Boreal songbirds and variable retention management: a fifteen-year perspective on avian conservation and forestry

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Boreal songbirds and variable retention management: a fifteen-year perspective on avian conservation and forestry

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Abstract

Partial retention harvest (PRH) has received attention as an alternative to clear-cutting yet most studies of its effects on boreal songbirds have been conducted shortly after harvest. We assessed responses of songbird assemblages to PRH over a 15-year post-harvest period at the EMEND experiment in the mixedwood forest of Alberta, Canada. Four partial retention levels (10, 20, 50 and 75% of stems) were applied in a series of ten-hectare “compartments” during winter 1998/99 with matching clear-cuts and unharvested control compartments in each of three replicates in four common mixedwood cover-types. Songbirds were surveyed using the point count method in 1998 (pre-harvest) and after harvest in 1999, 2000, 2005, 2006, 2012, and 2013. Partial retention harvests that left ≥20% of merchantable stems mitigated changes to songbird assemblages away from, and accelerated recovery toward, the unharvested benchmark. However, assemblages of 14- to 15-year-old controls differed from those observed prior to harvest, notably in composition of old-forest associated species, suggesting effects of experiment-scale processes and/or regional trends not attributable to forestry activities. Although retention levels ≥20% appear to better conserve old-forest birds than clear-cutting in the short term, long-term trade-offs with increasing harvest footprint to compensate for unharvested merchantable volume should be investigated.

Key words:
Forest management, Dispersed retention, Natural disturbance emulation, EMEND, Boreal songbird conservation
Introduction

The boreal forest provides breeding habitat for many Nearctic birds, earning it the moniker “North America’s bird nursery” (Blancher and Wells 2005). In the western boreal forest, both chronosquence studies (e.g., Schieck and Song 2006) and long-term longitudinal studies (e.g., Leston et al. 2018) have demonstrated the relationships between forest age and species turnover, and particularly the importance of older unharvested forest for species specializing on old forest habitats. The rapid increase of development and resource extraction in boreal forests throughout Canada since the 1990s, including the disturbance and/or fragmentation of older forests, has resulted in significant conservation concerns for boreal birds (Wells 2011).

Partial retention harvest (PRH) has been widely promoted as an alternative to clear-cutting to balance economic objectives with conservation goals (Gustafsson et al. 2012). Residual trees left within cutblocks emulate the spatial variability of post-fire legacies (Perera and Buse 2014), contributing to stand structural complexity and providing future sources of seeds, snags, and dead wood (Franklin et al. 1997). Landscape variation in residual tree density and arrangement is intended to promote the mosaic-like patterns of a burned forest, if not the ecological processes of wildfire (Hunter and Schmiegelow 2011).

The Ecosystem Management Emulating Natural Disturbance (EMEND; www.emendproject.org) experiment was established to compare effects of clear-cutting, PRH, and prescribed burning with unharvested controls on operation-sized blocks over a full harvest rotation of 80–100 years (Spence et al. 1999). While several studies have assessed the short-term effects of PRH on songbirds in the boreal forest (e.g., Harrison et al. 2005), long-term experimental studies are rare. The objective of this paper is to assess the effects of clear-cutting and PRH on songbird assemblages over a 15-year post-harvest period and compare these to
unharvested controls at EMEND. Unharvested controls were used as a benchmark for forest exceeding the rotation age: comparable bird data from experimentally burned stands were not available, and unharvested forest provides a useful reference for evaluating long-term recovery of boreal forest songbirds.

**Methods**


Harvest treatments (clear-cut (2%), 10%, 20%, 50%, 75% retention, or uncut controls) were applied to c. 10-ha compartments in four dominant tree cover-types (deciduous, deciduous with spruce understory, mixedwood, and coniferous). Harvest treatment by cover-type combinations were replicated three times (overall *n* = 72). Compartments were harvested in the winter of 1998/99 and allowed to regenerate without intervention.

**Data collection**

One or two point count stations were established in each of the 72 compartments in 1998 (*n* = 107). Stations were ≥50 m from compartment boundaries and ≥150 m apart where two
stations occurred in the same compartment. Breeding songbirds were surveyed at these stations in 1998, 1999 and 2000 (Harrison et al. 2005), 2005 and 2006 (F.K.A. Schmiegelow, unpubl. data), and 2012 and 2013.

This study is focused on songbirds (Order Passeriformes); however, pine siskins (*Spinus pinus*) and white-winged crossbills (*Loxia leucoptera*) were excluded due to concerns regarding irruptive and grouping behaviours, and corvids (Family Corvidae) were excluded because their territory sizes exceed the size of study compartments. Auditorily trained observers conducted unlimited-radius 5 min. point counts (Bibby et al. 2000) at each station between 0500–1000h, estimating distances to 50-, 100-, and >100-m intervals, over three survey rounds from late May to early July in all years (Harrison et al. 2005). Only observations within 50 m were analysed to increase spatial independence of data from each station and limit possible biases due to differences in detection rates over larger areas (e.g., Morissette et al. 2018). Observers alternated compartments among rounds to reduce potential observer bias.

Coniferous (softwood) and deciduous (hardwood) tree densities (Langor et al. 2006), and average sapling and shrub densities and heights (Macdonald and Volney 2007) were included to provide insight on stand-level vertical structure. Forest mensuration data were collected from six permanent 40x2 m strip plots randomly located in each EMEND compartment, and shrub data were collected from two 10x2 subplots at either end of each permanent plot, at approximately five-year intervals (for more details see Pinzon et al. 2016).

**Data analysis**

Species observations were summarized by taking the maximum count over the sampling rounds for each point count station (Toms et al. 2006), and the mean of the maximum observed abundance where two stations occurred in the same compartment. For most analyses, species
abundances were averaged for each pair of years (e.g., 1999 and 2000), and pairs of years were
treated as factors (time period). However, 1998 (the pre-harvest year) was considered a single
time period in all cases.

All analyses were performed in R (R Core Team 2018) unless otherwise noted.

Multivariate analysis of species composition change was performed with package “vegan”
(Oksanen et al. 2018), using redundancy analysis (RDA) of Hellinger-transformed species counts
(Legendre and Gallagher 2001). Species with \( \leq 2 \) total observations were removed prior to
analysis (McCune and Grace 2002). The species matrix was ordinated in response to forest
cover-type and a dummy variable representing the time period–treatment combinations to enable
inclusion of the pre-harvest year. Significance tests of model terms and ordination axes were
performed by permutation \( (n_{\text{perm}} = 999; \alpha = 0.05) \). Vectors representing environmental variables
were plotted \textit{a posteriori} on the ordination plot to indirectly examine the relationships between
species composition, experimental treatments, and forest structure (e.g., tree and shrub densities
and heights).

A second RDA following the same procedure was applied to the subset of species
considered “old forest associated” (Schiek and Song 2006) to verify whether overall species
composition changes potentially masked strong responses by rare and/or more disturbance-
sensitive species.

The RDAs described above provide a more complete picture of changes to species
composition relative to multiple treatment and environmental factors, but do not statistically
account for background changes to species composition within the unharvested controls.

Principal response curves using package “vegan” were used to verify the response of species
composition to harvest treatments over time relative to the controls (van den Brink and ter Braak

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Species counts were Hellinger-transformed and only post-harvest data were analysed due to collinearity between the pre-harvest time period and treatments. Species richness was estimated using coverage-based rarefaction (Chao and Jost 2012) with package iNEXT (Hsieh et al. 2016). Rarefaction provides richness estimates given an incomplete sample, and more generally, given imperfect detection within the sample (Chao and Jost 2012). “Coverage” refers to percent sampling completeness, estimated using the number of species that are observed ≤2 times in each sample (i.e., uncommon species). This rarefaction method discards fewer data than traditional individual-based rarefaction and provides less biased comparisons between assemblages (Chao and Jost 2012). Species richness was standardized to the minimum coverage across all samples; 95% bootstrap confidence intervals were calculated for each estimate using the 500 permutations. Non-overlapping confidence intervals indicate statistical significance at $\alpha \leq 0.05$ (Chao and Jost 2012).

Results

Species richness ($S$), rarefied to 96% sampling coverage, was 31.1 ± 1.77 (mean ± 95% CI) on average across all sites in the year prior to harvest (Fig. 1). Richness decreased significantly by 9.8 species in the clear-cuts ($S = 21.3 \pm 3.06$) and marginally by 4.7 species at 20% retention ($S = 26.3 \pm 2.82$) in the first two years post-harvest. After 7–8 years, richness increased significantly by 5.1 (75% retention) to 8.6 (unharvested) species ($S = 36.1 \pm 3.0$ and $39.7 \pm 3.4$, respectively) across all stands with ≥10% retention, with the exception of those with 20% retention, which gained only 3.4 species ($S = 34.5 \pm 2.70$). After 14–15 years, richness stabilized in three harvest treatments relative to the controls, with 1.2 ± 1.8, 3.3 ± 2.1, and 4.6 ± 2.8 more species in the clear-cuts, 20%, and 10% retention treatments, respectively; richness remained significantly higher by 4–6 species at both 50% and 75% retention ($S = 35.1 \pm 1.7$ and
37.2 ± 2.5, respectively). These two treatments continued to be characterized by high numbers of
15 species not observed in these blocks prior to harvest but which were seen at least once 14–15
years post-harvest. These observations included mourning warbler (Geothlypis philadelphia),
aldoer flycatcher (Empidonax alnorum), American robin (Turdus migratorius), and cedar
waxwing (Bombycilla cedrorum).

The RDA model of Hellinger-transformed species counts had an adjusted $R^2=0.26$
(overall proportion of variance explained). The first two canonical axes (Fig. 2) respectively
explained 36.9% and 29.5% of the constrained variance. Although statistically significant, axes
3–10 each accounted for less than 5% of the total variance. Tree cover-type (variance = 0.044, F
= 9.44, df = 3, p = 0.001) and the variable representing the combined effects of harvest treatment
and time period (var = 0.14, F = 5.18, df = 17, p = 0.001) were both included in the final model.
Ordination plots include ellipses representing one standard deviation around group centroids
(i.e., the average position of sites predicted for each treatment (Kindt and Coe 2005)) for each of
the three time periods: 1–2, 7–8, and 14–15 years after harvest (Figs 2a, b, and c, respectively).
Ellipses similarly represent the four cover-types (coniferous, mixed, deciduous with understory,
and deciduous) in Fig. 2d.

Species composition clearly changed relative to the controls as retention level decreased,
with the greatest differences observed in the clear-cuts (Figs 2a–c). Interaction between
treatment and time period is evident, as species composition in the harvested stands shifted from
negative to positive RDA2 values over time. Overlap among treatments similarly increased over
time, and considerable overlap is evident after 14–15 years—by this time period, overlap is
evident between the unharvested controls and compartments with 20–75% retention (Fig. 2c).
Interestingly, species composition differed between the pre-harvest stands and post-harvest
controls (Figs 2a–c), indicating changes over time in unharvested stands. Overlap between pre-
harvest stands and controls was lowest after 14–15 years (Fig. 2c).

The effect of cover-type follows a smooth gradient as the proportion of coniferous trees
increases. The moderate overlap at positive RDA1 values—coinciding with the plot area
occupied by clear-cuts and lower-retention treatments (Figs 2a–c)—illustrates the reduced
relationship between the original tree cover-type and species composition in stands of higher
harvest intensity (Fig. 2d).

For illustrative purposes, only species farthest from the origin were plotted to reduce
congestion (Fig. 2e). Where a vector’s angle from the origin closely matches the angle of another
plotted variable (including another species), their influences are positively correlated; vectors at
a 90° angle indicate no relationship, and where the vectors pull in opposite directions (180°) their
influences are negatively correlated (Legendre and Legendre 2012). At negative RDA1 values,
several species are positively correlated with unharvested stands, including golden-crowned
kinglet (GCKI, *Regulus satrapa*), yellow-rumped warbler (YRWA, *Setophaga coronata*), and
red-breasted nuthatch (RBNU, *Sitta canadensis*). Dark-eyed junco (DEJU, *Junco hyemalis*) and
several other sparrows characterise sites at high RDA1 and negative RDA2 values; this plot
region roughly corresponds with clear-cuts and low-retention stands in the first two post-harvest
years. Alder flycatcher (ALFL) characterises clear-cuts and low-retention stands 7–8 years after
harvest. Several species are positively correlated with 14- to 15-year-old low retention stands
including Tennessee warbler (TEWA, *Oreothlypis peregrina*), red-eyed vireo (REVI, *Vireo
olivaceus*), and least flycatcher (LEFL, *Empidonax minimus*). For a list of species codes see
Table 1.
Environmental vectors fitted *a posteriori* (Fig. 2f) suggest relationships between tree and shrub densities, species composition of songbirds, and treatment effects. Understandably, coniferous and large-diameter (>30 cm DBH) deciduous tree densities are strongly correlated with pre-harvest and unharvested sites. Strikingly, the lower half of the plot has almost no vectors, illustrating that as expected, clear-cuts and low-retention stands were negatively correlated with woody structure immediately post-harvest (Figs 2a, f). At positive RDA1 values and near RDA2 = 0, deciduous saplings appear to have dominated 7- to 8-year-old clear-cuts and low-retention stands, to the exclusion of most other woody vegetation (Figs 2b, f). After 14–15 years, shrubs and medium-diameter deciduous trees characterized harvested stands, while clear-cuts in particular were associated with tall deciduous saplings (Figs 2c, f). Interestingly, the position of the ellipse representing coniferous-dominated stands (Fig. 2d) indicates a strong negative relationship with shrub densities and heights, rather than a positive relationship with the density of coniferous trees (Fig. 2f).

The second RDA analysing only old-forest associated bird species showed a different trajectory of change over time (adjusted $R^2 = 0.17$) (Figs 3a–c). Immediately post-harvest, the size of the treatment ellipses decreased with decreasing retention levels, indicating a contraction of the species pool rather than a directional change (Fig. 3a). However, the subsequent two time periods revealed strong overlap among the 75% harvest and control compartments (the ellipse representing the control compartment almost completely hidden by the 75% retention ellipse), with increasing divergence seen in the lower retention levels, particularly $\leq 20\%$ retention (Figs 3b,c). Species associated with these lower retention levels include the blue-headed vireo (BHVI, *Vireo solitarius*), which typically nests below the canopy in forests with a well developed layer of shrubs and small trees (Morton and James 2014), and the Swainson’s thrush (SWTH,
Catharus ustulatus), which may be present but uncommon in younger forests (Schieck and Song 2006) (Fig. 3e). For a list of species codes see Table 1.

Verification using Principal Response Curves ($R^2 = 0.17$) confirmed the treatment patterns observed in the RDA of the full species set (Figs 2a–c). With background changes over time in the unharvested controls statistically accounted for, recovery of species composition after 14–15 years was evident, most strongly in the 20–75% retention treatments (Fig. 4). Individual species responses to the treatments follow expected patterns, with known old-forest species associated most strongly with unharvested controls. Notably, the strongest response was observed with the Ovenbird, a species categorized as a forest generalist by Schieck and Song (2006), which had the strongest association with unharvested stands. The thick leaf litter resulting from dense aspen regeneration in harvested stands might be expected to provide suitable habitat for this ground-nesting species. However, the high shrub regeneration observed in partial retention compartments (see Fig. 2f) may have reduced habitat quality for this species, which is generally associated with low understory cover (Porneluzi et al. 2011).

**Discussion**

Results of this study encourage optimism about use of PRH for conservation of boreal songbirds: ≥20% green tree retention mitigated harvest effects and accelerated species composition recovery toward the unharvested benchmark. In contrast, clear-cuts and stands with <20% retention supported different species compositions that changed substantially over a 15-year period with weaker convergence toward assemblages in the controls. However, the responses of species associated with old forests suggest that large unharvested areas remain an important component of landscape-level management.

*Partial retention harvest improves overall recovery and heterogeneity*
The changes in species composition over time highlight the role that a range of retention treatments can play in creating habitat to maintain a wide number of species. Increased species richness after 7–8 years supports this conclusion, although species losses in the first two years remind us that despite increasing the breadth of species composition, harvest leads to short-term reductions in local occupancy by pre-harvest species. The question is whether forest songbird assemblages will recover over time to conditions that would be fostered on unharvested landscapes.

In this light, it is worthwhile to re-examine the objectives of PRH, and by extension, the concept of emulating spatial natural disturbance patterns (Hunter 1993). Cyr et al. (2009) report that young forest stands are highly over-represented in the eastern boreal forest, compared with naturally-disturbed landscapes of the past; the western boreal forest, however, has a much higher historical fire frequency than eastern forests (Bergeron and Harper 2009). Given a relatively low expected proportion of stands >100 years within the boreal plains (23%; Bergeron and Harper 2009), two potential benefits of PRH become apparent. Where stands exceeding the rotation age are under-represented relative to the natural range of variation, it appears that habitats that support species composition of unharvested forests will be more quickly re-established by leaving ≥20% retention in some cutblocks (with caveats; see below).

Regions containing higher than expected proportions of old forest present opportunities to employ a range of harvest treatments, including partial retention and clear-cuts, to support a wider range of species by maintaining more diverse woody vegetation and vertical structure. However, the latter hypothesis would strongly benefit from explicit comparisons of PRH blocks and landscapes with burned forests of the same age class. It is unfortunate that it was not possible to make these comparisons with the existing bird dataset collected at EMEND, and research to
further test differences in species assemblages between burned and PRH forests are recommended (particularly longer-term studies). Other studies in western forests suggest that variable retention strategies support several bird guilds typical of postfire stands (e.g., shrub nesters), yet do not provide suitable habitat for species specializing on burned habitats (e.g., black-backed woodpeckers (*Picoides arcticus*) (e.g., Van Wilgenburg and Hobson 2008).

These findings indicate that regardless of harvest strategy, fire must continue to play an important role in western forests, particularly if management has reduced wildfire frequency well below the natural range of variation. Future studies of combined strategies including PRH and post-harvest prescribed burn may be of interest to determine stand- and landscape-level conditions necessary to maintain fire-associated species while balancing economic demands.

*Large areas of old forest remain important*

Species composition, particularly that of old-forest associated species, changed over time in the unharvested controls relative to the pre-harvest condition. While the overall treatment effects relative to the controls were not affected by these changes (Fig. 4), these results raise the possibility that 10-ha compartments are of insufficient size to prevent songbird species composition change within a harvested landscape. Changes in regional songbird populations may also be partially responsible for the observed differences, however testing our results against regional population trends was outside the scope of this study.

While it is possible that background population changes were responsible for the changes observed in the unharvested controls, it seems much more likely that unharvested reserves ≤10 ha are inadequate for maintaining old forest assemblages within a young harvested landscape (e.g., Schmiegelow et al. 1997). Forest edges support higher bird diversity than forest interior (Šálek et al. 2010) and increases of early-seral and generalist species may have contributed to
increased richness in EMEND compartments. Additionally, many of the species categorized as old-forest associates are known or suspected to be area-sensitive, including the bay-breasted warbler and black-throated green warbler (>100 ha old forest recommended; AESRD 2014) and Canada warbler (>100 ha patches recommended; AESRD 2014).

Recommendations about reserve size must be carefully weighed against the increased footprint that will result on harvested landscapes if green tree retention is increased while maintaining harvest volumes. Regardless, incorporation of PRH will challenge policy-makers and forest managers to balance conservation goals (e.g., old forest species vs. increased biodiversity), spatial footprint, and socio-economic impacts.

Conclusions

PRH was associated with a number of positive effects on songbird species composition relative to clear-cut harvesting in 10-ha study compartments. A range of harvest retention levels will likely contribute to overall biodiversity by supporting a wider range of species than clear-cuts and unharvested forest alone, or a single target retention level, and more closely emulate the variable conditions resulting from mixed-severity fire regimes. While ≥20% retention is a promising management strategy to promote more rapid recovery of assemblages of unharvested forest, large unharvested areas will remain important for conserving the most sensitive old-forest associates. Research in larger (>10 ha) partial retention stands is a logical next step to determine to what extent the small cutblocks at EMEND influenced patterns of avian assemblage change. Species composition change in small unharvested fragments is of concern on an increasingly fragmented landscape.

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References


## Table 1. Key to species codes from Figs 2e and 3e.

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Figure 1. Species richness estimates rarefied to 96% sampling coverage for each time period and treatment, with 95% bootstrap confidence intervals.

Figure 2. Redundancy analysis (RDA) of Hellinger-transformed species counts in response to retention level (treatment). Ellipses illustrate assemblage responses to harvest treatments a) 1–2 years, b) 7–8 years, and c) 14–15 years after harvest, as well as responses to d) tree cover-type (CD = coniferous, MX = mixedwood, DU = deciduous with spruce understory, and DD = deciduous). Species responses are shown in plot e), and vectors representing post hoc correlations of environmental vectors are shown in plot f). Note that a single ordination analysis was performed and variables are illustrated separately in each panel for clarity.

Figure 3. Redundancy analysis (RDA) of Hellinger-transformed species counts of old-forest associated species in response to retention level (treatment). Ellipses illustrate assemblage responses to harvest treatments a) 1–2 years, b) 7–8 years, and c) 14–15 years after harvest, as well as responses to d) tree cover-type (CD = coniferous, MX = mixedwood, DU = deciduous with spruce understory, and DD = deciduous). Species responses are shown in plot e), and vectors representing post hoc correlations of environmental vectors are shown in plot f). Note that a single ordination analysis was performed and variables are illustrated separately in each panel for clarity.

Figure 4. Principal response curve of Hellinger-transformed post-harvest species counts in response to retention level relative to the unharvested controls.
Pre-harvest

1-2 years
Clear-cut*
10%
20%*
50%
75%
Control

7-8 years
Clear-cut
10%*
20%
50%*
75%*
Control*

14-15 years
Clear-cut
10%
20%
50%*
75%*
Control

Rarefied species richness (coverage-based)