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The retention of non-commercial hardwoods in mixed stands maintains higher avian biodiversity than clear-cutting

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A diverse landscape can support a more diverse range of species and allow for more complex community structures. In forested habitats, openings and changes in tree composition allow for a higher species richness due to the greater chance of niche occupancy. Knowledge about these relationships may be useful for adapting forest harvesting strategies to, for example, support bird diversity conservation and studies are required to understand how different harvesting strategies influence forest structure and bird diversity. Here, we used Autonomous Recording Units (ARU) to record dawn signalling of forest birds between two forest-harvesting treatment types (complete clear-cuts and hardwood-retention patches) *vs* control forest patches in the John Prince Research Forest, British Columbia, Canada. We compared Species Richness and Shannon diversity as detected through identifying species in audio recordings, across treatments. The observed Species Richness and Shannon diversity did differ between the Retention treatment and Forest controls when controlling for number of individuals sampled, but both had higher Species Richness and Shannon diversity of passerine species than the Clear-cut treatments. When comparing species composition, we found that forest-associated species were disproportionately detected in Forest controls compared to Clear-cut treatments but detected at intermediate levels in Retention treatments. Species associated with early-seral habitats, though, had disproportionate detection in Clear-cut treatments compared to Forest controls, but also showed expected detections in Retention treatments. These results suggest that partial harvesting and retention of non-commercial hardwoods, can help retain forest-associated species while also helping attract early-seral avian species; this can help increase the overall diversity of the landscape while still making logging profitable. Further research should be conducted to determine the value of this retained habitat at different spatial scales to understand the impacts that it may have for larger-scale deployment.

Introduction

For forest habitats to support a diverse community of birds, the habitat structure needs to be somewhat heterogenous; having a mixture of standing live and dead trees, coniferous and deciduous tree species, fallen trees, shrubs and grassy openings creates more niche options for different, unique species (Hobson and Bayne 2000). Some species in such an avian community would be considered generalists and occupy a variety of different microhabitats within the larger forest, whereas others would be specialists found only in specific microhabitats (Mahon *et al.* 2016). Those forests which have the highest heterogeneity in their physical structure should support the highest avian diversity (Melin *et al.* 2018). Old growth forests, for example, provide an array of microhabitats created when large, mature trees fall, leaving gaps in the canopy that provide structural variance to the habitat (Andersson and Östlund 2004). When forests also face larger-scale natural disturbances, the communities of birds living within them will shift as the regenerating forests go through various successional phases on route to returning to old growth stands (Mahon *et al.* 2016).

Natural forest disturbances occur through fire, flooding, insect outbreaks and wind events. When managing forests for economic values, the associated anthropogenic disturbances can result in different forest conditions than those that would occur through natural disturbances (Uotila and Kouki 2005). Both natural and anthropogenic disturbances will disrupt the habitat, creating potential opportunities for new species (Väisänen *et al.* 1986), but also removing habitat options for others (Loehle and Eschenbach 2012). With the removal of mature trees from a forested landscape, wildlife species that depend on such features for nesting, breeding or feeding are less likely to be retained (Linden and Roloff 2013). Species associated more commonly with open or early-succession habitats, however, may colonize these open patches (Väisänen *et al.* 1986). Species that rely on standing

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trees for cavity nests and feeding, such as woodpeckers, may only occupy disturbance patches that either retain some standing deadwood, or reoccupy these patches once they are sufficiently revegetated (Tremblay *et al.* 2018). How the habitat rebounds following the disturbance (either naturally or through management) may also change the wildlife community. For example, traditional forest harvesting (i.e. clear-cut logging) is often followed by replanting with more simplistic stands of silviculturally valuable species (British Columbia Ministry of Forests 2000). The even-aged forest stands which this practice creates typically decreases the diversity of species settling in these stands compared to the original forest or naturally regenerated forests (Castaño-Villa *et al.* 2019). Species may also be limited in their ability to move through these habitats, restricting transit between remnant forest patches, as is seen with the Ovenbird, *Seiurus aurocapilla,* in spruce plantations (Villard and Hache 2012). By comparison, disturbances created through forest fires may open similar-sized patches as forest harvesting, but some standing deadwood may remain and the forest regenerates in classic succession order, eventually becoming a mixed stand. Studies suggest the avian community will return to its original state faster in some naturally disturbed, regenerating forests compared to clear-cut/replanted forests, depending on the frequency, severity, size of the fire area and time since the fire (Saab and Powell 2005).

Size, shape, scale and severity of the disturbance are also factors that affect wildlife communities in post-disturbance habitats (Redlich *et al.* 2018) and may also interact with the initial cause of the disturbance—whether natural or human-induced. Species diversity may be relatively high in areas with many small patches of disturbance intermixed among larger tracks of mature forest; such a mosaic of habitats can provide sufficient edge to attract new species to compensate for loss of some species that prefer continuous old forest conditions (Redlich *et al.* 2018, Leston *et al.* 2018). Species composition may also shift over time, transitioning from an initial increase in edge-associated species post-disturbance, to habitat specialists as the habitat ages. Following large fires, it may take up to 30 years for some species of the bird community to return to the area (Hobson and Schieck 1999). After clear-cut logging followed by silvicultural treatments, however, species richness may temporarily increase, but will not be as high in the long-term as a partial retention harvest (Hollie *et al.* 2020), suggesting that the nature of the disturbance can impact the ability of the community to rebound. One means of managing this is to employ harvesting techniques that better resemble natural disturbances, such as variable-retention harvesting systems (British Columbia Ministry of Forests 2003). This technique (also referred to as clear-cut with reserves) retains a proportion of the standing live and dead trees and creates vertical structure and vegetative diversity to the regenerating stand (Beese *et al.* 2019). When monitoring a community post-disturbance, there may be little overall change in measures of species richness and diversity, as retention patches may lose some habitat specialists but gain some habitat generalist species (Rosenvald and Lõhmus 2007, Lance and Phinney 2001). Therefore, to test the effectiveness of this management technique to facilitate transitions back to initial states, it is important to compare both the species richness and composition of variable-retention plots against traditional clear-cut harvesting. Techniques such as this are useful for retaining diversity, as many species are less affected by a natural disturbance to an unnatural one (Simon *et al.* 2002, Kardynal *et al.* 2009, Zimmerling *et al.* 2017). Even though the composition of the bird communities that occur in the harvested areas may be fluid during the transition back to mature forest, the number of species within the area (species richness) may remain similar by creating habitat for a mix of attracted and retained generalist species. This can be achieved by retaining herbaceous and shrub communities that are preferrable for the avian species being focussed on, as Fourcade *et al.* (2018) did in grassland habitats. Thus, techniques in resource extraction that attempt to mimic natural disturbances in species retention/attraction will need to consider both species diversity and species composition in post-disturbance monitoring.

In central British Columbia, timber harvest is the largest source of anthropogenic disturbance to forest ecosystems. Variable–retention harvesting that removes commercially valuable trees (typically conifer species in central British Columbia) while retaining a portion of the trees (typically non-commercial deciduous) is being tested in the region as a means of managing wildlife diversity and composition over the larger forested landscape. With standing trees still available, even at lower stem density and lower tree species richness, forest-adapted birds may continue to use these patches for supplementary foraging/nesting more than clear-cut patches (Lencinas *et al.* 2018). Further, open-habitat adapted species may also be attracted to these lower-density patches (Fourcade *et al.* 2018). Different types of retention harvesting will attract different species (Grodsky *et al.* 2016). Harvesting younger trees and leaving the mature 'veteran' trees will allow cavity nesters, raptors and insectivorous birds to use this habitat post-harvest (Franklin *et al.* 2019, Perry *et al.* 2018, Rodgers and Koper 2017). Harvesting coniferous trees and leaving deciduous species will allow woodpeckers and herbivores to utilize a mixed-age stand of deciduous species (Lencinas *et al.* 2018). There are many methods of harvesting that retain habitat for different species and measuring the effects of these methods may contribute to management strategies that offer a more balanced forest management system.

In this paper, we compare the species diversity and composition of the avian communities between experimental clear-cut patches and neighbouring deciduous (hardwood) retention patches in mixed-wood, sub-boreal forest ecosystem of central British Columbia. Our primary objective was to determine if species diversity was higher or lower in retention patches compared to similar-sized clear-cut forests and neighbouring communities of untreated mature forest (control). Our secondary objective was to determine if there is evidence that forest species were using the retention patches. Our prediction was that the retention patches would increase species richness by providing novel habitat, and species who often prefer forested habitats would utilize the hardwood retention patches more than they would utilize a clear-cut.

Methods

Study area

The study was conducted in the John Prince Research Forest, located approximately 25 km north of Fort St. James, British

Columbia, Canada (54.669432°N, 124.414230°W). We conducted the work on five recently harvested blocks (Figure 1A), blocks 1 and 2 were harvested in 2017, block 3 was harvested in 2016, block 4 was harvested in 2011, and block 5 was harvested in 2014. The average block size was 63.7 ha, ranging from 48.5 ha to 71.9 ha. Each harvest block ('Blocks' in Figure 1A) was separated by an average of 3.96 km from the closest other block. Within each of the five blocks, ~80 per cent of each block had been subject to complete tree removal (Clear-cut treatment) and another was selectively-harvested by removing commercial conifer species (White X Engleman's Spruce *Picea glauca x englemannii*, Douglas Fir *Pseudotsuga menziesii* and Lodgepole Pine *Pinus contorta*) and retaining non-commercial deciduous species (primarily Trembling Aspen, *Populus tremuloides* and Paper Birch, *Betula papyrifera*)—these areas were designated Retention treatments (Figure 1B). Hardwood retention treatments were typically consolidated into a single patch in all blocks, and this area was on the edge of the block bordering untreated neighbouring forests. As the Retention treatment was the smallest sampling unit (~15 ha), we selected a location with a radius of 100 m that fell within the treatment type for the placement of our ARU. We then selected another area within the same block that was approximately equidistant from the surrounding forest, but in which a 100 m radius would fall in a fully harvested area and designated this our Clear-cut treatment (Figure 1B). Finally, we then identified in each block an area of the neighbouring untreated forest (Forest control) of similar distance to the forest edge, and in which a 100 m radius included only unharvested forest, as our control (Figure 1B). The centroids of each of these three plots (Clear-cut and Retention treatments and Forest control) were on average 250 m from any other treatment/control within the same block. This selection of the plot treatment/controls was repeated in all five blocks in the study area. We then placed an autonomous recording unit (ARU) (SM4, Wildlife Acoustics) at the center of both of the treatments (Clear-cut or Retention), and the control (Forest treatment) in each block so that each treatment/control had five replicates.

Plot preparation

In 2018, we conducted sound detection tests to determine the range of the sound detection of the ARU. A Northern Cardinal song was played at 75 dB (at 1 m) using a Logitech X100 Bluetooth speaker from increasing distances (25 m, 50 m, 75 m and 100 m) on all sides of the ARUs at every plot (all Clear-cut, Retention and Forest plots at each of the five blocks). As Northern Cardinals are not found within the study area, they were easily distinguished from native singers in recordings. Further, their songs include broad frequency sweeps that cover much of the range of bird song in the region. These recordings were then analysed using Kaleidoscope software (v.5, Wildlife Acoustics) to determine the distance that songs were visible in spectrograms and could be recognized by auto-detection software, as well as sufficiently audible in recordings for trained observers to detect them. This indicated that the functional range of the ARU was ~75 m–100 m for passerine song.

We chose a mature tree at the center of each treatment plot within the block to mount the ARU. The mounting tree was chosen such that the outer detection radius of the ARU (~100 m) fell completely within the treatment type. As the treatment/control plot centroids (Figure 1B) were on average 250 m apart, the detection radius of the ARUs did not overlap with those of other treatments within the block (at least twice the detection distance from another ARU). If the plot center did not contain any mature trees, a pole was erected at the plot center to facilitate ARU mounting. The ARU was mounted to the tree/pole 2.5 m above ground (ag) by means of a small tree-climbing ladder.

We made recordings and tested equipment in the spring of 2018 as a pilot study and collected the data from 25 May to 15 July 2019, which is the breeding season for many of the species we were observing. We returned once every 2 weeks to change storage cards and replace batteries at all the plots.

Differences between the treatments were measured by counting trees and noting species at a randomly chosen plot within 5 m of the ARU mounting tree. Prior to sampling, plots were assessed for being representative of the habitat coverage within the broader detection radius of the ARU (75–100 m). Harvestable mature trees (>17.5 cm diameter at breast height) were counted within an 11.28 m radius plot at each plot (400 m^2 area), and both live and dead trees were tallied. The Forest controls had the highest number of standing mature trees among the three treatments (av 28.6 ± 6.6 SD/400 m^2), compared to the Retention treatment (av 7.8 ± 2.7/400m^2) and the Clear-cut treatment (av 0.2 ± 0.07/400 m^2). The basal area was also highest in the Forest controls, with an average of 29.54 m^2/ha, followed by the Retention treatments (11.23 m^2/ha), and the Clear-cut treatments (0.43 m^2/ha). Among the trees that were in the 400 m^2 plots, the Forest treatment had a mixed composition of deciduous (24 per cent) and coniferous trees (76 per cent), whereas the Retention was dominated by deciduous trees (95 per cent). There was only one tree found in all the Clear-cut plots, and it was deciduous. The average basal area retained in the Retention treatments was 38 per cent of the basal area in the Forest controls.

ARU settings

In the 2018 pilot season, the ARU's were set to record for 2 h each centered on dawn and dusk. During analysis of the pilot data, we found the peak period of song activity occurred within 30-minute centered at dawn. This period allowed high likelihood of detecting both early and late-starting signallers during the peak of dawn vocalizing, and the longer sampling period also allowed for greater possibility of detecting species that vocalize less frequently. As a result, in 2019 we set ARUs to record for 30-minute centered on dawn (civil twilight for date of recording) for analysis, and enumerated all species audible in the recordings. Due to the time required to manually transcribe these recordings, we chose to analyse recordings from every third day throughout the date range. If these recordings fell on a day of high wind or storms, we would select the next day with more audible conditions as a substitute; likewise, if the recording window centered on dawn had low-audibility conditions for the start or end of the recording, we shifted the time back or forward to conduct the 30-minute inventory during more audible conditions. This method gave more flexibility in usable recording days. This resulted in analysing a total of 150 30-minute recordings for the combination of treatments and blocks (three 30-minute recordings per sample day at each plot, corresponding to one each per

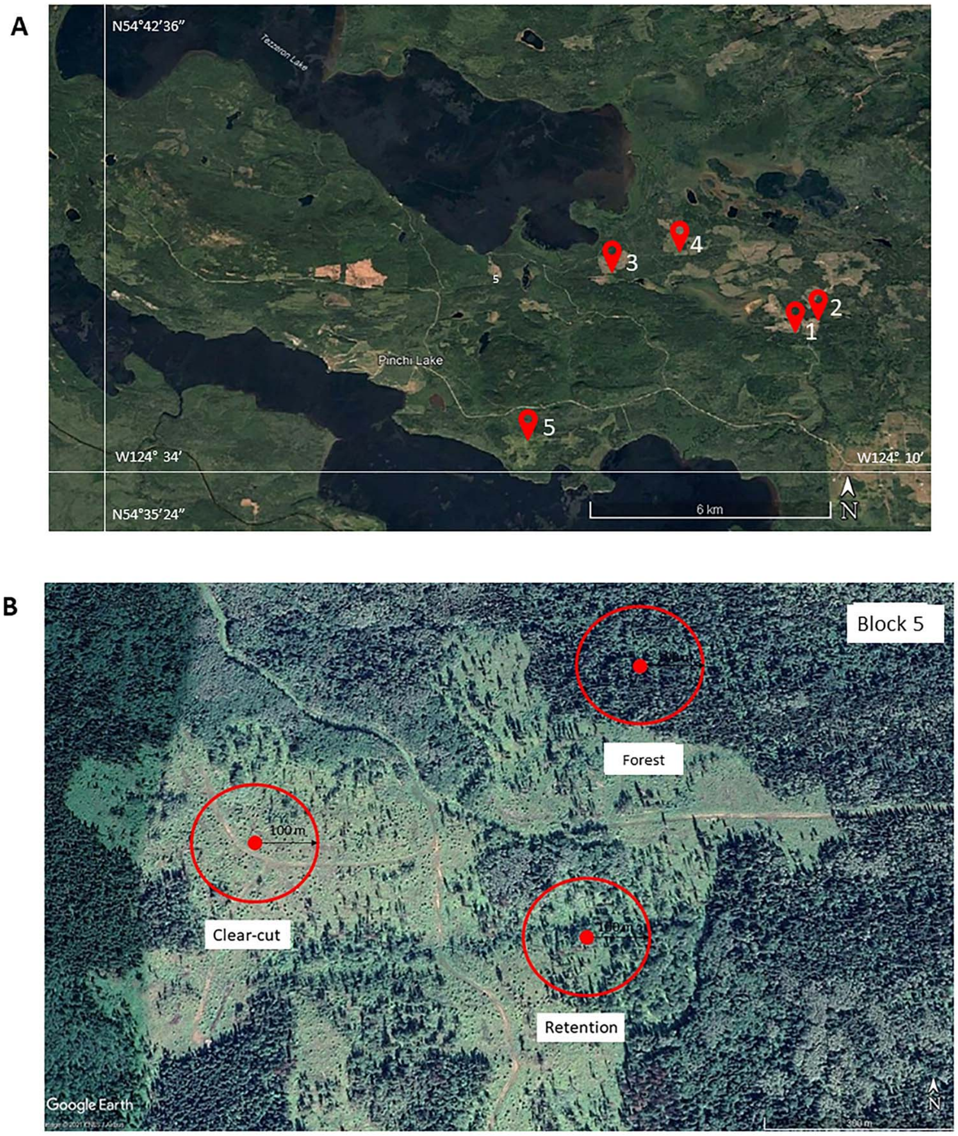

Figure 1. Overview of the study area with blocks numbered (A) and an example of the study design for each block (B). The large red circles indicate the sound detection radius of the ARU's within each treatment plot (Clear-cut, Hardwood Retention and Forest control), which was on average 100 m from the center of the plot (B). Satellite imagery was collected from Google Earth Pro (2021).

treatment, and 10 days of sampling at each of the five blocks over the date range).

The recordings were transcribed using spectrographic software (Kaleidoscope, Wildlife Acoustics). A trained observer identified the presence of each species detected within each recording, aided by reference vocalizations of local species (from personal recordings or sound archives, such as Xeno-canto or the Macaulay Library of Natural Sounds, Cornell University). Some species detected in ARU recordings—e.g. Common Loons (*Gavia gavia*), Barred Owls (*Strix varia*)—have sufficiently loud vocalizations that they could likely have been detected outside of the 100 m radius of the ARUs, and thus could not with certainty be ascribed to a particular habitat treatment. Several instances of these detections were cross-checked to confirm that they were heard simultaneously on at least two ARUs in different treatments within the same block. As such, we restricted analysis to detected species with vocalizations that would be unlikely to transmit to two ARUs in different treatment types simultaneously—this includes species in the passerines (Passeriformes), hummingbirds (Apodiformes), smaller owl species (Strigiformes), shorebirds (Charadriformes) and woodpecker (Piciformes) Orders (Table 1). Seven species of the 43 species that were detected were removed from the list of species analysed due to the loudness of their vocalizations.

To independently classify the habitat associations of the species identified in this study, we provided a species list to a group of five ornithologists (referred to as 'experts' in the following) and asked them to categorize the species as to

Table 1 Total number of detections of bird species by ARU in 2019 included in the analysis, as well as how each species was classified for habitat preferences by a panel of five classifiers

Species	Clear-cut (treatment)	Retention (treatment)	Forest (control)	Habitat classification	Agreement among classifiers (out of 5)
Alder Flycatcher	4	0	2	Early-seral Forest	5
American Robin	35	44	46	Early-seral Forest	4
Black-capped Chickadee	0	4	1	Early-seral Forest	3
Boreal Chickadee	0	3	1	Mature Forest	5
Brown Creeper	1	6	11	Mature Forest	5
Cedar Waxwing	7	12	8	Early-seral Forest	4
Common Raven	0	2	0	Early-seral Forest	4
Dark-eyed Junco	40	43	36	Early-seral Forest	4
Dusky Flycatcher	0	1	0	Early-seral Forest	5
Golden-crowned Kinglet	1	11	27	Mature Forest	5
Hammond’s Flycatcher	2	2	3	Mature Forest	5
Hermit Thrush	0	1	0	Mature Forest	5
Hummingbird sp	0	1	3	Early-seral Forest	5
Least Flycatcher	29	38	44	Early-seral Forest	5
Lincoln’s Sparrow	0	3	2	Early-seral Forest	5
MacGillivray’s Warbler	1	1	1	Early-seral Forest	4
Northern Pygmy Owl	0	0	1	Mature Forest	4
Northern Flicker	16	21	25	Early-seral Forest	5
Northern Waterthrush	5	18	25	Mature Forest	3
Olive-sided Flycatcher	5	5	13	Early-seral Forest	5
Pacific Wren	0	8	19	Mature Forest	4
Red-breasted Nuthatch	3	2	6	Mature Forest	5
Red-breasted Sapsucker	8	15	19	Mature Forest	5
Ruby-crowned Kinglet	0	4	2	Mature Forest	4
Swainson’s Thursh	31	43	47	Mature Forest	5
Tennessee Warbler	10	12	3	Early-seral Forest	5
Varied Thrush	3	7	2	Mature Forest	5
Western Tanager	2	0	0	Mature Forest	4
Western Wood PeeWee	5	4	8	Early-seral Forest	4
Willow Flycatcher	1	0	0	Early-seral Forest	5
Wilson’s Warbler	5	8	1	Early-seral Forest	5
Wilson’s Snipe	22	27	31	Open	4
White-throated Sparrow	39	44	46	Early-seral Forest	5
Yellow-bellied Sapsucker	0	1	1	Early-seral Forest	5
Yellow-rumped Warbler	7	3	4	Mature Forest	5

Options for classification were ‘Mature Forest’, ‘Early-seral Forest’ or ‘Open-habitat’ based on descriptions of habitat preferences in species accounts from ‘Birds of the World – online’. Classifications were made independently, and the Agreement (same classification independently arrived at) by experts is indicated.

whether their breeding habitat was characterized by either mature forest, early-seral habitat, or open-country habitat. This assessment was done using the ‘Habitat in Breeding Range’ descriptions under the ‘Habitat’ page from individual species accounts on the Bird of the World Online webpage (birdsoftheworld.org). The experts were provided with some key words associated with each habitat type to use in the classification; this included descriptors like: ‘old-growth’, ‘mature deciduous woodlands’ for our Mature Forest category; ‘edge’, ‘shrub’, ‘forest openings’, ‘young forest stands’ for our Early-seral category; and, ‘open’, ‘grasslands’, ‘fields’ for Open category. The experts categorized habitat associations for all species without reference to which treatment types the species had been detected in, nor how often they had been detected. We used agreement between the majority of the experts’ assignments (3/5) to assign a typical habitat category to each species, although in most cases agreement was usually 4/5 to 5/5 among the experts (average across all species was 4.6/5 for expert agreement).

Data analysis

We counted the number of days (any detections within the 30-minute recordings/day) in which a particular species was detected in each of the three treatments across dates sampled. This resulted in 1114 individual detections being identified from recordings, comprising 35 species detections across the three habitat classes over the course of the study. However, the number of individuals sampled in each habitat differed, with 282 detections in Clear-cuts, 394 in Retention plots and 438 in Forest plots. As estimates of species diversity are affected by the number of individual detections sampled, we used rarefaction to compare diversity estimates between our plots (Gotelli 2008, Chao *et al.* 2014). Rarefaction employs Monte Carlo subsampling from the observed relative abundance data at a given plot to determine estimated species diversity if a smaller number of individuals had been detected. The generated estimates (and their confidence intervals) at various points along the number of species sampled (from 1 to N for a particular plot) allows building an Interpolation curve. Extrapolation then allows a means of estimating how much species diversity is expected to increase at the plot if additional individuals had been sampled. This allows direct comparison of species diversity estimates between plots where different numbers of individuals were initially sampled—if the species diversity of one plot falls outside the 95 per cent CI of the rarefaction curve of another plot when controlling for number of individuals sampled, one can reliably say the two plots differ (Gotelli 2008, Chao *et al.* 2014).

We used our relative abundance dataset (number of individuals of each species detected within each treatment) using the package iNEXT (Chao *et al.* 2014, Hsieh *et al.* 2020) in R (v. 3.5.3. 2019, R Development Team) to Interpolate/Extrapolate Species Richness and determine Shannon Diversity estimates of samples by treatment type for comparison. Species Richness was calculated by specifying a Hill number (q) of 0 in iNEXT, whereas Shannon Diversity (the exponentional of Shannon entropy) used a Hill number of 1. We set the endpoint to which all plots would be extrapolated to at 800, approximately twice the total number of individuals sampled at both the Forest and Retention plots. We set the confidence limits at 95 per cent and used the default number of bootstrap replications (50) recommended by iNEXT (Hsieh *et al.* 2020). An excellent tutorial on the package and settings is available at https://cran.r-project.org/web/packages/iNEXT/vignettes/Introduction.html.

Each of the species detected was classified as Mature Forest, Early-Seral or Open species by our experts. We then compared the number of species showing these specific habitat preferences between the Clear-cut, Retention and Forest patches using Log likelihood ratio (G-test) with Williams' correction in the DeskTool package (v. 0.99.39) in R (v. 4.0.3. 2020, R Development Team).

Data availability

We provide counts of detected species and species association classifications as supplementary data. R code used in analysis is available upon request and is available on GitHub https://github.com/kenaotter/rarefaction.

Results

Avian Diversity, species richness and species composition between treatments

A total of 42 species were identified in ARU recordings in 2019, but nine of these species had vocalizations that were detected simultaneously on separated ARU in adjacent treatment types (American Bittern, Barred Owl, Canada Goose, Common Loon, Ruffed Grouse, Sandhill Crane and Pileated Woodpecker). This indicated that their locations could not reliably be classified to a specific treatment. These seven species were hence excluded from further analysis. The remaining 35 species include three species of woodpecker (Northern Flicker, Red-breasted Sapsucker and Yellow-bellied Sapsuckers), one species of small owl (Northern Pygmy Owl), one Charadriformes (Wilson's Snipe) and 29 species of passerines. A complete list of species and the habitats which were assigned to the species by our experts is provided as supplemental material.

The Shannon Diversity indices of the 2019 ARU data showed some differences between treatments (Figure 2A). Specifically, the Clear-cut treatment had a lower Shannon Diversity index than the other two treatments; this was determined by the interpolation curves (solid lines) of the other two treatments (Retention and Forest (control)) falling outside the 95 per cent confidence intervals at the point of total number of individuals sampled for the Clear-cut treatment (vertical dashed line in Figure 2A). This method of subsampling using interpolation lines allows direct comparison between plots while controlling for number of individuals sampled (Gottelli 2008). As the interpolation line for Forest controls fell within the 95 per cent CI of the Retention plot at the point of total individuals sampled, we detected no difference in the Shannon Diversity of these two plots.

The species richness indices of the 2019 ARU data had more overlap of the 95 per cent CI surrounding the interpolation/extrapolation curves than the Shannon Diversity indices. However, the Species Richness interpolation line for the Retention plot (Figure 2B) falls outside the 95 per cent confidence intervals at the point for the number of individuals sampled for the Clear-cut treatment, indicating that the Clear-cut had significantly lower species richness than the Retention plot when controlling for number of individuals sampled. Similarly, the Forest control plot was just outside the 95 per cent CI of the Clear-cut treatment, indicating a higher species richness. However, the estimated Species Richness for number of individuals sampled (points) and interpolation lines of both the Forest and Retention plots fell well within each other 95 per cent CI, indicating no detected difference in Species Richness.

Of the 35 species included in the analyses, 15 species were independently classified as being typically associated with Mature Forest, 19 with Early-seral Forest and only one (Wilson's Snipe) with Open-habitat (see supplemental material for individual classifications by species). There was strong congruence between expert classifiers in habitat associations for each species, with an average of 4.6 ± 0.6SD of the five experts independently assigning the same habitat classification to each of the 36 species.

The detection of species associated with the three habitat classes (Mature Forest, Early-seral Forest or Open Habitat) differed among our treatment types ($G = 20.57$, df = 4, $P = 0.0004$) (Figure 3). Inspection of the observed detections against expected values generated by the model indicate that Mature-forest associated species were detected significantly more than expected by chance within the Forest controls, and significantly less than expected by chance in the Clear-cut treatment, but observed detections were similar to expected

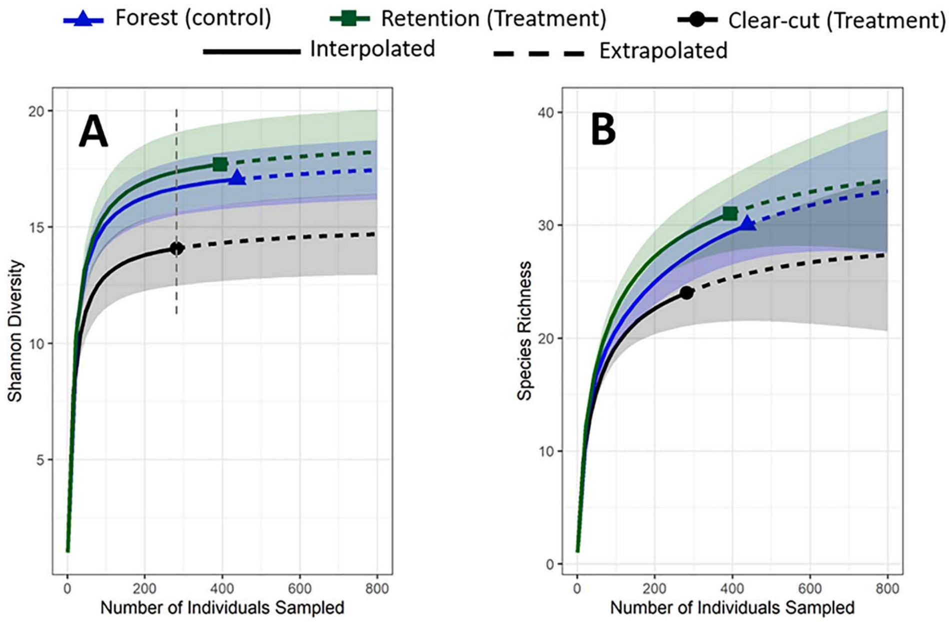

Figure 2. Shannon Diversity (A) and Species Richness (B) of bird detections in 2019 by treatment (Clear-cut, Hardwood Retention or Forest controls). Filled points (circle, square and triangle) on the line indicate the actual value for the number of individuals sampled at each plot. Solid lines are the back-interpolated estimates of Shannon Diversity (A) or Species Richness (B) at different smaller values of individuals sampled, and dashed lines are extrapolations of values if additional individuals had been sampled. Shaded areas are 95 per cent Confidence Intervals for the interpolated/extrapolated values. Comparing plots while controlling for number of individuals sampled is demonstrated by inserted vertical dashed line—the point on the interpolated Retention and Forest plots lays outside the 95 per cent CI of the Clear-cut plot, indicating that Shannon Diversity is higher for both these plots relative to the Clear-cut plot.

values within the Retention treatment. Early-seral Forest associated species were detected more than expected by chance in the Clear-cut treatments, significantly less than expected by chance in the Forest controls, but were similar to expected detections within the Retention treatments. The few Open-habitat associated species did not differ from expected values in any of the three treatments.

Discussion

Diversity

Our data suggests that Retention treatments dominated by deciduous species created a softer transition for settlement/use by avian species between the Forest controls and Clear-cut treatments. Species that were independently classified as 'Mature Forest'-associated were detected primarily in Forest plots but were also secondarily detected within Retention plots. The Species Richness and Shannon Diversity estimates of these two treatment types did not differ, but both were found to be higher than estimates for Clear-cuts. Thus, species associated primarily with forests may be able to use Retention sites as a habitat buffer, while the selective-retention of deciduous trees may also create potentially novel habitat that attracts Early-seral associated species (e.g. Tennessee Warblers and Western Wood Peewees) that contribute to increasing the overall diversity of the landscape. Although the retention itself did not have the highest species diversity, it may contribute to increasing the overall diversity when considering all three Treatment types collectively.

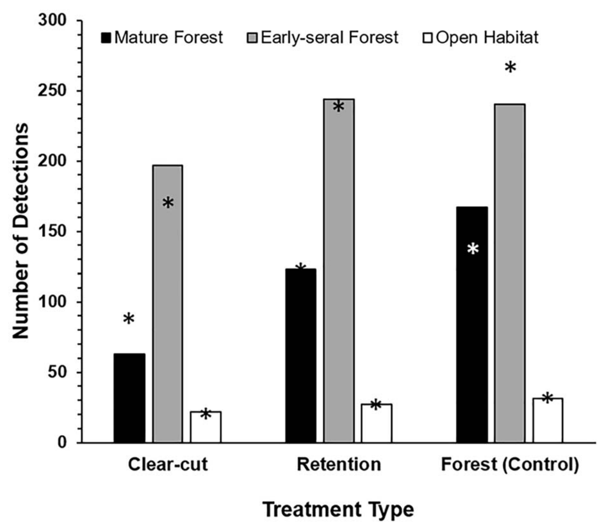

Figure 3. Detections of Mature Forest, Early-Seral Forest and Open Habitat associated avian species in each of the three treatment types: clear-cut patches, hardwood-retention patches and forest (control) patches. Asterisks for each column indicate the expected detections from a Log-likelihood test to which the observed detections (solid bars) were compared.

We found the Shannon diversity were similar for the Forest controls and Retention treatments, but lower in the Clear-cut treatments. When observing the habitat differences between these plots, the Forest control plots had double the number of mature stems, and a higher variety in tree species. This could account for why species classified as forest-associated were more likely to be detected in the Forest controls, as a more diverse forest community can support a more diverse bird community (Väisänen *et al.* 1986). The Forest controls also had a higher species richness than the Clear-cut treatments, but interestingly the species richness in Forest controls was not significantly different from the Retention treatment—this further suggest the Retention treatments could serve as a buffer to minimize the overall loss of species from the region.

The lowest Shannon diversity index was found in the Clear-cut treatment, which also had the lowest vertical vegetation structure available. Without this important vertical structure, there is little habitat available to most forest-dependent birds that are characteristic of the local ecosystem. This vertical structure is used as perches for foraging, singing, or provides nesting sites for non-ground nesting species (Laughlin *et al.* 2013). Without this structure, many species will not spend extensive time in these spaces, which could account for the lower species richness and diversity detected in recordings from these plots. Most of the species detected in these areas were either Open habitat or Early-seral Forest associated species. More vertical structure can support more forest-dependent species, as vertical niche differentiation occurs (Laughlin *et al.* 2013), which also supports the utility of integrating in selective-retention patches in logging management.

Species composition

There was only one species detected exclusively in the Forest control (Northern Pygmy Owl). There were, however, several species detected primarily in the Forest control, but also secondarily in the Retention treatment: Brown Creeper, Golden-crowned Kinglet and Pacific Wren. Most of these species are associated with mature coniferous forests and are rarely found in other habitats (Schieck and Hobson 2000). Our own independent experts categorized all as 'Mature Forest' associated species. This highlights the importance of maintaining a significant portion of the landscape in mature forest, as these species might otherwise be lost.

Hermit Thrushes, Dusky Flycatchers and Common Ravens were the only species solely detected in Retention treatments and not elsewhere. Two of these (Common Raven and Dusky Flycatcher) were species classified as being early-seral forest associated. We also found some species which had 50 per cent or more of their detections in the Retention treatments (Ruby-crowned Kinglets, Black-capped Chickadees, Boreal Chickadees, Varied Thrush and Wilson's Warblers). Several of these species were classified independently as species associated with early-seral habitat (e.g. Black-capped Chickadees and Wilson's Warblers), which includes edge habitat. Edge habitats are described as an interface between two adjacent and opposing habitats, such as the transition between forests and large openings (Boesing *et al.* 2018), which is represented by our Retention treatment areas. These early-seral species will use both the open and forested aspects of the edge for different daily activities, including foraging and nesting. The Retention treatments in this study may have helped make this transition less highly contrasted, extending the valued aspects of vertical structure and foraging availability for these species. Although the Retention plots were still considered 'forested', stem densities of mature trees in these plots were less than half that of Forest controls. This type of buffer effect may change the edge-effect dynamic of this forest, making this softer edge more accessible for both forest-associated species and clear-cut associated species, while potentially generating novel habitat for other species that are not associated with edge, mature mixed forest, or open country. This interpretation is reinforced in our study, as several of the species with 50 per cent or more of their detections within the Retention treatments were classified as mature-forest associated (e.g. Ruby-crowned Kinglets, Boreal Chickadees and Varied Thrush).

There were only two species detected exclusively in the Clear-cut areas (Western Tanager and Willow Flycatcher). Interestingly, neither of these two species were classified as open-habitat associated by our experts. Western Tanagers were classified as associated with Mature Forest and Willow Flycatchers with Early-seral Forests. The only species our experts linked to Open habitat was the Wilson's Snipe, yet this species was detected in all three treatment types and did not contribute sufficiently to detected differences between treatments among open-habitat associated species (Figure 3, Appendix Table). This likely stems from the habit of displaying snipe of signalling using diving aerial displays above territories, with sound generated from the whistling of their tail feathers. Such displays may have been conducted over neighbouring treatments, despite snipes typically preferring to nest in open-habitat. Our study did not suggest that Clear-cuts treatments would contribute significantly to an increase in landscape-level diversity, but this is likely the result of the scale of the study being limited to five comparison blocks. Inclusion of more blocks, especially larger clear-cuts in landscapes with more intensive forestry, may have resulted in detection of a greater number of open-habitat associated species. Species associated with Open-habitats are typically using open spaces for foraging (aerial predators and insectivores, as well as seed-eating species) or nesting (ground nesting birds) (Fourcade *et al.* 2018), and this may have been the case for Willow Flycatchers. Within our study, this may suggest that the retention is a more important habitat component for forest-dwelling species than for open-country species, and further studies could be conducted to determine the importance of retention habitats.

Decreased diversity associated with complete habitat clearing (e.g. Clear-cut treatments) that we found is similar to other studies conducted on bird communities around the world. Väisänen *et al.* (1986) found that the removal of mature forests in Finland reduced the number of forest-dependent species but increased the overall diversity by the addition of other species in the new habitat created. Many other studies have noted the general decrease in biodiversity found in clear-cuts, especially clear-cuts that are replanted as a monoculture stand (Rosenvald and Lõhmus 2007, Väisänen *et al.* 1986, Perry *et al.* 2018, Linden and Roloff 2013). Our results provide evidence that retention of forest elements can alleviate part of that diversity decline. Linden and Roloff (2013) looked at a different kind of selective-retention than our study, specifically snags, downed trees and younger green trees. They found that the retention of certain habitat elements increased the biodiversity in the forest that they were studying. Many studies have found that numerous bird species benefit from other specific habitat elements such as perches (Rodgers and Koper 2017) and legacy trees (Mazurek and Zielinski 2004) when left after a harvest or disturbance. Lance and Phinney (2001) also compared clear-cut, partial retention and forest patches in the central-interior of British Columbia on diversity of birds, and similarly found the lowest avian diversity in clear-cuts, whereas the retention and forest sites had similar species richness. This almost parallels the findings in our study. Lindenmayer *et al.* (2018) observed the effects of harvesting and fire on bird species richness, and found the highest richness was in the least disturbed sites, equivalent to our control Forest plots, but also suggested that retention patches are very effective to better maintain species richness when harvesting timber.

Selective-retention harvesting not only maintained better diversity in the short-term, as our study shows, but could also provide faster recovery of the habitat to a level near its original diversity. Schieck and Song (2006) have estimated that post-disturbance (fire), it may take up to 70 years for mature-forest adapted bird species to return to the area. Similar delays may be expected with complete forest removal by clear-cut harvesting. Integration of selective-harvesting and retention of mature non-commercial deciduous trees, such as realized in our Retention plots, may expedite the return of forest-adapted species (Schieck and Song 2006), and it would be of interest to continue tracking our plots over time to see if this is the case.

Other studies have found that clear-cuts do partially increase the overall diversity of a site by contributing new species associated with open habitat. Maintaining small cutblocks may help contribute to overall diversity, and all the species we encountered in these treatments were native to the region. Integration of clear-cut and retention sites to management does have utility, particularly if designing the clear-cuts in a manner that allows them to be quickly reoccupied (Vitz and Rodewald 2006), such as smaller sized clear-cuts.

Conclusions and management suggestions

The Retention treatments maintained comparable levels of Species Richness and Shannon Diversity to the Forest controls in our study, and thus contribute to the overall landscape-level diversity. This is due to several species being significantly more likely to be found in this treatment type than in either Forest controls or Clear-cut treatments. By providing this habitat buffer, the Retention treatments help to create a transition zone between the harvested and unharvested parts of the forest. Species utilizing the Forest controls and Clear-cut treatments primarily, were both found using the Retention treatment, so it has created a space where overlap between avian species guilds may occur.

Removal of all trees (clear-cuts) resulted in a decrease in avian diversity, likely due to the dependence of many forest-associated species on the vertical structure and canopy cover as vital habitat features. Variable-retention harvesting (Retention treatment) created a means of harvesting merchantable timber while maintaining avian diversity and significant habitat structure. This may provide a solution to combat the decline of biodiversity in British Columbian forests. Despite approximately half of the mature trees being removed from the landscape, the avian diversity remained close to that of the control neighbouring Forest controls. If coniferous trees were the target species of the harvest, which they often are in British Columbia, then leaving the remainder of the stand appears to benefit the local bird community. There is also evidence that suggests smaller clear-cuts are more tolerable for forest-adapted species, as they are more likely to utilize a small opening compared to a larger opening (Vitz and Rodewald 2006). This suggests that smaller clear-cuts, in combination with retention harvesting around the edges, could provide an economical method to harvest while minimizing the impacts on diversity. In a time when climate change threatens the forestry industry, making harvest changes such as this may have long-term positive impacts on the wildlife within the harvested forest. Climate change is also threatening bird species and their habitats (Stralberg *et al.* 2015), so making changes to harvesting that will benefit these species helps maintain healthy populations in the future, while making a more resilient landscape.

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