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## Combined long-term effects of variable tree regeneration and timber management on forest songbirds and timber production

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### ABSTRACT

The structure of forest stands is an important determinant of habitat use by songbirds, including species of conservation concern. In this paper, we investigate the combined long-term impacts of variable tree regeneration and timber management on stand structure, songbird occupancy probabilities, and timber production in northern hardwood forests. We develop species-specific relationships between bird species occupancy and forest stand structure for canopy-dependent black-throated green warbler (*Dendroica virens*), eastern wood-pewee (*Contopus virens*), least flycatcher (*Empidonax minimus*) and rose-breasted grosbeak (*Pheucticus ludovicianus*) from field data collected in northern hardwood forests of Michigan's Upper Peninsula. We integrate these bird-forest structure relationships with a forest simulation model that couples a forest-gap tree regeneration submodel developed from our field data with the US Forest Service Forest Vegetation Simulator (Ontario variant). Our bird occupancy models are better than null models for all species, and indicate species-specific responses to management-related forest structure variables. When simulated over a century, higher overall tree regeneration densities and greater proportions of commercially high value, deer browse-preferred, canopy tree *Acer saccharum* (sugar maple) than low-value, browse-avoided subcanopy tree *Ostrya virginiana* (ironwood) ensure conditions allowing larger harvests of merchantable timber and had greater impacts on bird occupancy probability change. Compared to full regeneration, no regeneration over 100 years reduces merchantable timber volumes by up to 25% and drives differences in bird occupancy probability change of up to 30%. We also find that harvest prescriptions can be tailored to affect both timber removal volumes and bird occupancy probability simultaneously, but only when regeneration is adequate. When regeneration is poor (e.g., 25% or less of trees succeed in regenerating), timber harvest prescriptions have a greater relative influence on bird species occupancy probabilities than on the volume of merchantable timber harvested. However, regeneration density and composition, particularly the density of *Acer saccharum* regenerating, have the greatest long-term effects on canopy bird occupancy probability. Our results imply that forest and wildlife managers need to work together to ensure tree regeneration density and composition are adequate for both timber production and the maintenance of habitat for avian species over the long-term. Where tree regeneration is currently poor (e.g., due to deer herbivory), forest and wildlife managers should pay particularly close attention to the long-term impacts of timber harvest prescriptions on bird species.

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### 1. Introduction

Variation in forest stand structure can have a strong influence on the use of these habitats by bird species across space and time (MacArthur and MacArthur, 1961; James, 1971; Cody, 1981;

Robinson and Holmes, 1982; Urban and Smith, 1989). Silvicultural practices in managed forests are key determinants of forest stand structure, and consequently, of occupancy by birds, including species of conservation concern (Thompson et al., 1995; Matteson et al., 2009). Although the general pattern of different bird species occupying forest stands with different structural characteristics is well recognized (e.g., Sallabanks et al., 2000), the combined impacts of timber harvest practices and variations in tree regeneration success on bird habitat use over many decades (due to

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changes in stand structure) are less clear. We examine these potential long-term impacts here, specifically with regards to a widely used uneven-aged timber management approach.

In uneven-aged timber management, single to small groups of trees are harvested to create forest-canopy gaps in which juvenile, shade-tolerant trees are expected to regenerate. Uneven-aged timber management is so-called because, over many harvests and with adequate regeneration, it results in the creation and/or maintenance of uneven tree-age and tree-size distributions (Nyland, 1998). If this occurs, stand structure can be assumed to be in quasi-equilibrium as removed canopy trees are replaced by younger regeneration cohorts in perpetuity. However, target residual stand structures (basal area, diameter-distribution, etc.) vary by land owner/manager with unclear long-term effects on bird occupancy. Furthermore, adequate regeneration of the same or ecologically and morphologically similar species as those removed is likely critical to the assumption of invariant stand structure. Variable or poor gap-tree regeneration can influence forest stand structure in lower strata immediately and in upper strata over the long term (i.e., many decades), as trees grow into the upper canopy (Woods, 2000). Therefore, in contrast to the immediate and much greater changes in forest structure produced by more intensive practices such as clear-cutting, impacts of uneven-aged management and variable regeneration are more subtle and take longer to manifest themselves, particularly in the overstory.

Several studies have shown that poor regeneration, primarily due to herbivory by white-tailed deer (*Odocoileus virginianus*), can influence bird populations by modifying stand structure (e.g., deCalesta, 1994; McShea and Rappole, 2000; Allombert et al., 2005). These studies mainly focus on understory vegetation, and although many bird species are dependent on structural features in under- and mid-story strata for nesting and foraging, others are more dependent on overstory characteristics (e.g., Annand and Thompson, 1997; Collins, 1983; De Graaf et al., 1985, 1998; Germaine et al., 1997; Goodale et al., 2009). To understand how these overstory specialists are likely to respond to management activities, we also need to evaluate the long-term dynamics of managed forests, as immediate changes in canopy characteristics due to tree removal are followed by expansion of the canopies of trees that remain, and gradual recruitment of understory trees into the canopy.

Many empirical studies examining impacts of forest structure on bird habitat have focused on short-term responses (e.g., less than 10 years post-harvest, Sallabanks et al., 2000; Forsman et al., 2010) because of the costs and logistical challenges of longer-term studies (but see, e.g., Shifley and Kabrick, 2002; Wallendorf et al., 2007 for longer-term empirical studies). Given difficulties of collecting long-term data, computer simulation tools are the primary means to evaluate the long-term effects of changes in management practices and regeneration success (e.g., Marzluff et al., 2002; Larson et al., 2004; Goldstein et al., 2003; Klaus et al., 2005; Shifley et al., 2000, 2006, 2008). For those interested in effects on birds, simulations can provide insight into how changes in timber harvest targets or herbivory rates are likely to influence habitat suitability for species that select breeding territories based on canopy characteristics. Thus, as we pursue goals of ecologically and economically sustainable forest management (e.g., Marzluff et al., 2002), simulations play a key role by allowing long-term impacts on overstory-dependent bird species to be weighed along with other costs and benefits of different management actions.

Previous simulation modeling studies have represented the impacts of variation in regeneration on long-term stand composition and structure explicitly (e.g., Mladenoff and Stearns, 1993; Kobe, 1996). Others have examined different forest types and harvest strategies across decades and centuries with varying degrees of stand-structure representation, from no structure representation

(e.g., Goldstein et al., 2003 modeled pine plantations as a function of stand age), through implicit representation (e.g., Shifley et al., 2006 represented stand species and size class – such as sapling and sawlog – for multiple forest types using the LANDIS model) to explicit representation (Marzluff et al., 2002, represented individual trees in conifer-hardwood stands using FVS). Of these, Marzluff et al. (2002) and Shifley et al. (2006) considered impacts on both birds and timber production.

Here, we investigate the combined long-term impacts of variable tree regeneration and uneven-aged timber management on stand structure, bird occupancy probabilities and timber production in northern hardwood forests. Northern hardwood forests in the Great Lakes region of the USA are an ideal ecosystem in which to evaluate these effects as they are managed nearly exclusively by selection silviculture, they provide habitat for many bird species of conservation concern (Matteson et al., 2009), harvest prescriptions vary among managers but often with variation driven by institutional factors rather than long-term expected outcomes (*pers. comm.* informal survey of regional forest managers), and large extents of these forests experience limited regeneration of desirable tree species due to high deer-browse pressure and other factors (Tilghman, 1989; Long et al., 2007; Powers and Nagel, 2009; Matonis et al., *in press*). In the northern hardwood forests of Michigan we study here, regeneration in areas with abundant deer is often characterized by low stem densities and/or domination by less browse-preferred and usually less commercially valuable tree species such as *Ostrya virginiana* (Mill.) (ironwood) and *Fagus grandifolia* (american beech), whereas areas with fewer deer are characterized by higher stem densities and/or domination by more browse-preferred species, especially commercially valuable *Acer saccharum* (sugar maple). In this paper, we investigate the impacts of different regeneration success rates (0–100% stocked), regeneration species compositions (sugar maple vs. ironwood) and timber harvest prescriptions (different residual stand structure criteria) on bird occupancy probabilities and harvested timber volumes over a century. To do so, we use field data to develop models to describe the relationships between bird occupancy probability and forest structure. We then use these relationships with the USFS Forest Vegetation Simulator and a forest-gap regeneration and growth model. The goal of our work is to improve understanding of the tradeoffs inherent to ensuring habitat for sensitive bird species and maintaining production of forest products.

## 2. Material and methods

### 2.1. Study area

Our data were collected in a 4,000 km<sup>2</sup> forested region of the Upper Peninsula of Michigan, USA (see Millington et al., 2010; Matonis et al., 2011). This region is dominated by upland northern hardwood, lowland conifer, aspen and mixed upland forest types juxtaposed in a mosaic across the rolling topography of the Menominee drumlin field. Predominant tree species in these forest cover types are sugar maple in upland northern hardwood stands, *Thuja occidentalis* (northern white-cedar) in lowland coniferous forest stands, and *Populus tremuloides* (trembling aspen) in aspen stands. These forest types provide habitat for numerous wildlife species including white-tailed deer and a diverse assemblage of songbirds (Laurent, 2005; Matteson et al., 2009).

Forest management for timber products is the primary land use in this region, and uneven-aged selection silviculture (both group and single-tree selection) dominates management of the region's northern hardwood stands. Consequently, harvesting and variation in harvesting (e.g., variation in intensity and frequency) are the predominant disturbance-based influences on northern hardwood

forest structure in the region, but variation in subsequent tree regeneration success rates, especially due to herbivory by abundant deer, are also likely to influence stand structure over the long-term (Kraft et al., 2004; Matteson et al., 2009; Matonis et al., in press). Harvest specifications vary with ownership and/or management goals, but stands are typically entered approximately every 10–20 years and 1/4 to 1/3 of the basal area is removed, leaving 16–18 m<sup>2</sup> ha<sup>-1</sup> (70–80 ft<sup>2</sup> acre<sup>-1</sup>) residual basal area (e.g., Schwartz et al., 2005). Land ownership in the study area is divided between land owned by the State of Michigan (42%), and private non-industrial (38%) and private industrial (20%) owners. We have documented that sugar maple regeneration density in harvest gaps varies widely across this region with a very large range, from zero to 25,000 stems per hectare (trees 1–2 m tall in 347 gaps with mean extended-gap area (Runkle, 1981) of 190 m<sup>2</sup> and range 80–915 m<sup>2</sup>, Matonis et al., in press). Across this region, a landscape-scale gradient in regeneration density in canopy gaps roughly coincides with winter deer distribution (Matonis et al., in press). In northern hardwood stands with higher deer densities, the commercially less-valuable and less browse-preferred subcanopy tree ironwood composes a greater proportion of regenerating trees (Miller, 2004; Matonis, 2009). In our model scenarios (Section 2.4) we explore the hypothetical extremes of variation in tree regeneration and composition implied by these patterns.

## 2.2. Bird occupancy modeling

To develop models of bird occupancy in forest stands (after MacKenzie, 2006; MacKenzie et al., 2006), we used records of bird species presence for 173 northern hardwood stands (Laurent et al., 2005). Bird species were marked as present if detected in any one of three surveys conducted at a permanently marked point in each stand within five hours of sunrise between June 10 and July 3 in 2001, 2002 or 2003 (all stands surveyed in the same year with no revisits in multiple years). Surveys were 10-min fixed-radius point counts (Ralph and Sauer, 1995) with species recorded as present if detected within 50 m of the observer. Stands were randomly selected from within larger plots that were chosen to maximize biotic and abiotic differences among plots and to sample the heterogeneity of the study area (Laurent et al., 2005). We focus our analysis on four species that favor northern hardwood stands and either nest or forage in the upper strata of stands (Collins, 1983; De Graaf et al., 1985; deCalesta, 1994; Matteson et al., 2009): *Dendroica virens* (black-throated green warbler, BTNW); *Contopus virens* (eastern wood-pewee, EAWP); *Empidonax minimus* (least flycatcher, LEFL); and *Pheucticus ludovicianus* (rose-breasted grosbeak, RBGR). All but the eastern wood-pewee are identified as “priority” species for bird conservation in the region (Matteson et al., 2009, although EAWP is on the threshold for this designation and is recognized as being in significant population decline), and all were detected frequently enough to develop useful occupancy models.

We evaluated seven overstory structure variables in the development of bird occupancy models for our northern hardwood sites. The particular variables we use can be readily obtained from both stand inventory data and the output of our stand regeneration, growth and harvest model (described in Section 2.3), and are the same as or similar to measures used in other bird habitat modeling (e.g., Jobs et al., 2004; Laurent, 2005; Smith et al., 2006). We use two measures of stand basal area (m<sup>2</sup> ha<sup>-1</sup>): the total stand basal area of all live stems (*TotBA*) and the stand basal area of non-*Acer* species (*NonAcerBA*). Basal area was measured using a 10 BAF prism (ft<sup>2</sup> acre<sup>-1</sup>) at three randomly located points in the stand. To characterize the structure of the canopy, we use the cumulative diameter-at-breast-height (cm) for trees with some part of their live-leaf canopy that intersects horizontal planes at 15 m (*SumDiam15 m*),

20 m (*SumDiam20 m*) and 25 m (*SumDiam25 m*) in height. As an index of canopy height (m) we use the maximum height of ‘non-emergent’ stand trees (i.e., trees with height < [1.25 × median tree height]) as we assume taller trees have emerged out of the canopy, *CanopyHeight*). Our seventh variable is the logarithm of canopy openness (*CanopyOpen*, %). For our field data canopy openness (*co*, %) was measured using a spherical densiometer, and for our simulated data we derive it from *TotBA* using the empirical relationship in our field data,  $co = 140.92 \times e^{-0.148 \times TotBA}$  (parameters significant with  $p < 0.001$  and  $r^2 = 0.69$ ). No correlations between these variables are greater than |0.66| except between *SumDiam25 m* and *CanopyHeight* (0.79). Field data for these variables were collected in the same northern hardwood stands as the bird surveys during 2001–2003 (Laurent, 2005).

We used a maximum-likelihood approach for modeling bird occupancy probability when detection is imperfect (MacKenzie, 2006; MacKenzie et al., 2006). These bird occupancy models use the logit link to linearize relationships between overstory structure covariates and the probability of occupancy,  $p$ , so that:

$$\text{logit}(p) = \beta_0 + \beta_1 x_1 + \dots + \beta_i x_i \quad (1)$$

We do not model detection probability as these variables cannot be represented in our regeneration and growth simulation model. To eliminate problems of over-fitting our models, we first examined univariate models for each species to select variables that might be useful in multivariate models. To do this we calculated the difference in the modified Akaike’s Information Criterion ( $AIC_c$ , Akaike, 1974 Burnham and Anderson, 2002) between each univariate model and the null model ( $\Delta AIC_{cnull} = AIC_{cnull} - AIC_c$ ). We also calculated Akaike weights ( $AIC_c$  wt), which can be interpreted as the approximate probabilities that a given model is the most useful for inference in the set of models considered. We included variables with  $\Delta AIC_{cnull} > 2$  (Burnham and Anderson, 2002) in multivariate models (both additive and interactive) for each species. Best multivariate and univariate models were ranked using  $AIC_c$  to find the model that maximized the tradeoff between model fit and complexity. We use  $AIC_c$  because for some of our multivariate models  $n/K < 40$  (where our sample size  $n = 173$  and  $K$  is the number of model parameters). The model with lowest  $AIC_c$  was used to estimate occupancy probability from the output of our forest stand regeneration, growth and harvest model. To fit occupancy probability models we used the ‘unmarked’ R package (version 0.8-6, Fiske and Chandler, 2010).

## 2.3. Forest stand regeneration, growth and harvest model

To examine the potential impacts of variation in uneven-aged timber harvest and regeneration density and composition on bird species occupancy probability in northern hardwood stands, we developed a forest stand regeneration, growth and harvest simulation model. This model couples a regeneration submodel with the US Forest Service individual-based forest growth model, Forest Vegetation Simulator (FVS). The forest regeneration submodel uses both (i) data collected in 2008 (Matonis, 2009) about the number, species composition, and size of saplings >2 m tall (which we assume to be above the height of deer browse) in 171 forest-canopy gaps (mean extended-gap area 186 m<sup>2</sup>, range 82–657 m<sup>2</sup>) across 29 stands harvested 8–12 years prior to data collection, and (ii) measurements of height growth on 233 SM and IW saplings collected from 141 gaps (mean extended-gap area 197 m<sup>2</sup>, range 82–657 m<sup>2</sup>) at 44 stands harvested 2–15 years prior to data collection. The regeneration submodel takes a phenomenological approach to simulate heights of gap saplings at one timestep (10 years) following timber harvest and grows them until they are 7 m tall, at which point they are passed to FVS for continued growth and mortality/harvest. This bespoke regeneration

submodel is required as FVS does not represent regeneration by seeding, and because regeneration success and composition in northern hardwood forests in the Great Lakes region are influenced by multiple factors (Matonis et al., in press). We use the FVS Ontario variant, which has been calibrated for Great Lakes Region northern hardwood forests (Lacerte et al., 2006; Sharma et al., 2008).

In our simulations, we specify regeneration success, regeneration species composition, and timber harvest rules and forecast the consequences for forest stand structure over 100 years. We represent only sugar maple (SM) and ironwood (IW) tree species. These species compose >70% of total tree basal area and sapling stems in our northern hardwood stands and they represent the strongest contrast between species in terms of commercial value (SM are more valuable), morphology (IW have much smaller maximum size), palatability to deer (SM are more palatable), and observed regeneration patterns (Matonis et al., in press). Sugar maple saplings were present in 71% of gap plots (184, 154 m<sup>2</sup> gap-centered circular plots in 31 stands) in northern stands, where there were fewer deer, with maximum densities equivalent to 25,140 saplings per ha, but completely absent from 96% of gap plots in southern stands (163 gap plots in 28 stands; Matonis et al., in press). In contrast, IW saplings were present in 54% of gap plots in southern stands with densities as high as 15,721 per hectare. Across all stands, SM and IW saplings were absent from 61% and 54% of all gap plots, respectively (Matonis et al., in press). Given such high variability in both regeneration composition and success we examine the full range of SM, IW and total regeneration success rates.

The regeneration submodel simulates the presence and growth of  $n$  or fewer trees in a gap, where  $n = \text{gap area}/CA_7$ . The parameter  $CA_7$  is the canopy area of any tree 7 m tall, and has a value of 13.79 m<sup>2</sup> (estimated from our empirical field data for 55 SM trees; compare with 12.2 m<sup>2</sup> estimated by Ek (1974) for 37 SM trees in Wisconsin). We simulate  $n$  or fewer trees because we are only concerned with the first trees that grow to 7 m to completely fill the gap at that height, thereby out-competing any other trees in the gap (i.e., the  $n$  'gap winners'). A tree that grows to 7 m tall is deemed a regeneration success. We do not simulate smaller saplings in the gap, which are unlikely to recruit into canopy positions due to self-thinning, herbivory, and other factors (e.g., see Sage et al., 2003) and thereby will have little impact on the future growing stock of a stand. We also do not have data about sapling mortality over time, which would be necessary if we were to model all regenerating saplings. In gaps with poor regeneration, there will be fewer than  $n$  saplings that regenerate and grow to 7 m.

Because we are interested in the effects of variable regeneration success on bird species occupancy probability, in our model scenarios (see Section 2.4) we fix the regeneration success rate ( $RSR$ ) as a boundary condition. For example, if  $n=6$  for a gap and  $RSR=50\%$ , the regeneration model simulates only three trees in that gap. For the same example gap, if  $RSR=100\%$  we would simulate six trees and if  $RSR=0\%$  we would simulate none. Once the appropriate number of trees has been generated in a gap, each tree is assigned a species based on the specified value of the sugar maple proportion ( $SMP$ ) boundary condition. The  $SMP$  indicates the proportion of regenerating trees that will be SM, with the remainder being IW. For example, if  $SMP=100\%$ , all regenerating trees will be sugar maple, if  $SMP=50\%$ , half of the regenerating trees will be SM and half IW, and if  $SMP=0\%$  all regenerating trees will be IW. Given our approach of representing only the  $n$  'gap winners', we cannot specify what  $RSR$  values represent in terms of tree density for saplings with height <7 m. However, our value of  $CA_7=13.79$  does imply that for  $RSR=100\%$  the density of 7 m tall trees is approximately 725 ha<sup>-1</sup>.

Once regenerating trees have been created and assigned a species, their height is estimated and they are grown to 7 m tall. Initial model tree heights ( $Ht$ , m) are modeled from our field data as a

function of canopy openness (proxy for light resources), and growth rates are modeled as a function of tree height, the time since harvest and whether the tree was present in the stand prior to harvest (and thereby 'released' by removal of resource constraints). Canopy openness and time since harvest were correlated in our field data, so we only use the variable that maximized model fit in our initial tree height and growth rates equations. Our field-based tree height data were not normally distributed so we used non-parametric bootstrapping to estimate the relationship to canopy openness:

$$Ht = \beta_x - (0.053 \times \text{CanopyOpen}) + \varepsilon, \varepsilon \sim \text{Normal}(\mu = 0, \sigma = 1.387) \quad (2)$$

where  $\beta_x$  is a tree height-rank parameter (Appendix A). The tree growth rate ( $GR$ , m year<sup>-1</sup>) for each tree species was also derived from our field data and is given by:

$$GR = \exp[\beta_6 + (\beta_7 \times AR) + (\beta_8 \times Ht) + (\beta_9 \times TSH)] + \varepsilon, \varepsilon \sim \text{Normal}(\mu = 0, \sigma) \quad (3)$$

where  $AR$  is 'advanced regeneration' (binomial; 1 if was tree present prior to harvest, else 0) and  $TSH$  is time since the gap was created (years; see Appendix B for parameter estimates and residual  $\sigma$  values). A tree is advanced regeneration if it was present in the stand understory (i.e., has height <7 m) prior to gap creation. To establish this, in each gap we surveyed, stem cross-sections were taken at 5 cm and breast height from one sugar maple and one ironwood sapling within three different height strata (1–2 m, 2–4 m and >4 m; when present). To determine whether saplings were present before or after harvest, sapling age at 5 cm was determined (number of rings counted on the cross section plus 0.5 years to account for the current year's growth). All sampled saplings  $\geq 3$  m were advanced regeneration, so  $AR=1$  for all simulated regenerating trees with  $Ht \geq 3$  m. For trees with  $Ht < 3$  m, the probability that a tree is advanced regeneration is estimated empirically from our field data:

$$P(AR|Ht < 3) = 1/1 + \exp[-(\beta_1 \times 0 + (\beta_1 \times Ht) + (\beta_2 \times TSH))] \quad (4)$$

(see Appendix C for parameter estimates).

The growth and harvest submodel (FVS) is aspatial and thus does not support simulation of the size and location of harvest gaps. Consequently, we estimate gap area following harvest in the forest-gap regeneration submodel. From the list of trees harvested in each stand, we cluster trees into groups (i.e., gaps) to fit the empirical Gamma distribution ( $k=3.196$ ,  $\theta=1.740$ ) of stump basal area per gap. In the model, gap area ( $GA$ , m<sup>2</sup>) is then estimated from the empirical relationship in our field data:

$$GA = 112.3 + (359.1 \times BA_5) + \varepsilon, \varepsilon \sim \text{Normal}(\mu = 0, \sigma = 85.1) \quad (5)$$

where  $BA_5$  is the basal area of stumps remaining in the gap following harvest (m<sup>2</sup> ha<sup>-1</sup>). Decrease in gap area through time due to overstory tree growth is modeled by assuming that branches of overstory trees at the edges of gaps grow laterally at an average rate of 8.97 cm year<sup>-1</sup> (normally-distributed error with  $\sigma=6.315$ , from the data presented in Webster and Lorimer, (2005), pers. comm. Webster). If gap area decreases to an area smaller than that able to support  $n$  trees before all  $n$  reach 7 m tall, the shortest tree of those remaining is removed from the model (this may occur in multiple timesteps).

#### 2.4. Model simulations

In our model simulations we investigated the effects of each combination of multiple  $RSR$  (100%, 50%, 25%, 12.5%, 0%) and  $SMP$  (100%, 50%, 25%, 12.5%, 0%) values in our model experiments (we

will refer to these as 'regeneration scenarios'). For each regeneration scenario we simulate the effects of three potential uneven-aged timber harvest prescriptions (Table 1). Prescriptions vary in target residual stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ), target harvest cycle (years), maximum residual tree diameter-at-breast-height (dbh, cm), and a target q-factor (dimensionless). The q-factor specifies the ratio of the tree density in each dbh size-class to its neighboring, larger, size-class; larger values result in dbh distributions with greater densities of smaller size-class trees and lower densities of larger size-class trees (Meyer, 1952). For all prescriptions the minimum removed SM tree dbh is 20 cm, 90% of all ironwood trees with dbh >12.5 cm are removed, the minimum stand removal basal area is  $5 \text{ m}^2 \text{ha}^{-1}$ , the minimum standing basal area before harvest is  $25 \text{ m}^2 \text{ha}^{-1}$ , and one legacy (seed) tree with dbh greater than the maximum residual tree dbh is allowed to remain (per ha). If the minimum standing basal area criteria is not met, or if the stand removal basal area criteria will not be met by harvest in a timestep (10 years interval), harvest does not occur until the first subsequent timestep in which the criteria are achieved. The values for these criteria were established by consulting with state, provincial and private industrial foresters working in the northern hardwood forests of upper Michigan, USA and Ontario, Canada (see Acknowledgements) and represent the range of harvest prescriptions currently employed across the region.

For each prescription and regeneration scenario, we simulate 35 northern hardwood stands randomly selected from the 173 stands for which we have inventories (i.e., 20% of our stand data) to reduce computational demands. For these stands, we initially compared results from three, five and seven model replicates for  $\text{RSR} = 100\%$  and  $\text{SMP} = 100\%$  with harvest Prescription A and found no significant difference between standard deviations of each set for merchantable timber removed and occupancy probability change for all bird species. Therefore, to minimize computational requirements, we use three model replicates for each scenario. From these replicates we calculate mean and 95% confidence intervals ( $1.96 \times$  standard error) of the state variables for the 35 stands for each prescription and regeneration scenario. These confidence intervals account for uncertainty in our bird occupancy and tree regeneration models and for stochastic variation in FVS growth and harvest. Our state variables are volume of merchantable timber harvested throughout the simulated century, percentage change in bird species occupancy probability between the initial stand state and the state 100 years subsequently, and bird species occupancy probability at year 100. To calculate the percentage change in bird species occupancy probability, we take the difference between the average of values for the first three 10-year timesteps and last three 10-year timesteps of each set of replicates. We use three-timestep averages to represent bird occupancy changes because timber harvest events produce potentially large changes in bird occupancy probabilities, and because the timing of timber harvest can vary between simulation replicates (being conditional on stand conditions). We also examine effects of harvest prescrip-

**Table 1**

Specification of uneven-aged timber harvest prescriptions used in simulations. Prescriptions vary in target residual stand basal area (*Residual BA*), target harvest cycle (*Harvest Cycle*), maximum residual tree diameter-at-breast-height (dbh, Max. dbh), and a target q-factor (*Q factor*, specifies the ratio of the tree density in each dbh size-class to its neighboring, larger, size-class; Meyer, 1952). All parameters specified here are targets, but individual simulations vary. Other aspects of prescriptions are constant for all prescriptions (see text, Section 2.4).

Prescription	Residual BA ( $\text{m}^2 \text{ha}^{-1}$ )	Harvest cycle (years)	Max. dbh (cm)	Q factor (dimensionless)
A	18.5	20	55	1.5
B	16.0	10	55	1.4
C	13.5	20	50	1.3

tions and regeneration scenarios on stand structure. Components of stand structure we consider are distributions of dbh, basal area and height for trees with dbh >10 cm. Merchantable timber volumes (trees with a top diameter of  $\geq 10$  cm) are calculated using the standard FVS Ontario equations (Sharma et al., 2008) and normalized by area and time (units in  $\text{m}^3 \text{ha}^{-1} \text{decade}^{-1}$ ).

### 3. Results

#### 3.1. Bird occupancy modeling

All four bird species were associated with at least one aspect of forest stand structure (i.e.,  $\Delta\text{AIC}_{\text{null}} > 2$  for models including at least one variable compared to null model; Table 2). Species were sensitive to different components of stand structure, with no component being important for all species. Canopy openness and canopy height each improved our ability to model species occupancy (i.e.,  $\Delta\text{AIC}_{\text{null}} > 2$ ) for two species. Bird species were sensitive to different levels of vertical forest structure, with BTNW being more common in stands with more dense lower-strata structure (i.e., *SumDiam15 m*) and LEFL and RBGR being more common in stands with increased abundance of upper-strata structure (i.e., *SumDiam25 m*). All stand structure components had positive influences on the occupancy of bird species in univariate models, with the exception of *CanopyOpen* which negatively affected the occupancy of BTNW. Stand occupancy models show that more than one independent variable was useful for explaining occupancy probability (i.e.,  $\Delta\text{AIC}_{\text{null}} > 2$ ) for BTNW, LEFL and RBGR, and that both additive and interactive models were important (Table 3).

#### 3.2. Impacts of timber harvest prescriptions and regeneration scenarios on stand structure and timber volumes

Differences in stand structure after 100 simulated years are generally greater between the regeneration scenarios we examine

**Table 2**

Univariate stand occupancy models for four bird species. These models for occupancy probability,  $p$ , are from bird and vegetation data collected in the field and have the form  $\text{logit}(p) = \beta_0 + \beta_x$ . All models with  $\text{AIC}_c$  less than the null model (no predictors) are shown. Models for which the difference between model  $\text{AIC}_c$  and null model  $\text{AIC}_c$  is greater than 2.0 are shown in bold and considered for inclusion in multivariate models (Table 3). Difference between an individual model  $\text{AIC}_c$  and the best model  $\text{AIC}_c$  is also shown ( $\Delta\text{AIC}_c$ ). Variables are described in the text (Section 2.2).

Species	Variables	$\text{AIC}_c$	$\Delta\text{AIC}_c$	$\text{AIC}_c$ (wt)	$\beta_x$
BTNW	<i>SumDiam15 m</i>	<b>617.9</b>	<b>0.0</b>	<b>0.46</b>	<b>0.784</b>
	<i>CanopyOpen</i>	<b>618.0</b>	<b>0.1</b>	<b>0.44</b>	<b>-0.672</b>
	<i>TotBA</i>	622.9	5.0	0.04	
	null	624.0	6.1		
EAWP	<i>CanopyHeight</i>	<b>669.1</b>	<b>0.0</b>	<b>0.45</b>	<b>0.479</b>
	<i>CanopyOpen</i>	671.1	2.0	0.17	
	null	672.5	3.4		
LEFL	<i>CanopyOpen</i>	<b>464.6</b>	<b>0.0</b>	<b>0.58</b>	<b>0.562</b>
	<i>CanopyHeight</i>	<b>465.7</b>	<b>1.1</b>	<b>0.34</b>	<b>0.588</b>
	<i>SumDiam25 m</i>	<b>470.3</b>	<b>5.7</b>	<b>0.03</b>	<b>0.377</b>
	<i>SumDiam15 m</i>	471.5	6.9	0.02	
	<i>TotBA</i>	473.0	8.4	0.01	
	null	473.0	8.4		
RBGR	<i>TotBA</i>	<b>648.4</b>	<b>0.0</b>	<b>0.29</b>	<b>0.776</b>
	<i>SumDiam25 m</i>	<b>648.9</b>	<b>0.5</b>	<b>0.23</b>	<b>1.780</b>
	<i>SumDiam20 m</i>	<b>649.0</b>	<b>0.6</b>	<b>0.22</b>	<b>0.839</b>
	<i>CanopyHeight</i>	650.7	2.3	0.09	
	null	651.4	3.0		

**Table 3**

Stand occupancy models for four bird species used with the regeneration, growth and harvest model. These models for occupancy probability,  $p$ , are from bird and vegetation data collected in the field and have the form  $\text{logit}(p) = \beta_0 + \beta_1 x_1 + \dots + \beta_k x_k$ . Values of  $AIC_c$  wt for each model are from model comparisons for all univariate and multivariate models using variables in Table 2. Parameter estimates ( $\beta$ ) for each variable in the highest-ranked model are also shown. Variables are described in the text (Section 2.2).

Species	Variables	$AIC_c$	$AIC_c$ wt	$\beta$
BTNW	Intercept	616.6	0.38	2.120
	CanopyOpen			-0.458
	SumDiam15 m			0.559
EAWP	Intercept	669.1	0.45	1.107
	CanopyHeight			0.479
LEFL	Intercept	448.4	0.49	-0.482
	CanopyHeight			0.629
	CanopyOpen			0.597
RBGR	Intercept	645.1	0.18	1.905
	TotBA			1.440
	SumDiam20 m			0.839
	TotBA:SumDiam20 m			1.256

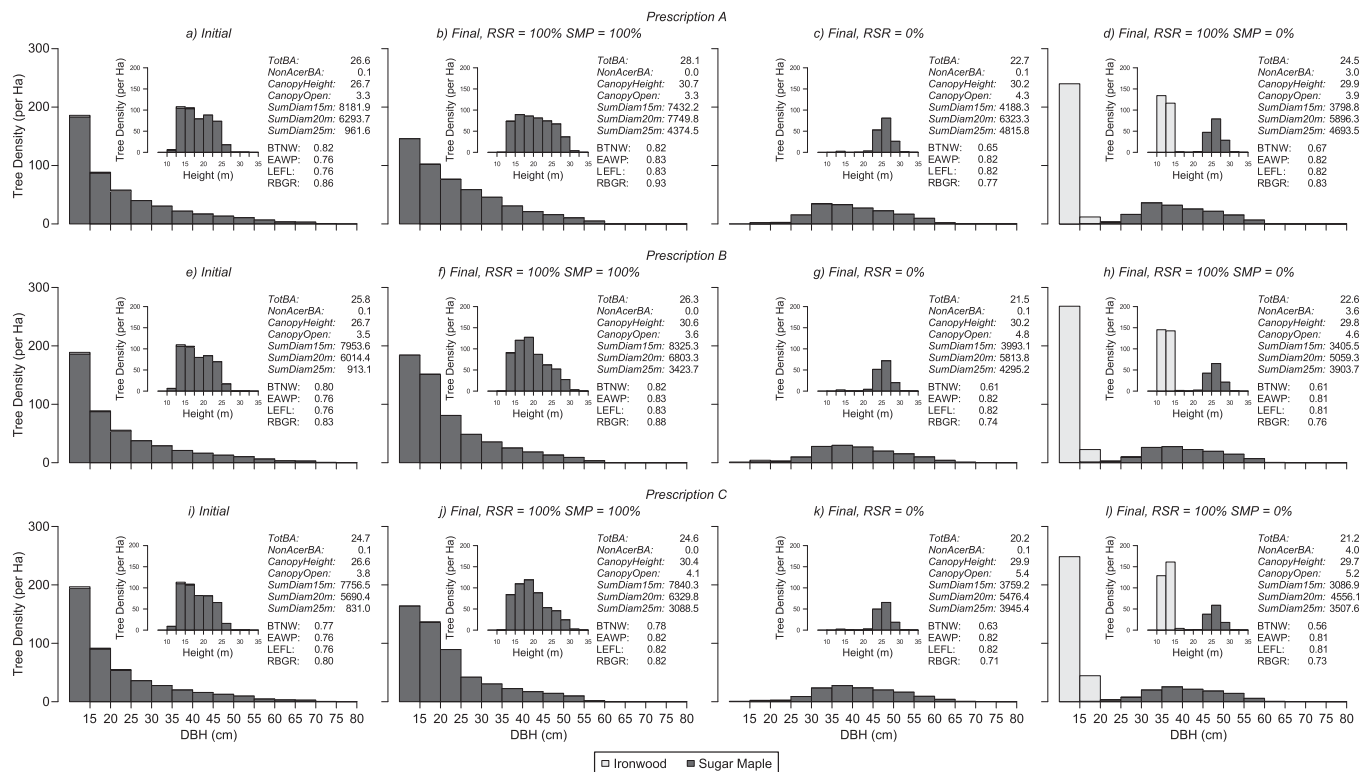
than between the harvest prescriptions (Fig. 1 shows extremes of regeneration scenarios for each prescription; see online supporting material for example animations). When  $RSR$  and  $SMP$  are large, final dbh distributions match the prescribed  $q$ -factor (e.g., Fig. 1b, f, and j), but for small  $RSR$  and  $SMP$ , harvest prescriptions have little effect on dbh, basal area and height distributions (Fig. 1c, d, g, h, k, and l). For small  $SMP$ , stand structure after 100 years is characterized by high ironwood tree density and basal area in smaller size-

classes, few trees in the >20 to <30 cm dbh size-classes, but with larger size-classes still adequately stocked by sugar maple (Fig. 1d, h, and l). This is because fewer sugar maple in a stand means lower stand basal area (small ironwood trees contribute little to basal area) which in turn reduces the frequency of timber harvest due to the minimum standing basal area rule. Final stand structure for  $RSR = 0\%$  results in similar structures as simulations with small  $SMP$ , but without high densities of ironwood in the smaller tree size-classes (Fig. 1c, g and k).

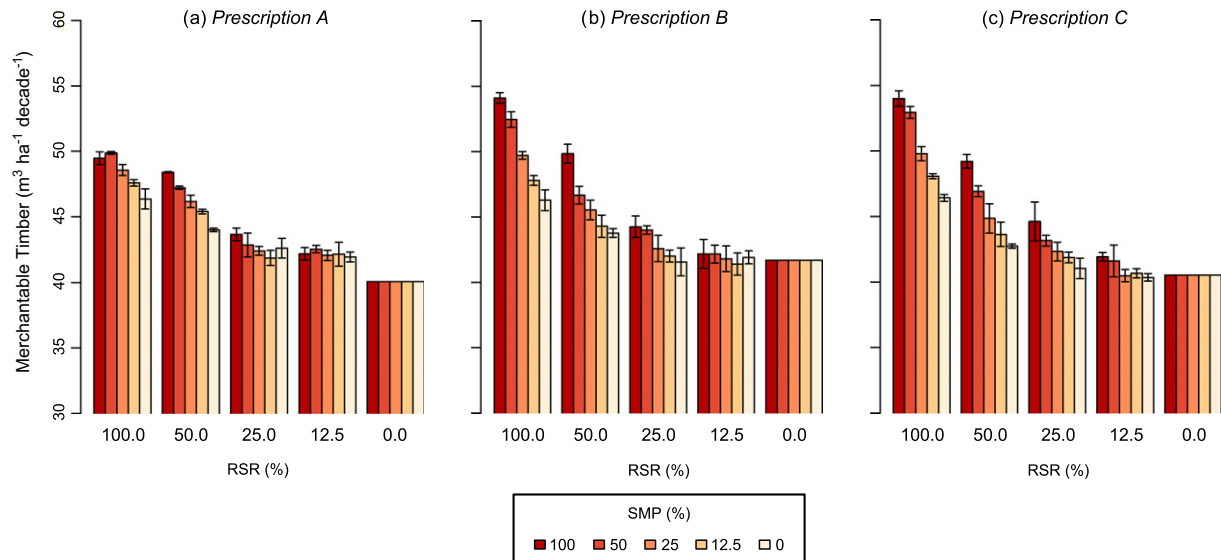
Of the three timber harvest prescriptions, Prescription A yields the least merchantable timber averaged across all stands and years (Fig. 2). Across all prescriptions, smaller  $SMP$  values yield smaller merchantable timber volumes (note that ironwood does not contribute to merchantable timber volumes). Harvested timber volumes are also consistently smaller for smaller  $RSR$  (for the same  $SMP$ ). Impacts of  $SMP$  and  $RSR$  on timber volumes are more pronounced for prescriptions with smaller target residual stand basal area and higher cutting frequency (e.g., difference between removal for  $RSR = 100\%$  and  $RSR = 0\%$  is greater for Prescription C than A).

3.3. Bird species responses to timber harvest prescriptions and regeneration scenarios

For all timber harvest prescriptions for the majority of  $RSR$  values, occupancy probability for LEFL and EAWP generally increase between initial and final stand state whereas occupancy probability for BTNW and RBGR generally decrease (Fig. 3). Exceptions are for BTNW and RBGR in scenarios with large  $RSR$  and  $SMP$  (in which change is positive). As  $RSR$  and  $SMP$  become smaller, BTNW and RBGR decrease in occupancy probability. In contrast, for large  $RSR$ , LEFL occupancy probability increases as  $SMP$  becomes smaller. Generally, differences in occupancy probability between  $SMP$  values are smaller for smaller  $RSR$ . Maximum changes in occupancy probability from initial conditions are: BTNW (-28.3%), RBGR



**Fig. 1.** Forest stand structure resulting from timber harvest prescriptions for initial stand conditions (a, e and i), final conditions with  $RSR = 100\%$  and  $SMP = 100\%$  (b, f, j), final conditions with  $RSR = 0\%$  (c, g and k), and final conditions with  $RSR = 100\%$  and  $SMP = 0\%$  (d, h and l). Final conditions are 100 simulated years after initial conditions. Tree density is plotted by diameter-at-breast-height (dbh) and height size-classes. Plots are for trees with dbh >10 cm only. Prescription specifications are presented in Table 1.



**Fig. 2.** Timber removals by regeneration scenario for timber harvest Prescriptions A (a), B (b), and C (c). Error bars are 95% confidence intervals from the standard error of three simulation replicates for each treatment. Prescription specifications are presented in Table 1.

(−13.6%), EAWP (+8.4%) and LEFL (+36.1%). Maximum differences in occupancy probability among harvest rules and regeneration scenarios are EAWP (1.8%), LEFL (15.7%), RBGR (22.2%) and BTNW (31.1%).

Generally, small *SMP* with large *RSR* (resulting in stands with many IW saplings but few SM) has similar effects on occupancy probabilities as small *RSR* (stands with few saplings of any species). This suggests that SM regeneration is a more important determinant of future forest structural attributes for the studied bird species than IW regeneration. For small *RSR* (i.e.,  $RSR \leq 25\%$ ), effects of *SMP* are negligible relative to 95% confidence intervals for EAWP, LEFL and RBGR. We observe equal differences in occupancy probability between *SMP* classes for a given *RSR* (i.e., difference in occupancy probability for a given species between *SMP* = 100% and 50% is equal to difference between *SMP* = 50% and 25%), indicating that change in occupancy probability per unit of *SMP* (for given *RSR*) is greater at smaller *SMP* (except RBGR for Prescription C, Fig. 3i).

Compared to the impacts of regeneration, and especially SM regeneration, the impacts of different harvest rules were more modest. Our results indicate that final occupancy probability for BTNW and RBGR will be greater for a given regeneration scenario for prescriptions with greater target residual basal area and q-factor (Prescription A > B > C; Fig. 4). In contrast, final occupancy probability for LEFL decreases with greater target residual basal area and q-factor (Prescription C > B > A), but differences between prescriptions for this species are smaller. Final occupancy probability does not vary between prescriptions for EAWP (given 95% confidence intervals). Final occupancy probability for BTNW and RBGR increases with increasing removed merchantable timber volume for all prescriptions, and has a weak decreasing trend for LEFL (Fig. 4). For *SMP* = 100%, differences in merchantable timber removed decrease between prescriptions as *RSR* becomes smaller, but differences in bird species' occupancy probability remain similar between prescriptions (except EAWP).

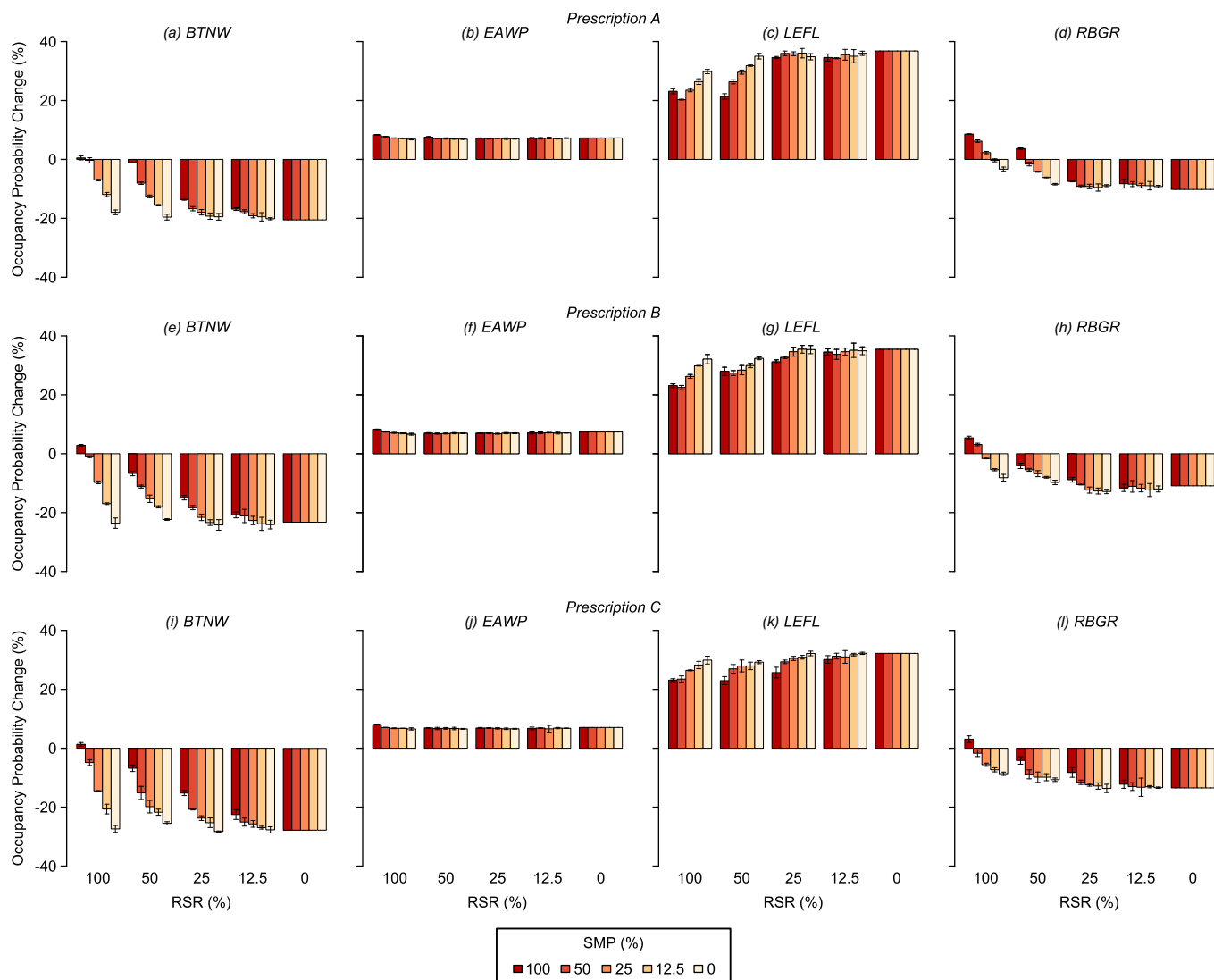
## 4. Discussion

### 4.1. Impacts of timber harvest and tree regeneration on canopy bird species

Our results show that over a 100-year timeframe bird species that specialize in overstory habitats respond uniquely to changes

in forest structure brought about by variation in timber harvest and regeneration composition and density. Regeneration density of sugar maple had the strongest long-term impacts on occupancy with ironwood regeneration and harvest prescriptions having more modest effects. Furthermore, 100-year average merchantable volume removals, which varied with harvest specifications and regeneration, were related to bird occupancy for three of the four species, positively for two species and negatively for one. Harvest prescriptions can be tailored to affect both timber removal volumes and bird occupancy probability simultaneously, but only when regeneration is adequate.

Change in occupancy probability over 100 years is generally negative for BTNW (mean of −17.1% across all scenarios and replicates) and RBGR (mean −7.5%), but positive for EAWP (mean +7%) and LEFL (mean +30%) (Fig. 3). These differences are due to the combinations of species specific occupancy-forest structure relationships and changes in stand structure. For example, whereas LEFL has a positive relationship with *CanopyOpen*, BTNW has a negative relationship (Table 3), and in the majority of scenarios for the prescriptions we investigated here *CanopyOpen* increases (because, averaged over all our stands, stand basal area decreases from the initial state, Fig. 1). Furthermore, different combinations of tree regeneration scenarios and timber harvest prescriptions can lead to different occupancy probability changes. For example, when SM regeneration success is high (i.e., regeneration success greater than 50% of which more than 50% is SM) RBGR occupancy probability increases over 100 years for all timber harvest prescriptions (Fig. 3). This is because both *TotBA* and *SumDiam20 m* increase compared to the initial stand conditions (e.g., Fig. 1b, f and j) and regeneration of the larger canopy tree species SM is required to increase values for these structural variables. Conversely, when SM proportion of regeneration is lower, RBGR change in occupancy probability becomes negative because smaller IW trees contribute little to basal area and *SumDiam20 m* – but the regeneration level at which it does varies by prescription (Fig. 3d, h and l). The only bird species for which change in occupancy probability does not vary between regeneration levels or prescriptions is EAWP (consistently +8–9%), because final *CanopyHeight* does not vary between regeneration scenarios or harvest prescriptions (Fig. 1). *Canopy-Height* varies little between scenarios because, even with very low *RSR* values, after 100 years trees that were in canopy and sub-canopy positions at time zero (initial conditions) are still adequate



**Fig. 3.** Mean stand percentage change in bird occupancy probability resulting from timber harvest prescriptions for black-throated green warbler (a, e and i), eastern wood-pewee (b, f and j), least flycatcher (c, g and k) and rose-breasted grosbeak (d, h and l) by regeneration scenario. Change is between start and end of 100-year simulations. Error bars are 95% confidence intervals from the standard error of three simulation replicates for each treatment. Prescription specifications are presented in Table 1.

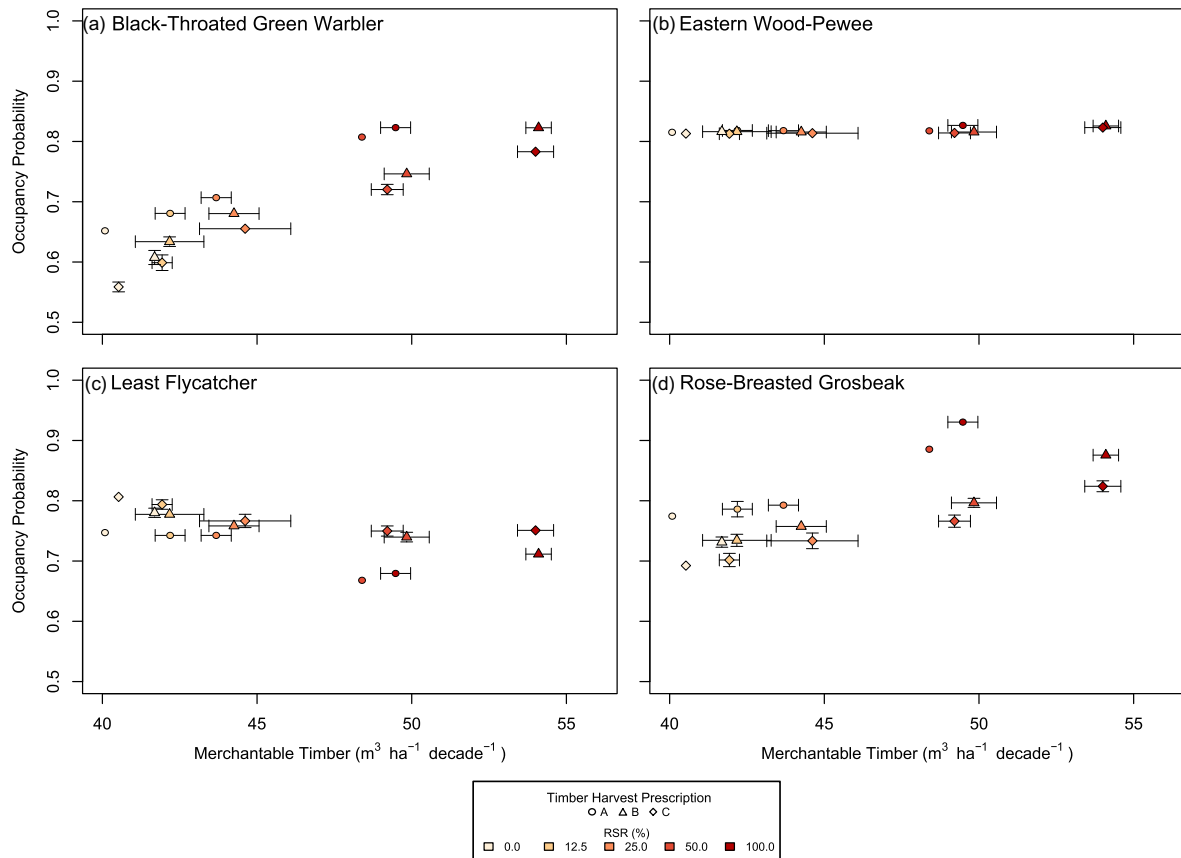
to populate the fully grown upper tree stratum (given tree growth rates and the minimum residual basal area harvest rules we used). Consistent increases in EAWP are observed because final *Canopy-Height* is consistently greater than initial values (averaged across all stands), as the initial condition of some stands is immature (relative to final conditions).

Differences in bird occupancy probability between *SMP* values are lower for low values of *RSR* than for high (Fig. 3). For example, across the three harvest prescriptions, change in occupancy probability of BTNW for *RSR* = 100% ranges from +3% to –27% across *SMP* values, but for *RSR* = 0% change in occupancy probability ranges from –17% to –28% (Fig. 3a, e and i). However, this result would likely be expected regardless of whether or not *RSR* is more important than *SMP* biologically, as since *RSR* determines the total number of saplings it limits the potential variation in *SMP*. For any value of *RSR*, when *SMP* is low, change in occupancy probability shows little variation indicating that *SM* regeneration density determines overstory structure (which drives differences in bird occupancy probability). Using BTNW as an example again, the decrease in occupancy probability for any given harvest prescription varies by a maximum of 3% across all values of *RSR* when *SMP* = 0% (except *RSR* = 0% for prescription C, Fig. 3a, e and i). This is because

the subcanopy, small tree species *IW* does not progress into larger size-classes (e.g., Fig. 1d, h and l), both because it does not grow as large as *SM* and because our harvest prescriptions demand that 90% of ironwood with *dbh* >12.5 cm is removed to create space for *SM* (a realistic assumption commercially).

Other studies have found both positive and negative effects of uneven-aged timber harvest for the bird species we examined here (Jobs et al., 2004; Holmes and Pitt, 2007). By taking a more detailed analysis than previous studies (i.e., by considering specific harvest prescriptions), we find evidence to suggest that different harvest approaches produce positive effects on some species and negative effects on others over the long term. Campbell et al. (2007) found EAWP responded positively to uneven-aged timber harvest. In our results, EAWP responds positively to uneven-aged management over the long term, regardless of regeneration rates (because *CanopyHeight*, averaged across all our stands, increases over time). Tozer et al. (2010) found that LEFL increased in response to intensive selection harvest (4.0 gaps  $\text{ha}^{-1}$  compared with standard 0.5 gaps  $\text{ha}^{-1}$ ) in the first or second year post-harvest in southern Ontario. Although we did not examine variation in gap density in our simulations, we do find that LEFL respond positively to harvest over the longer term, likely because our occupancy





**Fig. 4.** Mean stand bird occupancy probability and merchantable timber removed by regeneration success rate (RSR) and harvest prescription for black-throated green warbler (a), eastern wood-pewee (b), least flycatcher (c) and rose-breasted grosbeak (d). Occupancy probabilities are for year 100 of simulations. Simulations are for  $SMP = 100\%$ . Prescription specifications are presented in Table 1. Error bars are 95% confidence intervals from the standard error of three simulation replicates for each treatment.

probability model suggests LEFL prefer open stands (Table 3). For RBGR, Smith et al. (2006) found that stands with 'heavy removals' in deciduous woodlands of southern Ontario contained higher bird densities. In contrast, our results suggest RBGR have lowest occupancy probability for harvest prescriptions with lower residual basal area (i.e., 'heavier' harvest). However, all the prescriptions we examine here are 'heavy' as defined by Smith et al. (the 'heavy wood removal' they consider results in residual BA  $<20 m^2 ha^{-1}$ ). Finally, for a study area in New Brunswick, Canada, (Guenette and Villard, 2005), BTNW were found at greatest densities in stands with greater canopy closure and higher densities of large trees following harvest. Our findings are consistent with these results, illustrating that different intensity of timber harvest results in different responses over the long-term.

#### 4.2. Management implications

Of principle interest to forest managers, we find that when tree regeneration densities of commercially desirable trees are higher, managers can choose harvest prescriptions that benefit both timber volumes and bird species occupancy probability for canopy-structure dependent species. For example, our results suggest that when regeneration success is high, Prescriptions B and C will maximize merchantable timber while producing occupancy probabilities comparable to other prescriptions (compare prescriptions A, B and C for  $RSR = 100\%$  for each species in Fig. 4). However, when regeneration is poor (i.e., regeneration success of 25% or less), differences in timber volumes between prescriptions are reduced (given 95% confidence intervals), but differences in occupancy

probability between prescriptions remain. For instance, compare prescriptions A, B and C for  $RSR = 12.5\%$  in Fig. 4 (the exception to this is Prescription B for  $RSR = 0\%$  which has significantly greater timber output than the other prescriptions, likely because of the shorter harvest cycle). Our results show that, in general, when regeneration success is 25% or less, differences in occupancy probability for BTNW and RBGR between harvest prescriptions are greater than differences in merchantable timber removed (relative to 95% confidence intervals, Fig. 4a and d). For example, when regeneration success is 12.5%, timber yields do not vary significantly relative to confidence intervals between Prescriptions A and C (mean values decrease by approximately 2%), but BTNW and RBGR occupancy probabilities are significantly lower (by approximately 12% and 11%, respectively) between the prescriptions. Consequently, if maintaining high tree regeneration densities is not possible, forest managers should pay closer attention to the impacts of timber harvest prescriptions on bird species.

Maintaining high regeneration densities will likely be an issue in forests where deer are an important component of the economy (e.g., for sport hunting) and managers must consider the tradeoffs between deer population and tree regeneration. Deer herbivory is known to reduce stand timber value by slowing the recruitment of saplings to canopy positions (Marquis, 1981) and will also likely lead to changes in regeneration composition as deer preferentially browse some tree species over others (e.g., sugar maple over ironwood in northern hardwood stands, Beals et al., 1960; Miller, 2004; Matonis, 2009). Although we find total regeneration is generally more important for long-term bird species occupancy probability than maple proportion,

our results do suggest that lower proportions of maple in regeneration lead to greater changes in bird occupancy over the long term. Our approach can help forest and wildlife managers to identify appropriate timber harvest regimes together in forests where deer are a major driver of regeneration density and species composition. More useful still will be the explicit representation of deer within the modeling framework. Although the potential impacts of deer are implied by the regeneration scenarios we have investigated here (i.e., low regeneration densities, higher proportions of ironwood in regeneration; Matonis et al., *in press*), research that explicitly represents the spatially varying impacts of deer populations of different densities on long-term stand structure and habitat for other wildlife will provide deeper understanding of potential management actions. Linking this research to economic evaluation of both timber and songbirds in a spatially-explicit framework will also allow more rigorous analysis or tradeoffs and provide stronger justification for management actions.

Like all other models, the assumptions made throughout the modeling process must be understood when interpreting the management implications of our results. The resource-use modeling approach to bird occupancy probability we use (MacKenzie, 2006) assumes a closed population during sampling; our sampling strategy, which ensured all three detection surveys were performed within a month during the peak of the breeding season, likely did not violate this assumption. More generally, we assume that our models adequately reflect the variation that exists in the real world and that relationships between bird species occupancy and forest structure do not change through time, an assumption that would be violated by changes in inter-species relationships (e.g., predator-prey or inter-guild competition) or environmental conditions (e.g., forest species composition, climate) over time. However, our results for bird occupancy probability change are for a 100-year period and change will likely be exacerbated over longer time periods. Our regeneration sub-model assumes that shorter trees, of whatever species, will be out-competed by taller trees; although taller ironwood trees may delay recruitment of sugar maple they may not completely exclude it. Our modeling also does not account for the potential effects of the spatial context of forest stands (e.g., change in aspen cover across the landscape in which our hardwood stands are located) or disturbances other than timber harvest (such as wind, disease or insects). Hence, our projections, and approaches like this, should be used as one facet of management decision-making and used with awareness of its assumptions and limitations (Laurent et al., 2010). With these caveats understood, and along with continuing improvements (e.g. see Shifley et al., 2008), approaches like this do offer a useful means to explore potential alternative futures and formally examine the effects of multiple interacting drivers of long-term forest and habitat change.

## 5. Conclusions

In this paper we have presented the results of using bird-forest structure relationships with a forest-gap regeneration and growth model, both derived from empirical field data, to simulate the combined impacts of variable tree regeneration and uneven-aged timber management on stand structure, bird occupancy probabilities and merchantable timber harvest over a century. Our results imply that forest and wildlife managers (amongst others) will need to work together to ensure tree regeneration and prevent detrimental impacts on timber output and habitat for some avian species over the long-term. For example, we find that higher densities of regenerating sugar maple results in greater harvested merchantable timber volumes

and reduces the impacts of uneven-aged timber management prescriptions on bird occupancy probability over the long term. However, when regeneration is poor (e.g., regeneration success is 25% or less), harvest prescriptions have a greater relative influence on bird species occupancy probabilities than on the volumes of merchantable timber harvested. Importantly, our results suggest that ensuring high tree regeneration densities benefits both bird populations and timber production over the long term, and imply that that forest managers should take greater consideration of the long-term impacts of harvest prescriptions on bird species when tree regeneration is poor. This is further evidence that forest resource management cannot proceed in piecemeal fashion, and that coordinated management simultaneously serving multiple interests must be pursued.

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## Appendix A. Parameter estimates for initial regenerating tree heights model

Parameter estimates are for  $\beta_x$  in Eq. (2) where  $x$  is sapling rank category as follows; 1 = tallest tree, 2 = second tallest tree, 3 = third and fourth tallest trees, 4 = fifth and sixth tallest trees and 5 = seventh and shorter trees. Standard error of parameter estimates are shown in parentheses (all variables significant at  $p < 0.01$ ).

Parameter	Estimate
$\beta_1$	5.423 (0.916)
$\beta_2$	4.930 (0.211)
$\beta_3$	4.629 (0.212)
$\beta_4$	4.218 (0.256)
$\beta_5$	4.181 (0.349)

## Appendix B. Parameter estimates for tree growth rate equations

The model for sugar maple was derived from  $n = 135$  harvested saplings and that for ironwood from  $n = 98$ . Standard error of parameter estimates are shown in parentheses (all variables significant at  $p < 0.01$ ). The standard deviation of model residuals ( $\sigma$ ) is used to generate stochastic variation in model estimates. Parameters are for Eq. (3).

Parameter	Sugar maple	Ironwood
$\beta_6$	-1.679 (0.080)	-1.947 (0.119)
$\beta_7$	-0.571 (0.055)	-0.390 (0.068)
$\beta_8$	0.461 (0.035)	0.353 (0.031)
$\beta_9$	-0.076 (0.007)	-0.030 (0.011)
$\sigma$	0.211	0.238

### Appendix C. Parameter estimates for models to estimate probability that a tree is 'advanced regeneration'

The model for ironwood was derived from  $n = 139$  harvested saplings and for sugar maple from  $n = 165$ . Standard error of parameter estimates are shown in parentheses (all variables significant at  $p < 0.01$ ). Parameters are for Eq. (4).

Parameter	Ironwood	Sugar maple
$\beta_{10}$	4.986 (1.516)	-1.074 (0.733)
$\beta_{11}$	1.688 (0.541)	1.908 (0.391)
$\beta_{12}$	-0.784 (0.169)	-0.206 (0.060)

### Appendix D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.05.002.

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