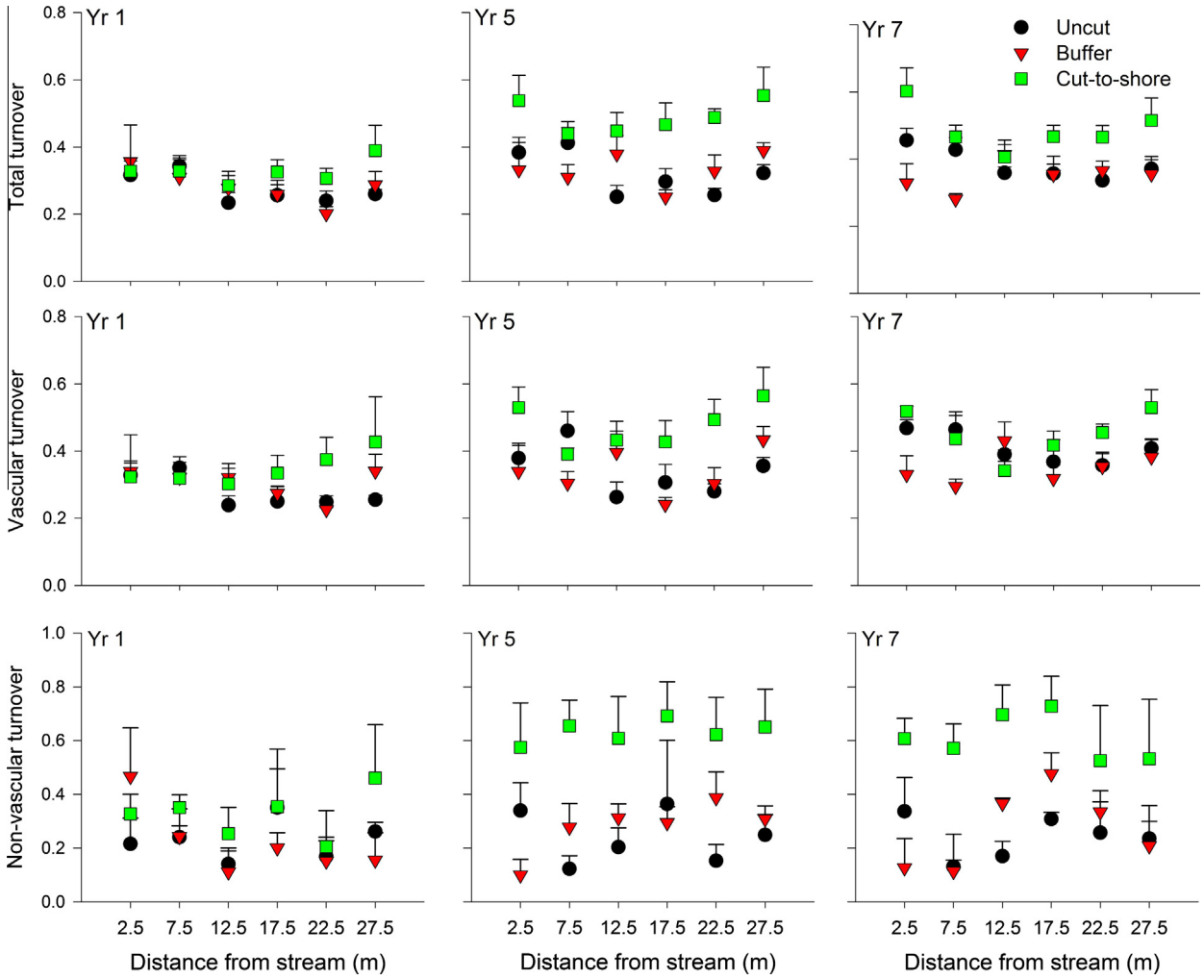

Fig. 4. Mean (+1 Standard Error) species turnover of total, vascular and non-vascular understory plant species over a seven year sampling period in relation to distance from stream in uncut, buffer, and cut-to-shore boreal watersheds.

or 7. Similar to Yr 0, most of the Yr 1 IS were associated with riparian habitat; however, none of the 31 indicator species identified in Yr 1 were associated with the upland community in the cut-to-shore treatment. The trends in Yrs 5 and 7 were similar. Species associations increased in the transition and upland communities in Yrs 5 and 7, relative to Yrs 0 and 1. As expected, most of these IS (e.g., *Epilobium angustifolium*, *Salix* spp., and *Polytrichium juniper*) have ruderal characteristics, such as highly dispersive propagules. Moreover, many of the transition and upland IS post-harvest were present in the streamside communities prior to disturbance (e.g., *Carex* spp. and *Mertansia paniculata*).

4. Discussion

Disturbance severity from cut-to-shore harvesting exerted strong controls on the dynamics of understory vegetation in boreal riparian forests, which was still evident seven years after the disturbance event. However, the dynamic responses strongly differed with the distance from the stream channel. Furthermore, vascular and non-vascular plants exhibited contrasting responses in their richness, abundance, turnover, and composition.

After an initial decrease, vascular species richness and abundance of understory vegetation was highest in the cut-to-shores sites, relative to the less disturbed treatments (i.e., buffer and uncut), but only in the transition and upland sites (10–30 m). Changes in vascular diversity in streamside plant communities was not detectable following cut-to-shore harvesting. It is generally accepted that resource availability is higher in riparian than upland forests and there is some evidence that vascular species growing in sites with higher resource availability are more resistant to disturbance (Hamilton and Haeussler, 2008; Slocum and Mendelssohn, 2008). However, we attribute the diverging disturbance-diversity relationships, to differing processes driving the communities from streamside to upland. In upland forests, the canopy exerts strong controls on the understory community composition, predominantly by limiting resource quantity (Hart and Chen, 2008). However, there is a lack of evidence for as strong a coupling of the canopy and understory in streamside communities relative to upland plant assemblages (Lyon and Sagers, 1998; Decocq, 2002), suggesting that hydrology, rather than the canopy drives understory riparian communities, and thus may be able to better cope with stand-replacing disturbances as long as hydrological processes are not significantly altered.

Specific microclimatic conditions are vital for growth and reproduction of non-vascular species (Rydgren et al., 2006). For the dominant boreal upland bryophytes (i.e., *Pleurozium schreberi, Hylocomnium splendens* and *Ptilium crista-castrensis*), the altered environment following stand-replacing disturbance, such as increased soil temperatures and decreased soil moisture, exceeds

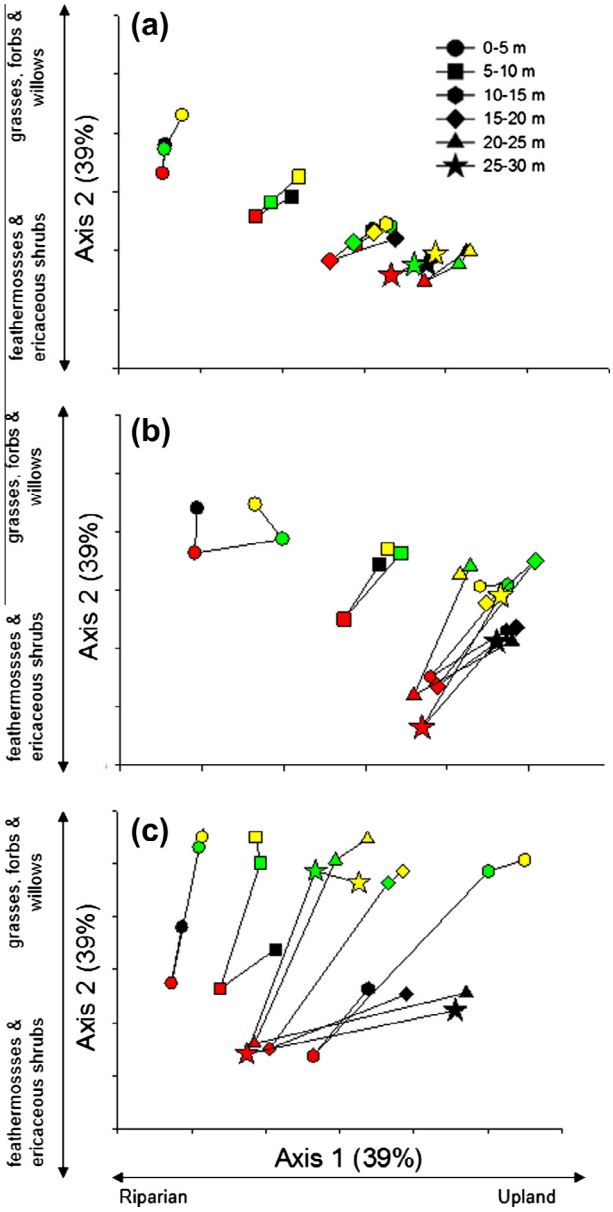

Fig. 5. NMS ordination of average site data from (a) uncut, (b) buffer, and (c) cut-to-shore sites over time in species space. Successional vectors connect Yr 0 (black), Yr 1 (white), Yr 5 (red), and Yr 7 (green). Axes 1, 2, and 3 account for 39%, 39%, and 17% of the understory variability, respective.

their tolerance, resulting in a decrease in their cover (Fenton and Frego, 2005; Hylander, 2005; Åström et al., 2007). In the present study, richness and abundance of non-vascular species did decrease following cut-to-shore treatment. Similar to studies from the Swedish boreal forest (Dynesius and Hylander, 2007; Dynesius et al., 2009), this response was much less pronounced in the streamside communities. We speculate that high moisture availability and shading from tall shrubs associated with riparian habitat (see Supplementary Data Table S1) buffers the effect of harvesting on bryophytes in streamside plots, and thus their response to harvesting isn't as marked as it is in the uplands.

Species turnover was consistently higher in the cut-to-shore treatment than both buffer and uncut plots, and the disturbance effect on turnover was greater in non-vascular than vascular species. Although shifts in richness and abundance following cut-to-shore treatment were greater in the upland than the streamside plots, we found that neither vascular nor non-vascular species turnover was mediated by distance from the stream channel. Immigration processes in streamside communities are enhanced because of hydrochory (i.e., flow facilitated propagules distribution) and better conditions for establishment, such as abundance of bare substrate (Planty-Tabacchi et al., 1996; Brown and Peet, 2003; Dynesius et al., 2009). However, lateral colonization from streamside into the upland, following disturbance, is also highly probable as species associated with upland habitat are able to tolerate low resource levels (i.e., light) at the trade-off of being less competitive in more productive habitats (Tilman, 1985). Our study indicated that numerous understory species previously restricted to the riparian sample plots, were able to colonize the transition and upland plots following canopy removal. For example, sedges (*Carex* spp.) were only associated with riparian habitat in Yr 0, but seven years after cut-to-shore they were associated with all distance ranges. Moreover, the ordination showed that the upland plots moved towards a more riparian community in species space.

Clear patterns emerged in understory species composition along the riparian ecotone and over time. After five years following the disturbance event, and still evident in Yr 7, cut-to-shore plots in the 10 to 30 m from stream diverged from a feathermoss and ericaceous shrub dominated community to one characterized by grasses, forbs and tall shrubs. However, all three treatments (uncut, buffer and cut-to-shore) had similar understory vegetation communities in the streamside plots (0–10 m from stream). Many of the species that increased in abundance in the cut-to-shore treatment were present before harvesting in the streamside plots. For example, *Calamagrostis canadensis*, is a widely distributed perennial rhizomatous grass common in Canadian boreal riparian forests (Lamb and Mallik, 2003), which may impede the colonization of invading species. Through both seed dispersal and clonal expansion, *C. canadensis* rapidly expands following timber harvesting (Lieffers et al., 1993). Most indicator species of the cut-to-shore riparian habitat in Yr 0 were still positively associated with the same habitat over time, whereas no species associated with cut-to-shore upland habitat in Yr 0, were associated with that habitat after harvesting. The alteration on the environment following timber harvesting disturbance had greater consequences on the growth and mortality of species associated with the upland plots relative to those growing streamside. These results were similar to a study comparing bryophyte communities before and after clearcutting in riparian and upland communities (Dynesius et al., 2009). However, there are no studies, in any forest system, comparing the entire understory community before and after complete canopy removal along a riparian ecotone.

Despite the difference in community composition in uncut and cut-to-shore plots, they were both similar to buffer plots in the 15–30 m range; indicating that these buffer plots contained both early and late seral species that characterize the cut-to-shore and uncut plots, respectively. Our results were comparable to a study in the central portion of the Canadian boreal forest that reported an increase in early seral vascular species into 15 m of the riparian buffer (Braithwaite and Mallik, 2011). These edge effects (i.e., detectable changes in the community reflective of abiotic and biotic processes at forest edges) from the adjacent clearcut may be related to microclimatic (i.e., canopy gap size, light transmittance, vapor pressure deficit, air temperature and soil temperature) changes within the buffer (Chen et al., 1995; Brosofske et al., 1997; Dong et al., 1998; Dignan and Bren, 2003); which have been reported to have negative effects on boreal upland bryophytes (Stewart and Mallik, 2006; Braithwaite and Mallik, 2011), facilitating colonization of vascular species.

A fundamental difficulty with field studies is untangling confounding effects caused by abiotic factors (Lawton et al., 1998; Gilliam and Roberts, 2003). The study area suffered from a severe drought from 2002 to 2003 (Government of Alberta), which was

Table 4
MRPP comparing understory composition among harvesting treatment over time. The value of the Agreement within group (*A*) and the significance of the association (*P*-value) after Holm correction are presented. Significant effects are shown in boldface type.

Site classification	Yr 0		Yr 1		Yr 5		Yr 7	
	A	*P*	*A*	*P*	*A*	*P*	*A*	*P*
0–5 m								
Uncut vs. Buffer	−0.03	0.70	−0.01	0.60	0.01	0.32	0.00	0.38
Buffer vs. Cut-to-shore	−0.03	0.85	−0.01	0.58	0.02	0.23	0.03	0.10
Uncut vs. Cut-to-shore	0.01	0.36	**0.05**	**<0.01**	0.05	0.08	0.03	0.16
5–10 m								
Uncut vs. Buffer	−0.03	0.75	0.01	0.32	−0.01	0.63	0.00	0.37
Buffer vs. Cut-to-shore	−0.02	0.63	−0.01	0.60	0.02	0.19	0.07	0.09
Uncut vs. Cut-to-shore	−0.04	0.84	0.03	0.08	0.01	0.25	0.08	0.11
10–15 m								
Uncut vs. Buffer	0.01	0.32	0.00	0.45	0.01	0.37	−0.01	0.54
Buffer vs. Cut-to-shore	0.01	0.32	−0.03	0.70	**0.04**	**0.05**	**0.05**	**0.03**
Uncut vs. Cut-to-shore	−0.04	0.84	0.01	0.32	**0.08**	**0.02**	**0.05**	**0.04**
15–20 m								
Uncut vs. Buffer	0.00	0.49	0.00	0.41	0.06	0.07	−0.02	0.73
Buffer vs. Cut-to-shore	−0.04	0.90	0.02	0.25	0.01	0.30	0.02	0.23
Uncut vs. Cut-to-shore	−0.04	0.86	0.01	0.32	**0.07**	**0.02**	**0.06**	**0.01**
20–25 m								
Uncut vs. Buffer	−0.05	0.77	−0.02	0.58	0.01	0.35	0.01	0.33
Buffer vs. Cut-to-shore	−0.04	0.75	0.07	0.06	0.01	0.37	0.01	0.34
Uncut vs. Cut-to-shore	−0.04	0.74	**0.10**	**0.01**	**0.08**	**0.04**	**0.08**	**0.03**
25–30 m								
Uncut vs. Buffer	−0.03	0.66	0.01	0.31	0.00	0.49	0.00	0.48
Buffer vs. Cut-to-shore	−0.07	0.89	0.01	0.37	0.05	0.04	0.03	0.16
Uncut vs. Cut-to-shore	0.00	0.45	**0.10**	**0.02**	**0.08**	**0.02**	**0.08**	**0.02**

the pre-harvest (i.e., Yr 0) sample period and may have affected the growth of post-harvest plant communities. Increased moisture availability to streamside plants, relative to those growing in the upland, may have buffered this effect. As a compensatory measure for annual abiotic fluctuations, we used both pre-harvest and uncut sites as a control to enhance our ability to interpret effects of harvesting across the riparian ecotone and reduce the possibility of inherent variability among treatments.

4.1. Management implications

Hydrological processes and disturbance regimes that structure riparian ecosystems impede competitive exclusion, enhance vascular diversity, and create an environment liable to meet the competitive and resource requirements of more species; including robust perennials able to tolerate stand-replacing disturbance through the survival of belowground plant parts. While this study provides evidence that changes in streamside plant communities following clearcut harvesting were less pronounced than those in upland plant communities, there are three caveats for management applications stemming directly from these results. First, this study illustrates early seral responses (up to 7 years after disturbance) and therefore it is possible that there continues to be changes in riparian communities as directional shifts in species composition and diversity have been shown to last for more than a decade (Thomas et al., 1999; Halpern et al., 2005; Belote et al., 2012). A longer term investigation into riparian dynamics following overstory harvesting is recommended. Second, in our study, ground disturbance was minimal to not confound effects of overstory removal. Specifically, harvesting was done during the winter months, when the ground was frozen, to minimize soil compaction, and mechanical site preparation (e.g., scarification) was restricted to be outside of 30 m from the stream channel. Extirpation and colonization processes may be exaggerated when ground disturbance is more severe. Third, vegetation responses may not parallel responses in other ecosystem processes such as nutrient leaching, soil erosion, changes to water quality and quantity, or other negative effects from harvesting. We strongly recommend that future studies focused on changes in riparian vegetation should attempt to link with our evolving knowledge of watershed processes following disturbance, such as patterns in surface and sub-surface hydrology.

In conclusion, we found that streamside communities, harvested with or without a 30 m riparian buffer had similar species diversity and composition to uncut forests. However, upland communities were less resistant to overstory harvest and subsequently were colonized by early successional species often present in pre-harvest riparian plots. Our study results have produced metrics for assessing response to riparian disturbance that should be applicable to other types of forest ecosystem and that can used to inform forest management planning and practices related to conservation of plant communities.

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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.2013.10.011.

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