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RESEARCH ARTICLE

Dynamics and recovery of forest understory biodiversity over 17 years following varying levels of retention harvesting

Samuel F. Bartels | **S. Ellen Macdonald**

Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada; and

Correspondence
S. Ellen Macdonald
Email: ellen.macdonald@ualberta.ca

Present address
Samuel F. Bartels, Department of Ecosystem Science and Management, University of Northern British Columbia, Prince George, British Columbia, Canada

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Abstract

1. Retention harvesting is advocated as an alternative to intensive timber harvesting, such as clear-cutting, to better maintain or facilitate recovery of biodiversity and other ecological values in managed forests. However, it is not clear how long the benefits of retention harvests persist.
2. We investigated responses of understory vascular plant cover, richness, diversity (inverse Simpson index) and composition to a gradient in dispersed retention (2% [clear- cut], 10%, 20%, 50% and 75% retention; unharvested reference [100% retention]) at 3, 6, 11, and 17 years after harvest, in four boreal mixedwood forest types (deciduous (broadleaf)-dominated, deciduous-dominated with conifer understory, mixed, and conifer-dominated) in western Canada.
3. Understory cover and richness tended to increase in the short-term (3 years), peaked at 6–11 years with differences following the gradient of harvesting intensity, then plateaued or declined in the second decade (17 years), by which time there were minimal or no differences among harvesting levels, including the reference. Responses for diversity were minimal. In contrast, composition varied along the gradient of harvesting intensity and showed little recovery towards the unharvested condition over the 17-year period. Generally, for plant community composition, clear-cut and lower retention treatments (10%, 20%) were similar to one another but differed from the higher retention and unharvested reference treatments.
4. *Synthesis and applications*: Retention harvests can moderate the negative impacts of harvesting and facilitate the recovery of biodiversity. Our results suggest that for the cover, richness and diversity of understory vascular plants, this moderating influence is weak and short-lived. However, higher levels of retention can temper changes in understory composition relative to the unharvested forest, but full recovery is likely to be slow and will be complicated by post-harvest regeneration dynamics.

KEYWORDS
boreal mixedwood forest, clear-cutting, forest conservation, forest harvest, sustainable forest management, understory vegetation, variable-retention harvest, vascular plant diversity

1 | INTRODUCTION

There is increasing recognition that traditional high-intensity clear-cut harvesting does not meet the biodiversity objectives of ecosystem-based management (Fedrowitz et al., 2014; Gustafsson et al., 2020). Retention harvesting, in which live trees are deliberately left behind in patches or as single trees during logging operations, has been widely acclaimed as an alternative (Fedrowitz et al., 2014; Gustafsson et al., 2010; Rosenvald & Lohmus, 2008) that can help maintain habitat elements, life-boat biodiversity and facilitate faster post-harvest recovery (Franklin et al., 1997; Lindenmayer et al., 2012; Rudolphi et al., 2014). Indeed, there is a growing body of evidence that retention harvesting (vs. clear-cutting) can help conserve biodiversity, including invertebrates (Pinzon et al., 2016; Work et al., 2010), large and small mammals (Franklin et al., 2019; Sullivan & Sullivan, 2001), herbaceous plants (Craig & Macdonald, 2009; Halpern et al., 2012; Johnson et al., 2014; Lilles et al., 2018; Macdonald & Fenniak, 2007) and bryophytes (Bartels et al., 2018; Caners et al., 2013; Perhans et al., 2009), with higher levels of retention being more effective. However, most prior studies span a relatively short time (<11 years) post-harvest; knowledge of longer-term responses is key for gauging the impact of retention harvesting as stands develop and the forest recovers.

Forest understory plants, known for their role as agents of change in forest condition (Nilsson & Wardle, 2005), show notable dynamic responses to forest disturbances, including harvesting. Understory vascular plant cover, richness and diversity tend to change dramatically following harvesting in boreal forests as increased resource availability promotes growth and greater evenness of remaining species, and as disturbance-adapted species colonize (Hart & Chen, 2006). Such responses can often show a lag of up to 10 years due to ecological inertia and effects of ecosystem memory in the almost-exclusively perennial understory community (Bergeron et al., 2017; Hart & Chen, 2006). All three of these metrics may increase or decline as stands approach canopy closure, with specific responses depending on life form, life history and functional traits, such as shade tolerance, reproductive strategy, colonizing ability and adaptation to disturbance (Aubin et al., 2013; Halpern et al., 2012; Roberts & Zhu, 2002).

Stand development in the boreal forest can follow multiple pathways resulting in broadleaf-, conifer- or mixed-species dominance at any stage of stand development (Bergeron et al., 2014; Chen & Popadiouk, 2002). Previous studies have suggested that understory plant communities in conifer-dominated boreal forests, along a moisture gradient within upland sites, may be more sensitive to harvesting than are mixedwoods (Echiverri & Ellen Macdonald, 2020; Macdonald & Fenniak, 2007). Given the strong influence of the overstory on understory plant communities (Bartemucci et al., 2006; Hart & Chen, 2006), it follows that understory responses will vary with forest type and harvesting intensity. Earlier studies suggested a threshold effect whereby a minimum of 10% to 20% dispersed retention is required to ameliorate the impacts of harvesting on understory plant communities (Craig & Macdonald, 2009; Macdonald & Fenniak, 2007) while other studies suggested 40% dispersed retention, or higher, are needed (Halpern et al., 2012). However, few studies have addressed the longer-term (>10 years) relationships between retention harvests and understory dynamics, and how these vary with harvesting intensity.

In this study, we investigated the response of understory vascular plants to a gradient of dispersed retention harvesting over a 17-year period based on data from permanent plots in a replicated large-scale experiment in the boreal mixedwood forests of western Canada. We specifically examined how understory vascular plant cover, richness (number of species), diversity (expressed as inverse of Simpson index) and composition compared across a gradient of harvesting intensity over time in four boreal forest types (i.e. deciduous (broadleaf)-dominated, deciduous with conifer understory, mixed deciduous-conifer, conifer-dominated). Due to increased resource availability (light, moisture) immediately following harvesting, we hypothesized: (H_1) an increase in understory species cover, richness and diversity, and significant differences in community composition between harvest treatments in the early years (<5 years) post-harvest, particularly in lower retention levels. We also hypothesized that (H_2) the response of the understory to harvesting would vary across the gradient of harvesting intensity, at least over the first decade, as the understory responds to the variation in canopy density, but that the differences would diminish thereafter in response to tree regeneration and redevelopment of the canopy. In response to the intensity of canopy removal (H_3) we expected shade-intolerant and early successional species to be associated with lower retention levels in the short-term post-harvest, but that such associations will weaken over time due to tree regeneration and canopy closure. In contrast, we expected shade-tolerant, mature forest species associated with the unharvested condition to be favoured by higher retention levels.

2 | MATERIALS AND METHODS

2.1 | Study location

The study location was the Ecosystem-based Management Emulating Natural Disturbance (EMEND) experiment in northwestern Alberta (56°46′13″N; 118°22′28″W), within the Lower Boreal Cordilleran Ecoregion (Strong & Leggat, 1992). The landscape has relatively gentle topography (677–880 m a.s.l.) and fine-textured luvisolic soils from glacio-lacustrine deposits (Kishchuk, 2004). Mean minimum and maximum annual temperatures are −4.2 and 7.3°C respectively; total annual precipitation is 483 mm with 63% as rainfall (30 year average 1981–2010, Manning, Alberta station; Environment Canada, 2010). The forest is dominated by trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss) and balsam poplar (*Populus balsamifera* L). The natural disturbance regime of the region is dominated by relatively frequent wildfire of variable severity (Bergeron et al., 2017).

2.2 | Experimental setup

The EMEND experiment includes a range of retention harvest treatments, each applied to three replicate ~10 ha compartments, in each of four boreal forest cover-types: (1) deciduous (broadleaf)-dominated (DDOM: >70% basal area of broadleaf (trembling aspen and balsam poplar) canopy species); (2) deciduous (broadleaf)-dominated with a developing conifer (white spruce) understory (DDOMU); (3) conifer-dominated (CDOM: >70% basal area of conifer (white spruce) canopy species); and (4) mixedwood (MX: mixed deciduous and conifer canopy with neither making up >70% of the canopy; Figure 1; see Table S1). The DDOM and DDOMU stands were 103 years post-fire, while the MX and CDOM stands were ~160 years post-fire, at the time of harvest (Bergeron et al., 2017). The six dispersed green-tree retention harvest treatments were: clear-cut (2%), 10%, 20%, 50% and 75% retention, and unharvested reference (100% retention). Harvesting, which targeted only tree species, was conducted in winter 1998/1999. The retention harvesting involved complete removal of trees within 5 m wide machine corridors with removal of different proportions of trees in intervening 15 m wide retention strips to achieve the desired retention level across the compartment, including the machine corridor. Trees were removed from retention strips more-or-less randomly, without favouring particular tree species or sizes (e.g. 'cut one, leave two'). Clear-cut harvesting followed standard operational procedures but with ~2% retention left as two small aggregated patches. Harvesting was conducted in winter under frozen ground conditions with snow cover, so ground disturbance was minimal. There was no machine traffic in the retention strips, where we sampled. The clearcut treatment would have experienced some machine traffic. Whole-tree harvesting was used with skidding to centralized

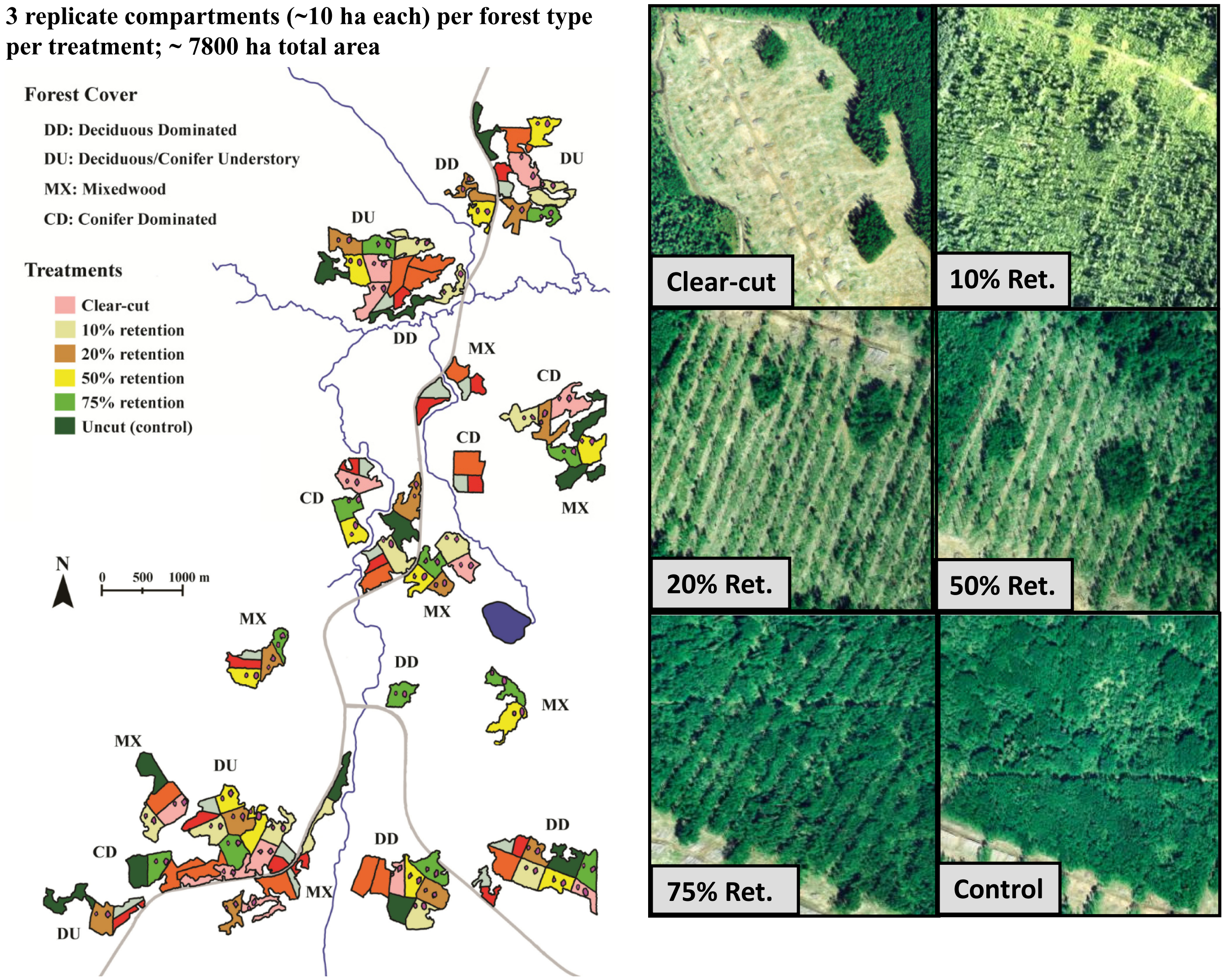

FIGURE 1 Layout of the Ecosystem Management Emulating Natural Disturbance experiment showing the spatial distribution of the six harvesting treatments (Clearcut, 10%, 20%, 50%, 75% retention, unharvested reference) applied to compartments (~10 ha each) replicated three times in each of the four forest types. Photographs show the treatments shortly after application. Each compartment included two small aggregated retention patches, which were not sampled in this study. Map colours of compartments not shown in the legend refer to additional treatments not considered in this study. See detailed information on experimental design in Section 2.

landings; thus, there was no logging slash left in the retention strips and only incidental amounts in the clearcut areas. The harvested stands and their understories, including the clearcuts, were left to naturally regenerate. Each combination of forest type and harvest treatment had 3 replicates (distances between stands ranged between 0.5–10 km), resulting in a total of 72 experimental compartments across the ~7800 ha total experimental area (Figure 1). Within each replicate compartment, six randomly situated permanent sampling sites were established (statistically, sub-samples). The harvesting was conducted as part of the operational harvest of partner companies. No permits or licences were required for field sampling. Detailed description of the experimental design and harvest treatments can be found at: http://emend.ualberta.ca.

2.3 | Understory vegetation data

At each permanent sample site, understory vascular plants were surveyed in: a 5×5 m quadrat for the shrub layer (all woody species, including tree seedlings or saplings <5 cm diameter at 1.3 m height), and a nested 2×2 m quadrat, for the herbaceous layer, including graminoids, forbs, and prostrate or trailing woody species. Given our focus on understanding the value of retention, quadrats in the retention harvesting treatments (10%, 20%, 50%, 75%) were located in the retention strips, not the machine corridors, which studies have shown can be quite similar to clearcuts in terms of understory cover and composition (Craig & Macdonald, 2009; Halpern et al., 2012). A visual estimate of percentage ground cover was made for each vascular plant species as the vertical projection of ground surface covered by the species within the appropriate quadrat. Use of experienced personnel combined with intensive training helped to ensure consistency and minimize bias. All vascular plants encountered were identified to species, either in the field or the laboratory. Understory surveys were conducted during peak vegetation cover (July–August) in 2001, 2004, 2009–2010, and 2015, corresponding to 3, 6, 11 and 17 years post-harvest. Time and logistical constraints encountered at the time of establishment of EMEND were such that only ~half of the plots we use herein were sampled in the pre-harvest year; we, therefore, used the unharvested compartments, for each forest cover type at each sampling time, as the reference. Nevertheless, earlier analysis of pre-harvest understory vegetation (the same metrics employed herein) for three of the four forest types (DDOMU missing) reassures us that there were no differences among compartments later assigned to different harvesting treatments (Fenniak, 2001).

2.4 | Statistical analyses

Understory (ground layer) vegetation response variables included: (1) abundance (sum of percent cover of individual species within a plot); (2) species richness (number of species per plot); (3) diversity (calculated as the reciprocal of Simpson index $\left(1/\sum Pi^2\right)$, where P_i is the proportional abundance (cover) of each species in a sample); and (4) species composition (average cover per species per compartment).

To analyse the changes in understory vascular plant cover, richness, and diversity among harvest treatments with time since harvest, we used linear mixed-effects models that accounted for the repeated measurements over time. The fixed factors were: retention harvest treatments, time since harvesting and their interaction; compartment, representing the experimental unit, and plot (sub-sample) within compartment were included as random effects. We specified the first-order autocorrelation structure and used the *corAR1*() function in the models to account for the repeated measurements or temporal autocorrelation (Crawley, 2013). The models were run separately for each forest type because preliminary analyses showed there were significant 3-way interactions among forest type (categorical variable, 4 levels), harvest treatment (categorical variable, 6 levels) and time since harvest (categorical variable, 4 levels). Separate analyses were performed for cover for the following vegetation categories: total (all vascular plant species pooled), tall woody (including shrubs plus tree species for which height in the plot was >1.5 m height but <5 cm diameter at 1.3 m height), short woody (including erect shrub species or trees of height <1.5 m), forbs (forbs plus prostrate or trailing woody species) and graminoids (included grasses and sedges). The linear mixed-effect models were performed by use of the *lme* (for cover and diversity; Gaussian distribution) and *glmer* (for species richness; Poisson distribution) functions in the NLME package (Pinheiro et al., 2022) and LME4 package (Bates et al., 2015), respectively, in R version 3.2.1 (R Development Core Team, 2015). The model residuals were checked to see whether they met the assumptions of normality and homogeneity of variance, and no data transformations were deemed necessary. When a main effect or the interaction term from the full model summary was significant ($\alpha = 0.05$), post-hoc tests ($\alpha = 0.05$, adjusted for multiple comparisons) were performed with the *lsmeans* function in the LSMEANS package (Lenth, 2016).

To determine the differences in species composition among retention harvesting treatments with time since harvesting, we used permutational multivariate analysis of variance (PERMANOVA) with the Bray-Curtis distance and 999 permutations. The analyses were done using a matrix of cover per species averaged across the six sampling sites per compartment to account for the fact that plots within compartment were subsamples. This was followed by post-hoc pairwise comparisons among treatments (using *pairwise.perm.manova* function) with a Bonferroni correction of the *p*-value. The PERMANOVA was performed in R using the *adonis* function in the 'Vegan' package (Oksanen et al., 2015).

To examine how the understory community composition in the harvesting treatments differed from that of unharvested reference treatments over time, we calculated the abundance-based total dissimilarity (sensu Baselga & Orme, 2012) using cover per species per compartment (averaged across the six sample plots) and based on the Bray-Curtis index (using the *beta.pair.abund* and *beta. bray* summary function in the 'Betapart' package; Baselga et al., 2021). We calculated the dissimilarity between each replicate harvested compartment and each of the three unharvested reference compartments of the same forest type, for each sampling year separately. For comparison, we calculated the dissimilarity values among the three unharvested (reference) compartment for each forest type, in each sampling year separately; from these, we calculated an overall average dissimilarity among unharvested compartments.

To assess how individual species contributed to variation in community composition among retention levels, we performed indicator species analysis (ISA; Dufrêne & Legendre, 1997). Separate analyses were conducted for each time period in each forest type. The ISA was performed in PC-ORD v.5 (MjM Software Design) with the default settings and the statistical significance of the indicator value for each species determined through Monte Carlo permutations. Given the large number of comparisons we only considered species that had an Indicator Value >25 and $p<0.05$ (sensu Dufrêne & Legendre, 1997). Post-hoc, we described the functional or physiological traits of the indicator species, such as shade tolerance, preferred habitat and successional status.

3 | RESULTS

We recorded 197 understory vascular plant species (122 forbs, 31 graminoids, 44 woody species including shrubs and trees) across the study plots (Table S2). Overall, 95 species were common to all the forest types whereas 27, 9, 27 and 30 species were unique to DDOM (165 species), DDOMU (137 species), MX (156) and CDOM (174 species), respectively.

Understory vascular plant cover, richness, diversity and composition varied among retention treatments and time post-harvest. The two-way interaction between harvest treatments and time since harvest was often significant but specifics varied among forest types and response variables (Table 1; Table S3). In addition to responses to harvesting, cover, richness and diversity also either increased or decreased with time in the unharvested compartments.

3.1 | Retention harvest treatment effects on cover, richness, and diversity

As hypothesized (H_1), the total cover of understory vascular plants tended to increase in the harvested treatments from years 3 to 6, particularly for the lower retention treatments, but then declined or levelled off by year 17 (Figure 2; Table S3). Also as hypothesized (H_2), differences in cover among the harvesting levels were greater in years 6 and 11 post-harvest, after which these differences weakened. Total cover did not differ among treatments (including the reference) 3 years post-harvest in any of the forest-cover types

TABLE 1 Effects of retention harvest treatment (H_{arvest}), time since harvesting (T_{ime}), and their interaction ($H_{arvest} \times T_{ime}$) on understory vascular plant cover, richness, diversity and composition in the four forest cover types. Results for I–III are based on linear mixed-effects models whereas IV are based on permutational analysis of variance (PERMANOVA). Values are *F*-statistic with *p*-values in parentheses.

	DDOM[a]			DDOMU			MX			CDOM		
Variable	H_{arvest}	T_{ime}	$H_{arvest} \times T_{ime}$	H_{arvest}	T_{ime}	$H_{arvest} \times T_{ime}$	H_{arvest}	T_{ime}	$H_{arvest} \times T_{ime}$	H_{arvest}	T_{ime}	$H_{arvest} \times T_{ime}$
I. Cover total	1.775 (0.193)	109. 942 (<0.001)	11.035 (<0.001)	3.705 (0.029)	76.675 (<0.001)	4.973 (<0.001)	0.248 (0.933)	98.803 (<0.001)	1.525 (0.095)	1.671 (0.216)	103.514 (<0.001)	5.682 (<0.001)
Tall woody	1.972 (0.155)	103.933 (<0.001)	8.205 (<0.001)	3.641 (0.031)	50.577 (<0.001)	6.105 (<0.001)	1.866 (0.174)	36.095 (<0.001)	2.047 (0.013)	4.710 (0.013)	55.089 (<0.001)	4.076 (<0.001)
Low woody	0.849 (0.541)	8.573 (<0.001)	4.557 (<0.001)	1.003 (0.457)	11.472 (<0.001)	2.123 (0.009)	0.581 (0.715)	50.788 (<0.001)	2.010 (0.015)	0.340 (0.879)	39.486 (<0.001)	1.525 (0.095)
Grass	4.167 (0.020)	6.337 (0.004)	2.924 (0.002)	1.654 (0.220)	18.053 (<0.001)	2.154 (0.008)	7.049 (0.003)	8.610 (<0.001)	0.945 (0.514)	1.546 (0.248)	12.438 (<0.001)	1.652 (0.060)
Forb	0.673 (0.652)	24.345 (<0.001)	2.616 (0.001)	1.391 (0.295)	26.640 (<0.001)	2.476 (0.002)	0.473 (0.790)	56.596 (<0.001)	1.889 (0.024)	0.331 (0.885)	51.493 (<0.001)	3.514 (<0.001)
II. Richness total	0.490 (0.778)	23.336 (<0.001)	3.927 (<0.001)	1.055 (0.431)	53.699 (<0.001)	2.351 (0.003)	0.271 (0.921)	63.256 (<0.001)	1.597 (0.074)	0.397 (0.842)	60.637 (<0.001)	2.326 (0.004)
III. Diversity total	0.281 (0.915)	4.501 (0.004)	2.928 (0.002)	0.936 (0.492)	8.789 (<0.001)	2.173 (0.007)	0.728 (0.616)	4.941 (0.002)	1.841 (0.029)	0.803 (0.569)	25.517 (<0.001)	2.363 (0.003)
IV. Composition total	3.982 (0.001)	3.857 (0.001)	0.486 (0.999)	3.936 (0.001)	4.296 (0.001)	0.533 (0.999)	3.697 (0.001)	5.690 (0.001)	0.520 (0.999)	3.186 (0.001)	5.211 (0.001)	0.481 (0.999)

[a] Results I–III are from mixed models that included compartment and plot within compartment as random terms to account for the fact that sample plots within compartments were sub-samples (not true replicates). Analyses were conducted separately for the four forest cover types: deciduous (broadleaf)-dominated (DDOM and DDOMU), mixed (MX), and conifer-dominated (CDOM) forests. $\alpha = 0.05$ was used to determine significance. Mean values and post-hoc tests for significant interaction effects are presented in Table S3. Differences in species composition (IV) were analysed by PERMANOVA based on Bray-Curtis distance.

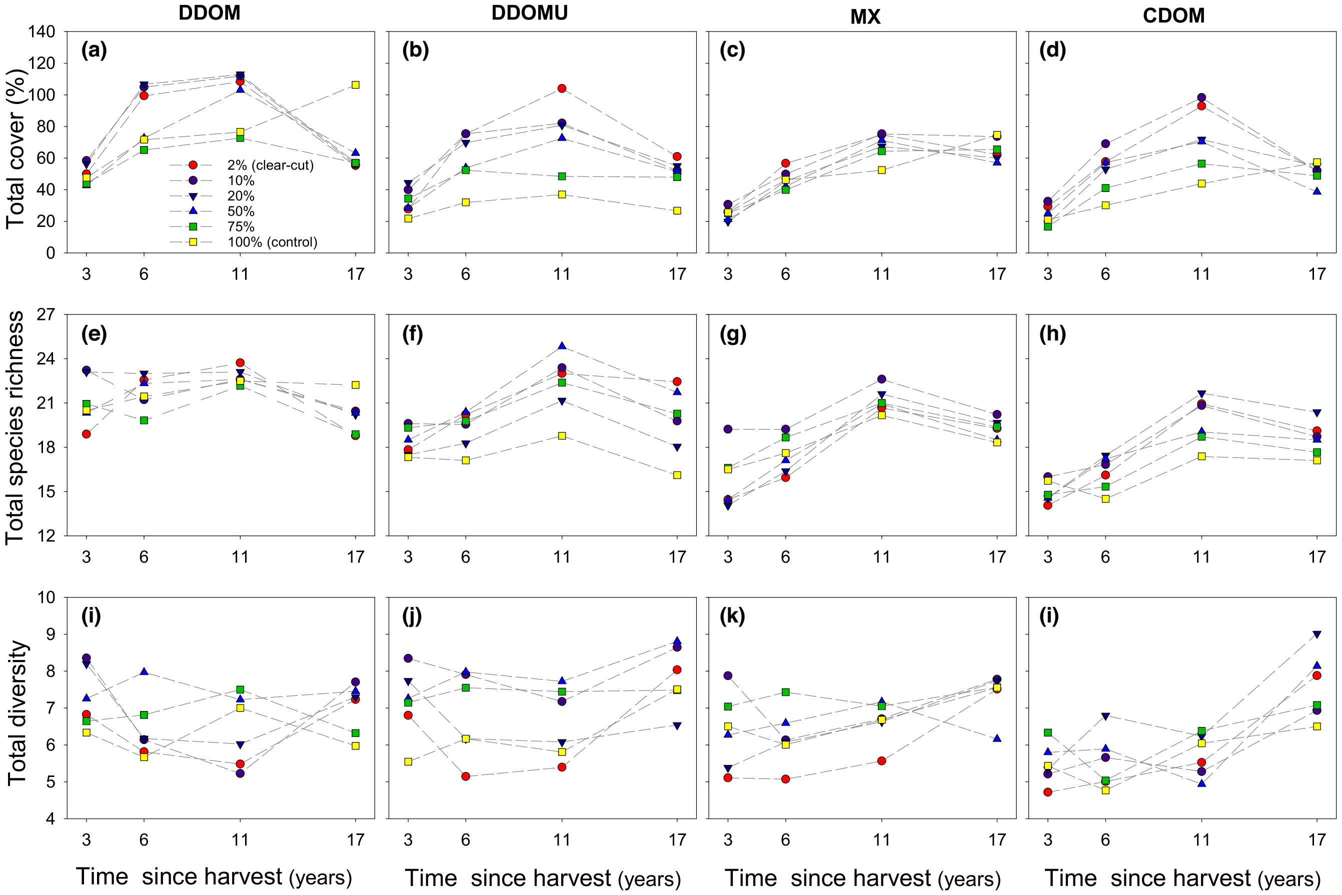

FIGURE 2 Trends in total understory vascular plant cover (a–d), species richness (number of species per plot; e–h), and diversity (inverse of Simpson index; i–l) in relation to retention harvest treatments (2% [clear- cut], 10%, 20%, 50% and 75% retention of original basal area vs. unharvested reference [100% retention]) and time since harvest (3, 6, 11 and 17 years) in DDOM, deciduous (broadleaf)- dominated (DDOM; a, e, i); DDOMU, deciduous-dominated with conifer understory (DDOMU; b, f, j); mixed (MX; c, g, k), and conifer-dominated (CDOM; d, h, l) forest. See Table S3 for summary data (mean and standard error) and results of post-hoc tests for significant interaction effects.

(Figure 2a–d; Table S3). In deciduous broadleaf-dominated forest (DDOM), at year 6 and 11, total cover was higher (10%–30% greater) in the lower (≤20%) retention than in higher (75%, unharvested reference) retention treatments. By year 17 the retention treatments no longer differed from one another but all had lower total cover than the reference, which had increased over time (Figure 2a; Table S3). Similar trends were also evident in the deciduous broadleaf with conifer understory (DDOMU) and conifer-dominated (CDOM) forest types. By year 17 in DDOMU, the retention treatments did not differ from one another but treatments with ≤50% retention still had higher total cover than the reference (by ~50%; Figure 2b; Table S3). For CDOM by year 17 there were no significant differences among treatments, including the reference (Figure 2d; Table S3). In the MX forest type, total cover also increased with time since harvest (6 and 11 years) before declining or levelling off but it never differed among any of the treatments, including the unharvested reference (Table S3; Figure 2c).

Cover of tall woody species, which included shrubs and regenerating saplings, explained much of the temporal trend in total cover for the harvest treatments in the DDOM, DDOMU and CDOM forest types (Figure S1). The trend of increasing total cover over time in the MX forest was underlain by increases in short woody species in the 75% retention and unharvested reference, while graminoid cover increased in the low retention treatments (Figure S1). In CDOM forest, increases in forb cover in the unharvested reference in year 17 helped explain the lack of differences with the harvested treatments at that time (Figure S1; Table S3).

We found some support for our hypothesis (H_1) that species richness (per plot) would increase post-harvesting, particularly in lower retention treatments, and then decline as this was the general trend for all forest-cover types (Table 1; Figure 2e–h; Table S3). However, there was little evidence for increasing differences among retention treatments over time (H_2) as there were very few significant differences among treatments (Table 1; Figure 2e–h; Table S3). For the DDOM forest at year 3, the clear-cut was significantly lower than 10% and 20% retention. For the DDOMU forest in years 11 and 17, the unharvested reference had lower richness than the 50% retention. In the CDOM forest in year 11, the unharvested reference had lower richness than the 20% retention (Figure 2e,f,h; Table S3). In the MX forest, total species richness never differed among the treatments (Figure 2g; Table 1).

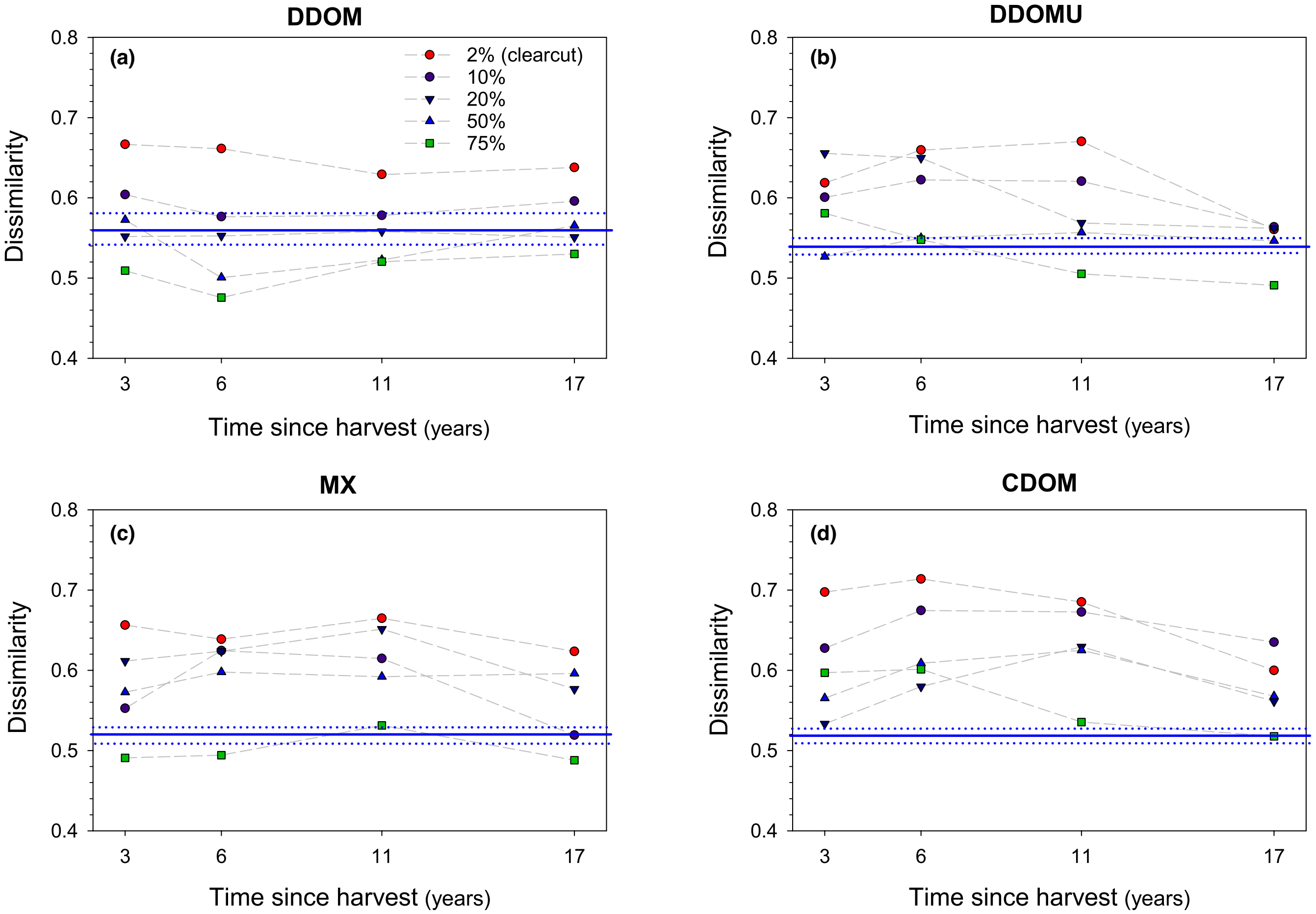

FIGURE 3 Comparison of understory vascular plant community composition, measured as the abundance-based total dissimilarity (based on Bray-Curtis index) between the retention harvest treatments and the relevant unharvested reference at 3, 6, 11 and 17 years post-harvest in (a) deciduous (broadleaf)- dominated (DDOM), (b) deciduous-dominated with conifer understory (DDOMU), (c) mixed (MX) and (d) conifer-dominated (CDOM) forests. Bray–Curtis dissimilarity ranges from 0 (samples with identical species composition) to 1 (samples with no species in common). The horizontal solid blue line shows, for reference, the mean (dashed lines represent 1 SE) dissimilarity among replicate unharvested compartments of each forest type, calculated as three pairwise comparisons within each year separately and then averaged over all 4 years. See also Table S5 for detailed results (mean, standard deviation and standard error) of the dissimilarity values.

The results for diversity did not support our hypotheses (H_1, H_2) as there were no consistent temporal trends and few differences among treatments (Figure 2i–l; Table 1; Table S3). In DDOM and DDOMU, total diversity in lower retention levels (i.e. ≤20%) declined from year 3 to 11 and then recovered by year 17; otherwise it did not vary over time or among treatments for DDOM and very rarely for DDOMU (Figure 2i,j; Table S3). In MX, total diversity tended to increase over time for lower retention levels but very rarely differed among treatments (Figure 2k; Table S3). In CDOM, total diversity increased in all treatments, including the unharvested reference, from year 11 to 17 but very rarely differed among treatments (Figure 2l; Table S3). Responses for diversity did not mirror those of richness but there was a bit of a trend for richness to decline from year 11 to 17 while diversity was tending to increase. This suggests that evenness was increasing and species' relative abundances were becoming more similar as they adjusted to the re-developing canopy.

3.2 | Differences in species composition and indicator species

As hypothesized (H_1) harvesting resulted in community composition that was dissimilar to the unharvested reference and this effect was more pronounced for lower retention levels (Table 1; Table S4). We did not, however, see the hypothesized (H_2) increases and then declines in these differences, as the time by treatment interaction was never significant (Table 1). The clearcut treatment always differed from both the 75% retention and the unharvested reference while the 10% and 20% retention also often differed from these two (Table S4). The three lower retention treatments (clearcut, 10%, 20%) never differed from the 50% retention, the 50% retention never differed from the 75% retention, and the 75% retention and unharvested reference never differed from one another (Table S4). However, the 50% retention differed from the reference for DDOMU, MX, and CDOM but not DDOM (Table S4).

The stronger effect of lower retention levels on community composition (H_1) is also supported by the evidence that dissimilarity between harvested compartments and the unharvested reference tended to be ordered along the gradient of harvesting intensity, while the lack of temporal trends contrasted with our expectation of recovery over time (H_2; Figure 3; see also Table S5). Interestingly, for all forest types the dissimilarity between the 75% retention and the unharvested reference was often comparable to, or even lower than, the average dissimilarity among unharvested compartments (Figure 3).

We found some evidence of stronger effects of harvesting in CDOM and weaker effects in MX. The MX forest showed no effects of harvesting on cover or richness and only two differences between harvesting treatments for diversity; CDOM, however, frequently showed significant effects of harvesting on all three metrics (Table S3). There was no such evidence for species composition (Table S4; Figure 3). Only the DDOM forest type showed some evidence of weaker effects of harvesting, with only the clear-cut having an understory species composition consistently different than the unharvested reference (Figure 3a; Table S4).

The ISA results supported our hypothesis (H_3) that shade-intolerant and early successional species would be associated with lower retention levels while shade-tolerant, mature forest species would be associated with higher retention levels and the unharvested reference (species traits from Aubin et al., 2012; E-Flora, 2021). Indicator species for the lower retention treatments (≤20%) included four disturbance-associated, shade-intolerant species that were indicators for multiple time periods and forest types: *Achillea millefolium*, *Epilobium angustifolium*, *Equisetum sylvaticum* and *Populus tremuloides* (reflecting abundant post-harvest vegetative regeneration; Table S6). Five shade-tolerant, common mature forest species were indicators of higher retention levels (>50%) or the unharvested reference in multiple time periods and forest types: *Cornus canadensis*, *Equisetum arvense*, *Mitella nuda*, *Viola renifolia* and *Pyrola asarifolia*. Other indicators of lower retention levels included shade intolerant forbs and grasses, and common forest understory forbs and shrubs while other indicator species for higher retention levels were common mature-forest forbs and shrubs (Table S6). Four species differed among the forest types in terms of which harvesting levels they were associated with: *Elymus innovatus*, *Linnaea borealis*, *Rosa acicularis* and *Vaccinium vitis-idaea*. We did not see evidence of the hypothesized (H_3) weakening of the association of shade-intolerant, early-successional species with lower retention levels; species were often found to be significant indicators of low retention levels in multiple years, including 17 years post-harvest (Table S6).

4 | DISCUSSION

As hypothesized (H_1), understory vascular plant cover and richness increased following harvesting with differences generally following the gradient of harvesting intensity. In contrast to expectations, diversity did not follow these trends. This suggests there were complex dynamic changes in species' relative abundances affecting evenness. We had expected the opening up of the canopy in these mature closed-canopy forests to lead to increased cover and richness, especially of shade-intolerant plant species, with responses scaling according to harvesting intensity (Halpern et al., 2012; Roberts & Zhu, 2002; Soler et al., 2016; Vanha-Majamaa et al., 2017). However, we did not see differences in cover and richness until year 6, even in the clearcut treatment which had experienced some ground disturbance during harvesting. This concurs with earlier studies that found retention harvesting had little or no effect on understory cover, richness, or diversity immediately after harvest (Macdonald & Fenniak, 2007; Roberts et al., 2016; Sullivan et al., 2001; Tatsumi et al., 2020). This absence of early effects of harvesting suggests a lagged response of the understory to the changed environmental conditions associated with harvesting (e.g. increased light transmission). While the mechanisms are not fully known, this could be attributed to several factors, including the degree of tolerance of individual species to resulting environmental conditions (microclimate) created by harvesting, seed bank persistence, as well as the balance between rates of colonization and extinction of constituent species. Earlier studies of this experiment highlighted the importance of ecological inertia or ecosystem memory, which manifest as a strong association of pre-harvest stand basal area and early post-harvest understory plant assemblages (Bergeron et al., 2017).

With time following retention harvesting, biotic communities may adjust to the post-disturbance environmental conditions and thus become more different than the unharvested condition before then slowly becoming more similar again as the canopy redevelops (Halpern et al., 2012; Roberts et al., 2016; Soler et al., 2016; Vanha-Majamaa et al., 2017). Trends in cover were consistent with our hypothesis (H_2) that differences in understory cover among harvesting treatments would increase over the first decade post-harvest as the understory adjusts to the varying levels of canopy retention, but these trends were weak or nonexistent for richness and diversity. By 6- and 11-years post-harvest understory vascular plant cover was 1.5 to 2 times higher in lower (≤50%) retention levels than in 75% retention or the reference. This was the trend for all but the mixed (MX) forest type, for which there were never any effects of harvesting on understory cover; this supports previous evidence, that understory plant communities of mixed forests are less sensitive to the effects of harvesting (Echiverri & Ellen Macdonald, 2020; Macdonald & Fenniak, 2007). It is likely that the positive effects of harvesting (in terms of increased resource availability) on understory vascular plant cover and richness begin to manifest at 6 to 11 years post-harvest after an initial lag, especially as open-habitat species colonize and dominate available growing space and resources (Halpern et al., 2012; Roberts et al., 2016). In our case, as revealed by the ISA, the almost exclusively perennial understory community at this stage following harvesting was dominated by both shade-intolerant and tolerant species that either resprouted after disturbance or germinated from a persistent seed bank that was relatively undisturbed during harvesting.

The fact that the harvest levels (clearcut to 75% retention) rarely differed from one another for cover, richness or diversity runs counter to the presumed benefits of retention (vs. clear-cutting) such as moderating the harvest-related loss of species, facilitating faster recovery and maintaining both closed-forest and open-forest associated species (Fedrowitz et al., 2014; Rosenvald & Lohmus, 2008; Rudolphi et al., 2014). However, the results for understory composition suggest higher levels of retention might be of some benefit. Retention levels from clearcut to 20% retention showed similar community composition that differed from the 75% retention and unharvested forest. The 50% retention treatment was intermediate, often not differing from higher or lower retention levels but still differing from the unharvested. Further, dissimilarity between harvested treatments and the unharvested reference generally followed the gradient of harvesting intensity and showed little recovery over the 17 years. This suggests retention provided a benefit in terms of conserving understory vascular plant communities but that recovery towards the unharvested condition is slow.

Previous studies have suggested that retention harvesting can result in recovery for at least some groups of understory plants within 8–11 years post-harvest (Halpern et al., 2012; Soler et al., 2016; Vanha-Majamaa et al., 2017), while others show that substantial differences are longer-lasting, especially for sensitive plant species (such as shade-tolerant, late-seral herbs; Blair et al., 2016; Halpern et al., 2012; Roberts et al., 2016; Vanha-Majamaa et al., 2017). Our results concur with previous studies, which showed continuing effects of harvesting, even with retention, on community composition 11+ years post-harvest (Roberts et al., 2016) and that higher levels of retention (≥40%) are needed to confer a conservation benefit (Halpern et al., 2012; Johnson et al., 2014). Overall, these results imply that species composition, unlike cover, richness and diversity, may take a long time to recover after harvesting, as also suggested previously (Hu et al., 2018), although future longer-term studies will be needed to quantify this.

Typically, increases in species richness and diversity following retention harvests are driven by colonization of ruderal species, including early successional and disturbance-dependent species, while forest-interior species might continue to persist (Roberts et al., 2016; Vanha-Majamaa et al., 2017) or might decline (Halpern et al., 2012). As expected, we found that disturbance-associated and shade-intolerant species were associated with lower retention treatments while mature-forest understory species, including shade-tolerant forbs, were associated with higher retention treatments and the unharvested reference.

The trends in understory vascular plant dynamics in response to harvesting differed among the four forest types, in general agreement with previous findings in boreal mixedwood forests (Hart & Chen, 2008; Macdonald & Fenniak, 2007). This reflects differences in effects of harvesting and subsequent stand regeneration on the understory environment. For cover, richness and diversity mixed forests showed very few differences among harvesting treatments, including the unharvested reference, but they showed no better recovery of species composition than the other forest types. The trend in conifer forests showed recovery of cover, richness and diversity (for the most part) comparable to the other forest types, but just as poor recovery of species composition.

The observed temporal trends were against a background of variation in the unharvested compartments of each forest type, underscoring the dynamic nature of natural forest stands and their constituent understory plant communities (Hart & Chen, 2006). The deciduous-dominated, mixed and conifer- dominated (DDOM, MX, CDOM) forest types all showed increasing total understory cover in the unharvested references over time. Given that the stands were at a mature age at the time the study began, this could reflect canopy break-up (Xing et al., 2018), which would result in increased resource availability for the understory. At the same time, the harvested stands were experiencing prolific vegetative regeneration of aspen (Gradowski et al., 2010), which would have greatly reduced light to the understory (Lieffers et al., 1999), suppressing ground layer vegetation. The end result for the deciduous-dominated forest type was that understory cover in the reference forest at year 17 was higher than in any of the harvested treatments. The decline in understory cover by year 17 in the deciduous broadleaf with conifer and the conifer forest types was likely similarly driven by aspen regeneration plus the influence of the white spruce on light and other microenvironmental conditions in the understory (Légaré et al., 2005; Lieffers et al., 2002; Messier et al., 1998). The temporal patterns for the unharvested treatments highlighted the dynamic nature of understory vegetation in these boreal forest stands, and the importance of having contemporary controls for assessing temporal patterns in responses to harvesting treatments.

This study provides important new insights into the potential benefits of retention harvesting for conserving understory vascular plants in boreal mixedwood forests. Overall, the benefits of retention harvesting, versus clear-cutting, on understory cover, richness, and diversity were relatively weak and short-lived. Species composition, however, is arguably a much better metric for assessing harvesting effects on biodiversity (e.g. as it accounts for increases in richness associated with early-seral species) and those results showed that higher retention levels (>50% retention) provided a benefit in terms of conserving understory communities. Still there was evidence for long-lasting impacts of harvesting, indicating that recovery to the unharvested condition will take more time; this will be further complicated by the variable regeneration dynamics of different forest types. Conservation of understory plant communities will thus likely require: high levels of retention, retention left in aggregated patches (perhaps with surrounding dispersed retention; Baker et al., 2016; Franklin et al., 2018; Halpern et al., 2012), or land-sparing approaches. Species of conservation concern will require special attention and any retention harvesting approach will need to consider effects on a broad suite of biotic groups and other forest values. We emphasize the importance of longer-term studies as a basis for management guidelines aimed at biodiversity conservation.

AUTHOR CONTRIBUTIONS

S. Ellen Macdonald, along with the other original investigators in the EMEND experiment, conceived of the project, designed the experiment and supervised data collection. Samuel F. Bartels analysed the data and led the writing of the manuscript. Both authors contributed equally to developing hypotheses, planning the data analyses, drawing inferences from the results, contributed critically to the drafts, and gave final approval for publication. *Statement on inclusion*: The two authors originate from different countries (Ghana, Canada), one of which is the country the study was conducted in (Canada). The EMEND experiment has, from the outset, involved extensive collaboration with stakeholders, including the provincial government, industrial partners and forestry community advisory groups.

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CONFLICT OF INTEREST STATEMENT

Both authors declare they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.dncjsxm3x (Bartels & Macdonald, 2023).

ORCID

Samuel F. Bartels https://orcid.org/0000-0003-2676-3295

S. Ellen Macdonald https://orcid.org/0000-0003-1750-1779

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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