Demographic response of a neotropical migrant songbird to forest management and climate change scenarios

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Abstract

Demographic models for species sensitive to human activities that are still relatively common are of particular interest to compare the relative influence of human land use and climate on population trends. Yet, data limitations often restrict our ability to interpret the numerical response of species to habitat alteration and climatic change adds to this challenge. In this study, we used habitat-specific demographic information from an individually-marked population of Ovenbird (Seiurus aurocapilla) and a forest timber supply model to project population trends over an 80-year horizon. We modelled changes in Ovenbird abundance, productivity, and population growth rate as a function of harvesting scenarios (no harvest, forestry-as-usual, and increased [10% or 20%] harvesting intensity) and projected impacts of climate change (0%, 10%, and 50% reductions in population size over the 80-year period), as well as contrasting assumptions about population dynamics (i.e. open vs. closed population). Among the many effects of climate change, it has been hypothesized that reductions in annual snow cover will occur, causing deeper and more frequent frost penetration into the soil and, in turn, a reduction in invertebrate (food) abundance during the following breeding season. Our models suggest that the study area currently is a demographic sink (k = 0.920) for Ovenbirds, although some habitat types still act as demographic sources. Over the first 7 years, a large decline in abundance of territorial males /C24% is projected, unless population levels are maintained through immigration. Interestingly, when we allowed for immigration from outside the study area, population growth rate remained <1 because a larger proportion of the population occupied habitat types acting as sinks. Over an 80-year period, the climate change scenarios we simulated were more likely to have negative impacts (5–49%) than forestry activities, whether we applied the current management plan or more intensive harvesting scenarios. To our knowledge, this study used some of the most detailed habitat-specific demographic information available for a North American forest songbird to model the relative influence of land use, climate, and population dynamics on population trends. Future studies should examine the possibility of synergistic effects between harvesting and climate change, to model their influence on Ovenbird or other species foraging on litter invertebrates.

1. Introduction

Forest ecosystems host a disproportionate amount of the world’s biodiversity (Gibson et al., 2011; Lindenmayer et al., 2012). It is important to understand the effects of human activities on these ecosystems and take actions to mitigate negative effects. Even though the numerical response of various taxa to management of forest ecosystems has been well documented (Fuller and Harrison, 2005; Edman et al., 2008; Vanderwel et al., 2009; Work et al., 2010), many authors have stressed the need for long-term demographic studies to fully understand the effects of forestry and other anthropogenic disturbances on population dynamics. Long-term monitoring of species abundance can be used to estimate population growth rates (Morris and Doak, 2002; MacKenzie et al., 2003), but this approach does not allow the identification of demographic processes having the greatest influence on observed patterns. With the exception of game species, most studies that have modelled the demographic response of wildlife to human land use have focused on species at risk (Morris and Doak, 2002; Ralls et al., 2002; but see Ball et al., 2003). These studies provide insights for management, but are often constrained by small sample size and rarely document the
mechanisms underlying population declines, which may differ (e.g. Allee effect; Stephens et al., 1999) from those acting on population dynamics when a species is not yet at risk (Beissinger and Westphal, 1998; Reed et al., 2002; Gilroy et al., 2012). Thus, it is important to also model the demographic response of species sensitive to human land use, yet still relatively common, i.e. focal species (Lambeck, 1997; e.g. Lindenmayer et al., 2000; Wintle et al., 2005). This “proactive” approach allows the development of adaptive management frameworks (e.g. Dzus et al., 2009) aiming to prevent sensitive species from becoming at risk (Abbitt et al., 2000).

In North America, many forestry companies have implemented sustainable forest management plans in an attempt to conserve biodiversity. For example, the extent and configuration of cutblocks and mixed-species plantations are increasingly focused on emulating natural disturbances (Crow and Perera, 2004; Long, 2009; Kuuluvainen and Grenfell, 2012). However, important issues have been raised (e.g. Klenk et al., 2008), including the fact that harvesting tends to differ from natural disturbances in its occurrence, extent, severity, and synchronicity across the landscape (Bergeron et al., 2002; Angers et al., 2005). Forestry activities tend to benefit species associated with early-seral forest and many of them are threatened in regions without active logging (Askins, 2001; Schlossberg et al., 2010; Sheehan et al., 2014). However, management of even-aged stands through clearcutting and plantation silviculture reduces the area of suitable habitat for species associated with late-seral stages (Barrientos, 2010; Mackay et al., 2014), whereas partial harvest systems in deciduous stands may decrease habitat quality for some taxa (Edman et al., 2008; Vanderwel et al., 2009; Work et al., 2010) owing to a gradual loss of old forest characteristics and simplification of vertical structure (Angers et al., 2005).

In addition to forest harvesting, there is growing concern about the effects of climate change on wildlife populations (Burrows et al., 2011; Davey et al. 2012; Reichert et al., 2012). In the northern hardwood forest of North America, complex interactions among abiotic factors are anticipated to alter the structure of species assemblages (Rodenhouse et al., 2008, 2009; Groffman et al., 2012). For example, long-term monitoring at Hubbard Brook Experimental Forest in north-central New Hampshire and recent climatic models suggest that snow cover events (i.e. number of times that the snowpack forms and dissipates during the year) will increase substantially (14–40%) by 2100, with a 20–79 day decrease in the number of snow-covered days owing to warmer temperatures (Campbell et al., 2010). These projections, along with the negative effects of experimental reduction in snow cover on abundance and richness of litter arthropods the following spring (Templier et al., 2012), suggest a mechanism by which ground-foraging birds feeding on invertebrates such as the Ovenbird may be affected by climate change (Groffman et al., 2012).

The Ovenbird (Seiurus aurocapilla) is considered to be one of the vertebrate species most sensitive to habitat alteration in the northern hardwood forest (Vanderwel et al., 2007, 2009). Declines in density or even local extinctions have been documented owing to intensive partial harvest treatments such as shelterwood harvesting (50–70% of tree removal; Vanderwel et al., 2009). When harvesting is less intensive (e.g. 30–40% tree removal through selection harvesting), reductions in Ovenbird density and productivity per unit area tend to be proportional to the wood volume removed (Pérot and Villard, 2009; Haché et al., 2013a; but see Morris et al., 2013). Nonetheless, this ground-foraging songbird remains regionally common (Pombidou et al., 2011), making it easier to develop demographic models and project future trends under alternative forest management scenarios (e.g. Larson et al., 2004). Depending on greenhouse gas emission scenarios, the bioclimatic models of Rodenhouse et al. (2008) projected that Ovenbird incidence in the Breeding Bird Survey (i.e. proportion of years per decade with species presence along a BBS route [Sauer et al., 2001], averaged for 1233 routes) would be 7.2–45.6% lower by the end of the century. Yet, very small differences in occurrence were projected (0% to –1.5%), suggesting that by the end of the century, the species would occupy the same area, but at lower densities. Similar patterns are projected for other ground-foraging species and neotropical migrants (Rodenhouse et al., 2008). Understanding how different land use and climatic scenarios will influence focal populations in intensively managed forest landscapes is critical to determine the relative importance of alternative threats and adjust conservation/management plans accordingly (e.g. Harris et al., 2014; Virkkala et al., 2014).

The objective of this study was to evaluate the effects of different forest management scenarios and climate change projections on a breeding population of Ovenbirds in northwestern New Brunswick, Canada. We combined empirical data on the demographic response of this species to habitat alteration (Haché and Villard, 2010; Haché et al., 2013a; Haché et al., 2014a; Vernouillet et al., 2014), projected timber yields from a forest timber supply model developed by J.D. Irving, Limited (Black Brook District), and anticipated impacts of climate change on our focal species to model the number of territorial males and young produced, as well as population growth rate ($\lambda$) over an 80-year period (2012–2091). We compared the status of a regional Ovenbird population over the projected period according to the current forest timber supply model (forestry-as-usual, hereafter FAU), reductions (10% and 20%) in the ratio of selection harvesting to shelterwood (i.e. larger areas managed through shelterwood), and a no-harvest scenario. These projections were combined with three scenarios of climatic change on breeding habitat quality: (1) no effect; (2) 10% reduction; and (3) 50% reduction in habitat quality by 2091 (after Rodenhouse et al., 2008). We considered changes in the density of breeding males and number of young produced to be proportionate to changes in habitat quality associated with climate change. This assumption was based on the documented response of Ovenbirds to the alteration of their habitat through selection harvesting (Haché et al., 2013a).

Source-sink dynamics, where demographic sources ($\lambda > 1$) maintain populations in demographic sinks ($\lambda < 1$), have been reported or at least suspected in many bird species (Pulliam, 1996; Rodenhouse et al., 1997; Murphy, 2001; Tittler et al., 2006). However, the spatial scale at which such population dynamics take place remains largely unknown (reviewed by Haché et al., 2014b). We considered two scenarios with respect to population dynamics. Specifically, we modelled Ovenbird population size: (1) irrespective of habitat-specific population growth rate, assuming that territory vacancies would be filled by birds from demographic sources outside the study area (i.e. open breeding population); and (2) considering intrinsic change in population size as a function of population growth rate in the absence of emigration or immigration (i.e. closed breeding population). Support for a closed population comes from stable isotope analyses indicating that most individuals recruited in individually-marked subpopulations in the study area had probably fledged locally (i.e. within the Black Brook District; Haché et al., 2014b).

2. Methods

2.1. Study area

The study was conducted in the Black Brook District, northwestern New Brunswick, Canada (47°23′N, 67°40′W). The land base covers 2000 km$^2$ and is privately owned by J.D. Irving, Limited.
Black Brook is one of the most intensively-managed forests in eastern North America (Montigny and MacLean, 2005). It is composed of deciduous stands (25% of total area; sugar maple [Acer saccharum], yellow birch [Betula alleghaniensis], and American beech [Fagus grandifolia]), coniferous stands (20%; black spruce [Picea mariana], white spruce [Picea glauca], and balsam fir [Abies balsamea]), mixedwood stands (18%), and conifer plantations (37%; see Etheridge et al., 2005 for details).

For 30 years, J.D. Irving, Limited has managed deciduous stands and deciduous-dominated mixedwood stands using selection harvest treatments, single-tree selection harvesting being the most widely used. This treatment typically removes 30–40% of the basal area (cross-sectional area at breast height [1.35 m] of all stems with a diameter > 10 cm) every 20–25 years. The creation of skid trails (5 m wide) accounts for ca. 20% of the basal area removed and the extra 10–20% is harvested from the residual forest between skid trails. Other treatments of similar intensity resulting in different configurations of residual trees such as strip and patch cuts (i.e. group selection) and pre-commercial thinning are applied sporadically. Alternatively, shelterwood harvesting removes 50–70% of the basal area and is applied to improve growing stock of deciduous and deciduous-dominated mixedwood stands and reduce the prevalence of American beech which is severely affected by beech bark disease. A second entry to remove the remaining commercial trees occurs when the deciduous regeneration is well established (ca. 25 years). Approximately 15 years after the second entry, improved stands are thereafter managed through a selection harvesting regime or another shelterwood treatment can be applied earlier if further improvement is required.

Since 1957, the company has focused largely on regeneration spruce species because they are less affected by eastern spruce budworm (Choristoneura fumiferana) than balsam fir, which otherwise would have predominated. The species most often planted were white and black spruce and, more recently, red and Norway spruce (Picea rubens: Picea abies) and white pine (Pinus strobus) are also being planted as species mixtures. Conifer plantations are generally harvested when they reach 40–50 years (G. Adams, J.D. Irving, Limited, pers. comm.). Naturally-regenerated conifer forests, dominated by black spruce and balsam fir, represent a small percentage of the district in long-range planning and are associated with riparian buffer strips, reserves, and lower productivity sites (G. Adams, J.D. Irving, Limited, pers. comm.).

2.2. Ecology and habitat-specific demography of the Ovenbird

The Ovenbird is a neotropical migratory songbird that reaches its highest density and productivity per unit area in mature deciduous and deciduous-dominated mixedwood stands with a relatively closed canopy and sparse understory (Pérot and Villard, 2009; Porneluzzi et al., 2011). It is a ground-nesting species foraging almost exclusively on litter invertebrates (Holmes and Robinson, 1988) and consuming prey proportional to their availability (Stenger, 1958).

Every year from 2006 to 2011, we monitored the demographic response of the Ovenbird to selection harvesting in five pairs of 25-ha study plots, including five treated plots and five controls. Specifically, we measured density, productivity per unit area, per capita productivity (Haché et al., 2013a), recruitment (Haché and Villard, 2010), and apparent survival of juveniles (Haché et al., 2014a) and adults (Vernouillet et al., 2014) during the first five years following a first entry selection cut, except juvenile survival (until day 14), which was measured during the fourth and fifth years post-harvest (Table 1). Reductions in density, productivity per unit area, and food abundance, and an increase in territory size were observed following selection harvesting, but these effects were no longer significant by the fifth year post-harvest (Haché et al., 2013a). Selection harvesting had no significant effect on apparent adult survival rate (Haché and Villard, 2010; Vernouillet et al., 2014), juvenile survival rate (Haché et al., 2014a), or per capita productivity (Haché et al., 2013a; see also Leblanc et al., 2011). Unfortunately, we could not determine the effects of 2nd or 3rd entry selection cuts as these treatments had yet to be applied in the study area or elsewhere in the region. In 2010, we also measured the density and productivity per unit area of Ovenbirds in recent (first year post-harvest; n = 3) and old shelterwood (16–20 years post-harvest; n = 3; 25-ha study plots) using the same protocol as Haché et al. (2013a). No individuals were detected during four surveys in recent shelterwood, while density (based on eight spot mapping visits) and productivity per unit area in old shelterwood were respectively 41%, and 66% lower than in recent selection cuts (i.e. mean values from 1 to 5 years post-harvest). Results from point count and spot mapping data suggest that Ovenbirds can also defend territories in mature conifer-dominated mixedwood and conifer stands and plantations (Guénette and Villard, 2005; MacKay et al., 2014). However, the abundance of territorial males varies as a function of the number of years following a clearcut. Thus, we reported density estimates for conifer stands in three categories (<10, 11–25, and >25 year since harvesting; see Appendix A for details).

2.3. Modelling approach

2.3.1. Step 1. Demographic model

We used the demographic information provided by the studies listed above to generate habitat-specific estimates of density, number of young produced, and population growth rate ($\lambda$; Table 1). Habitat-specific $\lambda$ was calculated as:

$$\lambda = \phi_A + (\psi \times (\phi_F \times \phi_A))$$

where $\phi_A$ is the apparent survival rate of adults, $\psi$ is the per capita productivity, and $\phi_F$ represents postfledging survival rate at day 14. We made the following assumptions: (1) survival rate of juveniles was the same as that of adults after day 14 (little mortality has been reported between day 14 and independence; Streby and Andersen, 2012, 2013; but see Dybala et al., 2013); (2) apparent survival of adults defending a territory in plantations and shelterwood was equal to that observed in recent selection cuts, until post-treatment density and productivity per unit area reached those of untreated deciduous stands; then, apparent adult survival was assumed to be the same as in untreated deciduous stands; and (3) individuals defending territories in conifer stands and spruce plantations do not produce young (see also Porneluzzi et al., 2011).

The sex ratio in adult songbirds is generally male-biased (e.g. 1.14:0.86, Donald, 2007; see also Amrhein et al., 2012). High pairing success has been reported in untreated deciduous stands and recent selection cuts (Bourque and Villard, 2001; Haché et al., 2013a). However, a male-biased sex ratio is expected in recent shelterwood and conifer stands owing to low habitat quality. This would lower the breeding success of males occupying these stands, or reduce it to zero (Table 1).

In post-harvest years for which we did not have empirical data, density and productivity per unit area in deciduous stands were extrapolated assuming a linear increase with the number of years post-harvest, while per capita productivity was assumed to remain constant (e.g. Haché et al., 2013a). Density and productivity per unit area in these stands were assumed to remain constant once they had reached the same values as in untreated stands (Table 1). Values were averaged over 5-year periods to coincide with the temporal resolution provided by the timber supply model used by the forestry company (see Step 2).
2.3.2. Step 2. Forest timber supply model

J.D. Irving. Limited generated its timber supply model for the Black Brook District using Woodstock, which is a linear programming optimization software that determines the optimum treatment schedule to maximize a value across a range of management constraints (Remsoft Inc., 1996). The simulation is based on an area file which is an aspatial representation of the study landbase that has been subdivided into landscape themes relative to management objectives. For example, attributes such as stand type, operability constraints, and ecoregion have been integrated. Individual stands were aggregated into strata based on similar age and stand characteristics. Management interventions included were selection harvest, shelterwood harvest, patch harvest, final harvest/tree planting, and precommercial and commercial thinning. Operability limits for these actions were based on J.D. Irving, Limited operation standards, along with the study landbase that has been subdivided into landscape themes based on an area file which is an aspatial representation of the study landbase that has been subdivided into landscape themes relative to management objectives. For example, attributes such as stand type, operability constraints, and ecoregion have been integrated. Individual stands were aggregated into strata based on similar age and stand characteristics. Management interventions included were selection harvest, shelterwood harvest, patch harvest, final harvest/tree planting, and precommercial and commercial thinning. Operability limits for these actions were based on J.D. Irving, Limited operation standards, along with the study landbase that has been subdivided into landscape themes.

2.3.3. Step 3. Forest management scenarios

First, we used the J.D. Irving, Limited forest timber supply model for the Black Brook district (i.e. forestry-as-usual; FAU) to model the Ovenbird population (abundance of territorial males, number of young produced, and population growth rate) over an 80-year period (2012–2091). We explored three additional management scenarios: (1) no harvesting (i.e. assuming the entire area is comprised of mature stands); (2) 10%; and (3) 20% decrease in the selection to shelterwood harvesting ratio relative to the FAU scenario (i.e. converting 10% and 20% of the area managed through selection harvesting into shelterwood throughout the 80-year period). The “no harvesting model” was meant to provide ecological benchmark values, whereas the two other scenarios quantified the effects of more intensive harvesting on the Ovenbird population. The no-harvest scenario may appear simplistic because it does not account for the effects of insect outbreaks or dieback on even-aged conifer stands. Such disturbances would create mosaics of stands of different age across the study area. Yet, this scenario is realistic for uneven-aged deciduous stands which are the most important for breeding Ovenbirds. Hence, we felt that predictions derived from this ecological benchmark would be useful to compare to those from the different harvesting and climate scenarios.

Because it does not account for natural disturbances, the timber supply model might underestimate the area harvested through salvage logging (see Meehl and Tebaldi, 2004 for anticipated increase in drought events). Salvage logging and stands with high tree mortality that cannot be salvaged are both expected to have similar effects as shelterwood harvesting on Ovenbird populations.

Table 1

<table>
<thead>
<tr>
<th>Year</th>
<th>Density (ha)</th>
<th>Productivity (ha)</th>
<th>Per capita Productivity (ha)</th>
<th>Survival Adult</th>
<th>Survival Juvenile</th>
<th>( \lambda )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Untreated deciduous</td>
<td>12.0 (±0.6)</td>
<td>21.5 (±1.7)</td>
<td>0.86 (±0.05)</td>
<td>0.73 (±0.02)</td>
<td>0.33</td>
<td>1.01</td>
</tr>
<tr>
<td>Select. harv. 1–5</td>
<td>8.8 (±0.4)</td>
<td>15.2 (±1.5)</td>
<td>0.81 (±0.06)</td>
<td>0.67 (±0.03)</td>
<td>0.30</td>
<td>0.92</td>
</tr>
<tr>
<td>&gt;5</td>
<td>12.0</td>
<td>21.5</td>
<td>0.86</td>
<td>0.73</td>
<td>0.33</td>
<td>1.01</td>
</tr>
<tr>
<td>Shelt. harv. 1–5</td>
<td>0.7</td>
<td>0.6</td>
<td>0.46</td>
<td>0.67</td>
<td>0.30</td>
<td>0.81</td>
</tr>
<tr>
<td>6–10</td>
<td>2.4</td>
<td>2.1</td>
<td>0.46</td>
<td>0.67</td>
<td>0.30</td>
<td>0.81</td>
</tr>
<tr>
<td>11–15</td>
<td>4.2</td>
<td>3.1</td>
<td>0.46</td>
<td>0.67</td>
<td>0.30</td>
<td>0.81</td>
</tr>
<tr>
<td>16–20b</td>
<td>5.9</td>
<td>5.1</td>
<td>0.46</td>
<td>0.67</td>
<td>0.30</td>
<td>0.81</td>
</tr>
<tr>
<td>21–25</td>
<td>7.6</td>
<td>6.6</td>
<td>0.46</td>
<td>0.67</td>
<td>0.30</td>
<td>0.81</td>
</tr>
<tr>
<td>&gt;25</td>
<td>9.4</td>
<td>16.2</td>
<td>0.81</td>
<td>0.67</td>
<td>0.30</td>
<td>0.92</td>
</tr>
<tr>
<td>Conifers 0–10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>11–25</td>
<td>0.7 (±0.3)</td>
<td>0</td>
<td>0</td>
<td>0.67</td>
<td>0.30</td>
<td>0.67</td>
</tr>
<tr>
<td>&gt;25</td>
<td>6.0</td>
<td>0</td>
<td>0</td>
<td>0.67</td>
<td>0.30</td>
<td>0.67</td>
</tr>
</tbody>
</table>

- a We estimated juvenile survival by multiplying postfledging survival (0.46; see Haché et al., 2014a for details) by adult survival.
- b We only had empirical data from the first and 16th years post-harvest. Values shown represent predicted means for the 5-year periods.
- c Density estimates from point count data were calibrated (see Appendix A) and we present mean predicted values from two datasets (Guénette and Villard, 2005; Mackay et al., 2014).
Hence, to some extent, the two more intensive harvesting scenarios can be used to mimic potential responses of forestry operations and, ultimately, Ovenbird populations, to natural disturbances. The main natural disturbances occurring in the study area are insect outbreaks and fires, but they are highly controlled and rarely influence the dynamics of deciduous stands (G. Adams, J.D. Irving, Limited, pers. comm.). Stand-replacing windthrow events tend to occur every 1000 years in forests of the Northeast (Seymour et al., 2002) and the analysis of an old growth forest landscape (i.e. mosaic of deciduous, mixedwood, and coniferous stands) of northern Maine indicated a canopy disturbance rate of 9.6% per decade (Fraver et al., 2009). However, disturbance agents such as drought and pathogens can interact with abiotic and biotic factors and the resulting dieback can create spatial heterogeneity and influence species composition (Hughes, 1960; Amos-Binks et al., 2010). Some mixedwood stands might also represent a natural transition following such natural disturbances (Amos-Binks et al., 2010). In the timber supply model, natural disturbances are not projected, except for natural senescence beyond a specific stand age. However, to some extent, harvest treatments are allocated to mimic natural disturbances in terms of area and volume harvested (Etheridge et al., 2006). Hence, landscape stochasticity (e.g. Wintle et al., 2005; Chisholm and Wintle, 2007) was not integrated into our models.

2.3.4. Step 4. Climate scenarios

The four forest management scenarios above assume no effect of climate change on our focal species. This is a realistic assumption as litter invertebrates might adapt, or the invertebrate community might change in response to climate change, maintaining similar overall abundance and biomass. Changes in prey community composition might have limited consequences on generalist insectivores such as the Ovenbird (Stenger, 1958). Alternatively, potential negative effects might be compensated by a longer growing season providing opportunities for additional breeding attempts or even double brooding, which has been documented in species such as a result of climate change (i.e. lower habitat quality in this scenario. For the Closed population scenario, Ovenbird population was only influenced by variation in local habitat quality in this scenario. For the Closed population scenario, abundance of territorial males and number of young produced as a function of two population dynamics scenarios. Projections were first generated irrespective of population growth rate (Open), assuming that surpluses or deficits of territorial males were compensated through immigration and emigration (i.e. large-scale source-sink dynamics; Tittler et al., 2006, 2009). The second scenario assumed that source-sink dynamics occurred over a spatial scale corresponding to the size of the study area and that population dynamics were only influenced by local population growth rate (Closed).

For the Open population scenario, density of territorial males and young produced per unit area (productivity) for each stand type and number of years post-harvest (Table 1) were multiplied by the area of each stand type. This was conducted for each year of the simulation period (using 5-year averages). Hence, the Ovenbird population was only influenced by variation in local habitat quality in this scenario. For the Closed population scenario, abundance of territorial males and number of young produced in year, were adjusted according to the population growth rate estimated in year,−1. We assumed that deciduous and deciduous-dominated mixedwood stands were saturated with Ovenbirds when they reached habitat-specific density estimates reported in Table 1. However, conifer stands were allowed to support higher densities to mimic crowding effects following years where > 1 and instances where population size in year, would support higher densities than at the beginning of the simulation. If individuals were added to the population in year, i.e. > 1 in year,−1, new individuals were assigned to the lowest quality habitat where males would be defending a territory (e.g. Shelterwood harvesting 11–15). In this example, new individuals were added to this stand type until the abundance (and corresponding number of young produced) reached the maximum value for this stand type (i.e. maximum abundance = 4.2 males × area; Table 1). The remaining individuals would then be added to the next more suitable habitat that would not be supporting territorial males in year,−1 (e.g. Shelterwood harvesting 6–10). Alternatively, if individuals had to be removed from the population in year, i.e. < 1 in year,−1, those defending a territory in the lowest quality habitat were removed. Using the same example as above, if Shelterwood harvesting 6–10 was the lowest quality habitat supporting territorial males territory size, density, and productivity per unit area are positively correlated with the abundance of litter invertebrates (Haché et al., 2013a). To model effects of lower food abundance on Ovenbirds, we decreased habitat-specific density and productivity per unit area by 0.7% (low) and 3.3% (high) every 5 years for the duration of the simulation period to obtain 10% and 50% reductions, respectively, by 2091. In these models, we assumed no effect of reduced food abundance on per capita productivity (as per Haché et al., 2013a; but see Seagle and Sturtevant, 2005). These two scenarios are consistent with projected declines in Ovenbird incidence in northeastern United States according to different emission scenarios and climatic models (Rodenhouse et al., 2008).
in years, individuals were first removed there and if more individuals had to be removed they would be selected among those in the second lowest quality habitat (Shelterwood harvesting 11–15). This process reflects the site-dependent regulation of population proposed by Rodenhouse et al. (1997). Algorithms were built to follow an automated process using Microsoft Excel 2010.

A total of 9 scenarios (i.e., 4 forest management outcomes, 3 climate change-related habitat alteration levels, and 2 population dynamics) were combined in 15, 15, and 5 models estimating abundance, number of young produced, and population growth rate, respectively, to determine the relative importance of different harvesting, climatic, and population dynamic scenarios on the status of the Ovenbird in Black Brook (see Table 2 for the scenario considered for each model). For population growth rate, we are only presenting results from the “no climate” models because the best information currently available suggests that the effects of a 10% or 50% reduction in habitat quality owing to climate change on population dynamics (e.g., per capita productivity and survival) would not influence population growth rate (Haché et al., 2013a), but would decrease the carrying capacity of the study area. Results are presented for the first year of the study (2012) and as mean annual values per 5-year period thereafter (2012–2016 = 2014, 2017–2021 = 2019, etc.).

3. Results

From 2012 to 2089, the projected area of deciduous forest remained relatively constant, at 38–46% of the total forested area (64,330–85,360 ha; Fig. 1). The area of untreated deciduous forest was projected to decline by 14,000 ha by 2024, but it followed a similar pattern in subsequent years. By the 10th year, the area managed through selection harvesting was projected to increase by ca. 8000 ha and remain relatively constant thereafter, while shelterwood harvesting remained at low levels throughout the projected period (0–4.8% of the forest land base, respectively). Lastly, the area covered by conifer stands was projected to vary between 56% and 62% of the total area. Areas for each treatment as a function of the number of years post-harvest under the forestry-as-usual (FAU) scenario are reported in Appendix B.

According to the FAU scenario without the effects of climate change, 46,070 territorial males would be present each year during the 2012–2016 period and values were projected to remain relatively constant throughout the projected period (47,000 ± 470 males; mean ± SE). Male abundance was projected to be 38,840 and 21,580, respectively, by 2089, under scenarios of low (−10%) and high (−50%) effects of climate change (i.e., lower habitat quality), respectively (Fig. 2). Under the FAU scenario without the effects of climate change, male abundance in 2012 was 25% lower than projected from the no harvest scenario without effects of climate change (61,870 males; Fig. 2A). By 2089, male abundance was higher under the FAU scenario without effects of climate change (43,160 males) and with a 10% reduction in habitat quality (38,840 males) than under the no harvest scenario with a 50% reduction in habitat quality (30,940 males).

Higher harvesting intensity (i.e., reducing the selection: shelterwood ratio by 10 and 20%) had less of an effect on the abundance of territorial males than the reduction in habitat quality caused by climate change. Indeed, compared to the FAU scenario, 1092 (±22) fewer males on average per period (−2.0% to −2.9%) were predicted if there was a 10% increase in harvesting intensity, while this difference was 2190 (±43) males for a 20% increase in harvesting intensity (Fig. 2B).

According to the FAU scenario without effects of climate change, the number of young produced also remained relatively

<table>
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<th>Population dynamics</th>
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Fig. 1. Area for each stand category used to model the future status of Ovenbird in Black Brook from 2012 to 2089. Predictions are from the J.D. Irving, Limited forest timber supply model.
constant throughout the projected period, at 59,900 (±920), on average, per period (Fig. 3). Interestingly, based on this scenario, productivity would currently (2012–2016) be only 6% lower than values projected from the no harvest scenario without effects of climate change (Fig. 3A). By 2089, the difference between the number of young produced under the FAU with a 10% reduction in habitat quality and a 20% increase in harvesting intensity was only 102 young (Fig. 3B). Differences between the number of young produced under the FAU scenario and a 10% increase in harvesting intensity was on average 2520 (±176), whereas this difference was, on average, 5040 (±352) young per period based on a 20% increase in harvesting intensity.
Based on the FAU harvesting scenario without effects of climate change, the study area acted as a demographic sink throughout the projected period (0.906 ± 0.009; Fig. 4). Mean population growth rate throughout the projected period was only slightly lower for 10% and 20% increases in harvesting intensity, with $\lambda = 0.901 \pm 0.002$ and 0.896 ± 0.003, respectively. The lowest $\lambda$ (0.869) was under the no harvest scenario (Appendix C). So far, the numbers of territorial males and young produced were estimated irrespective of population growth rate and assuming that population size was maintained by immigration and emigration. If population size was not maintained by immigration, a decline in abundance was projected to occur between 2012 and 2019 (−25%) and it would stay relatively constant thereafter (mean = 34,000 ± 560; Fig. 2C). This projected change in abundance would coincide with an increase in population growth rate by 0.071 during this period and have a mean value of 0.999 (±0.001) in subsequent periods (Fig. 4). Under a scenario assuming no immigration and a 50% reduction in habitat quality resulting from climate change, 14,750 males are projected to defend territories in the study area by the 2089 period, which is 32% less than the predicted value under the same conditions, but assuming that population size is maintained through immigration (i.e. without considering population growth rate; Fig. 2C). Interestingly, under the FAU scenario, the predicted number of young produced was identical whether population size was maintained by immigration or not.

4. Discussion

Our simulations reveal two important findings: (1) the projected effects of climate change on population size and productivity are expected to be greater, over the long term, than those of harvesting, but (2) model projections are very sensitive to population dynamics. When assuming that populations from outside the study area did not supply recruits (FAU scenario and no effect of climate change), the study area initially acted as a demographic sink ($\lambda = 0.920$), population size decreased by 25% by the end of the decade (2019) and it remained relatively stable thereafter. The study area currently supports ca. 25% fewer male Ovenbirds than it would if the entire study area was comprised of mature unharvested stands. However, the current landscape produces only ca. 6% fewer young.

Rodenhause et al. (2008) pointed out the important uncertainty that surrounds species response to climate change (see also Kujala et al., 2013). Future studies investigating the effects of varying weather conditions on the biomass and species composition of litter invertebrates would be needed to better predict the causal relationships between climate change and the status of ground-foraging species like the Ovenbird (e.g. White, 2008; Boggs and Inouye, 2012). The potential effects of regional differences in the amount of precipitation and elevation, and how they may influence snow cover and, in turn, litter invertebrates should be further evaluated. It is also exceedingly difficult to predict interactions among natural disturbances, human land use, invasive species, pathogens, or insect outbreaks and climate change. Thus, changes in stand composition and growth rate are difficult to anticipate (reviewed by Groffman et al., 2012; Selwood et al., 2015; see also Jarzyna et al., 2015). Although we do not know what tree species will dominate deciduous stands in Black Brook by 2089, the timber supply model was built to maintain a similar proportion of conifer and deciduous stands throughout the simulation period. The Ovenbird breeds in a broad range of deciduous and mixedwood stand types (Porneluzzi et al., 2011), suggesting that it is tolerant to tree species composition. The effects of climate change are therefore more likely to be associated with habitat degradation than with habitat loss due to shifts in stand composition in our study area (see also Rodenhause et al., 2008). Even under a low greenhouse gas emission scenario (10% reduction in habitat quality), climate change was projected to have more important effects on the number of male Ovenbirds in Black Brook than the high-intensity harvesting scenario (Fig. 2b). However, we cannot rule out the possibility that our scenarios without climate change effects are realistic given the uncertainty about species responses to climate change.

Although the Ovenbird population of the study area as a whole is likely acting as a demographic sink, our simulations suggest that source-sink dynamics are taking place within the study area. Untreated deciduous stands and selection cuts >5 years post-harvest are projected to act as demographic sources, whereas all other stand types would act as demographic sinks (Table 1). The low population growth rate estimated for our study area is mostly attributable to the large proportion of conifer stands (up to 60%). This proportion is projected to remain stable throughout the modelled period (57–62%). Although Ovenbirds are absent or present at low density in conifer stands, they would still host ca. 24% of territorial males (24–32% over the projected period), assuming a constant immigration rate. Under the no harvest scenario, where the study area is considered to be comprised only of mature stands, an increasing proportion of individuals were projected to defend territories in conifer stands (40%). This result reflects the fact that mature conifer stands support higher densities of Ovenbirds, in spite of their low population growth rate, than the younger, managed conifer stands that would be present in all other scenarios. Hence, conifer stands have a greater impact on the overall population growth rate in this scenario because they support more individuals. This also explains the lower population growth rate predicted under this scenario even though deciduous stands are expected to be more productive for Ovenbirds than in any other scenario (Fig. 4; Appendix C). However, in the absence of immigration, the percentage of breeding Ovenbirds in coniferous stands is projected to be <5% by 2019. This would increase population growth rate (i.e. higher proportion of individuals holding territories in demographic sources), where local recruitment would start compensating for adult mortality.

Considering the importance of the projected decline over a relatively short period under the FAU scenario, and the fact that the study area has been intensively managed for decades, population dynamics of Ovenbirds in our study area are probably influenced by immigration. Indeed, in the absence of immigration, the projected decline should have already taken place and local recruitment would be compensating for adult mortality. Future studies using a combination of intrinsic markers and tracking technologies are thus needed to determine the extent of natal dispersal movements. In the meantime, it would be important to monitor Ovenbird population trends within ca. 200 km around the study area to determine whether this region can act as a demographic source (Haché et al., 2014b; see also Lloyd et al., 2005; Bonnot et al., 2011).

An estimated 1–3 billion landbirds breed in the Canadian boreal forest (Blancher, 2003). Between 616,000 and 2,090,000 passerine nests are estimated to be lost to industrial forestry operations each year in Canada (Hobson et al., 2013). This translates into an annual loss of 564,000–1,330,000 potential recruits for Canadian bird populations (Hobson et al., 2013). Note that these numbers do not consider long-term negative effects of habitat loss and alteration caused by some silvicultural practices on reproductive success of many landbird species associated with mature forests. Thus, harvesting has important negative effects on forest bird assemblages. However, separate estimates for even-aged management (clearcuts) and partial harvest regimes for uneven-aged stands have not been produced. In northern hardwood stands, there is evidence that partial harvest treatments of moderate intensity (30–40% removal) could increase bird species diversity.
through the creation of early-seral habitat (Schlossberg et al., 2010; Haché et al., 2013b). Some mature forest specialists have lower abundances in early post-harvest years, but we are unaware of severe declines or local extinctions following such treatments in deciduous stands of North America (e.g. Vanderwel et al., 2009; Poulin et al., 2010; Haché et al., 2013b; Morris et al., 2013). However, the demographic response of mature forest birds to partial harvesting remains largely unknown (Hobson et al., 2013) and data currently available show contrasting responses among and within species (reviewed by Richmond et al., 2012). For example, although the Ovenbird is considered to be one of the most sensitive species to partial harvesting (Vanderwel et al., 2007, 2009), numerous lines of evidence from this and other studies (see 2.2. and Leblanc et al., 2011; but see Morris et al. 2013) suggest that it may be more tolerant to moderate alteration of its habitat than previously reported. The demographic response of the Ovenbird, combined with the creation of more suitable habitat for early-seral species, would be consistent with the intermediate disturbance hypothesis, which predicts a peak in species richness at intermediate levels of disturbance (Grime, 1973; Connell, 1978). Nonetheless, it would be unwise to assume that all mature forest songbirds are as tolerant to habitat alteration. For example, species such as the Brown Creeper (Certhia americana) and Olive-sided Flycatcher (Contopus cooperi) have a lower reproductive success in recent selection cuts or thinned plots (Robertson and Hutto, 2007; Poulin et al., 2010). Populations of these and ecologically-similar species should be closely monitored as forest management intensity increases.

The trend analyses reported in this study were based on the assumption that we could model population dynamics with some precision. Studies have provided contrasting estimates of $\lambda$ for Ovenbird populations. For example, in northern Wisconsin, Flaspohler et al. (2001) reported values of 1.11 and 1.18 for edge and interior habitats, respectively, whereas Leblanc et al. (2011) estimated $\lambda$ between 0.837 and 0.858 among four harvest treatments in deciduous stands from central Ontario (see also Podolsky et al., 2007). Many studies have reported that adult and juvenile survival were the most sensitive parameters used to estimate population growth rate (e.g. Schmutz et al., 1997; Flaspohler et al., 2001). Yet, to our knowledge, this is the first study modelling population dynamics of Ovenbirds based on apparent adult survival estimates specific to a study area. Owing to low return rates of birds banded as nestlings or juveniles (Greenwood and Harvey, 1982), survival during the first year (a.k.a. juvenile survival) remains largely unknown (Sillett and Holmes, 2002; Dybala et al., 2013). However, the combination of data on postfledging and adult survival rates provides the most realistic estimates of juvenile survival currently available for migratory bird species with large breeding ranges (Dybala et al., 2013; McKinnon-Louder et al., 2013). That being said, we recognize the uncertainty inherent to our modelling approach. For example, female-specific survival rates (e.g. Podolsky et al., 2007) and a better understanding of population dynamics in conifer stands and shelterwoods might yield slightly different population growth rates. In this study, we also assumed that the effects of selection harvesting on Ovenbird populations in subsequent entries would be similar to those reported following the first entry. Yet, more homogeneous stand structure and composition as well as a reduction in the density of large live trees (>39.1 cm) are expected after multiple entries (Angers et al., 2005) and the implications of such changes on breeding birds are unknown (e.g. Morris et al., 2013).

Ideally, population dynamics should be modelled throughout a species’ life cycle (Sillett and Holmes, 2002; Fafaby et al., 2013). We recognize that habitat loss/alteration and climate change also influence Ovenbirds on the wintering grounds and during migration. Conditions experienced by individuals during the nonbreeding season likely influence population dynamics on the breeding grounds over a spatial scale extending well beyond our study area, irrespective of breeding habitat quality. Hence, although we elected to focus on factors operating during the breeding season, nonbreeding habitat loss/alteration will have an additive effect.

Individual-based, spatially-explicit models would allow exploring effects of habitat loss vs. fragmentation on the breeding grounds (Wintle et al., 2005; Chisholm and Wintle, 2007). The Ovenbird has been shown to respond to landscape structure (Betts et al., 2006, 2007; Wallendorf et al., 2007; Villard and Haché, 2012) and, by the 15th year, the mean patch size of deciduous forest in Black Brook is projected to decrease by ca. 50% (Etheridge et al., 2006). Hence, landscape history (sensu Schrott et al., 2005) should be integrated in future models to better account for the complexity of forestry effects on our focal population. Nonetheless, to our knowledge, we used the most detailed habitat-specific demographic information available for a songbird breeding in an intensively managed forest of North America (see also Morris et al., 2013). Our simulations suggest that climate change will have more important effects on songbird populations breeding in the northern hardwood forest than forestry operations under the current forest management plan or more intensive scenarios. Although these findings should be interpreted with caution, they provide insight into future trends in bird populations and the opportunity to develop proactive conservation plans.

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Appendices A–C. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.10.002.

References


