Research Paper

How well does forestry in Ontario's boreal forest emulate natural disturbances from the perspective of birds?

J. Ryan Zimmerling[1], *Charles M. Francis*[2], *Christian Roy*[1] *and Anna M. Calvert*

[1]Canadian Wildlife Service, Environment and Climate Change Canada, Gatineau, Québec, Canada, [2]Canadian Wildlife Service, Environment and Climate Change Canada, Ottawa, Ontario, Canada

ABSTRACT. Emulating natural disturbance has become a paradigm for biodiversity retention in forest management. This study evaluates the extent to which harvest management practices have created stands that emulate natural fire disturbance from the perspective of bird communities in Ontario, Canada. We compared the relative abundance of forest landbirds at the stand level in mature forest (> 80 years old) with that in early-regenerating (0–20 years) and midgenerating (21–80 years) forests originating from fire or timber harvest across the boreal forest of Ontario using over 7000 point counts. Our results indicate that forest harvest management practices in Ontario have created stands that only partially emulate natural fire disturbances in terms of the bird community composition. Total bird abundance and species richness were significantly lower postharvest than postfire in midgenerating forests, although they did not differ in early-regenerating stands. Species-level comparisons revealed several differences between postharvest and postfire stands, as well as among age classes. Although no species was completely missing from any stand type, 8% of species in early- and 34% in midgenerating stands were detected significantly less often in postharvest than postfire forests. Some other species were found significantly more often in postharvest stands, while the majority of species detected (84% and 71% in early- and midgenerating stands, respectively) showed no significant difference between disturbance types. Collectively, these results suggest that widespread replacement of fire with logging as the dominant disturbance type will shift the relative abundance of species within Ontario's boreal forest bird community. Quantifying the population-level implications of these shifts requires extrapolating these stand level effects to the landscape level, while considering the actual or anticipated abundance and distribution of forest age classes across the province under different forest management regimes.

La foresterie en forêt boréale ontarienne réussit-elle à reproduire les perturbations naturelles telles que perçues par les oiseaux?

RÉSUMÉ. La reproduction des perturbations naturelles est devenue un paradigme pour la rétention de la biodiversité en aménagement forestier. La présente étude cherchait à évaluer à quel point les pratiques d'aménagement forestier ont généré des peuplements qui reproduisent les perturbations naturelles provenant de feux pour les communautés aviaires en Ontario, Canada. Nous avons comparé l'abondance relative des oiseaux terrestres forestiers à l'échelle du peuplement dans les forêts mûres (> 80 ans) avec celle observée dans de jeunes forêts en régénération (0-20 ans) ou des forêts d'âge moyen en régénération (21-80 ans) issus de feux ou de récolte forestière dans la forêt boréale de l'Ontario, au moyen de plus de 7000 points d'écoute. Nos résultats indiquent que les pratiques d'aménagement forestier en Ontario ont généré des peuplements qui reproduisent seulement partiellement les perturbations naturelles issues de feux en termes de composition de la communauté aviaire. L'abondance relative totale des oiseaux et la richesse spécifique étaient significativement plus faibles à la suite d'une coupe qu'à la suite d'un feu dans les peuplements d'âge moyen, mais elles n'étaient pas différentes dans les jeunes peuplements. Les comparaisons à l'échelle des espèces ont révélé plusieurs différences entre les peuplements après coupe ou après feu, de même que parmi les classes d'âge des forêts. Bien qu'aucune espèce ne fût absente dans les divers types de peuplements, 8 % des espèces dans les jeunes peuplements et 34 % des espèces dans les peuplements d'âge moyen ont été détectées significativement moins souvent dans les forêts récoltées que les forêts après feu. Certaines espèces ont été trouvées significativement plus souvent dans les peuplements récoltés, alors que la plupart des espèces détectées (84 et 71 % dans les jeunes peuplements et les peuplements d'âge moyen, respectivement) ne montraient pas de différences significatives entre les types de perturbations. Pris dans leur ensemble, nos résultats indiquent que la pratique répandue de substituer la récolte forestière au feu, comme type dominant de perturbations, entraînera des changements d'abondance relative des espèces dans les communautés aviaires de la forêt boréale de l'Ontario. Pour quantifier les effets de ces changements à l'échelle des populations, il faut extrapoler les effets observés à l'échelle du peuplement à celle du paysage, tout en considérant la quantité et la répartition actuelles ou anticipées des classes d'âge des forêts dans la province sous différents régimes d'aménagement forestier.

Key Words: *boreal; fire; forest management; harvest; natural disturbance emulation; Ontario; point count*

Address of Correspondent: J. Ryan Zimmerling, Canadian Wildlife Service, Environment and Climate Change Canada, Gatineau, Québec, Canada, Ryan.Zimmerling@canada.ca

INTRODUCTION

Retention of biodiversity in human dominated landscapes is important for long-term conservation of species and ecosystems. Although the extent of human impacts on natural landscapes continue to increase, only a limited portion is considered protected (15.4% globally as of 2014; Juffe-Bignoli et al. 2014), placing particular importance on conservation in human-managed areas. Conservation theory supports the importance of biodiversity to ecosystem function, stability, and productivity (e.g., Tilman et al. 1996, Cardinale et al. 2012). Ensuring the retention of a full complement of natural species is believed to be integral to sustainable communities (Mayfield et al. 2010), particularly in forest habitats (Paillet et al. 2010, Zhang et al. 2012), as emphasized by the Secretariat of the Convention on Biological Diversity (2014) and the North American Bird Conservation Initiative (2016).

Emulation of natural disturbance for biodiversity retention has become a key component of ecosystem-based forest management globally (e.g., Bunnell 1995, Perera and Buse 2004, Klenk et al. 2008, Sibley et al. 2012), including in the boreal forests across Canada (Senate Subcommittee on Boreal Forests 1999). This approach assumes that wildlife have adapted over time to forest disturbance resulting from wildfires and, to a lesser degree, insect outbreaks (Hunter 1993, Attiwill 1994, Haila et al. 1994, Niemelä 1999). Consequently, harvesting aimed at emulating the spatial and temporal changes resulting from these natural changes should minimize the loss of biodiversity (Bunnell 1995, Long 2009), at least at a coarse community scale that retains key habitat features required by most species (Cyr et al. 2009, Mayfield et al. 2010). Recent broad-scale assessments suggest that emulation of natural disturbance regimes in northern forests may be generally succeeding in maintaining many ecosystem functions and biodiversity (e.g., Long 2009, Börger and Nudds 2014), though some important knowledge gaps remain (Kuuluvainen and Grenfell 2012, Brandt et al. 2013).

Despite growing support for natural disturbance emulation in biodiversity conservation, empirical tests of this approach have not kept pace with theoretical predictions (Kuuluvainen and Grenfell 2012). Concern has also been raised that incomplete information on forest ecology and historical fire regimes might limit the effectiveness of this paradigm to achieve ecological sustainability (Tiedemann et al. 2000, Macdonald et al. 2004). Identified gaps include the need for improved emulation of natural fire-disturbance intervals (Cyr et al. 2009), incomplete long-term spatial and temporal data on anthropogenic forest change (Venier et al. 2014), and the absence of studies into the processes leading to observed differences in harvested vs. fire-disturbed forests (Wyshynski and Nudds 2009; though see Whitaker et al. 2008 for a measure of disturbance-specific demographic parameters, and Bélisle et al. 2007 for a test of evolutionary mechanisms). Predictions that timber harvesting may reduce biodiversity (e.g., Welsh and Venier 1996, Niemi et al. 1998, Askins 2000, Drever et al. 2006, Van Wilgenburg and Hobson 2008) are in contrast with recent evidence for the relative success of harvest management approaches in maintaining biodiversity (e.g., Lemelin et al. 2007, Wychynski and Nudds 2009, Börger and Nudds 2014). This disparity supports the need for continued empirical evaluation of how well harvesting mirrors natural forest processes.

Quantifying both community- and species-level differences in boreal birds between postharvest and postfire forests can be valuable for assessing the effectiveness of natural disturbance emulation (e.g., Rempel 2007, Van Wilgenburg and Hobson 2008). Several studies suggest that some bird species found in naturally disturbed forest stands are significantly less abundant in postharvest stands of similar types and ages, especially in the earliest successional stages but also several decades after harvest (e.g., Schulte and Niemi 1998, Hannon 1999, Imbeau et al. 1999, Simon et al. 2002). However, others find little difference for most species (e.g., Lemelin et al. 2007, Börger and Nudds 2014, Rempel et al. 2016). Lewis et al. (2016) found that waterfowl were relatively unaffected even by natural disturbance in the boreal forest. At the community scale, Drapeau et al. (2000) found that the mean number of mature forest bird species was significantly lower in human-altered landscapes of northern Québec than in naturally disturbed landscapes, largely because of a conversion from mixed-wood to deciduous cover. A broad review across North American forests suggests that such a conversion of mature forests could impact some regional bird populations and potentially jeopardize the ecological integrity of these habitats if harvest management practises are not further modified (Drever et al. 2006; see also Hobson and Bayne 2000, Venier et al. 2014).

Comprehensive data spanning a range of forest ages and postdisturbance time frames are important for assessing natural disturbance emulation. Because forest habitats are constantly changing with growth and decay, and as their inhabitants respond to habitat alteration, differences in bird communities between postfire and postharvest habitats may be dynamic (Schieck and Song 2006). For example, Hobson and Schieck (1999) showed that higher snag densities in recently burned vs. harvested mixed-wood forests of Alberta were correlated with initially greater abundance of cavity-nesting species, but that snag decay led to some convergence of bird communities after 28 years postdisturbance. By 60 years postharvest, Schieck and Hobson (2000) suggested these differences were virtually eliminated. Song (2002) also found that, as the forest canopy closed, both the bird communities and vegetation structure converged at about 50–60 years postdisturbance. Such findings have led to the general hypothesis that many birds of the boreal forest, where extreme periodic stand-replacing natural disturbances, e.g., fire and insect outbreak, have occurred frequently in the past, may be particularly resilient to disturbances caused by harvest management (Welsh 1987, Schmiegelow et al. 1997, Lemelin et al. 2007, Whitaker et al. 2008, Börger and Nudds 2014; but see discussions in Drever et al. 2006, Schmiegelow and Villard 2009).

Given the critical importance of the boreal forest to landbirds in Canada (Blancher 2003, Blancher and Wells 2005), and the large portion of the boreal forest subject to harvest management practices, the degree of resilience of boreal forest birds to industrial timber harvesting is of particular interest (Schmiegelow and Villard 2009). If birds do differ between naturally and anthropogenically disturbed boreal habitats, identifying the species most affected and the time frame of these effects might reveal mitigation strategies to reduce overall impacts on avian communities (Rempel et al. 2007, 2016). The primary objective of our study was therefore to evaluate the extent to which harvest management practices have emulated natural fire disturbances from the perspective of bird communities and individual bird

species across a large region of Ontario boreal forest. Using a large data set covering a wide area of northern Ontario, we contrasted postfire vs. postharvest forest bird communities of two age classes (< 20 yrs vs. 20–80 yrs postdisturbance), and also compared these bird communities with those of mature natural forests > 80 years postfire.

METHODS

Study area

This study was conducted throughout the Crown forests of Ontario where commercial timber harvesting occurs, a region that extends from the border of Manitoba to Québec, and covers an area of 240,000 km². The study area covered two bird conservation regions (BCRs; Fig. 1), which are characterized by their bird communities, habitats, and land uses. The Boreal Softwood Shield (BCR 8) primarily comprises dense boreal forest, which in comparison to the forests of southern Ontario has a limited diversity of tree species. Black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*) are the dominant species (Thompson 2000), and in various associations cover more than 60% of the landscape. The Boreal Hardwood Transition Forest (BCR 12) is characterized by a mosaic of deciduous, mixed, and coniferous stands covering more than 65% of the landscape (OMNR 2001). Species such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and red oak (*Quercus rubra*) are common in the southeast of the region, and boreal species such as black spruce, white birch, and jack pine more common in the north.

Fig. 1. Locations of the 329 10 x 10 km breeding bird atlas squares where sampling took place in the Boreal Softwood Shield and Boreal Hardwood Transition Bird Conservation Regions of Ontario.
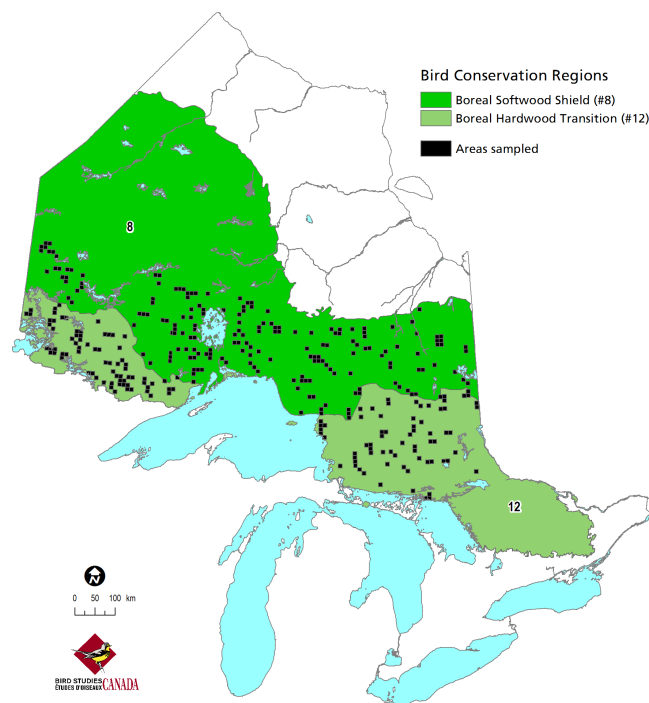
Field methods

Between 27 May and 19 July 2002 to 2004, bird communities were sampled using point counts in postfire and postharvest forests of various forest ages. The majority of point counts (66%) were conducted in late May or June and sampling dates were evenly distributed across disturbance histories. Sampling methods were adapted from those used for the second Ontario Breeding Bird Atlas (Cadman et al. 2007). Throughout the study area, 10 x 10 km squares were initially selected using stratified random sampling procedures to ensure that, whenever possible, both postfire and postharvest disturbances were adequately represented for each BCR. For both BCRs, postharvest disturbances were limited to clear-cuts; other types of harvesting, e.g., selective/partial harvesting, were excluded from sampling to avoid confounding our analyses. To maximize the number of areas that could be sampled per unit effort, the majority (85%) of sample sites were selected in areas with road access. However, special efforts were also made to sample unroaded areas, through air and canoe access, to ensure adequate coverage of areas that had not been subject to forest management.

Within each 10 x 10 km square, four separate U-shaped transects of six point count locations each were established. Transect starting locations were randomly chosen with the constraint that they must be at least 1.5 km apart on roads or on waterways, i.e., rivers or lakeshores. Roadside starting locations used the first four randomly selected points that met these criteria that had been generated for use during the Ontario Breeding Bird Atlas (Cadman et al. 2007). The maps provided to observers contained no disturbance or forest type information so that observers were unaware of disturbance history (postfire vs. postharvest) when conducting surveys unless there were obvious signs such as cut stumps. In roadless areas (> 1000 m from the nearest road), a similar protocol was used with the exception that starting points were defined by natural waterways, i.e., lakes or rivers, or geophysical features. Adjacent points in each U-shaped transect were separated by a minimum distance of 250 m. In most cases, two points (the first and last sampled) occurred on a roadside, two at 250 m from the road, and two at 500 m from the road. These six points composed a sampling cluster.

Observers were asked to select point count locations within a single habitat type, i.e., a single forest stand, in such a way that most of the habitat (> 70%) within a 100 m radius of the point was in the same forest stand. The precise coordinates of each point count location were recorded using a GPS. Each point was sampled only once during the breeding season, to maximize the number of different locations that could be sampled with the crews available. Thus, we traded off less precise information on individual locations with greater power to detect large-scale patterns.

The basic sampling protocol involved conducting point counts that were 5-min long within the first 5 hours after dawn. Typically, two clusters could be sampled by a single observer within the morning survey window. With highly skilled observers, preliminary trials suggested that 10-min point counts added < 1 additional species compared to 5-min point counts (Zimmerling, *unpublished data*), and would have decreased the number of stations that could be sampled. In addition, this protocol allowed surveys to be integrated into the Ontario Breeding Bird Atlas (Cadman et al. 2007). Surveyors recorded all species seen or heard,

with individuals detected within 100 m recorded separately from those beyond 100 m. To ensure that birds were within the treatment areas, only birds estimated to be within 100 m of the point count location were included in our analyses. Only adults were recorded. Point counts were conducted in favorable weather conditions and were not conducted during precipitation or in wind > 20 km/h, both of which reduce the detectability of singing birds. No playbacks or methods of increasing bird detections, e.g., "pishing" (see Zimmerling and Ankney 2000, Zimmerling 2005) were used during point counts. There was no relationship between the time of a survey within the morning.

To minimize the influence of variation among observers in detection probability during point counts (Farnsworth et al. 2005), all observers hired for field work were selected based on their ability to accurately and consistently identify species on recordings of actual point counts made the previous year in similar habitat. Moreover, to the extent possible, each observer conducted point counts in both BCR 8 and BCR 12 and within all habitat types, to reduce the risk that any residual variation among observers would be correlated with treatments.

Disturbance classification

Maps and digital data provided by forestry companies were used to determine disturbance type (harvest vs. fire) and forest age for each point count location, based on the coordinates reported by the field observers. However, in some regions, these maps and digital data were either incomplete or unavailable. Several forestry companies were unable to provide specific age class data prior to digitization in the early 1980s. In such instances, a combination of vegetation data, hard-copy maps, discussions with forest practitioners, forest resource inventory data, and remotely sensed landcover data were used to determine treatment history.

Disturbance data were categorized into two types: disturbances originating from fire (hereafter postfire) and disturbances originating from timber harvesting (hereafter postharvest). Point counts in other disturbance types, e.g., windthrow and insect outbreaks, were excluded from analysis because sample sizes were too small and the resulting postdisturbance landscapes are structurally and chemically different than those produced by fire (e.g., Campbell 2001).

For all analyses, forests were categorized into three age classes based on time since disturbance: early-regenerating (< 20 years since disturbance; i.e., disturbed between 1983 and 2004), midregenerating (20–80 years; i.e., disturbed 1921–1982), and mature (> 80 years; last disturbed prior to 1920). We were unable to use more precise age categories because this information was lacking for most previous logged sites. Relatively precise information on year of most recent harvest (± 2 years) was only available for about 5% of previously harvested sites, and decade of most recent harvest for only 11% more. Thus, for most logged sites we were only able to determine whether the most recent disturbance was more than or less than 20 years. Although better information was available on fires, we needed to use the same categories for comparison. The oldest age class (> 80 years) was only relevant for postfire disturbance, because large-scale modern commercial forestry operations did not begin in most of the study area until after the 1920s. The resulting five age/disturbance habitat types (early-postfire, midpostfire, mature-postfire, early-postharvest, midpostharvest) were assessed throughout our analyses.

We focused our analyses on landbird species (see Appendix 1 for full list of species analyzed) because point counts are well suited to surveying these species in forested habitats, and other taxa that rely on the boreal forest, e.g., waterfowl, shorebirds, and marshbirds, are generally rarely detected and hence usually had inadequate sample sizes. Landbird taxa with sufficient sample sizes for analysis included hawks, grouse, woodpeckers, and passerines.

Data analysis

Two levels of analysis, at community- and species-levels, were completed. The community-level analysis examined the total bird abundance and species richness detected at each point count location. Preliminary analysis indicated that both community level metrics were overdispersed so we used a negative binomial model to analyze the data (Eq. 1).

$$Y_i \sim \text{NB}(\mu_i, \phi) \qquad (1)$$

where Y is the number of birds or species observed at plot i, μ is the mean, and ϕ is the parameter that controls overdispersion relative to the square of the mean. This parametrization of the Negative binomial is commonly referred as the NB2 (Lindén and Mäntyniemi 2011).

$$\log(\mu_i) = \text{BCR}_i + \text{Age}_i + \text{Disturbance}_i \\ + \text{Age} \times \text{Disturbance}_i \qquad (2)$$

We used BCR, disturbance type, age class, and an interaction between disturbance type and age class as explanatory variables on the log scale for the mean (Eq. 2). We initially included a random effect for cluster, but this did not improve model fit, so it was dropped.

The species-level analysis examined the relative abundance of individual species within postharvest and postfire point count locations. To compare species abundance among age classes, we only considered data from postfire disturbances because none of the mature forest stands had previously been logged. Comparisons among disturbance types were done separately for each of the younger age classes. Species were included in the analysis only if they were detected at a minimum of 72 point count locations, i.e., 1% of all point counts. Individual species models were fitted via a negative binomial regression with disturbance type, age class, and an interaction between disturbance type and age class as explanatory variables and BCR as a covariate. The model also included a random effect for cluster to account for the possibility of autocorrelation among points in the same cluster, e.g., clumped species distributions.

All regressions were fitted in a Bayesian framework that was implemented in Stan (Carpenter et al. 2017) from R using the rstan package (Stan Development Team 2016). We used noninformative priors for all parameters. Model convergence was visually evaluated and verified using the Gelman-Rubin statistic (R^2; Gelman et al. 2014). One of the major advantages of using a Bayesian approach fitted using Markov chain Monte Carlo (MCMC) is that derived parameters and their credible intervals can be estimated from the posterior distribution (Kéry 2010, Kruschke 2014). In our case, the contrasts between the disturbance type, age class, and interactions were derived directly from the model output. Contrasts between two levels of an

explanatory variable, e.g., postfire vs. postharvest, represent the natural log of the ratio between the expected values of those two levels and are presented with 95% Bayesian credible intervals (BCI). Differences were considered significant if the 95% BCI did not overlap zero. In some cases, these were back-transformed into percentage differences.

RESULTS

A total of 7114 point counts, clustered in 1354 clusters in 329 atlas squares across the boreal forest of Ontario (Fig. 1), were included in the analyses. Of those point counts, 27% (N = 1902) were conducted in early-regenerating stands, 32% (N = 2287) in midregenerating stands, and 41% (N = 2925) in mature stands; 66% (N = 4716) of the stations were in postfire stands while 34% (N = 2398) of the stations were in postharvest stands. A total of 68,574 individuals birds were recorded during the point counts, representing 106 landbird species. However only 62 species were recorded on at least at 1% of all point counts and were therefore used for analysis (N = 65,487 individuals; see Appendix 1 for included species and their scientific names).

Community level results

We did not find consistent differences between BCRs in species richness (contrast between estimated means: = 0.020; 95% Bayesian credible interval [−0.003 - 0.044]) or total abundance (= 0.017 [−0.009 - 0.042]). In postfire forests, numbers of individuals per point count and of species per point count were highest in early-regenerating stands, slightly lower in mature stands and lowest in midregenerating stands (Fig. 2). Contrasts show that estimated species richness was not significantly (1.3% [−3.4 - 5.7%]) higher in early-regenerating than mature stands, but total abundance was 9.1% (3.9 - 14.4%) higher in early-regenerating stands. Species richness was 9.7% (6.7 - 12.6%) lower and total abundance was 9.5% (6.2 - 12.7%) lower in midregenerating stands when compared to mature stands.

In midregenerating stands, both species richness (−5.7% [−9.4 - −1.8%]) and total abundance (−7.1% [−11.3 - −2.8%]) were significantly lower in postharvest stands (Fig. 2). However, postharvest early stands did not differ significantly from postfire early-regenerating stands for either species richness (2.1% [−2.7 - 7.0%]) or total abundance (−1.7% [−6.7 - 3.6%]).

Species level results

As expected, many species differed in abundance between mature and younger forests (Fig. 3, Table 1; see Appendix 2 for estimated average abundance of all species in each stand type). Overall, 20 species (31%) were significantly less abundant in early-regenerating stands than in mature stands while 16 species (26%) were significantly more abundant in early-regenerating stands than in mature stands (Fig. 3, third column; Table 1). Similarly, 19 species (31%) were significantly less abundant in midregenerating than mature stands, while 5 species (8%) were significantly more abundant in midregenerating stands than in mature stands (Fig. 3, fourth column; Table 1). Overall, 28 species (45%) were consistently more abundant in mature forest than in either early- or midregenerating forests, of which 11 (18%) were significant in both contrasts: American Redstart (*Setophaga ruticilla*), Blackburnian Warbler (*Setophaga fusca*), Brown Creeper (*Certhia americana*), Black-throated Green Warbler

Fig. 2. Predicted total number of individuals (a) and number of species (b) observed per point count in early-regenerating, midregenerating, and mature forest stands, for postfire (left; black) and postharvest (right; grey) habitats in Bird Conservation Region 8 in Ontario. Dots represent the mean and bars represent the 95% Bayesian credible intervals.
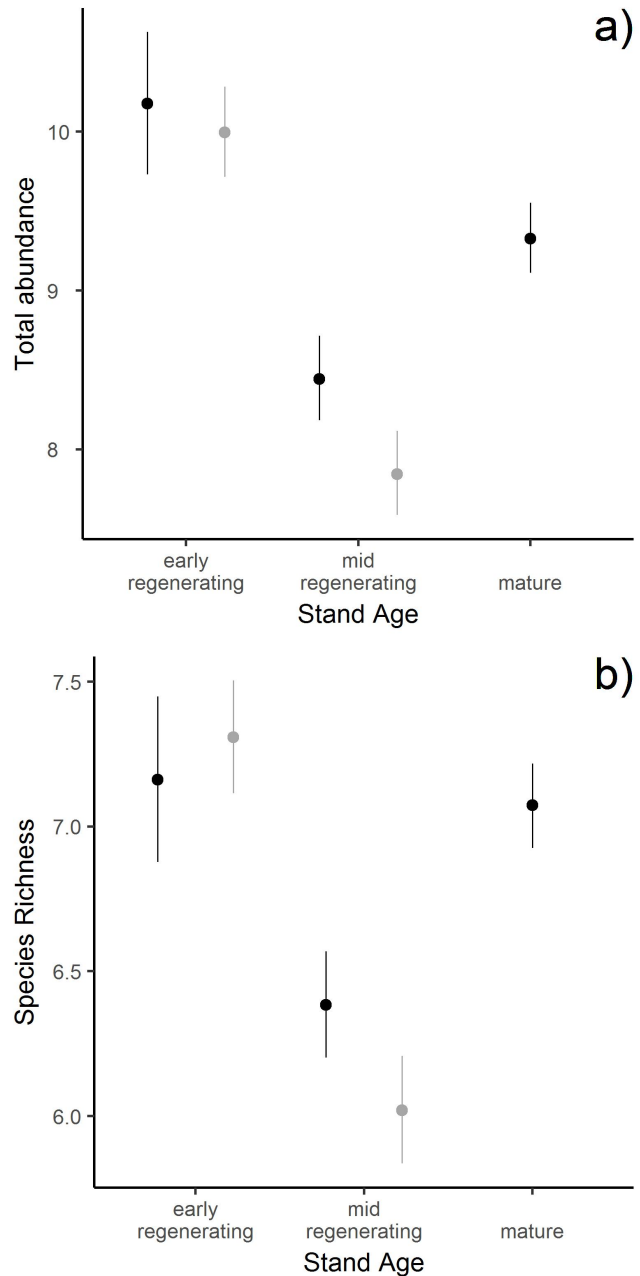
(*Setophaga virens*), Magnolia Warbler (*Setophaga magnolia*), Northern Parula (*Setophaga americana*), Purple Finch (*Haemorhous purpureus*), Red-breasted Nuthatch (*Sitta canadensis*), Swainson's Thrush (*Catharus ustulatus*), Winter Wren (*Troglodytes hiemalis*), and Yellow-bellied Sapsucker

Fig. 3. Contrasts between disturbance types (harvest vs. fire) and age classes (early- or midregenerating vs. mature) in estimated abundance of boreal bird species in northern Ontario forest stands. Species are ordered according to the values in the first column. Negative values indicate species that were less abundant in postharvest than postfire stands (first two columns), or less abundant in early- or midregenerating than mature stands (last two columns). The scale is natural log, such that a value of 0.7 corresponds to double (or half) the abundance. Dots represent the mean and bars represent the 95% Bayesian credible intervals. Black is used when the 95% credible intervals of the estimates do not overlap zero. See Appendix 1 for vernacular and scientific names of all species listed.
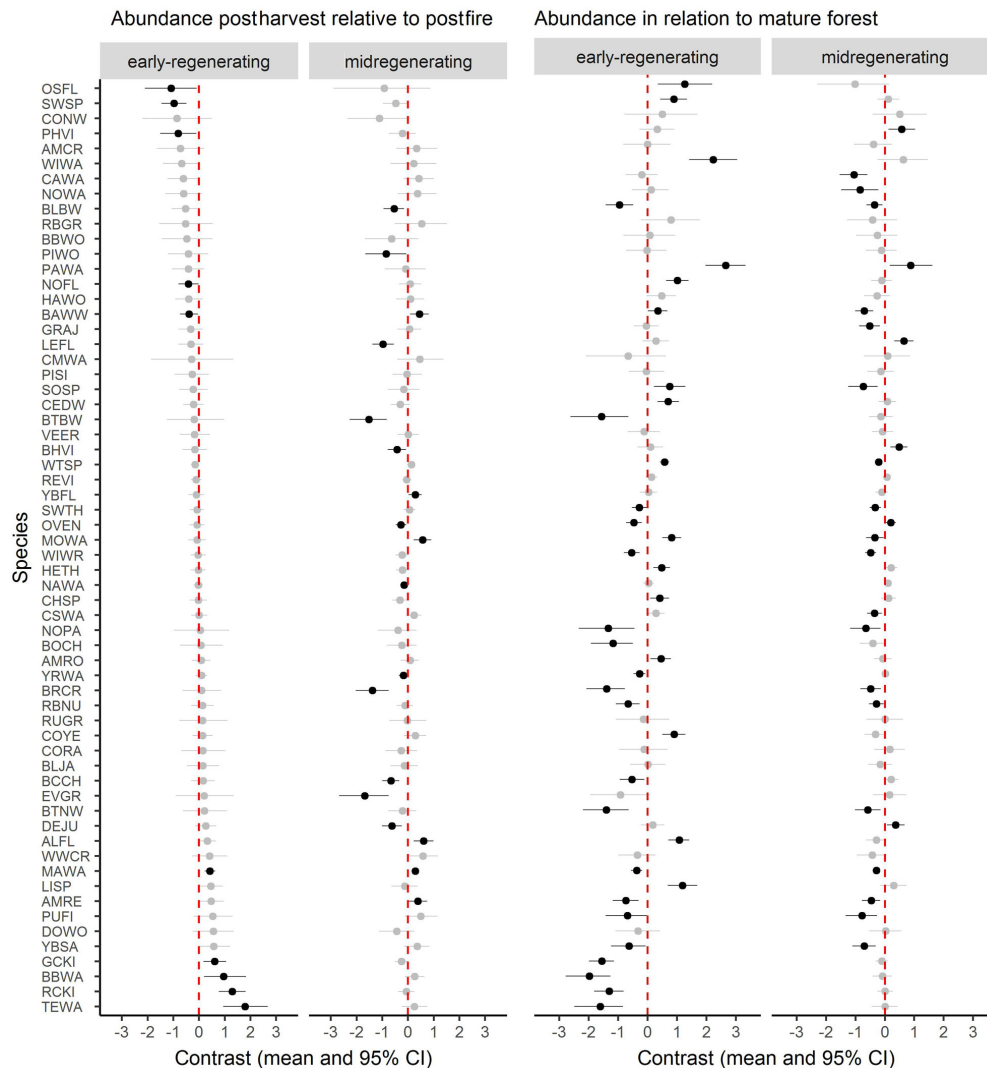
(*Sphyrapicus varius*). Conversely, 21 species (34%) were consistently more abundant in the younger age classes, though only 1 was significant in both contrasts: Palm Warbler (*Setophaga palmarum*). Four species (6%) were significantly more abundant in early-regenerating stands in relation to mature forests, but significantly less abundant in midregenerating forests: Black-and-white Warbler (*Mniotilta varia*), Mourning Warbler (*Geothlypis philadelphia*), Song Sparrow (*Melospiza melodia*), and White-throated Sparrow (*Zonotrichia albicollis*), while one species was significantly less abundant in early-regenerating stands, but more

abundant in midregenerating stands, in relation to mature stands: Ovenbird (*Seiurus aurocapilla*).

Several species were less abundant postharvest than postfire in regenerating forests, while others showed the opposite pattern, and the differences were not always consistent across age classes. In early-regenerating stands, 5 species (8%) were significantly less abundant postharvest than postfire, and 5 species (8 %) were significantly more abundant postharvest than postfire (Fig. 3, first column; Table 2). The differences were more pronounced in midregenerating forest stands, where 12 species (19%) were

significantly less abundant postharvest, and 6 species (10%) were significantly more abundant postharvest (Fig. 3, fourth column; Table 2). Only one species (Magnolia Warbler) was consistently more abundant in postharvest stands. One species (Black-and-white Warbler) was less abundant in postharvest habitat in early-regenerating stands but more abundant in harvested habitat in midregenerating stands (Fig. 3; Appendix 3).

Table 1. Numbers of boreal landbird species in northern Ontario that were more or less abundant in mature forest relative to early- or midregenerating stands, classified by the direction and significance of the contrast, where significant [sig] or nonsignificant [ns] was based on whether or not the Bayesian credible intervals include zero. For instance, 11 species were significantly less abundant in early-regenerating than mature stands and were also significantly less abundant in midregenerating than mature stands (bottom left cell). See Figure 3 [third and fourth columns] and Appendix 3 (panel a) for individual species contrast values.

	Early << Mature (sig)	Early < Mature (ns)	Early > Mature (ns)	Early >> Mature (sig)	Total
Mid >> Mature (sig)	1	0	4	1	6
Mid > Mature (ns)	3	5	3	6	17
Mid < Mature (ns)	5	5	5	5	20
Mid << Mature (sig)	11	2	2	4	19
Total	20	12	14	16	62

A comparison of disturbance-contrasts (i.e., mean estimated abundance ratios between postharvest vs. postfire stands) with the age-contrasts (mean estimated abundance ratios between mature vs. early/midregenerating stands) suggests a link between age- and disturbance-associations of many boreal bird species (Table 3). Nearly two-thirds of species (20/32) that were less abundant in early-regenerating than mature stands were also more abundant postharvest than postfire, with five species significant in both contrasts: Bay-breasted Warbler (*Setophaga castanea*), Golden-crowned Kinglet (*Regulus satrapa*), Magnolia Warbler, Ruby-crowned Kinglet (*Regulus calendula*), Tennessee Warbler (*Oreothlypis peregrina*), while three-quarter of species (23/30) that were more abundant in early-regenerating than mature stands were less abundant postharvest than postfire, with four species significant for both contrasts: Black-and-white Warbler, Olive-sided Flycatcher (*Contopus cooperi*), Northern Flicker (*Colaptes auratus*), Swamp Sparrow (*Melospiza georgiana*; Table 3). Most species (21/23) with higher abundance in midregenerating than mature stands also showed lower abundance in postharvest than postfire stands, with four species significant for both contrasts: Least Flycatcher (*Empidonax minimus*), Dark-eyed Junco (*Junco hyemalis*), Blue-headed Vireo (*Vireo solitarius*), Ovenbird, and 62% of species (24/39) that were less abundant in midregenerating than mature stands showed greater abundance in postharvest than postfire stands, also with four species significant for both contrasts: Mourning Warbler, Black-and-white Warbler, Magnolia Warbler, American Redstart (Table 3). There were no

species that were significantly less abundant in early-regenerating than mature forests while also significantly less abundant postharvest than postfire, and also no species that were more abundant in midregenerating than mature forests while also significantly more abundant postharvest than postfire (Table 3).

Table 2. Numbers of boreal landbird species that were more or less abundant postharvest than postfire in northern Ontario in early- vs. midregenerating stands, classified by the direction and significance of the contrast, where significant [sig] or nonsignificant [ns] was based on whether or not the Bayesian credible intervals include zero. For instance, no species were significantly less abundant in postharvest than postfire stands of both early- and midregenerating age classes (bottom left cell). See Figure 3 [first two columns] and Appendix 3 (panel b) for individual species contrast values.

	Early-regenerating				
	Harvest << Fire (sig)	Harvest < Fire (ns)	Harvest > Fire (ns)	Harvest >> Fire (sig)	Total
Midregenerating					
Harvest >> Fire (sig)	1	2	2	1	6
Harvest > Fire (ns)	1	11	6	2	20
Harvest < Fire (ns)	3	10	9	2	24
Harvest << Fire (sig)	0	7	5	0	12
Total	5	30	22	5	62

DISCUSSION

Our results generally are consistent with the idea that boreal inhabitants may be particularly resilient to harvesting, possibly the result of their historical exposure to regular natural disturbances (e.g., Schmiegelow et al. 1997, Lemelin et al. 2007, Whitaker et al. 2008, Börger and Nudds 2014). The majority of landbird species sampled (84% for early- and 71% for midregenerating stands) showed similar abundance, i.e., nonsignificant difference, between postharvest and postfire forests, which suggests that past harvest management has created some habitats that are generally as suitable for these species as forests originating from fires. No species were found exclusively in postfire or postharvest forests. Similarly, Rempel et al. (2016) found that although several forest condition indicators, e.g., conifer/deciduous ratios or edge density, differed between naturally and anthropogenically disturbed sites, occupancy rates of most (11/14) species were similar between disturbance types.

Nevertheless, our comparisons between postharvest and postfire landscapes indicate that harvesting in Ontario has not completely emulated natural disturbance for some species of boreal birds. At the community scale, our results indicate lower species richness and abundance in postharvest than postfire stands, but only at the intermediate (midregenerating) age class. At the species level, many species showed significantly higher or lower abundance in postharvest relative to postfire forests in either early- (10 species) or midregenerating (18 species) stands. However, few species

Table 3. Numbers of boreal landbird species in northern Ontario that were more or less abundant in mature than younger stands, versus more or less abundant postfire than postharvest, for early- and midregenerating stands. Values are classified by the direction and significance of the contrast, where significant [sig] or nonsignificant [ns] was based on whether or not the Bayesian credible intervals include zero. For instance, in early-regenerating forests, there were four species that were significantly less abundant postharvest than postfire while also being significantly more abundant in younger than mature stands (top left cell). See Figure 3 and Appendix 3 (panels c and d) for individual species contrast values.

	Early-regenerating					Midregenerating				
	Harvest << Fire (sig)	Harvest < Fire (ns)	Harvest > Fire (ns)	Harvest >> Fire (sig)	Total	Harvest << Fire (sig)	Harvest < Fire (ns)	Harvest > Fire (ns)	Harvest >> Fire (sig)	Total
Younger >> Mature (sig)	4	8	4	0	16	4	2	0	0	6
Younger > Mature (ns)	1	10	3	0	14	4	11	2	0	17
Younger < Mature (ns)	0	7	5	0	12	2	6	10	2	20
Younger << Mature (sig)	0	5	10	5	20	2	5	8	4	19
Total	5	30	22	5	62	12	24	20	6	62

exhibited consistent differences in both age classes, suggesting that harvest alters species composition, but that its impacts vary with successional age (e.g., Hobson and Schieck 1999, Schieck and Song 2006). Several other studies in boreal forests have reported greater compositional dissimilarities between burned and harvested sites immediately following disturbance than at later successional stages (Hobson and Schieck 1999, Imbeau et al. 1999, Schieck and Hobson 2000, Morissette et al. 2002, Hannon and Drapeau 2005). Although we did not find this, it is also important to note that the midregenerating harvested forests in our study would have been affected by harvest practises that occurred before widespread adoption of efforts to emulate natural disturbance (see Drapeau et al. 2000). For example, there would not have been efforts to retain residual forest cover (i.e., wildlife trees, snags), downed woody debris, and other structure, and silviculture practices may have differed, all of which may have contributed to some of the greater differences in midregenerating stands. Additionally, because precise information on the year of harvest was unavailable for most stands, we cannot preclude the possibility that the average age of midregenerating postharvest and postfire stands differed, further influencing bird community assemblages in midregenerating stands.

Our findings are also consistent with other evidence that vegetation successional patterns affect bird community composition after disturbance (e.g., Schulte and Niemi 1998, Hobson and Schieck 1999, Thompson et al. 1999, McRae et al. 2001, Simon et al. 2002). Community-level estimates were consistent with the idea that species richness in temperate forests is generally greater in younger successional communities, because recently disturbed ecosystems typically have greater nutrient availability and energy exchange than older ecosystems (Gower et al. 1996). At the species scale, many species associated with open habitat showed greater abundance in early-regenerating than older stands, e.g., Alder Flycatcher (*Empidonax alnorum*), Cedar Waxwing (*Bombycilla cedrorum*), Common Yellowthroat (*Geothlypis trichas*), Northern Flicker. Other species peaked in abundance in mature forest, e.g., Brown Creeper, Northern Parula, Red-breasted Nuthatch, Swainson's Thrush, Winter Wren, suggesting they prefer more mature trees, more complex structure or large patches of contiguous forest. Few species showed greatest abundance in midregenerating stands, perhaps because these stands no longer have the high nutrient richness of early stands and do not yet have the quality of mature forests. Finch et al. (1997) argue that such responses of individual species should be a key concern for forest managers because each species' response is unique, and because management strategies are often species-specific. Additionally, associations between age-contrasts and disturbance-contrasts suggest that species that are more abundant in early-regenerating than mature stands are less abundant in postharvest than postfire forests and vice versa, although the factors driving this association are unknown. This suggests that changing from predominantly fire disturbance to predominantly harvest disturbance could have greatest impacts on early successional species.

Although we would not anticipate a total loss of any boreal species with harvesting in this region, our results imply a probable shift in relative abundance for a number of species, including mature-forest inhabitants. Our study was not able to compare mature, i.e., > 80 years, postfire forests with mature postharvest forests, but some species were most abundant in large tracts of forests that are older than rotational age. For example, 18% of all species analyzed, including Blackburnian Warbler, Brown Creeper, Red-breasted Nuthatch, Swainson's Thrush, and Winter Wren, were significantly more abundant in mature forests than in either early- or midregenerating stands. Other authors (e.g., Titterington et al. 1979, Welsh 1981, Schieck et al. 1995, Cumming and Diamond 2002) have found similar associations with mature forest. We found that all mature-forest species also occurred in early- and midregenerating postdisturbance forests, albeit at lower densities, suggesting that they may find some habitat in managed areas. Blancher et al. (2009) did not find any difference in population trend between birds associated with mature forest and those preferring early successional stages, but this may reflect, in part, the extent of remaining intact forest. Previous studies (e.g., Drapeau et al. 2000, Campbell 2001) have projected that species associated with mature forests will significantly decline over the next 40 years as a result of forest harvesting, due to reductions in the remaining area of mature forest. This supports the idea that maintaining mature forests in a portion of the harvested landscape is necessary for effective emulation of natural disturbances.

Blancher et al. (2009) did not find any difference in population trend between birds associated with mature forest and those preferring early successional stages, but this may reflect, in part, the fact that only a limited part of the landscape has been harvested.

Understanding the underlying reasons for differences between postharvest and postfire communities could help improve management techniques to more closely emulate natural disturbance (Rempel et al. 2016). For instance, snag density is an important structural feature that differs between postharvest and postfire forests (Zimmerling, *unpublished data*). In the years immediately following an intensive fire, species that use shrubs and understory vegetation for nesting and foraging will have very little habitat, whereas those that use snags will have abundant habitat (e.g., Imbeau et al. 1999, Hannon and Drapeau 2005). In contrast, many harvesting methods leave behind few snags. Although the present study was not designed to target snag-nesters and foragers, several snag-specialist species were indeed more abundant in postfire forests (e.g., Northern Flicker and Olive-sided Flycatcher, though only in early-regenerating stands) than in postharvest forests, a result consistent with other studies despite differences in forest type and geographic location (Hutto 1995, Morissette et al. 2002). However, given that patterns between guilds, e.g., snag-specialist, and disturbance histories were inconsistent, our results may not be readily generalizable. Fire suppression since the 1950s in the southern boreal continues to reduce the amount of younger, burned forests with numerous snags, and thus recent changes in forest management guidelines and practices in Ontario to increase wildlife tree retention, including snags, to an average of 25 trees / ha may be especially important (OMNR 2001, 2010).

Collectively, our results suggest that if harvest becomes an increasingly common disturbance in Ontario's boreal region, there will be important changes in species composition within the forest bird community. Quantifying the population-scale impacts of these shifts requires extrapolation of these stand-level effects to the landscape-level, by accounting for the projected amounts of each habitat type in the landscape (see Drapeau et al. 2000). Effective emulation of natural disturbances must consider landscape-scale habitat change in burned vs. harvested areas in the context of current and future forest age class distribution, and across a range of alternative forest management strategies.

CONCLUSION

The boreal forest is a critical habitat for North American wildlife (Blancher 2003, Blancher and Wells 2005, Brandt et al. 2013), and population declines in many bird species have been partially attributed to harvest management (e.g., Schmiegelow and Monkkonen 2002). We found that more than half of the boreal landbird species responded similarly to disturbances by fire and harvest, perhaps attesting to both the success of management efforts to emulate natural disturbances, as well as the resilience of many boreal birds (e.g., Schmiegelow et al. 1997, Lemelin et al. 2007). Nonetheless, important differences in abundance between disturbance types in both early- and midregenerating stands suggest that the extent to which harvest emulates natural disturbances depends on forest age, as well as specific habitat features. Thus relative species abundance could vary with future harvesting, even if most species manage to persist.

It is not realistic to expect any degree of harvest management to fully replicate the natural habitat diversity of postfire forests. Forestry research would benefit from quantification of how widely managed forests can diverge from natural habitats without severely compromising biodiversity and sustainability (Delong and Tanner 1996, Perry 1998, Drever et al. 2006, Rempel et al. 2016), with the objective of planning harvest to replicate natural disturbance events as closely as possible. Boreal forest inhabitants require a complex landscape matrix of diverse habitat features, including trees of various ages and structures as affirmed by our results. It is thus the retention or replication of these conditions in harvesting that is required to meet the coarse-filter needs of entire boreal forest bird communities (Bergeron et al. 2002, Vitz and Rodewald 2006, Rempel et al. 2007). In Ontario, forest harvest guidelines have recently been updated (OMNR 2010), but further evaluation is needed to determine how well they meeting the coarse-filter needs of wildlife. Harvest management of Canada's boreal region needs to incorporate long-term and landscape-scale monitoring of both forest habitats and wildlife in ways that recognize spatial and temporal variability in abundance and the dynamic nature of these ecosystems (Thompson and Harestad 2004, Venier et al. 2014).

Responses to this article can be read online at:
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Appendix 1. English and scientific names of boreal bird species evaluated in this study, number of individuals (*n*), and percent of all point counts on which the species was detected (% point counts), ordered alphabetically by their 4-letter abbreviation codes.

Code	English name	Scientific name	*n*	% point counts
ALFL	Alder Flycatcher	*Empidonax alnorum*	1229	12.7
AMCR	American Crow	*Corvus brachyrhynchos*	207	2.5
AMRE	American Redstart	*Setophaga ruticilla*	1089	12.1
AMRO	American Robin	*Turdus migratorius*	1040	12.1
BAWW	Black-and-white Warbler	*Mniotilta varia*	824	10.7
BBWA	Bay-breasted Warbler	*Setophaga castanea*	538	6.7
BBWO	Black-backed Woodpecker	*Picoides arcticus*	96	1.2
BCCH	Black-capped Chickadee	*Poecile atricapillus*	1332	12.3
BHVI	Blue-headed Vireo	*Vireo solitaries*	648	7.8
BLBW	Blackburnian Warbler	*Setophaga fusca*	738	9.1
BLJA	Blue Jay	*Cyanocitta cristata*	455	5.1
BOCH	Boreal Chickadee	*Poecile hudsonicus*	247	2.8
BRCR	Brown Creeper	*Certhia americana*	363	4.7
BTBW	Black-throated Blue Warbler	*Setophaga caerulescens*	415	5.0
BTNW	Black-throated Green Warbler	*Setophaga virens*	695	7.6
CAWA	Canada Warbler	*Cardellina canadensis*	345	4.3
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	1194	10.2
CHSP	Chipping Sparrow	*Spizella passerina*	1262	13.7
CMWA	Cape May Warbler	*Setophaga tigrina*	84	1.1
CONW	Connecticut Warbler	*Oporornis agilis*	105	1.3
CORA	Common Raven	*Corvus corax*	337	3.3
COYE	Common Yellowthroat	*Geothlypis trichas*	1030	11.1
CSWA	Chestnut-sided Warbler	*Setophaga pensylvanica*	1607	17.7
DEJU	Dark-eye Junco	*Junco hyemalis*	849	9.9
DOWO	Downy Woodpecker	*Picoides pubescens*	179	2.2
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*	196	1.7
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	1399	15.6
GRAJ	Gray Jay	*Perisoreus canadensis*	634	6.4
HAWO	Hairy Woodpecker	*Picoides villosus*	293	3.7
HETH	Hermit Thrush	*Catharus guttatus*	2261	23.3
LEFL	Least Flycatcher	*Empidonax minimus*	1073	9.6
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	873	8.7
MAWA	Magnolia Warbler	*Setophaga magnolia*	3804	40.6
MOWA	Mourning Warbler	*Geothlypis philadelphia*	1335	14.4
NAWA	Nashville Warbler	*Oreothlypis ruficapilla*	5939	53.2
NOFL	Northern Flicker	*Colaptes auratus*	550	6.9
NOPA	Northern Parula	*Setophaga americana*	241	3.1

NOWA	Northern Waterthrush	*Parkesia noveboracensis*	229	2.8
OSFL	Olive-sided Flycatcher	*Contopus cooperi*	76	1.0
OVEN	Ovenbird	*Seiurus aurocapilla*	3303	33.6
PAWA	Palm Warbler	*Setophaga palmarum*	414	4.5
PHVI	Philadelphia Vireo	*Vireo philadelphicus*	170	2.2
PISI	Pine Siskin	*Spinus pinus*	321	3.3
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	159	2.1
PUFI	Purple Finch	*Haemorhous purpureus*	210	2.8
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	116	1.4
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	957	11.6
RCKI	Ruby-crowned Kinglet	*Regulus calendula*	1196	14.2
REVI	Red-eyed Vireo	*Vireo olivaceus*	4760	43.7
RUGR	Ruffed Grouse	*Bonasa umbellus*	217	3.0
SOSP	Song Sparrow	*Melospiza melodia*	558	5.9
SWSP	Swamp Sparrow	*Melospiza georgiana*	498	5.6
SWTH	Swainson's Thrush	*Catharus ustulatus*	2669	27.7
TEWA	Tennessee Warbler	*Oreothlypis peregrina*	391	4.7
VEER	Veery	*Catharus fuscescens*	826	8.9
WIWA	Wilson's Warbler	*Cardellina pusilla*	144	1.7
WIWR	Winter Wren	*Troglodytes hiemalis*	1890	23.2
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	7088	54.5
WWCR	White-winged Crossbill	*Loxia leucoptera*	958	6.2
YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*	1584	18.6
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*	460	5.8
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	2785	31.3

Appendix 2. Predicted mean number of boreal birds detected per point count per species in each of five habitat types in northern Ontario forest stands, after adjusting for differences among Bird Conservation Regions and treating transects as a random effect (see Methods for model details). Values are plotted by age class (ER: early-regenerating, MR: midregenerating, M: mature) and by disturbance type (black = postfire, grey = postharvest). Dots represent the mean and bars represent the 95% Bayesian credible intervals. See Appendix 1 for full English and scientific names corresponding to each species' 4-letter code.
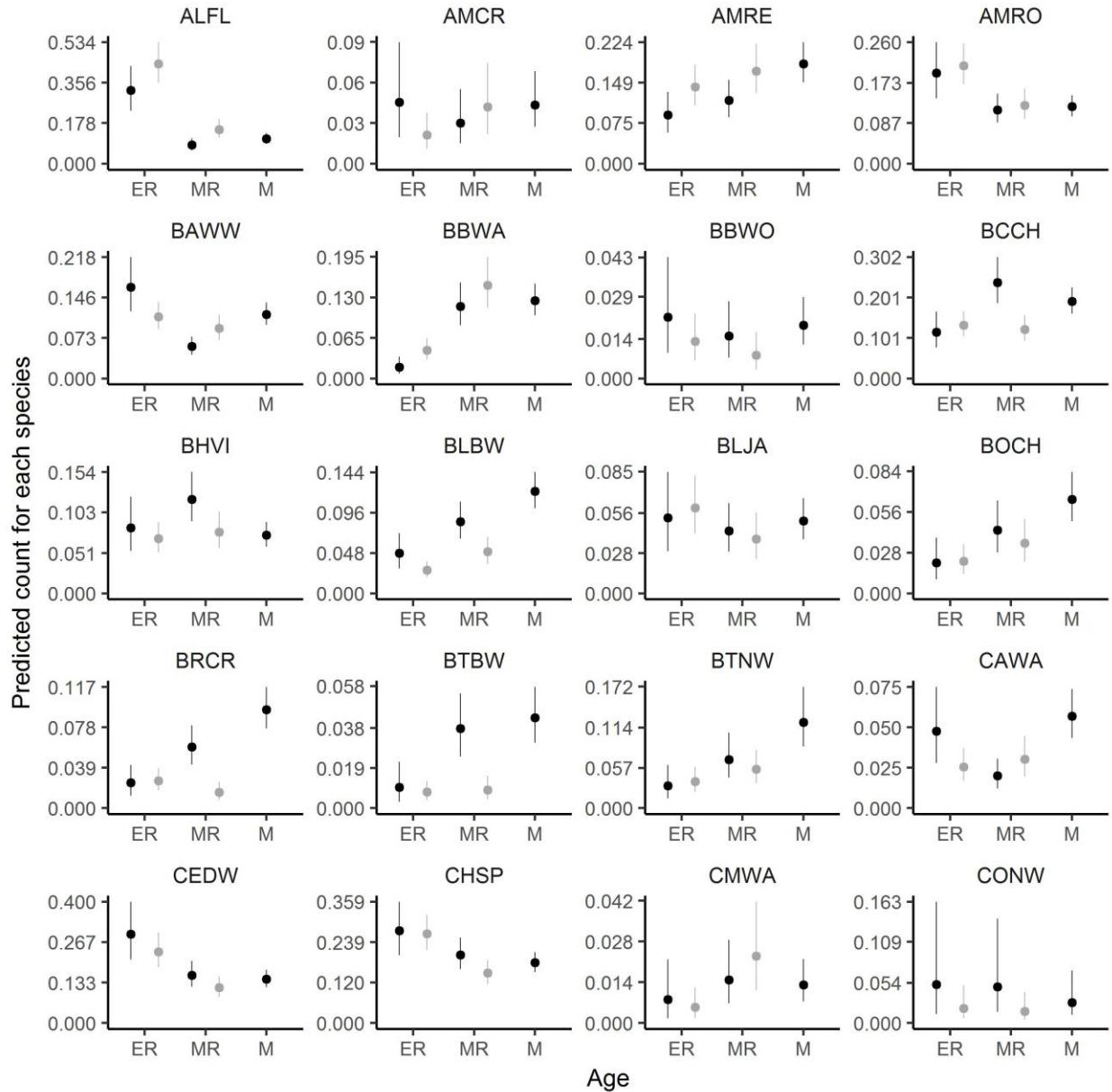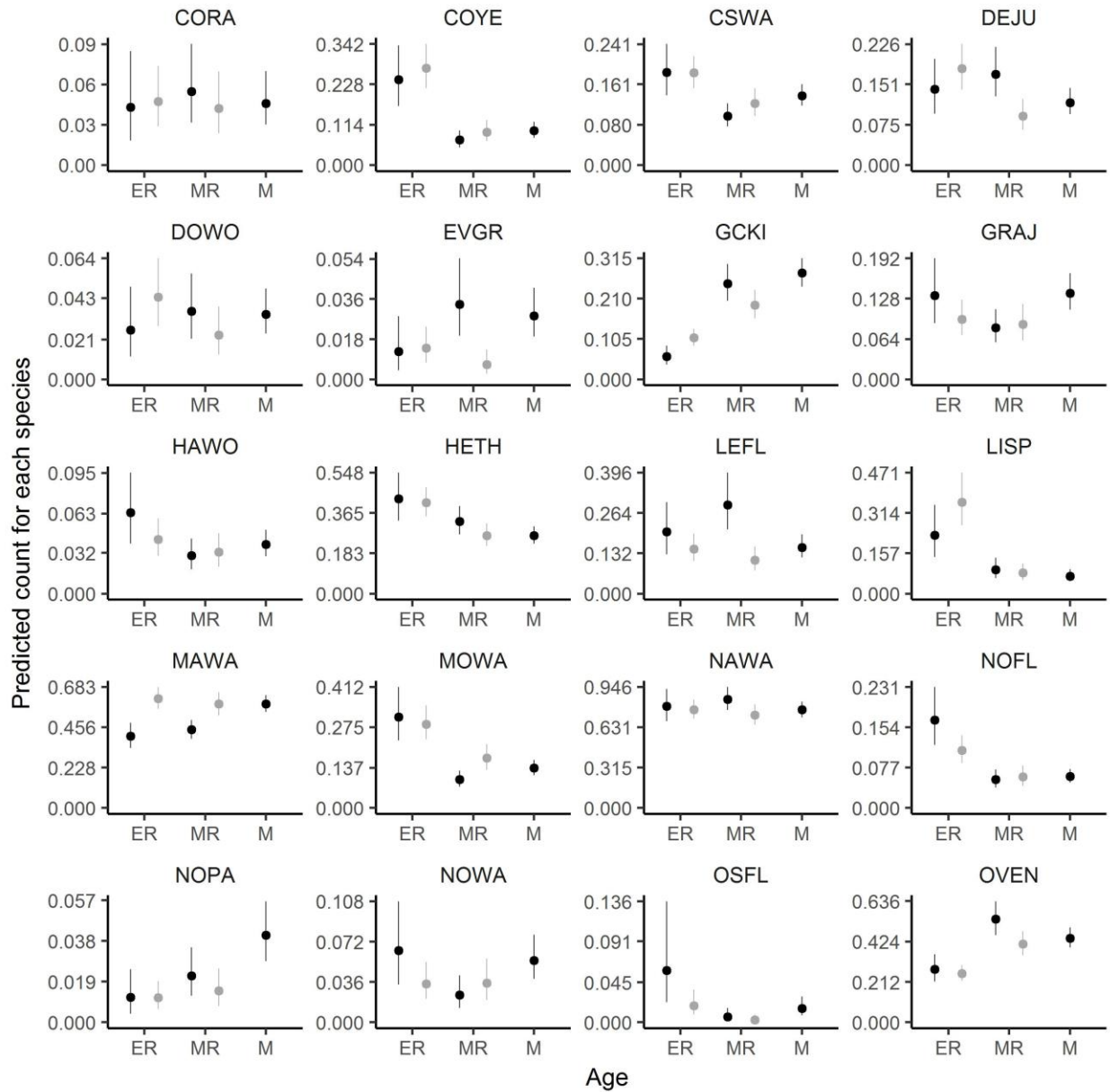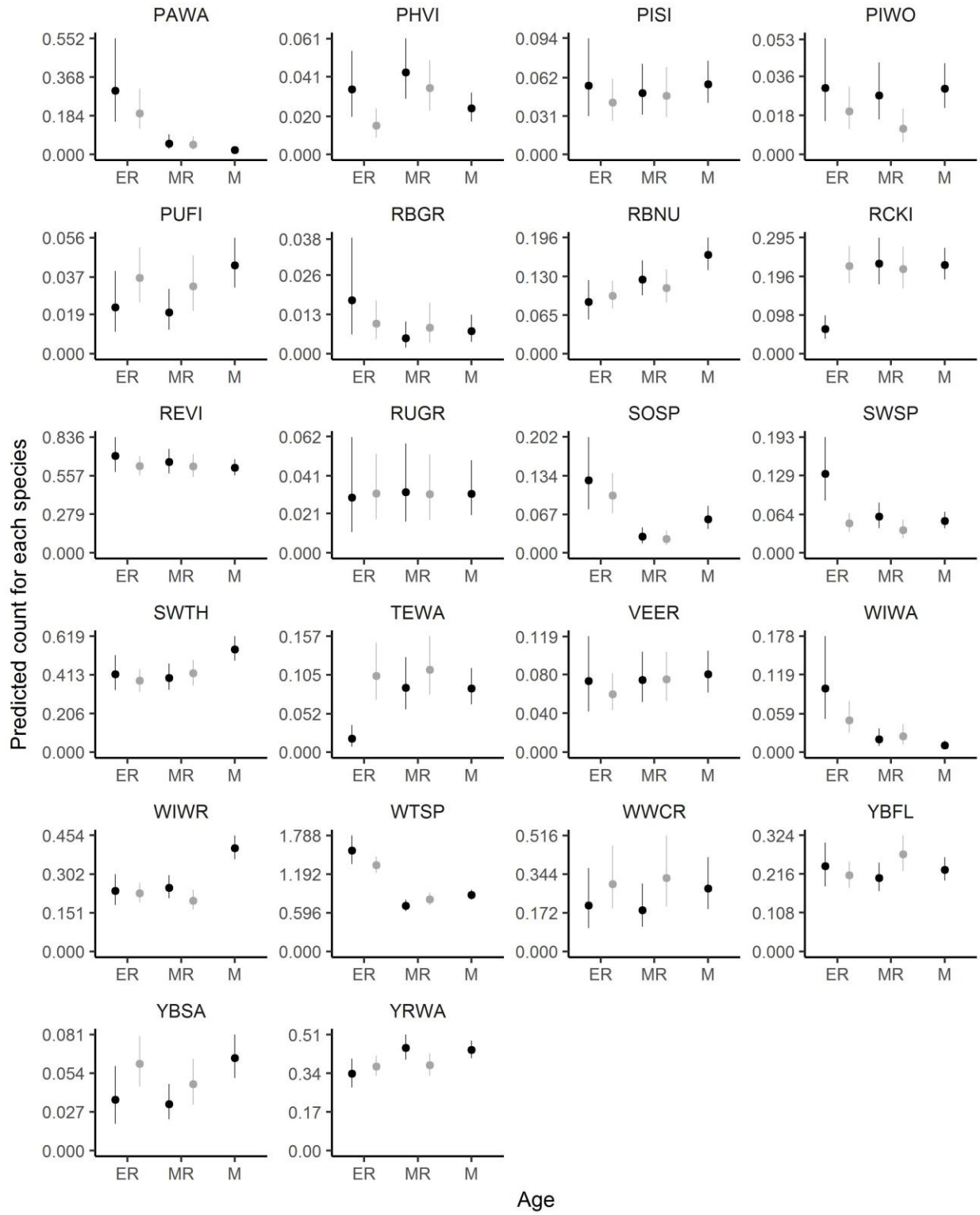
Appendix 3. Comparisons of contrasts for individual species between **(a)** early-regenerating postfire vs. mature forest compared with midregenerating postfire vs. mature forest; **(b)** harvest vs. fire in early-regenerating compared to harvest vs. fire in midregenerating forests; **(c)** harvest vs. fire in early-regenerating forests compared to early-regenerating postfire vs. mature forest; and **(d)** harvest vs. fire in midregenerating stands compared to midregenerating post-fire vs. mature forest. Dots represent the estimated contrast on the natural logarithmic scale (where a value of 0.7 corresponds to double (or half) the abundance). For example, species in the upper half of (a) occurred more frequently in midregenerating postfire forest than mature forest, and species on the right side of (a) were also more abundant in early-regenerating postfire forest than mature forest. Black labels indicate species for which both contrasts were significant (95% credible intervals do not overlap zero); blue labels indicate species for which the contrast on the x-axis was significant but not the contrast on the y-axis; green labels indicate species for which the contrast on the y-axis was significant but not the contrast on the x-axis; and grey labels identify species for which neither contrast was significant.