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Compositional stability of boreal understorey vegetation after overstorey harvesting across a riparian ecotone

Rebecca L. MacDonald, Han Y.H. Chen, Samuel F. Bartels, Brian J. Palik & Ellie E. Prepas

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boreal forest; disturbance; diversity–stability hypothesis; riparian vegetation; succession; understorey plants

Nomenclature
Marie-Victorin et al. (2002)

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MacDonald, R.L. (rmacdon2@lakeheadu.ca)[1],
Chen, H.Y. H. (corresponding author, hchen1@lakeheadu.ca,)[1],
Bartels, S.F. (sfbartel@lakeheadu.ca)[1],
Palik, B.J. (bpalik@fs.fed.us)[2],
Prepas, E.E. (ellie.prepas@lakeheadu.ca)[1]

[1]Faculty of Natural Resources Management, Lakehead University, Thunder Bay, ON P7B 5E1, Canada;
[2]Center for Research on Ecosystem Change, Northern Research Station, USDA Forest Service, Grand Rapids, MN 55744, USA

Abstract

Questions: Understanding factors that contribute to the stability of an ecosystem following harvesting is central to predicting responses of boreal ecosystems to increasing human disturbances. While the response of understorey vegetation to harvesting is well understood for upland sites, little is known about compositional stability of riparian understorey vegetation. We examined how compositional stability changes with or without harvesting along an upland to streamside gradient and tested whether compositional stability is affected by pre-harvest species diversity and composition.

Location: Lower Foothills sub-region of the Boreal Plain, ca. 20 km northwest of Whitecourt, Alberta, CA.

Methods: We repeatedly sampled understorey vegetation of four winter-harvested and four unharvested sites in western Canadian boreal forest. Species covers were measured during the summer prior to harvesting in 2003 (year 0) and in 2004, 2008 and 2010 (1, 5 and 7 yrs after, respectively). We used non-metric multidimensional scaling to ordinate plots using species covers, and measured vector length in the ordination space to quantify floristic dissimilarity of each plot between year 0 and years 1, 5 and 7, an inverse measure of compositional stability.

Results: Floristic dissimilarity between year 0 and subsequent years was significantly greater in harvested than unharvested sites for all subsequent sampling years. Furthermore, along the upland to stream gradient, floristic dissimilarity was larger on upland than stream sites. Additional analyses revealed that floristic dissimilarity was related negatively to pre-harvesting species richness and evenness, but positively to bryophyte cover.

Conclusions: Our results demonstrate that understorey compositional stability is strongly influenced by harvesting, and streamside communities are more stable than upland communities. Our results indicate that compositional stability of understorey vegetation in response to harvesting is associated positively with pre-disturbance species richness and evenness, but negatively with bryophyte dominance.

Introduction

Understanding community changes following a perturbation has been a focus of ecologists for over half a century, with particular attention being directed towards the role of biodiversity on aggregate properties such as biomass and nutrient cycling (Elton 1958; Frank & McNaughton 1991; Tilman et al. 2006). In forest ecosystems, understorey vegetation accounts for the majority of diversity (Gilliam 2007; Halpern & Lutz 2013) and affects overstorey succession and productivity (Royo & Carson 2006), nutrient cycling (Nilsson & Wardle 2005) and wildlife habitat (Johnson et al. 2003). Corresponding with global trends in resource consumption (Foley et al. 2005), approximately one million hectares are harvested each year in North American boreal forest (Canadian Council of Forest

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Ministers 2005), leading to a significant shift in dominant disturbance regimes. Therefore, understanding the response of understorey communities to harvesting is imperative.

Compositional stability, the measure of change in community membership and abundance following a disturbance, depends on the balance between local extirpation and colonization by new species (Halpern 1988; Sankaran & McNaughton 1999; Belote et al. 2012). Overstorey characteristics, particularly canopy removal through harvesting, have a profound impact on resource availability for understorey plant communities (Halpern 1988; Whitney & Foster 1988; De Grandpré & Bergeron 1997; Hart & Chen 2008; Bartels & Chen 2010, 2013; Belote et al. 2012), but the strength of overstorey controls on understorey communities remains debated (Halpern & Lutz 2013). Furthermore, current understanding of harvesting effects on understorey vegetation is largely restricted to upland forests (De Grandpré & Bergeron 1997; Hart & Chen 2006, 2008; Belote et al. 2012) except a particular focus on bryophyte assemblages (Dynesius et al. 2009). It remains unclear whether the response of riparian understorey vegetation to harvesting is similar to that of upland understorey vegetation.

A community's response to disturbance may vary dependent on pre-disturbance species diversity and species characteristics of communities (Sankaran & McNaughton 1999; Wittebolle et al. 2009). Prominent in these investigations is the 'insurance hypothesis' (Yachi & Loreau 1999), which states that communities with higher biodiversity are more likely to contain species that can survive a given environmental perturbation. Thus, high biodiversity impedes or prevents the establishment of non-resident colonizing species, and diverse communities are more able to resist community change. Alternatively, however, greater compositional shifts may occur as pre-disturbance richness increases because more species in the local pool might represent more species available in the adjacent pool, and therefore the composition might reorganize in more different combinations by random chance. Although the majority of diversity–stability research has focused on species richness, the dominance structure within the community (evenness) may also affect stability (Wittebolle et al. 2009). Theoretical evidence suggests that community stability is only enhanced by diversity when evenness is high (Hillebrand et al. 2008).

Understorey vegetation in riparian forests is characteristically of high species diversity as a result of higher resource quantity and heterogeneity of streamside habitats, imparted by hydrological processes and natural disturbance regimes (Naiman et al. 1993). By contrast, upland understorey communities, driven mainly by light availability, are relatively species-poor and dominated by species that require overstorey shading (Nilsson & Wardle 2005; Hart & Chen 2008; Liu & Bao 2014). We therefore expect that upland sites would have a lower compositional stability than streamside communities following overstorey removal by harvesting if high pre-disturbance biodiversity impedes the establishment of non-resident colonizing species. Alternatively, a higher compositional stability may occur in upland sites than streamside communities if more local species result in diverse species reorganizations through random chance.

Species or functional group composition within the vegetation community is also likely an important factor in predicting effects of ecosystems to disturbance. For example, herbaceous species in forests may respond differently to stand-replacing disturbances than bryophyte species (Hart & Chen 2008; Liu & Bao 2014). Following canopy removal, light levels, air and soil temperatures and soil resource availability increase, creating an environment that is generally more favourable for vascular plants (Hart & Chen 2006; Belote et al. 2012). These conditions, as well as high pH and low moisture content in the thin organic layer following canopy removal, exceed the tolerance of many bryophyte species (Åström et al. 2007), resulting in bryophyte declines (Hart & Chen 2008; Liu & Bao 2014). Bryophytes are highly sensitive to disturbances, and in systems like the boreal forest, where bryophyte species contribute a major proportion to ground-layer species abundance and diversity in the upland forest understorey than streamside (Hart & Chen 2008; Dynesius et al. 2009), compositional response to harvesting may be strongly influenced by abundance of bryophyte species.

Here, we measure compositional stability of understorey plant communities following harvesting across a riparian–upland gradient using pre- and post-harvest data from permanent sampling plots. Our objectives were to examine (1) whether compositional stability differs between harvested and unharvested sites; (2) whether compositional stability differs along a riparian–upland gradient; and (3) whether compositional stability is influenced positively by pre-harvested species diversity and negatively by abundance of bryophytes.

Methods

Study area

The study was conducted in the Lower Foothills sub-region of the Boreal Plain, ca. 20 km northwest of Whitecourt, Alberta, Canada. The climate is sub-humid and the precipitation is variable: long-term (1978–2009) total annual precipitation recorded at Whitecourt (782 m a.s.l.) ranged from 364 to 786 mm (Environment Canada 2014). The rolling topography occurs on moderately fine to fine-textured till or glaciolacustrine parent material. The characteristic forest 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.) on well-drained sites, and black spruce [*Picea mariana* (Mill.) BSP] and tamarack [*Larix laricina* (*DuRoi*) K. Koch] on poorly drained sites. Understorey vegetation is depauperate relative to central Canadian boreal systems (Qian et al. 1998). Forest of the study area originated from stand-replacing fire in 1940.

Experimental design and data collection

Four headwater stream sites were clear-cut to the stream during January to March 2004. Chemical site preparation consisted of aerial application of Vision® (Monsanto, St. Louis, MO, US) in August 2004, which was applied >30 m away from the stream, and thus did not directly influence our study plots. We also sampled four headwater stream reference sites that were not harvested to monitor temporal understorey vegetation dynamics without disturbance. At each site, three randomly located, 30-m long transects were established, running perpendicular from the stream to the upland transition zone. Two 1-m^2 understorey (the component of the understorey <1.5-m tall) vegetation plots were randomly located within each of the following distance ranges from the stream channel bank: 0–5, 5–10, 10–15, 15–20, 20–25 and 25–30 m, for a total of 12 plots per transect and 36 plots per site. Transects and permanent vegetation plots were marked with GPS, as well as physically marked with corner and centre posts.

Vegetation sampling was conducted during the periods of peak vegetation cover of all ground species in the summer (July through August) in 2003 (year 0) and the summers of 2004 (year 1), 2008 (year 5) and 2010 (year 7). Sampling included all vascular (shrub and herbaceous species) and nonvascular (bryophytes and lichens included) plants. We attempted to identify all plants to species level in the field; however some plants, e.g. *Carex* spp., were identified only to genus due to the difficulty of their identification without flowers or fruits. Percentage cover (0–100%) of each plant species or genus in each plot was estimated by eye following the procedure described in Mueller-Dombois & Ellenberg (1974).

Statistical analyses

We quantified temporal compositional stability by measuring changes in species composition after disturbance relative to before disturbance (or year 0). Within each site, species-specific percentage cover of the six 1-m^2 plots within each distance range at each sampling time (year 0, 1, 5 or 7) was averaged to represent mean response of a sampling unit, i.e. a specific distance range within each site, prior to statistical analysis. Trends in the compositional data were examined using non-metric multidimensional scaling (NMS). NMS is well suited for community data, because it uses non-metric rank ordering to perceptually map data; NMS avoids assumptions of normality and homogeneity of variance that are required in traditional ordination techniques (MjM Software Design, Gleneden Beach, OR, US). NMS was carried out using PC-ORD v 5 (MjM Software Design) and was set to the slow and thorough auto-pilot mode to select the optimal solution (i.e. dimensionality). Floristic dissimilarity (FD) from year 0 to years 1, 5 and 7 of each sampling unit was measured as Euclidean distance in NMS ordination space. Compositional stability is inversely related to the Euclidean distance: stability is maximum when the sample unit maintains its initial position in ordination space (i.e. Euclidean distance = 0).

To test the effects of harvesting and distance from stream on FD, we used repeated measures general linear models (rGLM). We used harvesting as a categorical fixed factor, distance from stream as a continuous fixed factor, FD as the response variable and sampling year as the repeated measure. Floristic dissimilarity was natural log-transformed to satisfy linear model assumptions of normality and homogenous variance. For each rGLM, we tested the sphericity (i.e. symmetry of the covariance matrix) using Mauchly's criterion test, which is suitable for assessing the validity of the sphericity assumption that underlies repeated measures analysis of variance (Mauchly 1940), and applied the Huynh-Feldt correction to our results if the assumption was violated (Huynh & Feldt 1976). We calculated the effect size (η^2) to estimate the proportion of the total variance attributed to an effect (Tabachnick & Fidell 1989).

We examined the correlation among pre-disturbance species richness, evenness and percentage cover of bryophytes and distance from stream. To examine whether FD is associated with pre-harvest species richness, evenness and percentage cover of bryophytes, we used simple linear regression analysis. Species richness (S) is a measurement of the total number of species in each sample unit. The percentage cover of bryophytes is the sum of covers of all ground-layer bryophyte species. To calculate evenness, we used the (Pielou 1969) index (J'):

$$J' = H' \cdot \ln(S)^{-1} \tag{1}$$

where H' is the Shannon-Weiner diversity index and S is species richness of the sample unit. Total cover is the summation of cover of all species in each plot.

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Results

Non-metric multi-dimensional scaling showed distinct compositional patterns between harvested and unharvested sites and distance from stream among sampling years (Fig. 1). In ordination space, communities close to the stream were grouped further apart than communities distant from the stream. The best NMS ordination was reached in a three-dimensional solution with a final stress of 6.32, in which axes 1, 2 and 3 had r^2-values of 0.40, 0.21 and 0.17, respectively. Pre-disturbance species richness was not negatively related to distance from stream, whereas pre-disturbance bryophyte cover increased with distance from stream, and there was not a significant relationship between species evenness and distance from stream (Fig. 2a–c). There were strong correlations among pre-disturbance species richness, species evenness and bryophyte cover (Fig. 2d–f).

Floristic dissimilarity between year 0 and subsequent years was significantly higher in harvested than unharvested sites for all subsequent sampling years (Table 1, Fig. 3). Furthermore, FD after harvest increased with distance from stream for all sampling years, whereas it did not change with distance from stream for unharvested sites (Table 1, Fig. 4). There was no difference in FD among sampling years, nor was there an interaction between sampling year and disturbance or distance from stream (Table 1). In harvested sites, the abundance of several common species in the riparian zone, such as *Calamagrostis canadensis*, *Athyrium filix-femina* and *Lonicera involucrata*, among others, declined with increasing distance from the stream, whereas

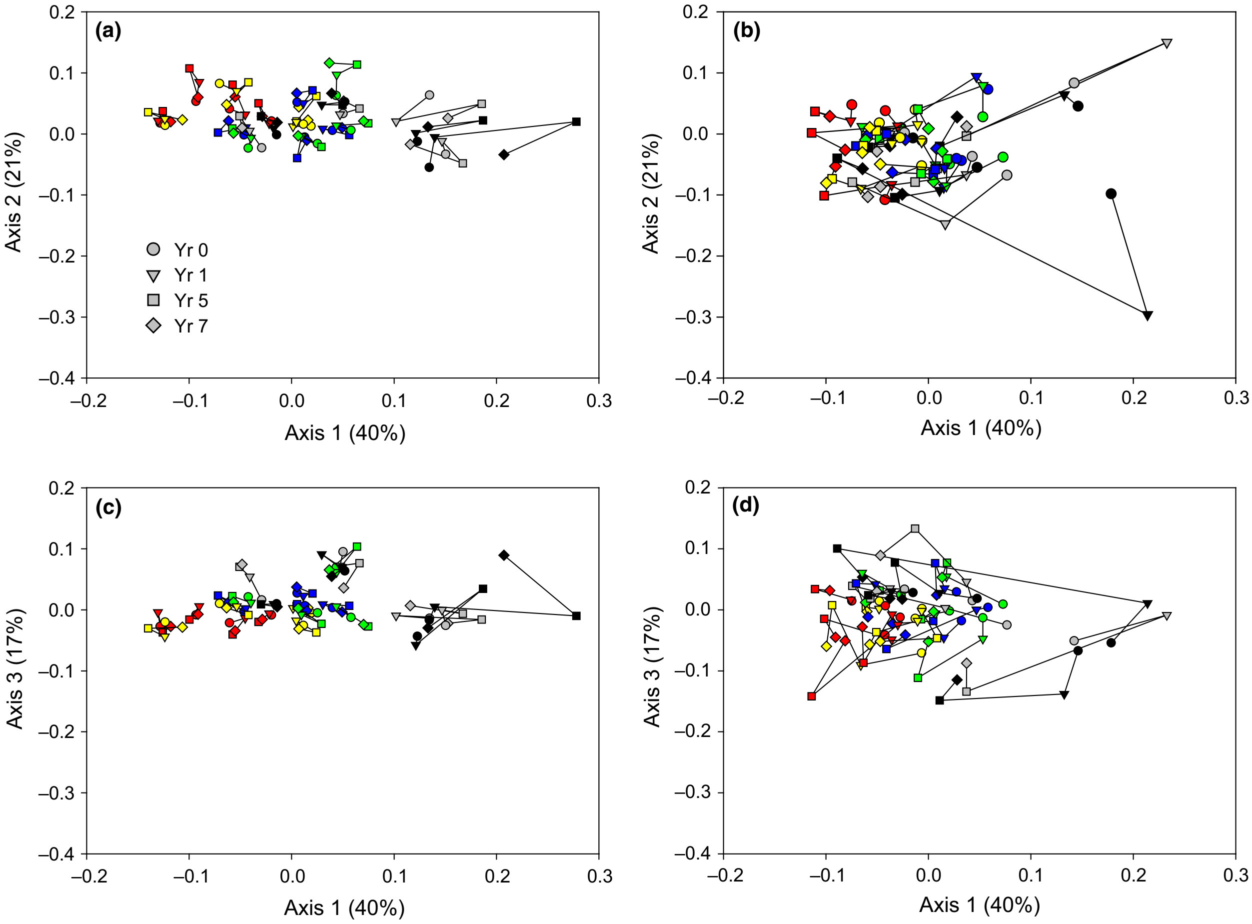

Fig. 1. Non-metric multidimensional scaling ordination of understorey species across riparian ecotones on Canadian Boreal Plain watersheds over time. A final stress of 6.32 was reached in a three-dimensional solution in which Axes 1, 2 and 3 explained 78% (40%, 21% and 17%, respectively) of the understorey compositional variability. Within the ordination space: (**a**) unharvested (axis 1 vs axis 2), (**b**) harvested (axis 1 vs axis 2), (**c**) unharvested (axis 1 vs axis 3) and (**d**) harvested (axis 1 vs axis 3), successional trajectories were formed by sequentially connecting points representing the early successional pathway of the same community over time. Colours represent distance from stream: 0–5 m (red), 5–10 m (yellow), 10–15 m (blue), 15–20 (green), 20–25 m (grey) and 25–30 m (black). Pre-disturbance condition is represented by the initial point for each trajectory. The second, third and fourth subsequent points corresponds with year 1, 5 and 7 post-harvest, respectively.

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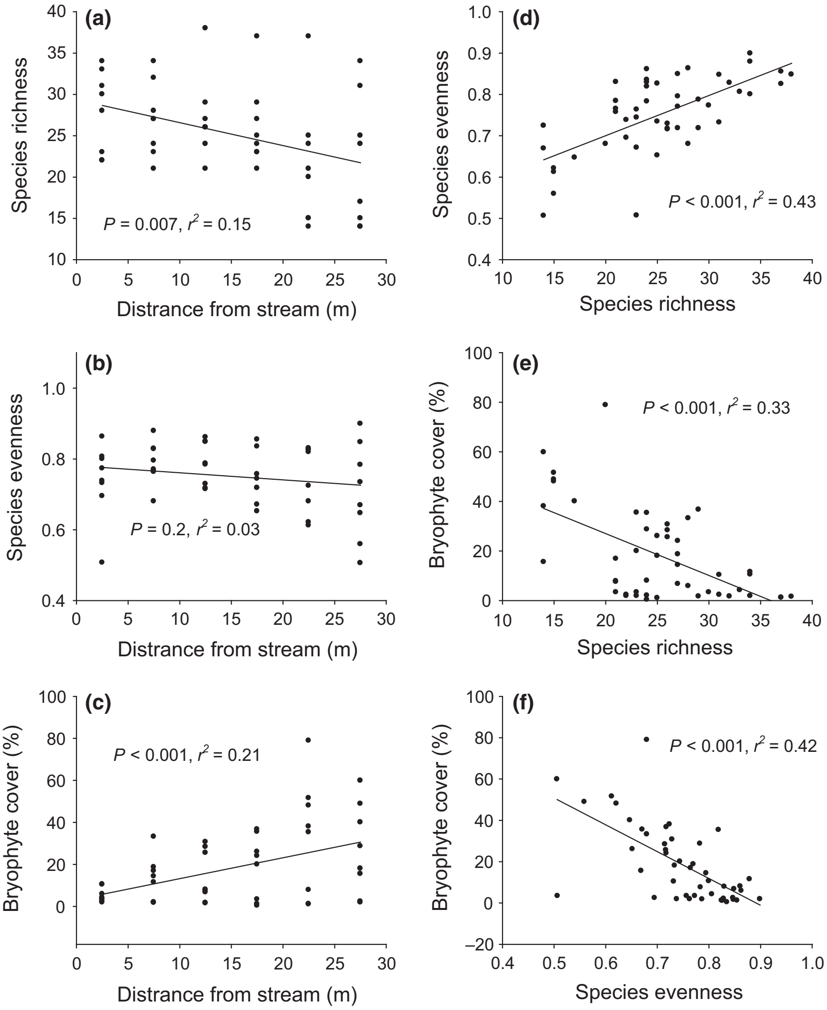

Fig. 2. Relationships between distance from stream and pre-disturbance community attributes. (**a**) species richness (number of species per plot) and distance from stream; (**b**) species evenness and distance from stream; (**c**) bryophyte cover (%) and distance from stream; (**d**) species richness and species evenness; (**e**) bryophyte cover (%) and species richness; and (**f**) bryophyte cover (%) and species evenness.

other species such as *Epilobium angustifolium* and *Linnea borealis* increased with increasing distance from stream (Appendix S1).

Regression analysis revealed that FD between pre- and post-harvest communities was related negatively to pre-disturbance species richness (Fig. 5a) and species evenness (Fig. 5b), but positively to total bryophyte cover in all sampling years (Fig. 5c). The predictive power of species richness and bryophyte cover on FD decreased over time, as indicated by decreasing percentage of variance accounted for by the respective predictors (Fig 5a–c). In unharvested communities, FD temporal variation was not related to species richness measured in year 0 (Fig. 5a), but was positively related to evenness in years 5 and 7 (Fig, 5b) and positively to bryophyte cover in all subsequent sampling years (Fig. 5c).

Discussion

Along boreal riparian–upland gradients, understorey plant communities following harvesting have strongly shifted. The strong compositional shift after harvesting is consistent with previous understorey vegetation studies in upland forests (Halpern 1988; De Grandpré & Bergeron 1997; Hart & Chen 2008; Belote et al. 2012). Our results provide direct evidence for a lateral pattern of compositional stability along riparian–upland gradients. Complementary to a specific focus on bryophyte assemblages (Dynesius et al. 2009), our study demonstrates that compositional stability of all plant species after harvesting is lower in upland than streamside communities.

Species closer to the stream are adapted to grow in a resource-rich environment highly influenced by stream

Table 1. Floristic dissimilarity (natural log-transformed vector length between pre- and post-harvest sample plots in NMS ordination space) in relation to harvesting, distance from stream and sampling year.

Source	*df*	*F*	*P*	η^2
Between Subjects				
Harvesting	1	37.87	0.01	0.13
Distance	1	6.61	0.08	0.07
Harvesting × Distance	1	3.26	0.02	0.12
Error 1	44			
Within Subjects				
Year	2	1.99	0.15*	0.04
Year × Harvesting	2	0.64	0.52*	0.01
Year × Distance	2	2.36	0.11*	0.05
Year × Harvesting × Distance	2	0.01	0.99*	0.01
Error 2	88			

*Huynh-Feldt correction was applied to correct for sphericity.

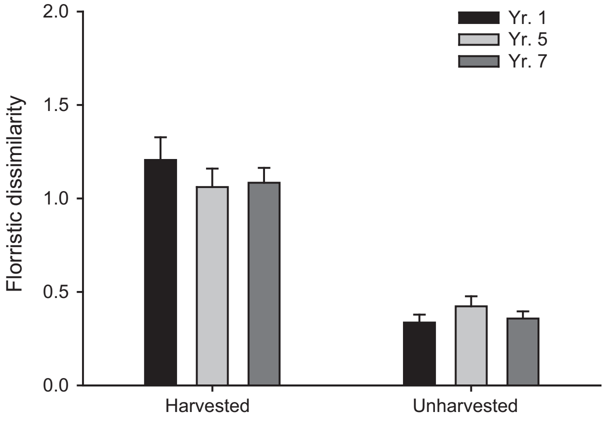

Fig. 3. Floristic dissimilarity between year 0 and years 1, 5 and 7 for harvested and unharvested sites. Values are means ± 1SE.

hydrology (Naiman et al. 1993). In upland conditions, forest canopy drives the composition of the understorey strata by exerting strong controls on resource availability (e.g. light, nutrients and water; Halpern 1988; De Grandpré & Bergeron 1997; Hart & Chen 2008; Bartels & Chen 2010; Belote et al. 2012) as well as providing detritus inputs (Whitney & Foster 1988). In contrast, there is less coupling between the canopy and streamside understorey vegetation (Lyon & Sagers 1998; Decocq 2002; Dynesius et al. 2009).

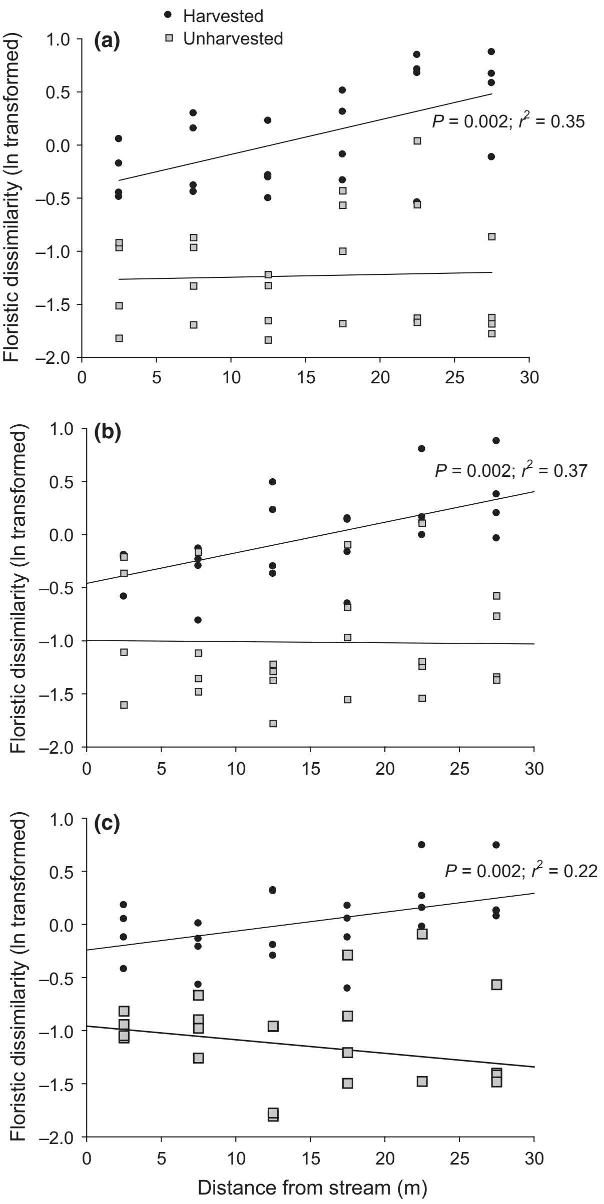

Fig. 4. Floristic dissimilarity in relation to distance from stream in harvested and unharvested sites between year 0 and (**a**) year 1, (**b**) year 5 and (**c**) year 7.

We found positive relationships between compositional stability following harvest and pre-harvest species richness. A positive relationship between compositional stability and pre-disturbance species richness could be a result of fewer species lost following disturbance (Sankaran & McNaughton 1999) and/or fewer colonizing species following disturbance in species-rich than species-poor communities. Our analysis of individual plant species responses to harvesting shows there was a similar number of colonizing species in both species-rich and -poor communities; resident species in the species-rich communities generally remained present through time, whereas more shifts to colonizing species occurred in species-poor communities (MacDonald et al. 2014). These results suggest that the communities with high species richness improve compositional stability following harvest through less species loss than the communities with low species richness.

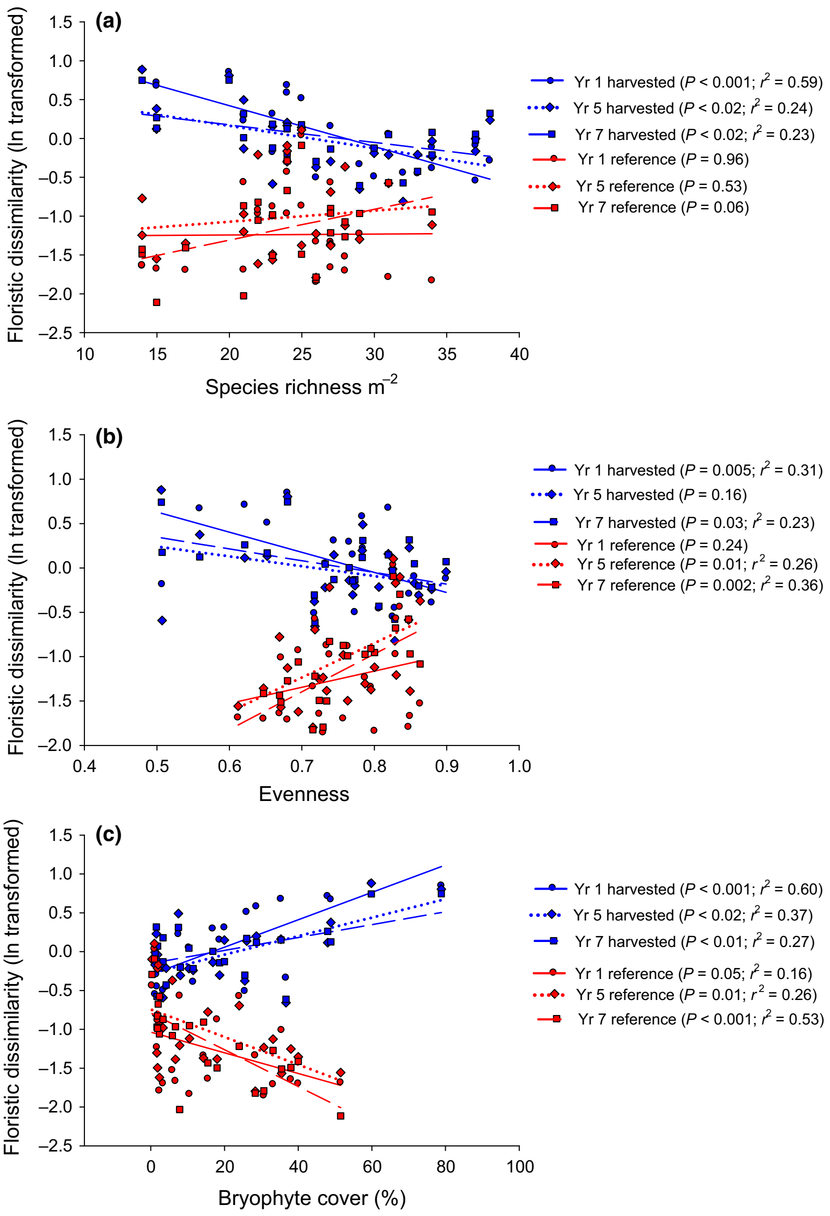

Fig. 5. Floristic dissimilarity between year 0 and years 1, 5, and 7 in relation to year 0 species richness, evenness and bryophyte cover. (**a**) Species richness, (**b**) evenness and (**c**) bryophyte species percentage cover in harvested and unharvested plots. Floristic dissimilarity was quantified by vector length in NMS scaling ordination space (Fig. 1).

We also found positive relationships between compositional stability following harvest and pre-harvest species evenness. This result complements the findings of strong positive influences of species evenness on ecosystem functionality in manipulated environments (Wittebolle et al. 2009). Our findings provide evidence that high species evenness improves community compositional stability following a major stand-replacing disturbance in natural environments. Communities with greater evenness are often represented by multiple functional groups (such as reproductive or growth strategies; Mwangi et al. 2007).

We found that dominance of bryophytes negatively affected compositional stability following harvesting. The strength of the relationships between post-harvest compositional stability and pre-disturbance bryophyte cover was much stronger than that to pre-disturbance species evenness. This indicates bryophyte cover has a strong influence, in addition to its contribution to species evenness, on compositional stability. The strong influence of bryophytes on post-disturbance compositional stability is attributable to their strong sensitivity to canopy removal after harvesting (Åström et al. 2007; Hart & Chen 2008; Liu & Bao 2014).

In conclusion, we show strong compositional shifts of understorey vegetation following overstorey harvest. Furthermore, streamside understorey plant communities were more compositionally stable than upland plant communities following the harvest. Our analysis shows that compositional stability is positively affected by pre-harvest species richness and evenness, but communities with high bryophyte dominance are less compositionally stable after harvest. Our observational study validates some important mechanisms that affect community stability following disturbances or environmental stresses found in controlled experiments (Sankaran & McNaughton 1999; Tilman et al. 2006; Wittebolle et al. 2009). Unlike manipulated experiments, however, relative influences of the observed effects of species richness and evenness and bryophyte cover are difficult to discern because of the inherently strong correlations among pre-disturbance attributes across a riparian ecotone. Nevertheless, our results show evidence that pre-disturbance species richness, species evenness and functional group evenness collectively contribute to community compositional stability in natural environments.

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References

Åström, M., Dynesius, M., Hylander, K. & Nilsson, C. 2007. Slope aspect modifies community responses to clear-cutting in boreal forests. *Ecology* 88: 749–788.

Bartels, S.F. & Chen, H.Y.H. 2010. Is understory plant species diversity driven by resource quantity or resource heterogeneity? *Ecology* 91: 1931–1938.

Bartels, S.F. & Chen, H.Y.H. 2013. Interactions between overstorey and understorey vegetation along an overstorey compositional gradient. *Journal of Vegetation Science* 24: 543–552.

Belote, R.T., Jones, R.H. & Wieboldt, T.F. 2012. Compositional stability and diversity of vascular plant communities following logging disturbance in Appalachian forests. *Ecological Applications* 22: 502–516.

Canadian Council of Forest Ministers 2005. *Criteria and indicators of sustainable forest management in Canada-National status 2005.* Natural Resources Canada, Canadian Forest Service, Ontario, CA.

De Grandpré, L. & Bergeron, Y. 1997. Diversity and stability of understorey communities following disturbance in the southern boreal forest. *Journal of Ecology* 85: 777–784.

Decocq, G. 2002. Patterns of plant species and community diversity at different organization levels in a forested riparian landscape. *Journal of Vegetation Science* 13: 91–106.

Dynesius, M., Hylander, K. & Nilsson, C. 2009. High resilience of bryophyte assemblages in streamside compared to upland forests. *Ecology* 90: 1042–1054.

Elton, C.S. 1958. *The ecology of invasions by plants and animals*. Methuen, London, UK.

Environment Canada. 2014. Canadian Climate Normals 1981–2010. Available at http://climate.weatheroffice.gc.ca/climate_normals/index_e.html Accessed 25 June 2013.

Frank, D.A. & McNaughton, S.J. 1991. Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos* 62: 360–362.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., (...) & Snyder, P.K. 2005. Global consequences of land use. *Science* 309: 570–574.

Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57: 845–858.

Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69: 1703–1715.

Halpern, C.B. & Lutz, J.A. 2013. Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory–understory interactions. *Ecological Monographs* 83: 221–237.

Hart, S.A. & Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. *Critical Reviews in Plant Sciences* 25: 381–397.

Hart, S.A. & Chen, H.Y.H. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. *Ecological Monographs* 78: 123–140.

Hillebrand, H., Bennett, D.M. & Cadotte, M.W. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89: 1510–1520.

Huynh, H. & Feldt, L.S. 1976. Estimation of the box correction for the degrees of freedom from sample data in the randomized block and split plot designs. *Journal of Educational Statistics* 1: 69–82.

Johnson, C.J., Alexander, N.D., Wheate, R.D. & Parker, K.L. 2003. Characterizing woodland caribou habitat in sub-boreal and boreal forests. *Forest Ecology and Management* 180: 241–248.

Liu, X. & Bao, W.K. 2014. Understory plant assemblages present distinct short-term responses to the clear-cutting of an old-growth spruce forest near an alpine timberline. *Canadian Journal of Forest Research* 44: 562–571.

Doi: 10.1111/jvs.12272

Lyon, J. & Sagers, C.L. 1998. Structure of herbaceous plant assemblages in a forested riparian landscape. *Plant Ecology* 138: 1–16.

MacDonald, R.L., Chen, H.Y.H., Palik, B.P. & Prepas, E.E. 2014. Influence of harvesting on understory vegetation along a boreal riparian–upland gradient. *Forest Ecology and Management* 312: 138–147.

Mauchly, J.W. 1940. Significance test for sphericity of a normal n-variate distribution. *The Annals of Mathematical Statistics* 11: 204–209.

Marie-Victorin, Rouleau, E. & Brouillet, L. 2002. *Flore Laurentienne*, 3rd ed. Gaëtan Morin, Montreal, CA.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. Wiley and Sons, New York, NY, US.

Mwangi, P.N., Schmitz, M., Scherber, C., Roscher, C., Schumacher, J., Scherer-Lorenzen, M., Weisser, W.W. & Schmid, B. 2007. Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology* 95: 65–78.

Naiman, R.J., Decamps, H. & Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3: 209–212.

Nilsson, M.C. & Wardle, D.A. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment* 3: 421–428.

Pielou, E.C. 1969. *Ecological diversity and it's measurement: an introduction to mathematical ecology*. John Wiley & Sons, Toronto, CA.

Qian, H., Klinka, K. & Kayashara, G.J. 1998. Longitudinal patterns of plant diversity in the North American boreal forest. *Plant Ecology* 138: 161–178.

Royo, A.A. & Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36: 1345–1362.

Sankaran, M. & McNaughton, S.J. 1999. Determinants of biodiversity regulate compositional stability of communities. *Nature* 401: 691–693.

Tabachnick, B.G. & Fidell, L.S. 1989. *Using multivariate statistics*, 2nd ed. Harper & Row, New York, NY, US.

Tilman, D., Reich, P.B. & Knops, J.M.H. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441: 629–632.

Whitney, G.G. & Foster, D.R. 1988. Overstorey composition and age as determinants of the understorey flora of woods of central New England. *Journal of Ecology* 76: 867–876.

Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K., De Vos, P., Verstraete, W. & Boon, N. 2009. Initial community evenness favours functionality under selective stress. *Nature* 458: 623–626.

Yachi, S. & Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* 96: 1463–1468.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Mean percentage cover of understorey species (in alphabetical order) of year 1, 5 and 7 measurements in reference sites and clear-cut sites across a riparian–upland gradient.