Effects of alternative forest management on biomass and species diversity in the face of climate change in the northern Great Lakes region (USA)

Matthew J. Duveneck, Robert M. Scheller, and Mark A. White

Abstract: Northern Great Lakes forests represent an ecotone in the boreal–temperate transition zone and are expected to change dramatically with climate change. Managers are increasingly seeking adaptation strategies to manage these forests. We explored the efficacy of two alternative management scenarios compared with business-as-usual (BAU) management: expanding forest reserves meant to preserve forest identity and increase resistance, and modified silviculture meant to preserve forest function and increase adaptive capacity. Our study landscapes encompassed northeastern Minnesota and northern Lower Michigan, which are predicted to experience significant changes in a future climate and represent a gradient of latitude, forest type, and management. We used the LANDIS-II forest simulation model to simulate forest change under current climate, low emissions climate, and high emissions climate futures. Our results suggest that under a low emissions climate scenario, expanded reserves and modified silviculture strategies can be effective at increasing resistance by preserving forest composition, including legacy species (e.g., balsam fir (Abies balsamea (L.) Mill.)), and increasing adaptive capacity by maintaining or increasing aboveground biomass compared with BAU management. Under a high emissions climate scenario, the expanded reserve strategy was not effective at preserving legacy species; however, the modified silviculture strategy was effective at increasing aboveground biomass compared with BAU management. These results highlight alternative management options and limitations in the face of climate change.

Key words: adaptation, alternative silviculture, climate change, expanded reserves, forest management, forest simulation model, LANDIS-II, Michigan (USA), Minnesota (USA), resistance.

Introduction

There is interest in preserving boreal-temperate forest ecosystems as found in the northern Great Lakes region. In addition to being a “haven for biodiversity” (Bradshaw et al. 2009), these forests provide a large carbon sink (D’Amato et al. 2011), wood products for the timber industry (D’Amato et al. 2009), suitable wildlife habitat for numerous charismatic or endangered species (Heinselman 1996), and numerous recreational opportunities. Given the limits of a forest’s ability to naturally adapt to climate change (Iverson et al. 2008; Soja et al. 2007), natural resource managers are increasingly interested in novel techniques to enhance adaptive capacity, that is, the amount that a forest can change while providing the ecosystem services upon which we depend (Millar et al. 2007; Seidl et al. 2011; Spies et al. 2010). In addition, there is a growing acceptance that effective management must occur at a regional extent (Menz et al. 2013).
Designing for resistance with forest reserves

Creating or maintaining forest reserves along connected corridors may be considered a resistance strategy to provide disturbance refugia for vulnerable species (Millar et al. 2007). Current forest reserves such as the Boundary Waters Canoe Area Wilderness (BWCA) in northeastern Minnesota provide landscapes with limited human management and high connectivity (Heinselman 1996). Increased connectivity facilitates tree species migration in response to climate change (Iverson et al. 2004), and refugia have the potential to harbor genetic and species diversity (McLachlan et al. 2005). Compared with managed forests, unmanaged old-growth forests may provide more biomass storage, greater structural complexity, and higher volumes of standing dead and downed wood (Silver et al. 2013). To date, little research has addressed the role that forest reserves (i.e., forested areas without extractive harvest) may play in increasing connectivity and providing refugia in the face of climate change.

Under current best management practices, riparian corridors are generally protected from extractive activities at a limited distance from the high water mark. Riparian zones can limit erosion and sedimentation, increase shading thereby reducing stream temperatures, increase coarse woody debris, and increase fish and wildlife habitat (Lee et al. 2004). Riparian corridors also provide aquatic and terrestrial species with the ability to migrate easily to more suitable climate conditions (Rudnick et al. 2012). Expanding the width of these existing reserves will create larger areas of connected corridors with the potential for greater within-reserve heterogeneity.

Modified silviculture regimes to increase adaptive capacity

Altering existing silviculture practices to manage for climate change can be considered a strategy to increase adaptive capacity. Specific tactics can potentially increase structural (e.g., age) or compositional (e.g., species) diversity. Risk of a damaging forest pathogen associated with a single species or a single age cohort can be minimized by creating diverse stands, thereby reducing the risk (Walker et al. 1999). By supporting redundant functional species with different environmental tolerances, adaptive capacity is enhanced (Walker 1992). With so much uncertainty in climate change projections (Intergovernmental Panel on Climate Change [IPCC] 2007) and the resultant impacts on forests (Duveneck et al. 2014; Scheller and Mladenoff 2005; Xu et al. 2009), management can strategically allow forests to adapt to future conditions (Puettmann 2011). Specific silviculture systems for increasing adaptive capacity include extended rotation prescriptions (Silver et al. 2013), managing for asynchrony with patch harvesting, and planting future climate-suited species (Millar et al. 2007).

With favorable environmental conditions, productive forests are often managed in low-diversity stands, favoring competitive exclusion over complementarity. Under stressed conditions, however, complementarity may be favored over competitive exclusion, creating a positive correlation between diversity and productivity (Paquette and Messier 2011). Some evidence suggests (through simulation modeling) that an increasingly positive relationship between forest productivity and tree diversity will develop in the Great Lakes region under increasingly higher emissions scenarios and declining productivity (Duveneck et al. 2014). Managing for diversity may increase productivity that might otherwise decline under anticipated climate change.

In Minnesota, and presumably throughout the Great Lakes region, there is a trend toward decreased use of clearcuts, increased patch cutting, and increased rotation ages (D’Amato et al. 2009). Intermediate treatments (i.e., low- to moderate-intensity harvesting) have much different impacts on carbon cycling than large-scale clearcuts. With longer rotation ages, or less frequent harvests, more carbon is retained in a more stable pool of soil carbon (Aber et al. 1982). More frequent harvests result in more carbon being exported off site.

Managing forests for carbon sequestration

Current forests play a pivotal role in carbon sequestration and management (Jandl et al. 2007). Managers are increasingly interested in the trade-offs between the ability of forests to adapt to climate change and forests contribution to climate change mitigation through carbon sequestration (D’Amato et al. 2011; Steenberg et al. 2011). Both reserve expansion and altering current silviculture treatments have the potential to increase carbon storage while increasing the adaptive capacity to sequester more carbon by increasing structural and compositional diversity.

Our objectives were to assess the ability of alternative management scenarios to increase or maintain representative forest ecosystem services under climate change. Our assessment compared business-as-usual (BAU) management with two alternative management strategies in northeastern Minnesota and northern Lower Michigan as a simulation experiment relying on a spatially dynamic model. We assessed the trade-offs between resisting and adapting to climate change. Specifically, we addressed the following question. In the face of climate change, how might alternative management strategies affect future aboveground biomass, harvested timber, tree species diversity, and forest type?

Methods

Study area

We selected the northern Great Lakes region to study these questions as scientists predict large changes in the climate in the midcontinent (IPCC 2007) and the boreal–temperate forest transition zone within the region is especially vulnerable to environmental changes (Fischelli et al. 2013). This area represents 26 million hectares of mixed boreal–temperate forests in the northern Great Lakes region (Northern Institute of Applied Climate Science 2013). Within the region, we chose two landscapes, northeastern Minnesota and northern Lower Michigan, representing a gradient of latitude, forest type, and management (Fig. 1). Minnesota is cooler, centered in the boreal–temperate ecotone, and is more intensively managed. Michigan is in the temperate hardwood region and has a more diverse suite of tree species and forest types. Disturbance regimes, timber management, forest types, species composition, and climate change effects under BAU management are described previously for each landscape (Duveneck et al. 2014; Ravenscroft et al. 2010).
For the Minnesota landscape, we used previously estimated timber harvest regimes (Tables 1 and 2), fire and wind regimes (<0.6% area disturbed·year−1), initial communities, delineated ecoregions, and tree species parameters (Duveneck et al. 2014). Alternative management scenarios were meant to represent plausible futures as adjustments to BAU. For each management scenario, we assessed three climate scenarios: (i) current climate, (ii) low emissions climate future, and (iii) high emissions climate future. To compare our results between landscapes and prior research (Duveneck et al. 2014), we used as consistent an approach as possible to parameterize the scenarios. For all simulations, we used a 2 ha cell resolution and a 150-year time horizon starting at year 2000. The 16 198 and 25 436 km² of forest were represented by 809 887 and 1 271 793 cells in the Minnesota and Michigan landscapes, respectively.

We assessed forest dynamics using the LANDIS-II v6.0 forest landscape model (Scheller et al. 2007) (see Duveneck et al. 2014) for model input data). LANDIS-II is flexible in scale, process-driven, and has successfully reproduced dynamics of many forested ecosystems (e.g., Gustafson et al. 2010; Ravenoscroft et al. 2010). LANDIS-II operates across interconnected cells within climate and soil regions (“ecoregions”). The model simulates succession, disturbance, and management. Spatial interactions are incorporated within each study area and among processes (e.g., climate change, harvesting, fire, wind, and seed dispersal). LANDIS-II incorporates multiple user chosen extensions that interact with each other. Each extension ran at a 5-year time step.

We used the LANDIS-II Biomass Succession extension (v3.1), which regulates the succession mechanisms of growth, competition, and mortality for species–cohorts (Scheller and Mladenoff 2004). To calculate species-specific parameters (i.e., maximum aboveground net primary productivity per year (ANPPmax), and probability of establishment (Pest)), we used the PnET-II for LANDIS-II model (Xu et al. 2009). PnET incorporates climate data (temperature, precipitation, and photosynthetic active radiation (PAR)) along with soil water holding capacity (SWHC) and species-specific physiological parameters (e.g., foliar nitrogen content and maximum foliar mass area) for each climate–soil region on the landscape (Duveneck et al. 2014). ANPPmax and Pest are incorporated into the LANDIS-II Biomass Succession extension. ANPPmax determines the maximum growth possible of aboveground biomass for a species–cohort (Scheller and Mladenoff 2004). Growth is further limited by competition and a growth curve parameter that determines how fast simulated ANPP reaches ANPPmax. Age-related biomass decline is defined by a mortality curve that represents an increasing decline in biomass as the species reaches its maximum longevity. Pest determines the probability of a new cohort establishing, given a local seed source and adequate light, and is based on a climate envelope approach (Xu et al. 2009). To start a simulation, the Biomass Succession extension goes through a “spin-up” phase in which the past growth of current species–cohorts is simulated up to the starting year. Therefore, spin-up time is based on the age of the oldest cohort.

We used the Biomass Harvest extension (v2.1) to simulate harvest scenarios (Gustafson et al. 2000). Specific prescriptions were applied to management areas based on ownership groups. Stands are delineated within management areas. At each 5-year time step, the extension selects stands for treatment based on user-defined criteria. Stand selection criteria is based on forest types present, and species–cohorts mature within management areas matching prescriptions (Tables 1 and 2). Simulated biomass is removed from cells within stands based on prescription-specific criteria. For each management area, specific rotation periods define the amount of the management area treated at each time step (Gustafson et al. 2000).

We used the Base Fire (v3.0) (He and Mladenoff 1999) and Base Wind (v2.0) (Scheller and Mladenoff 2004) extensions to simulate fire and wind disturbance. To quantify spatially explicit species aboveground biomass (AGB) (g·m−2) and to classify forest type, we utilized the Biomass Output extension (v2.0) and the Biomass Re-class extension (v2.0), respectively. To process outputs and visualize results, we used the raster library in R (R Core Team 2011). Within each landscape, we used previously developed BAU timber harvest regimes (Tables 1 and 2), fire and wind regimes (<0.6% area disturbed·year−1), initial communities, delineated ecoregions, and tree species parameters (Duveneck et al. 2014).

Climate data

We simulated the current climate scenario based on randomly assigning 30 years of observed PRISM climate (1969–1999) to future simulation years (Daly and Gibson 2002). We simulated low and high emissions climate scenarios to bracket a range of uncertain futures. For the low-emissions climate, we used the IPCC B1 emission scenario and the parallel climate model (PCM) global circulation model (GCM). For the high-emissions climate, we used the IPCC A1FI emission scenario and the Geophysical Fluid Dynamics Laboratory (GFDL) GCM (IPCC 2007). In each landscape, we delineated unique climate regions (Duveneck et al. 2014) based on current climate observations where relatively homogeneous climate was observed (Daly and Gibson 2002). For each unique climate region, we downscaled and accessed temperature and precipitation data from the USGS Geo Data Portal (http://cida.usgs.gov/climate/gdp). To estimate projected PAR, we accessed projected radiation data from 17 meteorological stations in the Michigan landscape. After observing the low variability in PAR across observation sites, we used mean PAR within each climate region. For the Minnesota landscape, we used previously estimated PAR within each climate region (Ravenoscroft et al. 2010).

To simulate forest change to year 2150, we imputed monthly climate variables (maximum and minimum temperature, precipitation, and PAR) for the 50 years beyond the range of IPCC climate projections (IPCC 2007). The initial 100 years of climate projections encompassed an increase in temperature in all seasons in both emissions scenarios; however, the precipitation projections were more variable (Duveneck et al. 2014; Stoner et al. 2012). We imputed the final 50 years of climate data using the Amelia library (Honaker et al. 2011) in R (R Core Team 2011) based on the variability in each of the climate variables within the original 100 years of data. For the temperature projections, we included a linear regressed increase in imputed temperature.

Alternative management scenarios

We simulated expansion of existing forest reserves as a resistance strategy and simulated a modified silviculture regime as a strategy to increase adaptive capacity. We represented forest reserves as sites devoid of any timber harvesting. We used the Protected Areas Database (The Conservation Biology Institute 2010) to delineate areas in each study region that had existing formal...
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Table 1. Common silviculture prescriptions used in northeastern Minnesota business-as-usual (BAU) management scenarios and the associated adjustments used in the modified silviculture scenario.

<table>
<thead>
<tr>
<th>BAU landscape treated per time step (%)</th>
<th>USDA PNIF</th>
<th>MN DNR &amp; CO</th>
<th>USDA FS</th>
<th>PIF</th>
<th>BAU planted species following harvest</th>
<th>Modified silviculture adjustment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen clearcut</td>
<td>2.81</td>
<td>4.41</td>
<td>6.80</td>
<td>6.10</td>
<td>White spruce, white pine, and red pine</td>
<td>-40 Removed white spruce</td>
</tr>
<tr>
<td>Upland spruce clearcut</td>
<td>1.61</td>
<td>1.99</td>
<td>1.66</td>
<td>1.90</td>
<td>Jack pine and red pine</td>
<td>-10 Removed jack pine</td>
</tr>
<tr>
<td>Red pine clearcut</td>
<td>0.18</td>
<td>0.29</td>
<td>0.18</td>
<td>0.19</td>
<td>Red pine</td>
<td>-10</td>
</tr>
<tr>
<td>Northern hardwood clearcut</td>
<td>0.60</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-100</td>
</tr>
<tr>
<td>Northern hardwood patch cut</td>
<td>0.68</td>
<td>3.03</td>
<td>3.01</td>
<td>2.65</td>
<td>Oak species</td>
<td>25 Added northern hardwoods and oak species</td>
</tr>
<tr>
<td>Oak shelterwood</td>
<td>0.09</td>
<td>0.08</td>
<td>0.10</td>
<td>0.10</td>
<td>Oak species</td>
<td>-10 Removed white spruce</td>
</tr>
<tr>
<td>Red pine clearcut</td>
<td>0.12</td>
<td>0.23</td>
<td>0.13</td>
<td>0.08</td>
<td>Red pine and white spruce</td>
<td>-10</td>
</tr>
<tr>
<td>White pine clearcut</td>
<td>0.09</td>
<td>0.09</td>
<td>0.08</td>
<td>0.07</td>
<td>White pine</td>
<td>-10</td>
</tr>
</tbody>
</table>

Note: Common landowner groups: PNIF, private non-industrial forests; USDA FS, U.S. Department of Agriculture Forest Service; MN DNR & CO, Minnesota Department of Natural Resources and county lands; PIF, private industrial forests. Planted northern hardwoods include black cherry, yellow birch, American elm, and American basswood. Planted oak species include black oak, northern red oak, and bur oak. Within individual prescriptions, patch sizes were also reduced in modified silviculture prescriptions.

Table 2. Common silviculture prescriptions used in northern Lower Michigan business-as-usual (BAU) management scenarios and the associated adjustments used in the modified silviculture scenario.

<table>
<thead>
<tr>
<th>BAU landscape treated per time step (%)</th>
<th>USDA PNIF</th>
<th>USDA FS</th>
<th>MI DNR</th>
<th>PIF</th>
<th>BAU planted species following harvest</th>
<th>Modified silviculture adjustment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen–birch clearcut</td>
<td>0.06</td>
<td>1.72</td>
<td>2.39</td>
<td>3.49</td>
<td>Red pine and jack pine</td>
<td>-50 Northern hardwoods</td>
</tr>
<tr>
<td>Jack pine clearcut</td>
<td>0.12</td>
<td>0.82</td>
<td>0.53</td>
<td>0.05</td>
<td>Red pine and jack pine</td>
<td>-15</td>
</tr>
<tr>
<td>Northern hardwood shelterwood</td>
<td>0.01</td>
<td>0.08</td>
<td>0.09</td>
<td>0.06</td>
<td>Oak species</td>
<td>-25</td>
</tr>
<tr>
<td>Northern hardwood patch cut</td>
<td>0.16</td>
<td>0.52</td>
<td>0.59</td>
<td>0.29</td>
<td>Oak species</td>
<td>-15 Oak species</td>
</tr>
<tr>
<td>Oak patch cut</td>
<td>1.04</td>
<td>1.27</td>
<td>1.05</td>
<td>0.47</td>
<td>Oak species</td>
<td>25</td>
</tr>
<tr>
<td>Oak shelterwood</td>
<td>0.42</td>
<td>0.51</td>
<td>0.38</td>
<td>0.19</td>
<td>Oak species</td>
<td>-15</td>
</tr>
<tr>
<td>Oak thinning</td>
<td>1.43</td>
<td>1.75</td>
<td>1.31</td>
<td>0.64</td>
<td>Oak species</td>
<td>0</td>
</tr>
<tr>
<td>Birch shelterwood</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.02</td>
<td>Oak species</td>
<td>-100</td>
</tr>
<tr>
<td>Red pine clearcut</td>
<td>0.05</td>
<td>0.23</td>
<td>0.15</td>
<td>0.02</td>
<td>Red pine and jack pine</td>
<td>-15</td>
</tr>
<tr>
<td>Red pine patch cut</td>
<td>0.16</td>
<td>0.36</td>
<td>0.23</td>
<td>0.03</td>
<td>Oak species</td>
<td>0</td>
</tr>
<tr>
<td>Red pine shelterwood</td>
<td>0.04</td>
<td>0.09</td>
<td>0.06</td>
<td>0.01</td>
<td>Oak species</td>
<td>-15</td>
</tr>
<tr>
<td>Red pine thinning</td>
<td>0.52</td>
<td>1.16</td>
<td>0.73</td>
<td>0.10</td>
<td>Oak species</td>
<td>0</td>
</tr>
<tr>
<td>Upland spruce–fir clearcut</td>
<td>0.10</td>
<td>0.54</td>
<td>0.95</td>
<td>1.62</td>
<td>Oak species</td>
<td>-15 Oak species</td>
</tr>
<tr>
<td>Swamp Hardwoods clearcut</td>
<td>0.02</td>
<td>0.11</td>
<td>0.16</td>
<td>0.50</td>
<td>Oak species</td>
<td>-15 Northern hardwoods</td>
</tr>
<tr>
<td>Swamp hardwoods patch cut</td>
<td>0.10</td>
<td>0.06</td>
<td>0.08</td>
<td>0.25</td>
<td>Oak species</td>
<td>0</td>
</tr>
<tr>
<td>Swamp hardwoods shelterwood</td>
<td>0.05</td>
<td>0.03</td>
<td>0.04</td>
<td>0.11</td>
<td>Oak species</td>
<td>-15</td>
</tr>
<tr>
<td>Swamp hardwoods thinning</td>
<td>0.02</td>
<td>0.01</td>
<td>0.02</td>
<td>0.05</td>
<td>Oak species</td>
<td>0</td>
</tr>
<tr>
<td>White pine clearcut</td>
<td>0.07</td>
<td>0.15</td>
<td>0.11</td>
<td>0.06</td>
<td>Oak species</td>
<td>-15</td>
</tr>
<tr>
<td>White pine patch cut</td>
<td>0.30</td>
<td>0.47</td>
<td>0.35</td>
<td>0.20</td>
<td>Oak species</td>
<td>0</td>
</tr>
<tr>
<td>White pine shelterwood</td>
<td>0.12</td>
<td>0.19</td>
<td>0.14</td>
<td>0.08</td>
<td>Oak species</td>
<td>-15</td>
</tr>
<tr>
<td>White pine thinning</td>
<td>0.31</td>
<td>0.48</td>
<td>0.36</td>
<td>0.20</td>
<td>Oak species</td>
<td>0</td>
</tr>
</tbody>
</table>

Note: Common landowner groups: PNIF, private non-industrial forests; USDA FS, U.S. Department of Agriculture Forest Service; MI DNR, Michigan Department of Natural Resources; PIF, private industrial forests. Planted northern hardwoods include black cherry, yellow birch, American basswood, American elm, and sugar maple. Planted oak species include black oak, white oak, northern pin oak, and northern red oak. Within individual prescriptions, patch sizes were also reduced in modified silviculture prescriptions.

To simulate modified silviculture, we altered BAU prescriptions (Duveneck et al. 2014) based on increasing uneven-aged silviculture systems and increasing regeneration of northern hardwoods and oak species (e.g., American basswood (Tilia americana L.), black maple. Planted oak species include white oak, northern red oak, and bur oak. Within individual prescriptions, patch sizes were also reduced in modified silviculture prescriptions.

protection status. These reserves include the large BWCA in Minnesota, state parks, and state natural areas. In northern Lower Michigan, fewer large reserve areas exist; however, under our BAU scenario, we randomly selected 38% of private non-industrial forest (PNIF) cells as forest reserves under the assumption that 62% of PNIF lands are actively managed for timber (Butler 2008). In our expanded reserve scenario, we created a forest reserve buffering 1500 m on either side of major river corridors. The rivers included the Cloquet and St. Louis rivers in northeastern Minnesota and the Manistee, Au Sable, and Muskegon rivers in northern Lower Michigan. In addition to the river reserves, we created a 1000 m buffer along the Great Lakes shore boundaries in both study areas (Fig. 2). Under BAU management, 13% and 11% of the forested landscape was in reserves in the Minnesota and Michigan landscapes, respectively. Under our expanded reserve scenario, simulated river and lake buffers resulted in 18% of forested lands in reserves in each landscape. Although the increase in reserve area in the Michigan landscape was larger, the percent area under active management was comparable to the Minnesota landscape in both the BAU and expanded reserve scenarios.
cherry (*Prunus serotina* Ehrh.), American elm (*Ulmus americana* L.), white oak (*Quercus alba* L.), northern pin oak (*Quercus ellipsoidalis* E.J. Hill), and northern red oak (*Quercus rubra* L.) (Tables 1 and 2).

Rather than prescribe identical harvest prescriptions to each landscape, we adjusted the BAU prescriptions in each landscape to decrease harvested AGB by approximately 60% from BAU management. Generally, these adjustments resulted in a reduction in clearcuts, an increase in northern hardwood patch cuts, and planting of native northern hardwoods and oaks currently present on the landscapes, albeit in low abundance.

**Data analysis**

Stochastic variation in model outputs is largely influenced by natural disturbance events (i.e., fire and wind). We examined the stochastic variation within scenarios by replicating each simulation five times. We chose a small number of replicates due to the long run time necessary for each simulation and the resulting low variance between replicates. Maximum AGB variance at year 2150 was <2% of the mean AGB within each simulation. Due to the low stochastic variation of natural disturbance events relative to the size of the landscapes, we randomly selected one replicate from each clearcut, an increase in northern hardwood patch cuts, and planting of native northern hardwoods and oaks currently present on the landscapes, albeit in low abundance.

To examine the effects of reserve expansion, we compared the AGB of the BAU scenario with the AGB of the expanded reserve scenario (by species and total biomass). To understand dynamics within reserves, we compared average simulated AGB within reserves with that outside reserves. We examined spruce–fir species (balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) BSP)) as the group of species most vulnerable to climate change related decline (Duveneck et al. 2014). In addition to spruce–fir AGB, we assessed AGB total and species diversity within and outside reserves. We compared within- and outside-reserve AGB and diversity by spatially separating outputs that occur within and outside reserve areas (Fig. 2) using the raster library in R (R Core Team 2011).

**Results**

**Aboveground biomass**

Modified silviculture and, to some extent, expanded reserves increased total AGB relative to BAU for all climate scenarios in both landscapes (Fig. 3).
Alternative management was more effective at increasing AGB in the Minnesota landscape than in the Michigan landscape (Fig. 6). In both landscapes, the high emissions climate scenarios resulted in the lowest simulated diversity. Compared with BAU management, the expanded reserve scenario resulted in a limited increase in diversity. The modified silviculture scenario in the Minnesota landscape resulted in larger increases in diversity compared with BAU and expanded reserve management in all three climate scenarios. Compared with BAU management, the modified silviculture scenario in the Michigan landscape resulted in a small decrease in diversity under the current and low emissions climate scenario and a small increase in diversity under the high emissions climate scenario.

Under the expanded reserve management scenario, our simulations of forest reserves resulted in generally higher diversity compared with managed forests outside reserves (Fig. 5). This effect was most pronounced in the high emissions climate scenario in the Minnesota landscape. In the Michigan landscape, the effect of reserves on diversity was negligible.

Diversity

Average tree species diversity in each cell was lower in the Minnesota landscape than in the Michigan landscape (Fig. 6). In both landscapes, the high emissions climate scenarios resulted in the lowest simulated diversity. Compared with BAU management, the expanded reserve scenario resulted in a limited increase in diversity. The modified silviculture scenario in the Minnesota landscape resulted in larger increases in diversity compared with BAU and expanded reserve management in all three climate scenarios. Compared with BAU management, the modified silviculture scenario in the Michigan landscape resulted in a small decrease in diversity under the current and low emissions climate scenario and a small increase in diversity under the high emissions climate scenario.

Forest type

The Minnesota landscape simulations resulted in larger species-group changes in AGB than in Michigan (Table 3). The Minnesota landscape also exhibited large variability in the spatial distribution of forest type given climate and management differences (Fig. 7). Under the current and low emissions climate simulations, the spruce–fir forest type persisted within the reserves of the expanded reserves scenario at year 2150 (Fig. 7). Under the high emissions climate scenario, abundance of the northern hardwood forest types increased in reserves by year 2150, resembling the spatial distribution of BAU management.

The Minnesota modified silviculture scenario resulted in a more heterogeneous spatial distribution of forest type compared with BAU management (Fig. 7). The higher diversity of forest types under modified silviculture was represented by a decrease in aspen–birch forest type and an increase in white pine and northern hardwoods forest types. Under modified silviculture, the current and low emissions climate scenarios resulted in an increase in the spruce–fir forest type, but not the high emissions climate scenario.

Discussion

Forest managers and policy makers are increasingly seeking best management strategies to manage forests in the context of climate change (Millar et al. 2007; Seidl et al. 2011). Successful management in the Great Lakes region to increase resistance and...
Table 3. Initial percentage of aboveground biomass (AGB) in each species group and percent change (+ or −) at simulation year 2150 for each climate and management scenario in each landscape.

<table>
<thead>
<tr>
<th>Species Group</th>
<th>Current Initial % AGB</th>
<th>Low emissions BAU</th>
<th>XR</th>
<th>MS</th>
<th>BAU</th>
<th>XR</th>
<th>MS</th>
<th>BAU</th>
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Note: Current, current climate; BAU, business-as-usual management; XR, expanded reserves; MS, modified silviculture.

Adaptive capacity to the effects of climate change may be limited under a high emissions climate future.

**Forest reserves**

In our low emissions climate simulations, the expanded reserves did function as a resistance strategy. Spruce–fir forest types in the Minnesota landscape (Fig. 7) and spruce–fir species AGB in both landscapes (Fig. 5) persisted more in the reserve areas than in actively managed forests. These species are shade tolerant and common within minimally disturbed late successional forests (Heinselman 1996). Under our high emissions climate scenario, however, the forest reserves provided limited refuge to the spruce–fir species (Fig. 5) and spruce–fir forest types (Fig. 7). These results are consistent with other research that found adaptive forest management for climate change to be less successful under increasingly higher emissions climate scenarios (Buma and Wessman 2013). For populations with long generation times (i.e., tree species), limiting external stressors has been identified as a climate management priority (Moritz and Agudo 2013). Our expanded reserve scenario may be considered a successful resistance strategy in the context of providing refuge with limited disturbance along environmental gradients (Rudnick et al. 2012). There is support to conserving the trailing edge of a species migration such as balsam fir in the boreal–temperate ecotone. Genetically, a species within the trailing edge of its range will have adapted to more extreme conditions having had more generations (Hampe and Petit 2005).

As expected, forest reserves provided more simulated on-site AGB than actively managed forests (Fig. 5), which is consistent with previous research comparing managed vs. unmanaged stands (Powers et al. 2012). An increase in AGB implies higher on-site carbon storage. While managing for carbon storage in the Great Lakes region does not currently provide a direct financial benefit, there is a growing interest in managing forests specifically for climate mitigation (Malmsheimer et al. 2008). Our results indicate, a decrease in AGB is expected under the high emissions climate scenario compared with the current climate scenario. For this reason, there may be an increased interest in maintaining, if not increasing, AGB on the landscapes.

The higher simulated alpha diversity within reserves (Fig. 5) suggests that the forest reserves under low-frequency natural disturbance regimes may result in an increase in diversity over the long term. Conversely, the diversity of actively managed forests with mixed frequency of disturbance may increase less. At the landscape scale, the expanded reserves scenario resulted in very little change in simulated diversity compared with the BAU scenario (Fig. 6). These results suggest that at the 2 ha cell size, forest reserves may have the potential to increase forest alpha diversity. This is consistent with empirically measured increasing heterogeneity in less disturbed forests at a subhactare grain size (Bradford and Kastendick 2010). Our results do not include old-growth gap dynamics within a grain size less than 2 ha, and we do not suggest that our results would necessarily scale down to a smaller grain size (Urban 2005).

While attempting to increase resistance, forest reserves may increase adaptive capacity by increasing alpha diversity. This may be considered counter to carefully managed disturbances as opportunities for desirable change (Buma and Wessman 2013; Puettmann 2011). While we did not measure genetic adaptability, the evolutionary adaptability of forests to the effects of climate change can be improved with shorter generation times (Kuparinen et al. 2010). Forest reserves in landscapes with low natural disturbance frequency will have long generation times. To some extent, shorter generation times can be managed for by adjusting harvest rotation periods within actively managed forests (Puettmann 2011).

Regardless of the success of the resistance goal of providing refuge to spruce–fir and increased carbon storage, additional ecosystem services can be enhanced through expanded forest reserves. Specifically, forest reserves along riparian corridors have the potential to increase wildlife habitat and connectivity (Collingham and Huntley 2006; Rudnick et al. 2012). Riparian zone functions relating to stream flows, large woody debris inputs, and water temperature can also be maintained or enhanced by buffer zones (Lee et al. 2004). Large forest reserves such as the BWCA allow landscape-scale processes to occur (e.g., fire) with limited anthropogenic restrictions (Heinselman 1996). These sites provide natural laboratories for studying the interactions and processes between species, climate change, pollution, invasive species, and other processes (Heinselman 1973).

In the warmer Michigan landscape, the reserve areas had less of an effect on spruce–fir species (Fig. 5) than in Minnesota. This is likely due to climate and management differences between the landscapes (Duveneck et al. 2014). The interaction between climate and the competitive advantage of spruce–fir species (i.e., shade tolerance) in reserve areas allow larger increases where the conditions are more favorable. In addition, the less intensively managed Michigan landscape had less contrast in spruce–fir AGB and diversity between reserves and actively managed forests. Finally, the Minnesota landscape initially contained more spruce–fir AGB within the boreal–temperate ecotone. To receive the largest gains in ecosystem services (with limited resources), landscapes with less intensive BAU management may not be appropriate for reserve selection.

**Modified silviculture**

Our modified silviculture scenarios were moderately successful at increasing adaptive capacity. Recent research has considered trade-offs between forest adaptation and mitigation strategies.
Although our research did not consider belowground carbon storage, our results suggest that modified silviculture may increase climate mitigation by increasing aboveground biomass and may increase adaptation by increasing species diversity. A complex forest with high diversity can promote low abundance.
species capable of responding to changing environmental conditions (Walker et al. 1999). Our modified silviculture scenario was designed to increase heterogeneity with less frequent even-aged silviculture systems and more frequent smaller patch cuts. In addition to heterogeneity, the modified silviculture scenario was designed to favor and plant species expected to respond well to climate change (Tables 1 and 2). For planting to be successful, a substantial financial investment in successful artificial regeneration is required.

By managing for heterogeneity and adaptation, the modified silviculture scenario generally resulted in both increased on-site AGB (Fig. 3) and diversity (Fig. 6) at the expense of a decline in boreal tree species (Fig. 4) and a decrease in harvested timber (Fig. 3). In the case of white spruce in the Minnesota landscape, the BAU scenario includes planting white spruce following red pine clearcut prescriptions (Table 1). Under the modified silviculture prescription, we ceased planting white spruce, which resulted in a decline in white spruce AGB compared with BAU management. For forest policy makers, a trade-off exists between harvested and on-site AGB. The modified silviculture scenario represents a change in priority to increase on-site AGB at the expense of a reduction in harvested AGB. The modified silviculture scenario, however, may result in higher value timber products compared with BAU management products. For example, short-rotation even-aged silviculture systems will produce lower value products compared with group selection harvested with a patch-cut or extended-rotation silviculture system (White 2011). This may at least partially offset losses due to the reduction in harvested AGB.

Modified silviculture increased diversity in the Michigan landscape only under the high emissions scenario. The Michigan landscape showed less contrast between BAU and modified silviculture where there are less frequent even-aged silviculture prescriptions under BAU management compared with the Minnesota landscape (Duveneck et al. 2014). In addition, the current species composition of the Michigan landscape is more typical of a northern temperate forest than is the boreal–temperate Minnesota landscape (Curtis 1959). The alternative management in the Michigan landscape has less influence on composition and productivity. This suggests that opportunities to adapt existing BAU management may be easier to implement in the Minnesota landscape; however, BAU management may be better poised to naturally adapt to climate change in the Michigan landscape. Adaptive management in Michigan could focus on species and silviculture characteristics of the central hardwood region south and west of the study region. This might be more effective at increasing diversity, especially under the high emissions climate scenario.

Uncertainty and model limitations

A tremendous amount of uncertainty exists in the emissions scenarios and GCMs (IPCC 2007). Our choice of low and high future emissions scenarios was meant to bracket a range of future uncertainty. Recent carbon emission observations, however, suggest that our present global carbon emission trajectory is on track or above that of the high emissions (A1FI) climate scenario that we used in our projections (Jennings 2012).

Our simulations should not be interpreted as predictions. Rather, our results are plausible future scenarios with increasing
future uncertainty. Our model results are simplifications of reality based on the available data. We did not include species migrating from outside the landscape, effects of large unregulated browse damage (e.g., Fischelli et al. 2012), CO₂ fertilization (e.g., Reich and Hobbie 2012), or ozone pollution (e.g., Ainsworth et al. 2012). We recognize that a large amount of uncertainty exists in how landowners’ priorities will shift regarding management. Our alternative management scenarios were based on informed speculation and adjustments to BAU forest management (Duveneck et al. 2014). Future management will depend on dynamic individual management priorities, market fluctuations, and policy restrictions.

Conclusions

In contrast to other adaptation studies simulating an increase in biomass under climate change (e.g., Steenberg et al. 2011), our results suggest a decline in both harvested and on-site AGB under the high emissions climate scenario. Therefore, our results suggest a strong need to consider alternative management options to maintain AGB. Under a low emissions climate scenario, the ability to manage for climate change was much greater than under the high emissions climate scenario. The expanded reserve scenario was effective at preserving legacy species under the low emissions climate scenario. Under the high emissions climate scenario, our alternative management scenarios provided a limited ability to manage for climate adaptation; alternative management does show some promise for increasing adaptive capacity. Additional management alternatives should be explored in the future to match effective management to conditions provided by a changing climate.

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