Stand-level response of breeding forest songbirds to multiple levels of partial-cut harvest in four boreal forest types

R. Bruce Harrison, Fiona K.A. Schmiegelow, and Robin Naidoo

Abstract: We investigated whether impacts on boreal forest songbird communities in northwestern Alberta could be mitigated through a harvesting system that attempts to emulate the local natural disturbance regime. The EMEND (Ecosystem Management by Emulating Natural Disturbance) project is a multidisciplinary experiment to compare clearcuts and partial-retention cuts in four upland cover types with uncut forest and with experimentally burned stands. We studied breeding birds at EMEND between 1998 (pretreatment) and 2000, focusing on their responses to partial harvesting. Partial cuts were generally intermediate (and varied in a linear fashion) between clearcuts and undisturbed forest for community and species measures. Species that declined in abundance in partial cuts were typically dependent on shrubs and trees, whereas species that benefited were typically ground nesters. While partial cutting offered some advantages over clear-cutting in conserving short-term avian diversity, we suggest that low retention levels (i.e., 10%, 20%) cannot be justified from this perspective. The benefits that accrued in these treatments were relatively small, and species that declined or disappeared were typically characteristic of mature forest habitats. Higher retention levels (i.e., 50%, 75%) may conserve some species of concern, but the extent to which these treatments offer productivity advantages over lower residuals requires further study.

Résumé : Les auteurs ont voulu vérifier si les impacts sur les communautés de passereaux forestiers dans le nord-ouest de l'Alberta pouvaient être atténués par un système de récolte qui tente d'émuler le régime local de perturbations naturelles. Le projet EMEND (« Ecosystem Management by Emulating Natural Disturbance », c.-à-d. aménagement écosystémique par l'émulation des perturbations naturelles) est une expérimentation multidisciplinaire visant à comparer les coupes à blanc et les coupes partielles à rétention avec des forêts non coupées et des peuplements issus d'un brûlage expérimental dans quatre types de couverts mésiques. Ils ont étudié les oiseaux nicheurs à EMEND entre 1998 (prétraitement) et 2000 en ciblant leurs réponses à la récolte partielle. Les coupes partielles étaient en général intermédiaires (et variaient selon un profil linéaire) entre les coupes à blanc et la forêt non perturbée en ce qui a trait aux mesures de communauté et d'espèce. Les espèces dont l'abondance diminuait dans les coupes partielles étaient typiquement dépendantes des arbres et arbustes, tandis que celles qui en bénéficiaient étaient des nicheurs au sol. Bien que la coupe partielle offre certains avantages par rapport à la coupe à blanc en conservant à court terme la diversité aviaire, ils ne croyent pas que de faibles niveaux de rétention (c.-à-d. 10 %, 20 %) soient justifiables de ce point de vue. Les bénéfices obtenus par ces traitements sont relativement faibles et les espèces qui ont diminué ou sont disparues étaient typiquement caractéristiques des forêts matures. Des niveaux plus élevés de rétention c.-à-d. 50 %, 75 %) peuvent conserver certaines espèces visées, mais il faudra d'autres études pour déterminer dans quelle mesure ces traitements offrent des avantages en termes de productivité par rapport aux niveaux plus faibles de rétention.

Introduction

The response of forest birds to harvesting has been the subject of considerable research over the past few decades. At the stand level, forest harvesting creates conditions amenable to species favouring early-successional habitats (i.e., Crawford et al. 1981; Thompson et al. 1992) and generally leads to a decrease in the number of habitat dimensions available to birds (DesGranges and Rondeau 1993). In other words, the forest characteristics that create ecological niches for birds are those that are reduced by harvesting: vegetation composition and layering (MacArthur and MacArthur 1961; Franzreb and Ohmart 1978), snags and coarse woody debris (Niemi and Hanowski 1984; Hansen et al. 1991; Westworth and Telfer 1993), and stand age (Schieck and Nietfeld 1995; Kirk et al. 1996).

Received 24 November 2004. Accepted 1 April 2005. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 5 August 2005.

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 doi: 10.1139/X05-076

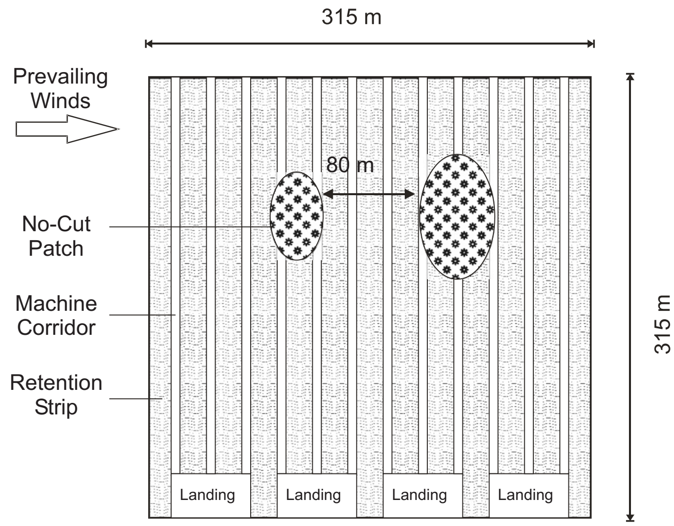
Recently, efforts have been made to mitigate harvesting impacts on ecological integrity through a natural disturbance paradigm, which suggests that critical processes inherent in forest systems might be maintained by emulating natural disturbance patterns (Hunter 1993*a;* Haila 1994; Brawn et al. 2001), for instance, via partial cutting. Natural disturbances such as fire (the major agent of stand replacement in the western boreal forest) typically leave structural legacies of live and dead woody material, reducing the contrast between disturbed and undisturbed stands (Hansen et al. 1991). If partial cutting can leave behind similar legacies, harvesting might better approximate natural patterns (Lee et al. 1997), and the impact of tree removal may be lessened (Merrill et al. 1998; Schieck and Hobson 2000).

The usefulness of the natural disturbance approach at present lacks substantial empirical support. There is debate as to whether logging can effectively mimic fire (DesGranges and Rondeau 1993; Hutto 1995) in terms of site disturbance, soil fertility, and residual snags and woody debris. Comparisons of fire- and logging-origin stands indicate convergence over time for spider communities (Buddle et al. 2000), but only partial convergence in terms of vegetation (Crites 1999) and bird communities (Schulte and Niemi 1998; Hobson and Schieck 1999; Schieck and Hobson 2000; Simon et al. 2002). More specifically, the effects of partial cutting on bird communities have been studied throughout western North America, including areas in the western United States (Franzreb and Ohmart 1978; Medin and Booth 1989; Anderson and Crompton 2002), the Pacific Northwest (Hansen et al. 1995; Beese and Bryant 1999; Hayes et al. 2003), and the British Columbia Interior (Steventon et al. 1998; Lance and Phinney 2001; Leupin et al. 2004). In the boreal mixedwood forest of western Canada, Norton and Hannon (1997), Tittler (1998), and Tittler et al. (2001) examined the effects of group retention harvesting in deciduous-dominated forest in northeastern Alberta. In general, these studies have indicated that partially harvested stands initially retain a portion of the mature forest bird community not found in clearcuts, while still allowing the incursion of some early-successional species.

The EMEND (Ecosystem Management by Emulating Natural Disturbance) project is a multidisciplinary research project initiated in 1995 in northwestern Alberta, Canada. EMEND is an attempt to model harvest and regeneration of upland mixedwood forests on natural disturbance regimes via a comparison of partial-retention cuts (human-caused disturbances) with stands burned at a variety of intensities (natural disturbances). Unharvested controls were also maintained. EMEND represented a good opportunity to test whether traditional logging practices in the boreal mixedwood forest could be modified at the stand level to better accommodate nontimber values, such as avian biodiversity.

In this paper we detail 3 years of field study (1998–2000) of the effects of partial cutting on songbird communities at EMEND, as detected by point count sampling. Six levels of tree retention were examined in four cover types. Based, in part, on trends found in other partial-cut studies in western North America, we predicted that partial cuts would be intermediate between clearcuts and unharvested controls for all community measures, in all forest cover types, and that measures would vary linearly with level of tree retention. We also predicted that guilds and species dependent on shrub or tree cover for nesting and foraging would be most negatively impacted by harvesting and that their abundance would also vary linearly with level of retention.

Fig. 1. Schematic representation of compartmental layout at EMEND, Alberta, Canada.



Materials and methods

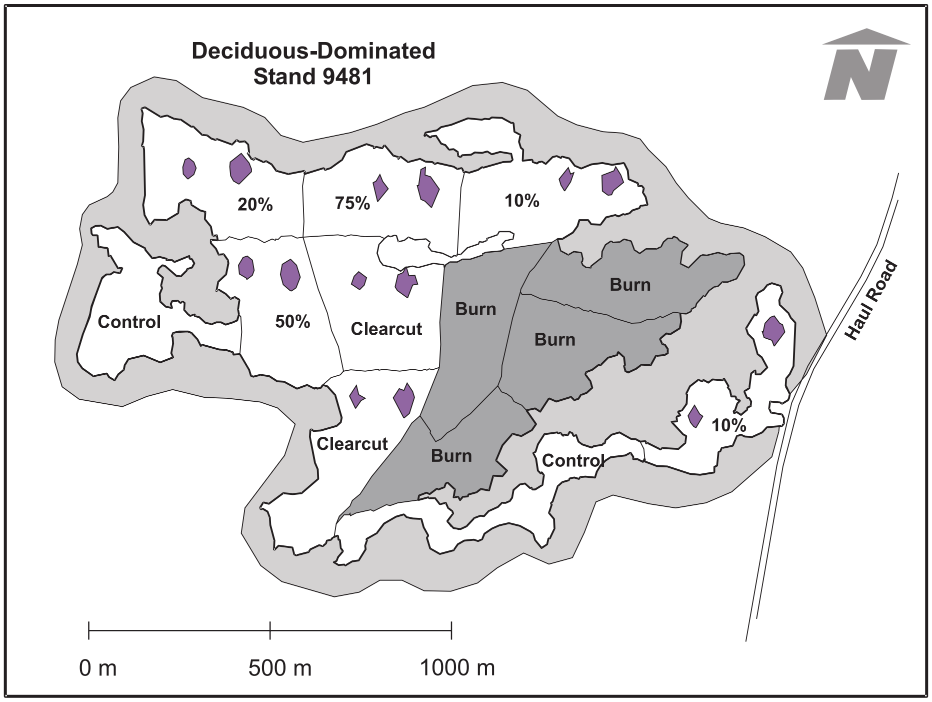
Study area

The EMEND project is located in an area of upland boreal mixedwood forest near Peace River in northwestern Alberta (56°44′N, 118°20′W). Dominant tree species in this region include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). Older stands are characterized by white spruce (*Picea glauca* (Moench) Voss), and wet areas of black spruce (*Picea mariana* (Mill.) B.S.P.) are interspersed throughout the landscape. Understory vegetation on mesic sites is commonly composed of wild rose (*Rosa* spp.), low-bush cranberry (*Viburnum edule* (Michx.) Raf.), and alder (*Alnus crispa* (Ait.) Pursh, *Alnus rugosa* (Du Rois) Spreng.). The topography is generally low and rolling, with some plateaus, and soils are typically luvisolic (Strong and Leggat 1981).

Experimental design

EMEND is a large-scale experiment (>1000 ha) designed to systematically study combinations of two driving variables: forest canopy composition and amount of residual structure left after harvest. Four mature forest cover types were represented: (1) deciduous dominated (80%–95%); (2) deciduous dominated with coniferous understory (extensive and at least 50% of canopy height); (3) mixed (conifer and deciduous composition each 35%–65%); (4) conifer dominated (80%–95%). Deciduous trees were primarily trembling aspen, with a secondary balsam poplar component; coniferous trees were almost exclusively white spruce. Within each cover type, six levels of tree retention were chosen: 0% (clearcut), 10%, 20%, 50%, 75%, and 100% (control). Three replicates of each treatment were selected for

Fig. 2. Example of spatial arrangement of treatment and control compartments in one block at EMEND, Alberta, Canada. Dark polygons within treatment compartments represent retention ellipses. Burn treatments were part of EMEND experimental design, but had not been carried out at the time of this study.



each forest type. Here, we use "retention" and "residual" synonymously.

Site selection occurred in 1997; baseline data were collected in the spring–summer of 1998, and harvesting treatments were implemented in the winter of 1998–1999 in cutblocks or "compartments", each approximately 8–10 ha in size. Harvesting was in a uniform shelterwood strip pattern (Fig. 1), with 15 m wide retention strips separated by 5 m wide machine corridors, oriented in a north–south direction (perpendicular to prevailing winds). Different levels of tree retention were attained by varying the degree of tree extraction from retention strips. Two additional elliptical patches (0.25 and 0.5 ha) of trees were retained in most of the harvested compartments for use as intrastand controls for other studies. Compartments were arranged in a partially blocked design, with constrained allocation of treatment types, and were separated from the surrounding landscape by 50–100 m forested buffers. Typically, blocks were at least 500 m apart, and controls were at least 1000 m apart. Within blocks, treated compartments were usually adjacent to two or more treatments, whereas controls were usually adjacent to only one treatment and surrounded on three sides by undisturbed forest (Fig. 2). Posttreatment bird sampling was conducted in 1999 and 2000. Harvesting implications have been interpreted in relation to preharvest conditions and uncut control stands.

Vegetation surveys

The composition and structure of the vegetation surrounding each bird sampling station was measured in August 1998 using a protocol modified from Martin (1992*a*). Circular plots of 0.04 ha were centered on the station. Ground cover in seven categories was estimated to the nearest 5%, in four nested 1-m^2 quadrats. Stems of shrubs between 50 and 140 cm high were also counted within these quadrats. Saplings (dbh <2.5 cm) and poles (dbh 2.5–8 cm) were counted by species in a 0.008-ha nested subplot, and trees in four diameter classes (8–15, 15–23, 23–38, and >38 cm) were tallied by species for the entire plot. We also recorded the number of snags in five diameter classes (8–12, 12–15, 15–23, 23–38, and >38 cm). Posttreatment vegetation was surveyed in 2000 using the same methodology in the same compartments. Plots that overlapped retention ellipses were moved outside the ellipse in a randomly chosen direction to better represent treatment-related changes.

Bird surveys

We used a fixed-radius point count method (Hutto et al. 1986) to estimate relative abundance within compartments. Every combination of cover type and treatment was sampled, and each compartment contained one or two randomly situated points, depending on its configuration. We visited each point three times in 1998 and five times in both 1999 and 2000 during the breeding season (mid-May to early July). During each visit, observers recorded all birds seen and heard within a given radius around the point, over a 5-min sampling interval. Approximately half the point count stations were 100 m radius counts, where observations were noted within two concentric circles: one at 50 m and one at 100 m. At the remaining points, observations were limited to one 50 m radius circle because of compartment size constraints. Birds observed flying over the point were recorded in the field but excluded from all analyses. The methodology was standardized to reduce possible sources of seasonal, diurnal, and environmental bias, within and between years (Verner 1985), and observers were trained in detection and counting techniques. Points were situated a minimum of 50 m (small radii) or 100 m (large radii) from compartment boundaries and a minimum of 150 m (all radii) from other points in the same compartment. No overlap of sampling radii occurred.

Analyses

Prior to performing analyses, data were tested for normality using scatterplots, quantile–quantile plots, and Kolmogorov–Smirnov tests and for homoscedasticity using Levene's test (Conover 1980). Least-squares regression was used to test for significant linear or curvilinear trends in means among treatment levels. Curvilinear models were tested where they appeared to empirically fit the data and were compared to linear models based on whether they reduced the residual sum of squares. One-way fixed factor analysis of variance (ANOVA) was used to identify significant differences among treatment means, with significance levels adjusted via a sequential Bonferroni technique for multiple tests (Rice 1990). The Tukey correction for unplanned multiple comparisons was used in some instances (Neter et al. 1985). Because the number of stations varied among compartments, a weighting factor was incorporated into analyses where appropriate. If necessary, data were transformed to meet assumptions of parametric tests, and if assumptions could not be met, weight estimation regression (in which data points within a group are weighted by the inverse of their group variance; SPSS Inc. 1999) and Kruskal–Wallis ANOVA were used. Because sample sizes were relatively small and variation was typically high, outliers were not removed and an α of 0.10 was used for all tests. This increased power and lessened the possibility of type II errors, which may have important consequences for monitoring of species (Thompson and Schwalbach 1995; Steidl et al. 1997). For some statistics, we lacked confidence in the form of the underlying population distribution; we therefore used a method of bootstrapping (Efron and Tibshirani 1998) to estimate means and standard errors and used regression coefficients with bias-corrected confidence intervals.

Vegetation

The 1998 and 2000 vegetation data sets contained 82 shared variables. We combined variables that appeared similar in terms of habitat value, then used principal components analysis and correlation analysis to identify 12 "representative" variables for each cover type, which were then compared using one-way ANOVA. While a multivariate ANOVA was preferred, the assumptions (Scheiner 1993) could not be met. Data could not be directly compared between years using a repeated measures ANOVA, as some survey points could not be relocated after harvest.

Birds

Point count analyses included only birds recorded within the 50 m radius circles. This restriction meant a potential loss of statistical power (due to smaller data sets), but it prevented potential biases in species detectability at distances between 50 and 100 m (Wolf et al. 1995; Schieck 1999) and minimized variations in detectability among harvest-retention levels and cover types. Using a smaller count radius also increased the independence of stations within the same compartment, reduced possible edge effects at compartment boundaries, and ensured that vegetation measurements were in closer proximity to bird locations. We further restricted analyses to those species that may be reliably detected using diurnal visual and auditory cues. Species with territories that typically exceed the compartment size at EMEND (i.e., woodpeckers) were also removed.

Table 1. Breeding weights assigned to bird observations during point count surveys.

Behaviour or observation type	Rank
Family group or juvenile	2.0
Adult carrying food or nesting material	2.0
Pair or nest	2.0
Distraction display	2.0
Singing or countersinging male	1.0
Territorial dispute	1.0
Calling adult	0.5
Adult observed visually	0.5

All but the control compartments contained two retention ellipses, which we expected to influence bird presence. Because the locations of the ellipses were not determined until after preharvest data collection, point counts were not situated in a systematic manner with regard to the ellipses, and the overlap between ellipses and count radius was greater in some stations than others. Consequently, data from some compartments were influenced more by the ellipses than others. As a result, birds observed exclusively within an ellipse during a count were excluded from the count, and bird abundances at the station were adjusted for the reduced sampling area. This adjustment was made for affected stations in the 0%, 10%, and 20% treatments only; at higher levels, observers found it too difficult to distinguish retention ellipses from retained forest during a count. Stations that overlapped with ellipses for more than half their radius were excluded from analyses (n = 4).

To better link abundance to breeding status, a weighted ranking system (Schmiegelow et al. 1997; Table 1) was used. Species abundance within each compartment was calculated as the mean rank per station per round.

Species richness was calculated as the number of species detected per station, in all counts, within each year. Rarefaction was used to compensate for differential sampling effort between compartments by standardizing all samples to a common size of one station (see James and Wamer 1982). Similarity of communities between pre- and post-harvest years was measured using the Morisita–Horn index (Magurran 1988), which is not sensitive to rare species occurrence and small sample sizes. Species were also grouped into foraging and nesting guilds based on Ehrlich et al. (1988). Foraging guilds were defined by method of feeding, including aerial gleaning, bark gleaning, foliage gleaning, and ground foraging; nesting guilds were defined by nest location and included cavity, ground, and shrub–tree. For species abundances, treatment means were compared to the control value using independent sample Student's t tests to account for experiment-wide fluctuations in species abundance (i.e., interannual variation in numbers). Data are primarily expressed as changes in mean treatment values between 1998 and 2000, but changes between 1998 and 1999 are presented where they exhibit

Table 2. Significant linear regressions of vegetation variables in 2000, in each forest cover type at EMEND, Alberta, Canada.

			Linear regression		
Cover type	Layer	Variable	p[a]	R^2	Slope[b]
DEC	Ground cover	% litter	<0.001	0.777	+
		% DWD	0.001	0.503	–
	Shrub	Low shrub stems	0.079	0.181	–
	Canopy	Large snags[c]	<0.001	0.508	+
		All snags	<0.001	0.574	+
		Deciduous poles	0.008	0.361	+
		Deciduos trees	(<0.001)	0.915	+
DEC–UND	Ground cover	% shrub	0.061	0.203	–
		% DWD	<0.001	0.513	–
	Canopy	Small snags	0.001	0.487	+
		Large snags[c]	0.003	0.436	+
		All snags	<0.001	0.688	+
		Deciduous trees	<0.001	0.557	+
		Coniferous stems	(<0.001)	0.747	+
MIX	Ground cover	% moss	0.035	0.249	+
		% DWD	0.003	0.424	–
	Canopy	Small snags	(0.030)	0.390	+
		Large snags[c]	(<0.001)	0.842	+
		All snags	(<0.001)	0.722	+
		Deciduous stems	0.034	0.251	+
		Coniferous stems	(<0.001)	0.746	+
CON	Ground cover	% all green	0.006	0.388	+
		% moss	0.015	0.316	+
		% DWD	<0.001	0.544	–
	Canopy	Large snags[c]	0.006	0.391	+
		All snags	0.010	0.350	+
		Coniferous stems	<0.001	0.559	+

Note: DWD, downed woody debris.
[a]p values in parentheses were determined by weight estimation regression.
[b]Direction of relationship: + denotes rise with increasing retention level; – denotes drop with increasing retention level.
[c]dbh >12 cm.

different patterns. Analysis of covariance (ANCOVA) was used to compare regression relationships between time periods.

Results

Vegetation

Preharvest tree densities ranged from a low of 930 trees/ha in deciduous (DEC) sites to a high of 1494 trees/ha in deciduous–understory (DEC–UND) sites. ANOVA detected no preharvest differences between treatments for any of the vegetation characteristics measured in 1998, in any cover type, but some variables exhibited significant linear regressions in certain cover types. In DEC–UND sites, ground-litter cover declined slightly with increasing subsequent residual level ($p = 0.046$, $R^2 = 0.226$). Similar slight declines were observed in mixed (MIX) sites for ground shrub cover ($p = 0.055$, $R^2 = 0.211$) and low shrub stems ($p = 0.037$, $R^2 = 0.244$) and in coniferous (CON) sites for deciduous stems ($p = 0.018$, $R^2 = 0.301$). Each of these variables was included as a covariate in tests of bird indices in 1998, but since none were found to have a significant effect, they were excluded from further analyses. In every case, the observed preharvest trend was absent or reversed in the postharvest surveys, and therefore, if anything, resulted in conservative tests relative to our hypotheses. Analyses of a larger (unpublished) vegetation data set collected in 1998 by other EMEND researchers revealed similar results.

A number of variables in each cover type displayed a significant linear trend among treatments after harvest (Table 2).

Birds

In DEC and MIX sites, species richness between 1998 and 2000 increased linearly as residual level increased, primarily due to loss of species from the clearcuts and increases in the controls (Fig. 3). Coniferous sites exhibited a significant cubic (or third-order polynomial) relationship for the same period, although a linear trend similar to that for the other two cover types was observed between 1998 and 1999 ($p = 0.006$, $R^2 = 0.388$). An overall increase in richness across treatments between the first and second postharvest year was detected in three of the cover types (DEC sites: $p = 0.001$; MIX sites: $p = 0.010$; CON sites: $p = 0.038$).

The similarity of bird communities occupying the same compartments in 1998 and 2000 also increased linearly as

Fig. 3. Mean changes in bird species richness per sampling station between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada. Probability and goodness-of-fit measures correspond to cubic regression in coniferous sites and linear regression in all others. Line slopes for significant relationships (with 95% confidence interval) are as follows: deciduous = 6.7 (4.3–8.9); mixed = 4.5 (0.6–7.7).

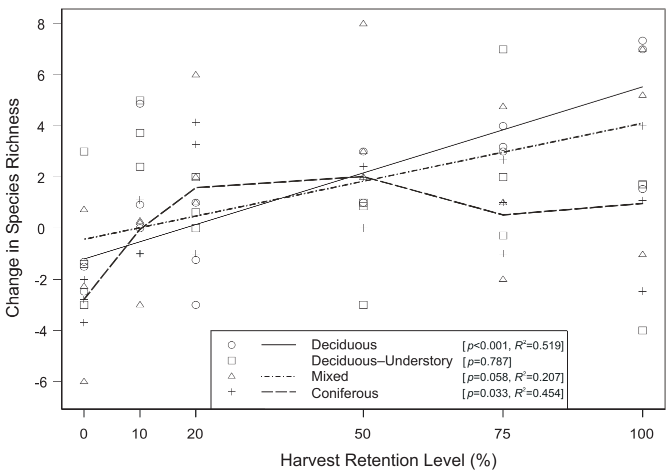
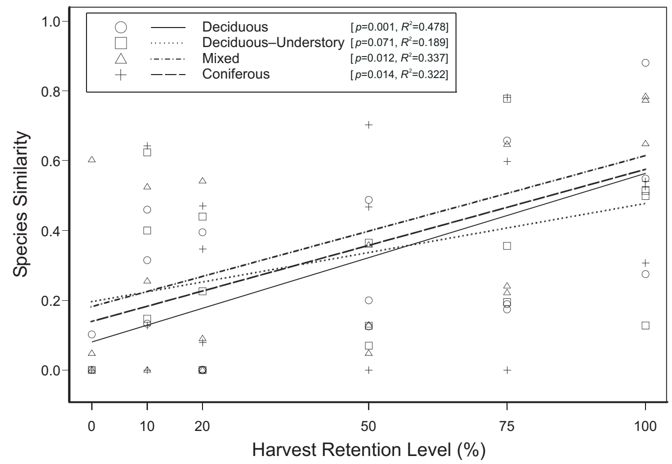


Fig. 4. Mean species similarity per compartment between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada. Probability and goodness-of-fit measures correspond to linear regression in all sites. Line slopes for significant relationships (with 95% confidence interval) are as follows: deciduous = 0.47 (0.25–0.73); deciduous–understory = 0.27 (0.02–0.49); mixed = 0.43 (0.15–0.68); coniferous = 0.42 (0.26–0.61).



residual level increased in all four cover types (Fig. 4), due in part to the low similarity (or complete turnover) of bird communities in clearcuts between years. An overall increase in similarity across treatments between the first and second postharvest year was detected for MIX sites ($p = 0.032$).

Of the 71 forest bird species detected between 1998 and 2000, foraging guilds consisted of aerial foragers (16 species = 23%), bark gleaners (9 species = 13%), foliage gleaners (23 species = 32%), and ground gleaners (23 species = 32%). Nesting guilds consisted of cavity nesters (15 species = 21%), ground nesters (22 species = 31%), and shrub–tree nesters (34 species = 48%). For some guilds (aerial foragers, bark gleaners, and cavity nesters), per-station bird abundances were low because of a paucity of species and the relatively small sampling area, and therefore data were not analyzed.

Among foraging guilds between 1998 and 2000 (Fig. 5), foliage gleaner abundance increased linearly as residual level increased in three cover types. The remaining cover type (DEC–UND) exhibited a significant cubic relationship for the same period, although a linear trend similar to that for the other cover types was observed between 1998 and 1999 ($p = 0.017$, $R^2 = 0.309$). Conversely, ground forager abundance declined linearly as residual level increased in three cover types. Among nesting guilds (Fig. 6), the abundance of shrub–tree nesters increased linearly as residual level increased in three cover types, and in the fourth type (DEC–UND), a similar linear trend was observed between 1998 and 1999 ($p = 0.088$, $R^2 = 0.172$). Ground nester abundance declined linearly in MIX and CON sites.

An overall increase in abundance across treatments between the first and second postharvest year was detected for foliage gleaners in three cover types (DEC: $p = 0.023$; DEC–UND: $p = 0.099$; MIX: $p = 0.008$), ground foragers in three cover types (DEC: $p = 0.038$; MIX: $p = 0.014$; CON: $p = 0.001$), ground nesters in all cover types (DEC: $p = 0.002$; DEC–UND: $p = 0.007$; MIX: $p = 0.015$; CON: $p = 0.001$), and shrub–tree nesters in one cover type (MIX: $p = 0.008$).

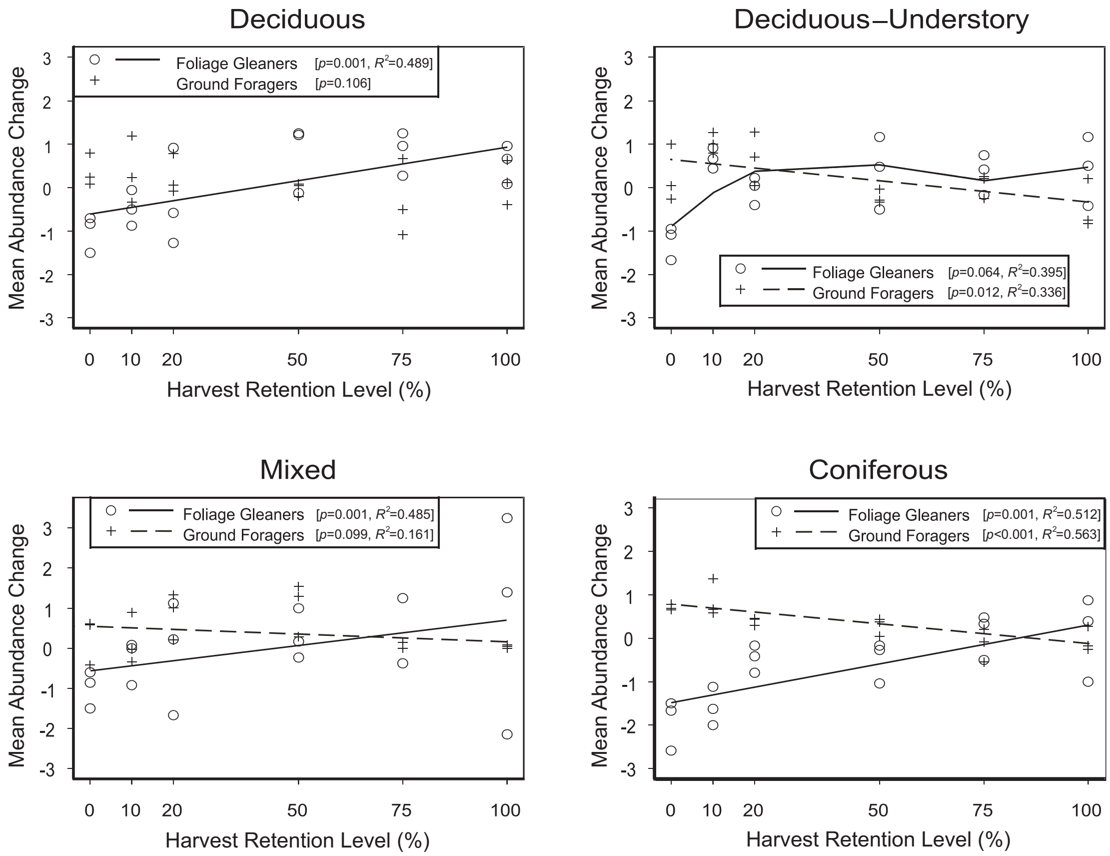
Changes in annual abundances were analyzed for the 15–20 most abundant species in each cover type, or those detected in at least 5 of the 18 compartments, to ensure each analyzed species was represented in two or more compartments in at least two treatments (Appendix A). Only a few species in each cover type exhibited statistically significant mean abundance changes relative to the controls, or significant linear regression trends (Table 3). Small samples resulted in generally low power for these tests. In qualitative terms, among species with enough observations to be analyzed, the 10% and 20% residual treatments exhibited slightly fewer local "extinctions", or species losses, than the clearcuts, where almost all declines were extinctions, and slightly more extinctions than the 50% and 75% residuals (Table 4). Controls experienced almost no extinctions in any cover type.

Discussion

Bird community response

Our prediction that community measures in partial cuts would vary linearly with level of retention was generally supported. In DEC and MIX sites, less retention resulted in lower species richness. In CON sites, a cubic relationship was observed, indicating that the "midrange" retention levels retained species to a greater degree than in other cover types. In DEC–UND sites, no pattern was evident, but the extensive coniferous understory and more complex vegetative structure may have "buffered" species loss in harvest treatments. Interestingly, the number of species postharvest actually increased in the higher residuals (50%, 75%, 100%) in most cover types, partly because of an overall rise in richness observed across all treatments in 2000 (as compared to 1999). The reasons for this trend (and the increases in overall abundance exhibited by guilds in 2000 relative to 1999) are unclear, but may be related to regional population fluctuations and a slightly more intensive sampling regime. We do not

Fig. 5. Mean changes in foraging guild abundances per station between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada. Probability and goodness-of-fit measures correspond to cubic regression for deciduous–understory foliage gleaners and linear regression for all others. Foliage gleaner line slopes for significant relationships (with 95% confidence interval) are as follows: deciduous = 1.56 (0.90–2.00); mixed = 2.17 (0.98–3.35); coniferous = 1.80 (0.83–2.55). Ground forager line slopes for significant relationships are as follows: deciduous–understory = –1.02 (–1.52 to –0.29); mixed = –0.33 (–0.72 to 0.07); coniferous = –0.91 (–1.29 to –0.56).

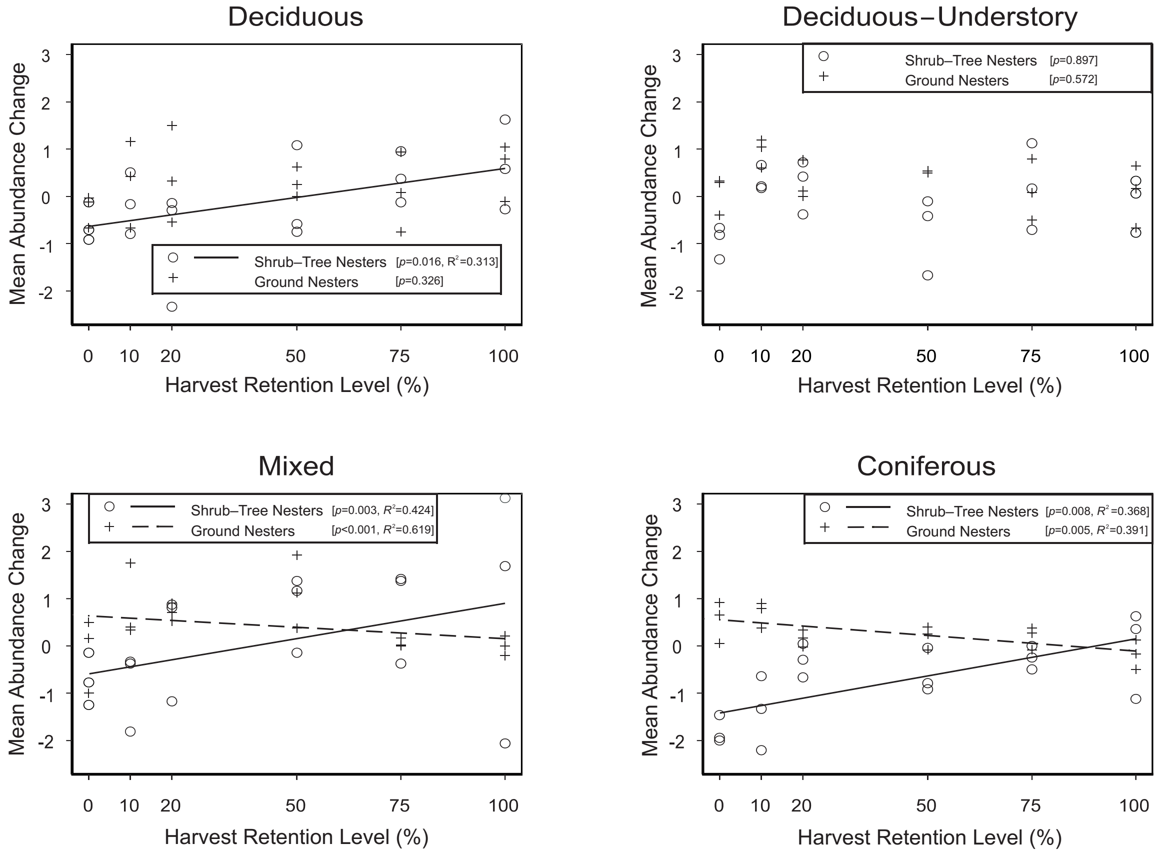


believe increases in the uncut stands reflect posttreatment crowding effects, as controls were typically separated from treatments by a forest buffer on three sides. Additionally, most of the data were collected in the second postharvest year, and studies in similar forests in northeastern Alberta have shown crowding to be relatively ephemeral in these systems (see Schmiegelow et al. 1997; Schmiegelow and Hannon 1999). Patterns of community similarity followed a similar trend in all four cover types: the lower the retention level, the lower the similarity between pre- and post-harvest communities.

Bird response by guild and species

Our second prediction, that guilds and species dependent on shrub or tree cover would be most negatively impacted by partial cutting, was also supported. Guild trends were linear: less retention resulted in lower foliage gleaner and shrub–tree nester abundance (three cover types), but higher ground forager abundance (three cover types) and ground nester abundance (two cover types). Species data were more variable, and many comparisons lacked statistical power, but a distinct pattern emerged. In all cover types, most declines relative to controls occurred in the lower residual treatments (0%, 10%, 20%), by species typically dependent on shrubs or trees for nesting and foraging (i.e., Golden-crowned Kinglet (*Regulus satrapa*), Red-eyed Vireo (*Vireo olivaceus*), Swainson's Thrush (*Catharus ustulatus*), Yellow-rumped Warbler (*Dendroica coronata*)). The Ovenbird (*Seiurus aurocapilla*), which also declined in lower residual treatments, is a ground nester and forager, but requires the presence of canopy trees: Schieck and Nietfeld (1995) classify it as most abundant in mature aspen mixedwood forests in Alberta. Even at higher residual treatments, some species declined in abundance (i.e., Golden-crowned Kinglet, Ovenbird, Swainson's Thrush), and while most declines were not statistically significant, we believe they indicate generally lower habitat quality for these species. Losses typically persisted through both years in all cover types. Most increases relative to the controls were also exhibited in the lower residuals, by ground nesting and foraging species (i.e., Dark-eyed Junco (*Junco hyemalis*), Lincoln's Sparrow (*Melospiza lincolnii*), White-throated Sparrow (*Zonotrichia albicollis*)). An exception to this pattern in all cover types was the Chipping Sparrow (*Spizella passerina*), a ground forager that is generally considered a shrub–tree nester. However, we observed this species nesting on the ground on several occasions in 2000. Mourning Warbler (*Oporornis Philadelphia*) and Tennessee Warbler (*Vermivora peregrina*), both ground nesters, exhibited the same colonization tendency: increases were not observed until the second

Fig. 6. Mean changes in nesting guild abundances per station between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada. Probability and goodness-of-fit measures correspond to linear regression in all sites. Shrub–tree nester line slopes for significant relationships (with 95% confidence interval) are as follows: deciduous = 1.24 (0.41–2.17); mixed = 2.27 (0.87–3.68); coniferous = 1.58 (0.58–2.26). Ground nester line slopes for significant relationships are as follows: mixed = –1.00 (–1.41 to –0.58); coniferous = –0.65 (–1.09 to –0.23).



year postharvest, by which time shrub and sapling regrowth may have been sufficient to satisfy their foraging needs.

In northeastern Alberta, partial cuts in hardwood stands (~10%, 30%, 40%) were also intermediate to clearcuts and controls in most measures after 1 year (Norton and Hannon 1997). Forest dwellers (dependent on trees and shrubs) benefited from increasing residual tree retention, but ground dwellers were generally unaffected. Three years postlogging, species that benefited from the partial cuts tended to be habitat generalists; most forest dwellers had abandoned the partial cuts (Tittler et al. 2001). Accordingly, community similarity was found to be lower between year 0 (preharvest) and year 3 than between year 0 and year 1 (Tittler 1998), perhaps resulting from an initial failure of some species to breed successfully or from competition between forest-dwelling and early-successional species (i.e., ecological lags in response). Tittler et al. (2001) also observed a shift towards species characteristic of open habitats in the third year postharvest, hypothesizing that lags in vegetation regeneration and dispersal resulted in delayed colonization. We detected a similar pattern at EMEND: ground nesters increased between the first and second years postharvest in low-retention treatments in all cover types, and ground foragers increased in all but DEC–UND sites, with most increases attributable to species classified by Tittler et al. as open-habitat birds.

Other forest ecosystems across North America exhibit similar patterns: as a rule, partially harvested stands retain a portion of the mature forest bird community not found in clearcuts, although at lower numbers, while supporting some early-successional species (i.e., Franzreb and Ohmart 1978; Hansen et al. 1995; Costello et al. 2000; Hayes et al. 2003). Bird abundances and species richness are generally proportional to degree of retention, although some studies have detected greater species diversity and (or) abundance in partial cuts compared to that on uncut sites (i.e., Annand and Thompson 1997; Simon et al. 2000; Lance and Phinney 2001; Anderson and Crompton 2002). Whether this effect is observed may depend on regional bird community composition and duration of study. At EMEND, few early-successional colonist species were present in the regional species pool because of the relatively intact condition of the forest; thus, we expected that short-term gains in partial cuts would be outnumbered by losses of mature forest species. This expectation was generally not borne out, as species richness rose across most partial-cut treatments in 2000; however, richness still increased linearly with retention level because of a contemporaneous rise in the uncut controls. All studies report loss of some mature forest-dependent species, typically from groups that nest or forage in the canopy (i.e., Franzreb and Ohmart 1978; Hayes et al. 2003) or which glean bark and nest in cavities (i.e., Medin and Booth 1989; Anderson and Crompton 2002). Species benefiting from partial cuts typically belong to ground-foraging or ground-nesting guilds (i.e., Beese and

Table 3. Significant mean species abundance changes (relative to controls) and regressions observed between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada.

			Harvest retention level%[c]					Linear regression[d]			
Cover type	Species[a]	Foraging guild, nest guild[b]	0	10	20	50	75	p	R^2	Slope	95% CI
DEC	DEJU	G, G	+					ns			
	WTSP	G, G		+				(0.077)	0.183	–0.26	–0.55 to –0.03
	CAWA	A, G					–	ns			
	REVI	A, ST	–		–			(<0.001)	0.595	0.36	0.20 to 0.52
	TEWA	F, G	–					(0.001)	0.492	0.40	0.18 to 0.61
	GCKI	F, ST			–			ns			
	YRWA	F, ST		–	–			0.059	0.206	0.44	0.20 to 0.63
	RBNU	B, C	–					ns			
	YBSA	B, C					–	ns			
DEC–UND	DEJU	G, G		+				0.039	0.241	–0.28	–0.46 to –0.06
	LISP	G, G		+				ns			
	OVEN	G, G						0.033	0.253	0.39	0.12 to 0.76
	CHSP	G, ST			+			0.028	0.266	–0.47	–0.77 to –0.20
	YRWA	F, ST	–					ns			
MIX	DEJU	G, G			+	+		ns			
	OVEN	G, G		–				ns			
	WTSP	G, G		+				ns			
	CHSP	G, ST				+		ns			
	MOWA	F, G		+				ns			
	SWTH	F, ST	–	–		–		0.021	0.290	0.21	0.07 to 0.38
	YRWA	F, ST				+		ns			
CON	DEJU	G, G	+					0.026	0.275	–0.35	–0.55 to –0.19
	LISP	G, G						(0.086)	0.173	–0.15	–0.32 to 0.02
	GRJA	G, ST				+		ns			
	BTNW	F, ST		–				ns			
	GCKI	F, ST	–		–	–		(0.015)	0.315	0.49	0.11 to 0.88
	WETA	F, ST		–				ns			
	WWCR	F, ST					+	ns			
	YRWA	F, ST	–	–	–			(<0.001)	0.803	1.05	0.77 to 1.32
	RBNU	B, C					+	ns			

[a]BTNW, Black-throated Green Warbler; CAWA, Canada Warbler; CHSP, Chipping Sparrow; DEJU, Dark-eyed Junco; GCKI, Golden-crowned Kinglet; GRJA, Gray Jay; LISP, Lincoln's Sparrow; MOWA, Mourning Warbler; OVEN, Ovenbird; RBNU, Red-breasted Nuthatch; REVI, Red-eyed Vireo; SWTH, Swainson's Thrush; TEWA, Tennessee Warbler; WETA, Western Tanager; WTSP, White-throated Sparrow; WWCR, White-winged Crossbill; YBSA, Yellow-bellied Sapsucker; YRWA, Yellow-rumped Warbler.

[b]Foraging guilds: A, aerial; B, bark; F, foliage; G, ground. Nesting guilds: C, cavity; G, ground; ST, shrub or tree.

[c]Changes compared to control values using independent sample Student's t tests, $\alpha = 0.10$.

[d]p values in parentheses were determined by weight estimation regression; ns, not significant; positive slope indicates an increase in abundance with increasing retention; negative slope indicates a decrease in abundance with increasing retention; CI denotes confidence interval.

Bryant 1999; Simon et al. 2000). Finally, most studies agree that partial cutting cannot accommodate all native bird species. Addressing this objective requires a variety of management approaches across multiple spatial scales, including the retention of unharvested areas (i.e., landscape-level retention) to accommodate the needs of sensitive species.

None of the species observed at EMEND are on the national list of species at risk prepared by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004), nor are any designated as threatened or endangered provincially in Alberta. However, several species are designated as "sensitive" provincially, indicating that special attention may be required to prevent them from becoming at risk (Alberta Sustainable Resource Development 2003). Two of these, the Black-throated Green Warbler (*Dendroica virens*; in CON sites) and the Canada Warbler (*Wilsonia canadensis*; in DEC sites), exhibited significant decreases in harvest treatments. Most of the other species were observed too infrequently for resultant data to be analyzed, yet several are considered sensitive to forestry activities in boreal mixedwood forests (Hannon et al. 2004). Resident species, as a group, are of particular conservation concern in boreal forests (Schmiegelow and Mönkkönen 2002) and are often not well sampled during conventional point count survey periods because of the earlier onset of breeding activities. Alternate survey techniques are thus required to evaluate responses of these species to partial cutting.

Caveats

Short temporal scale

While this study had the advantage of a strong pre- and post-harvest design, we monitored only short-term responses;

Table 4. Mean species abundance changes observed between 1998 and 2000, as a result of partial harvest (categories represent 0%–100% harvest retention levels) of different forest cover types at EMEND, Alberta, Canada.

	DEC[b]						DEC–UND[b]						MIX[b]						CON[b]					
Species[a]	0	10	20	50	75	100	0	10	20	50	75	100	0	10	20	50	75	100	0	10	20	50	75	100
AMRE		+			+	c		e		e	e													
BCCH	c	c	c	c	c	c	e	c			c	c												
BOCH														c	–	e		–	e			–	c	c
BTNW													e	e		–	+	–	e	e*	–	c	e	–
CAWA	e	e	e	e	–*	+																		
CHSP	c	+	c		c		c	c	c*	+	+	–	+	+	c	c*	c	c	c	+	c	–	+	c
CMWA																				e		e	e	–
COWA	e	–	e	–		+																		
DEJU	c*	c	c	c	c		c	c*	+	c	c		nc	+	c*	c*	c	+	c*	c	nc	+	+	–
GCKI	e	e	e*		–		e		e	–	e	–	e	e	e	–	e	–	e*	–	–*	–*	–	–
GRJA								+	–	e	c	e	–	e	–	–	e	–	e	+	–	c*	–	–
LEFL	e	c		e		–																		
LISP	c	c		c			c	c*			c								c	c	c			
MOWA	c	c	c	c	c	c							c	+*		c	c							
OVEN	e	e	e	e	–	+	e	e	e	–	–	–		e*	e	e	e	e						
PISI																c		–	e		e	e	e	e
RBGR					c	c																		
RBNU	e*	c	+	e	–			c	e	e		+	e	–	e	–	e	+	e	–	+	–	+*	–
REVI	e*	–	e*	nc	c	c																		
SWTH	e	e	c	–	+	–	e	–	–	e	e	–	e*	e*	c	e*	–	+	e	e	e	e		nc
TEWA	e*	+	+	c	+	+	c	+	c	c	+	+	e	+	c	e	–	+	e	–	+		c	–
WAVI	e	e	e		+	+	e	e	c	–	–	–												
WETA																				e*	e		c	c
WIWR																			e		+	+	–	+
WTSP	+	+*	+	–	+	nc	c	+	c	+	+		c	+*	c	c	c		c	c	–	c	c	–
WWCR															c			–	e	c		+	+*	–
YBSA	0	+	0	c	e*	c																		
YRWA	e	–*	–*	+	+	+	e*	+	–	+	–	+	–	+	–	+*	+	+	e*	–*	–*	+	+	+

Note: Changes marked with an asterisk are significant relative to changes in controls during same period.

[a]AMRE, American Redstart; BCCH, Black-capped Chickadee; BOCH, Boreal Chickadee; BTNW, Black-throated Green Warbler; CAWA, Canada Warbler; CHSP, Chipping Sparrow; CMWA, Cape May Warbler; COWA, Connecticut Warbler; DEJU, Dark-eyed Junco; GCKI, Golden-crowned Kinglet; GRJA, Gray Jay; LEFL, Least Flycatcher; LISP, Lincoln's Sparrow; MOWA, Mourning Warbler; OVEN, Ovenbird; PISI, Pine Siskin; RBGR, Rose-breasted Grosbeak; RBNU, Red-breasted Nuthatch; REVI, Red-eyed Vireo; SWTH, Swainson's Thrush; TEWA, Tennessee Warbler; WAVI, Warbling Vireo; WETA, Western Tanager; WIWR, Winter Wren; WTSP, White-throated Sparrow; WWCR, White-winged Crossbill; YBSA, Yellow-bellied Sapsucker; YRWA, Yellow-rumped Warbler.

[b]Changes were compared to control values using independent sample Student's *t* tests, $\alpha = 0.10$; "–" indicates species decreased in abundance in that retention level between 1998 and 2000; "+" indicates species increased in abundance between 1998 and 2000; "e" denotes a local extinction, where species disappeared between 1998 and 2000; "c" denotes a local colonization, where species was detected in 2000 but not in 1998; "nc" indicates species did not change in abundance between 1998 and 2000.

how these may relate to longer-term patterns is unclear. For example, retaining mature trees in deciduous-dominated stands may promote the growth of shade-tolerant white spruce (Bella and Gál 1996) over aspen and may consequently be reflected in future bird communities by favouring species associated with coniferous trees. Regrowth may result in increased similarity between low- and high-retention stands within cover types. Schieck and Hobson (2000) detected partial convergence of bird communities over 15–30 years between small and large retention patches in boreal mixedwood forests, probably due to growth of trees in surrounding cutover areas. Alternatively, while higher retention stands are initially more structurally complex (Sullivan et al. 2001; Lee et al. 1997.), there may be convergence over time within residual patches if, for example, snag loss outweighs snag recruitment. Clearly, longer term monitoring at EMEND is necessary to accurately assess response and provide reliable management recommendations.

Assumption of link between abundance and productivity

Abundance data, such as that derived from point counts, are frequently used to infer habitat quality, under the assumption that individuals will occur at greater densities in better quality habitats (with associated higher survival and reproduction rates). However, density alone can be misleading (see van Horne 1983; Vickery et al. 1992*a*). For example, song output can be a deceptive indicator of pairing status, since unpaired males may sing more frequently than paired males (Gibbs and Wenny 1993). To test this assumption, Harrison (2002) concurrently studied breeding behaviours of Swainson's Thrush (*Catharus ustulatus*) at EMEND and found that populations in partial cuts appeared to consist almost entirely of nonreproducing birds. This suggests the results presented here should be considered optimistic, at best.

Compartment size considerations

A maximum of two point count stations could be situated within each 10-ha compartment at EMEND. This resulted in small sample sizes for many species, and the concomitant high variability compromised our ability to detect changes postharvest. Furthermore, 10 ha may be too small a patch for some species in western forests (Hannon 1993). For example, the Ovenbird has been classified as an "area-sensitive species" because of its reliance on large patches of homogeneous mature forest habitat (Freemark and Collins 1992; Thompson et al. 1993), and pairing success among Ovenbirds has been positively correlated to forest patch size and distance from edge (Van Horn et al. 1995; Burke and Nol 1998). It is possible that in-block retention strategies over a large expanse might be suitable for Ovenbirds and possibly other area-sensitive species, but we could not detect this at EMEND.

Landscape context

The EMEND Project was designed to address questions at the level of the stand, and resultant data must be supplemented by broader scale information. The distribution of birds may depend on factors such as patch area, degree of fragmentation, and connectivity (Walters 1998; Villard et al. 1999; Brotons et al. 2003); hence, species presence and abundance may depend upon landscape context. In addition, metapopulation theory suggests that low-quality or "sink" bird populations may be sustained through immigration from neighboring subpopulations (i.e., Pulliam 1988; Martin 1992*b*), and therefore local assemblages may be as much a reflection of neighboring habitats as of local habitat conditions (McGarigal and McComb 1995; Drapeau et al. 2000). Consequently, caution should be exercised in both the interpretation of stand-level responses and in extrapolating these to evaluate habitat disturbance at a larger scale.

Management implications

In-block retention of live trees through partial cutting represents one facet of an ecosystem-based approach to forest management modeled after a natural disturbance regime. It is apparent that the needs of all forest species will not be met by partial cutting, as evidenced by the species lost from even the high-retention partial cuts at EMEND. However, consistent with other partial-retention studies in western North America, a portion of the mature forest bird community at EMEND did not disappear from partial cuts, suggesting some advantages over clear-cutting for conservation of avian diversity. Nevertheless, concurrent behaviour monitoring at EMEND (Harrison 2002) cautions against naive interpretation of these result: the presence of mature forest species in partial cuts was not reflected in reproductive activity, a measure of the quality of these habitats. We suggest that lower retention treatments (10%, 20%) cannot, therefore, be justified from a short-term avian diversity perspective. Higher retention levels (50%, 75%) may confer greater biodiversity advantages, but monitoring of reproductive activity should be undertaken to assess whether these treatments offer productivity advantages over lower retention levels, particular for species with known sensitivities to forest harvesting (i.e., Black-throated Green Warbler and Canada Warbler).

EMEND consists of a wider range of harvest retention levels than most other partial-cut studies in western North America. This permitted simultaneous evaluation of the operational feasibility and ecological benefit of varying retention levels. Based on expected increased economic costs, and associated logistical challenges, it is likely that in the absence of a significant shift in policy, at best 10% or 20% retention levels will be implemented on a widespread basis within existing forest tenures in Alberta. These levels are generally consistent with the amounts of live residual patches that typically remain after wildfires in western (Lee et al. 2002) and eastern boreal forests (Bergeron et al. 2002). Such patches are large enough to have been detected historically using relatively coarse-scale remotely sensed data (i.e., aerial photography). Clearly, a large proportion of the forest bird community was lost when low levels of retained trees were left dispersed throughout harvested blocks. In northeastern Alberta, Schieck et al. (2000) and Schieck and Hobson (2000) found that retaining trees in a clumped rather than a scattered pattern resulted in bird communities that were more similar to those in old-growth forest, a strategy consistent with site-level patch retention based on natural disturbance. There nevertheless remains a paucity of information regarding variation in live-stem retention resulting from variation in severity within burns, which is arguably the more appropriate basis for establishing in-block retention levels of residual live material following harvest.

Management questions regarding retention are usually posed as binary choices for fixed levels of retention at a stand level (i.e., At 10% retention, is an aggregated or dispersed strategy more advantageous?) or formulated as a trade-off across spatial scales (i.e., Given that 10% of the merchantable volume will not be harvested, is it better to retain this as structure within harvested stands or as larger patches distributed across a given land base?). However, these are artificial dichotomies from the perspective of a natural disturbance regime, which operates at multiple scales. Under a given fire regime, characterized by a particular fire frequency, fire size, and fire severity, some areas will escape burning altogether, and thus a portion of a region will consist of stands considerably older than the fire cycle. Within burned areas, unburned patches (often referred to as fire skips) will persist. Finally, variation in fire severity will result in variation in the number of live stems remaining within a burned stands. There exist few data on this latter attribute of fire regimes, but recent figures from central Alberta (Stepnisky 2003) and western Quebec (Bergeron et al. 2002) suggest that values of 50% and greater are not uncommon, dependent, in part, on forest type. Furthermore, Stambaugh (2003) found that lightly to moderately burned areas (i.e., those with naturally high retention of live trees) supported breeding songbird populations equivalent to those in old, unburned stands. Thus, from an ecological perspective, high levels of in-block retention may be justified in some cases. While this has obvious implications for timber supply, it must also be considered in the broader context of ecosystem management based on an understanding of natural system dynamics.

EMEND attempts to address the question of “How much residual is enough?” in a natural disturbance approach to forest management at the stand level. This is a vital question, but is not the only challenge faced by planners. In order for biodiversity to coexist with industrial forestry, management must also understand the effects of natural disturbances in terms of spatial patterns (i.e., size and configuration of openings) and temporal scale (i.e., frequency of harvest) (Hunter 1993*b*; Lee et al. 2002). This requires managing for spatial and temporal heterogeneity on many scales simultaneously (Hunter 1990). Haila et al. (1994) suggest identifying critical scales for a set of taxa and using these as guidelines for planning forest operations over a large area. Our study has provided some information for one vertebrate taxon; nonetheless, we caution against applying these results to other taxonomic groups, which may respond to disturbance in very different ways, on much smaller or larger scales. We also emphasize that our recommendations are based on short-term research only, and any management action based on them should be accompanied by a longer term monitoring scheme (i.e., an adaptive management approach).

Acknowledgements

This research was part of a larger study, the EMEND project, and could not have been undertaken without the hard work of all those who participated in EMEND. L. Christensen, C. Dow, and S. Quinn helped collect the data. Financial support was provided by the Manning Diversified Forest Products Research Trust Fund, Canadian Forest Products Ltd., Daishowa-Marubeni International Ltd., the Natural Sciences and Engineering Research Council of Canada (NSERC), the Sustainable Forest Management Network Centres of Excellence, and the Canadian Circumpolar Institute of the University of Alberta. The authors also thank J. Spence, J. Beck, and S. Hannon for their assistance. Comments from P. Drapeau and an additional anonymous review improved the manuscript.

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Appendix A

Appendix appears on the following page.

Table A1. Species codes, common names, and scientific names for bird species detected at EMEND in at least 5 of 18 compartments, in at least one cover type.

Species code	Common name	Scientific name	Foraging guild[a]	Nesting guild[b]
AMRE	American Redstart	*Setophaga ruticilla*	A	ST
BCCH	Black-capped Chickadee	*Parus atricapillus*	F	C
BOCH	Boreal Chickadee	*Parus hudsonicus*	F	C
BTNW	Black-throated Green Warbler	*Dendroica virens*	F	ST
CAWA	Canada Warbler	*Wilsonia canadensis*	A	G
CHSP	Chipping Sparrow	*Spizella passerina*	G	ST
CMWA	Cape May Warbler	*Dendroica tigrina*	F	ST
COWA	Connecticut Warbler	*Oporornis philadelphia*	G	G
DEJU	Dark-eyed Junco	*Junco hyemalis*	G	G
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	F	ST
GRJA	Gray Jay	*Perisoreus canadensis*	G	ST
LEFL	Least Flycatcher	*Empidonax minimus*	A	ST
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	G	G
MOWA	Mourning Warbler	*Oporornis philadelphia*	F	G
OVEN	Ovenbird	*Seiurus aurocapilla*	G	G
PISI	Pine Siskin	*Carduelis pinus*	F	ST
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	F	ST
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	B	C
REVI	Red-eyed Vireo	*Vireo olivaceus*	A	ST
SWTH	Swainson's Thrush	*Catharus ustulatus*	F	ST
TEWA	Tennessee Warbler	*Vermivora peregrina*	F	G
WAVI	Warbling Vireo	*Vireo gilvus*	F	ST
WETA	Western Tanager	*Piranga ludoviciana*	F	ST
WIWR	Winter Wren	*Troglodytes troglodytes*	G	C
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	G	G
WWCR	White-winged Crossbill	*Loxia leucoptera*	F	ST
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*	B	C
YRWA	Yellow-rumped Warbler	*Dendroica coronata*	F	ST

[a]Foraging guilds: A, aerial foragers; B, bark gleaners; F, foliage gleaners; G, ground foragers.
[b]Nesting guilds: C, cavity nesters; G, ground nesters; ST, shrub or tree nesters.