



Climate adaptive silviculture strategies: How do they impact growth, yield, diversity and value in forested landscapes?



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ABSTRACT

Forest managers have been wrestling with questions of how best to prepare today's forests for a future climate that may be quite different from the climate under which they were established. We used the LANDIS forest landscape model to conduct a factorial simulation experiment to assess the landscape-wide effects of alternative cutting and planting practices in northern Wisconsin (USA) under three climate change scenarios simulated for 300 years to allow demographic legacies to be overcome by the experimental treatments. Our objective was to assess the relative ability of actionable components of silvicultural strategies to maintain productivity and economical and ecological values of forests under future climates compared to a "business as usual" (BAU) silviculture scenario representing current sustained yield practices. We found that the general effect of climate change was to increase the biomass of all species (CO₂ fertilization and increased growing season), although the most cold-adapted species eventually declined under warming climate scenarios. Two alternative silvicultural strategies produced clearly different outcomes compared to the BAU scenario. Total landscape tree biomass was least under BAU, reflecting its high biomass removal rates, and greatest under the most aggressive climate-adapted silviculture strategy coupled with a high CO₂ climate scenario due to increased growth and relatively high removal rates. Harvested outputs responded to both climate and silvicultural strategy, with the high CO₂ scenario reducing biomass available for harvesting compared to a moderate CO₂ scenario, except under the aggressive climate-adapted strategy. Our study suggests that creative silvicultural practices can be developed (and tested) to maintain productive and ecologically healthy forests under future climate conditions.

1. Introduction

Forest managers are wrestling with questions of how to best prepare today's forests for a future climate that may be quite different than the climate under which they were established. Adaptation strategies, or management actions that enable ecosystems to accommodate change, have been proposed and categorized broadly into resistance, resilience, and response options (Millar et al., 2007). In North America, the profession of forestry was founded on the premise of providing a sustainable supply of timber, water, and other goods and services from forests, and this led to the development of uneven-aged and even-aged silvicultural methods for predictably managing the regeneration, composition, development, health and quality of many commercial forest types (Pinchot, 1947). This traditional approach of managing for "stability" has been challenged due to the inherent "surprises" occurring within dynamic and complex ecological systems (Holling and Meffe, 1996).

Over the past few decades, ecologically-based strategies were developed for resilience after disturbance that facilitate the return of an ecosystem to pre-disturbance conditions, such as retention, close-to-nature, and natural disturbance-based forestry (Messier et al., 2015). A key component of ecologically-based management is maintaining a diversity of trees species, because tree diversity has been shown to enhance or stabilize productivity in response to environmental change (Loreau et al., 2001, Paquette and Messier, 2011, Ammer, 2019). Management for a full suite of ecosystem services, in addition to timber, is now an integral part of contemporary forest management considerations in the U.S. Strategies to enable rapid response to novel conditions are new areas of research and include complex adaptive systems concepts (Messier et al., 2015).

A recent survey of forest management literature revealed that a common theme in proposed strategies for climate adaptation is to implement management strategies to diversify (composition and

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structure) existing forest communities (e.g., Lindenmayer et al., 2012) and to increase the abundance of species that are better suited to future climatic conditions (Ontl et al., 2018) as a restoration (*sensu* Rissman et al., 2018) and resilience (*sensu* Millar et al., 2007) strategy. This often includes altering retention guidelines to increase biodiversity, gap cutting to increase spatial heterogeneity, other approaches to diversify stand structure, and “enrichment planting” to supplement local, native species diversity (Swanston et al., 2016). Another, more controversial option, is “assisted migration” of species that do not currently occur in an area, but that might thrive under the climate of the future and help fill ecological niches vacated by species expected to decline under future climate (Williams and Dumroese, 2013). The majority of management recommendations for climate adaptation in the literature focus on maintaining existing ecological patterns and processes using adaptation methods, with only 14% of recommendations suggested active interventions to transform ecosystems into better adapted configurations (Hagerman and Pelai, 2018). The recommendations around ecological patterns and processes are often focused on principles of ecological forestry, or on retaining trees and biological legacies at harvest, using a variety of tools to enhance diversity in forest composition and structure, and using long cutting cycles to allow for recovery after harvest (Franklin et al., 2007). For example, Rissman et al. (2018) propose a framework that combines restoration, maintenance (persistence), and transition-to-novelty, with managers setting the relative implementation of each strategy in the context of the ecological system and the threats it faces. Formally established guidelines for implementing this framework are few and can be considered experimental (Janowiak et al., 2014a).

Managing forests within transitional ecotones pose special issues. For instance, the mixed Laurentian forests of the Great Lakes region of North America represent a transitional ecotone between biomes, or the transition from boreal conifer-dominated forests of the north to temperate deciduous-dominated forests of the south. Transitional ecotones between biomes represent areas of potentially abrupt change in response to climate change (e.g., Frelich and Reich, 2010). The species diversity of these forests, particularly mixedwood combinations of boreal and temperate species, makes this ecotone a sensitive region for climate change effects on forest composition (Fisichelli et al., 2014), with important implications for biodiversity such as migratory forest birds (Niemi et al., 2016). Additionally, identifying appropriate management strategies to sustain mixedwood stands can be difficult due to differing shade tolerances, growth patterns, and site preferences of component species (Kabrick et al., 2017).

Part of the difficulty in projecting future tree species compositional change due to climate is that current and projected changes are multifaceted (Reyer et al., 2015). For example, it is unclear how climate change will interact with other anthropogenic changes, such as dramatic changes to historic fire regimes (Hanberry and Nowacki, 2016, Meunier et al., 2019), to affect the persistence of fire-adapted species such as pines and oaks. Indeed, both pines (*Pinus* spp.) and oaks (*Quercus* spp.) represent important habitat and food resources for a wide variety of wildlife species (Naylor, 1994, McShea and Healy, 2002), but not necessarily the same wildlife species. One potential outcome of a warming climate may be the regional replacement of pines by oak species. Such a potential outcome already relies on active silviculture to counter the regional trend toward homogenization of forests by more mesic and fire-intolerant tree species such as red maple (Abrams 1998, Schulte et al., 2007).

It is possible that climate-induced drought stress may eventually moderate such regional trends, although elevated carbon dioxide (CO₂) that drives a warming climate is thought to also enhance drought tolerance across a broad range of taxa (Peñuelas et al., 2011). Further, CO₂ fertilization is anticipated to enhance tree growth and productivity (Franks et al., 2013, Gustafson et al., 2018b), but tree species vary widely in their response to enriched CO₂ (Kallarackal and Roby, 2012). Warming climate lengthens growing seasons, and in some scenarios, the

lengthening is dramatic, resulting in large increases in forest productivity (Duveneck and Thompson, 2017), although individual species may be negatively impacted by heat stress in mid-summer (Teskey et al., 2015). Meanwhile, invasive species, such as the emerald ash borer (EAB), threaten entire genera of species, further degrading the diversity and resilience of forested ecosystems (Reyer et al., 2015). Such complex and interactive changes highlight the need for flexible and adaptive forest management and silvicultural strategies (Rissman et al., 2018).

A common lament by those looking for guidance on how to manage forests in the face of climate change is that most recommended strategies are general, focusing on restoring local disturbance regimes and native species diversity, and that there are few aggressive, transformative recommendations such as assisted migration (Nagel et al., 2017, Hagerman and Pelai, 2018). Additionally, there is little research addressing the efficiency of proposed transitional forest management strategies because a long time duration is needed to assess the response of forests to silvicultural treatments. It commonly takes decades for the consequences of stand-scale treatments to become evident, and it is difficult to scale short-term, stand-level results to the temporal and spatial scales at which forest dynamics and climate change play out. In the short term there is little certainty as to whether proposed strategies will work as expected, or how much additional management effort will be required in future decades to make a difference in outcomes. Forest landscape models with direct links to climatic and atmospheric drivers (Gustafson, 2013) provide a powerful tool to conduct virtual experiments at the relevant temporal and spatial scales to provide insight into the relative long-term effectiveness of alternative strategies for adapting forested landscapes to climate change, but very few studies have yet applied such tools to study the efficacy of climate adaptive silvicultural strategies at landscape temporal and spatial scales.

In this study, we used the LANDIS forest landscape model (Scheller et al., 2007) to conduct a factorial simulation experiment to assess the effect of alternative cutting and planting practices on forest composition and productivity under three climate change scenarios. The model has both direct links to climate drivers and flexibility to simulate traditional and novel silvicultural strategies. Our objective was to assess the relative ability of actionable components of silvicultural strategies to produce productive and ecologically functioning forests under future climates compared to a current sustained yield silviculture practices (BAU) baseline. Critical functional response variables included harvested output (biomass), aboveground biomass stocks, tree species and age class diversity, and the relative dominance of species groups related to economic, ecosystem, and wildlife habitat characteristics. Our expectation was that under progressively higher CO₂ scenarios, BAU strategies will produce declining productivity (tree biomass accumulation) and ecological diversity, while climate change adaptation strategies will produce stable or increasing productivity and diversity.

Our experimental design allowed us to evaluate several hypotheses. (1) CO₂ fertilization and growing season length will cause the climate factor to have a greater effect on response variables than the silviculture factor. (2) Ecosystem goods and services (indicated by the biomass of species of high economic, ecologic, or mast production, and biomass harvested) will be highest for the CCA treatment under both RCP 6.0 and 8.5 because this strategy best adapts forests to climate change. (3) Site-scale species richness will be highest for CCA under RCP 8.5 because it has the most aggressive planting practices. (4) Coniferous forest types will decline for all silvicultural treatments under RCP 8.5 due to the general loss of boreal species, but will decline the least under DIV, which plants the most conifer species. (5) All response variables will respond most favorably to CCA under RCP 8.5 because it was designed to be adaptable to climate change. Conversely, all response variables except biomass harvested will respond least favorably to BAU under all climate scenarios because it was designed to maximize biomass output without consideration of climate change. DIV will respond most favorably to the intermediate RCP 6.0 climate scenario because it

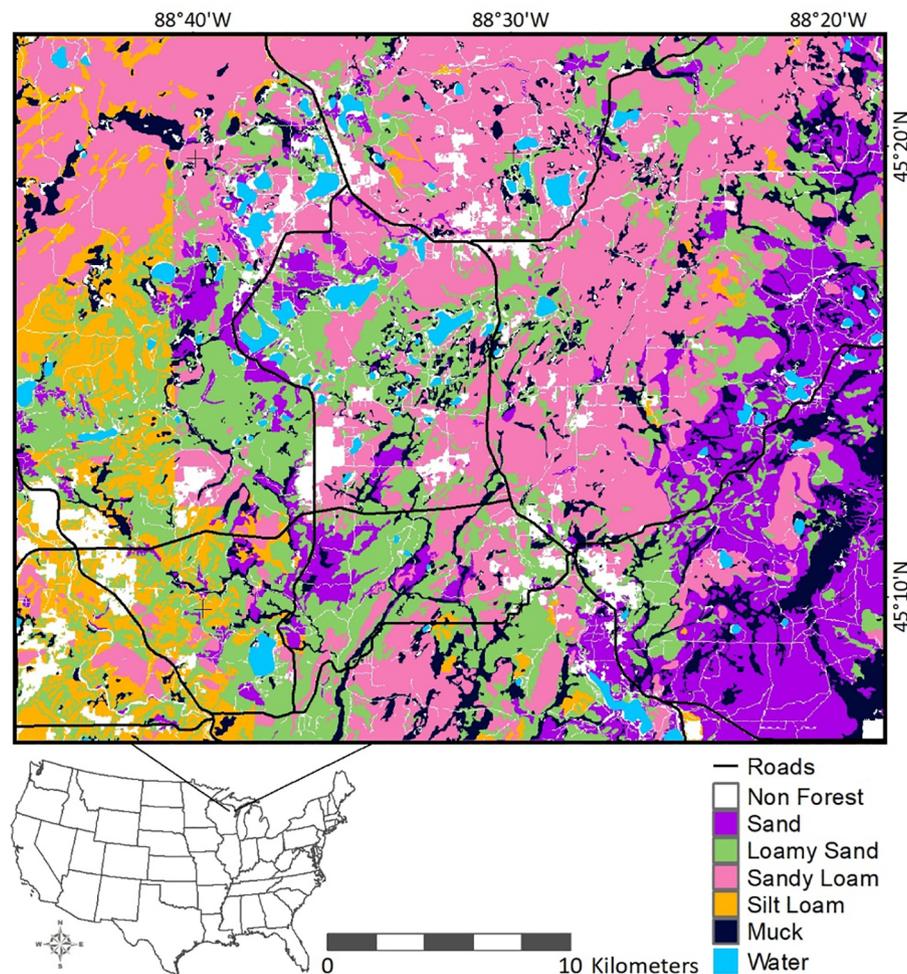


Fig. 1. Study area (104,471 ha) location in Oconto county (Wisconsin, USA), showing the general soil types affecting soil water availability and respective forest community types.

represents an intermediate climate-adapted silvicultural strategy. (6) CCA will best maintain biomass available for harvest and species diversity under both RCP 6.0 and 8.5 because it was the most specifically climate-adaptive strategy. Biomass harvested may also be higher than BAU under RCP2.6, demonstrating that this strategy is effective even if climate does not change much.

2. Methods

We conducted our simulation experiment on a 104,471 ha Laurentian mixed forest ecosystem in Oconto County, Wisconsin (USA) (Fig. 1, Table 1). Forested ecosystems in the study landscape are strongly influenced by glacial landforms that create a sharp soil moisture gradient from west (mesic) to east (xeric), with interspersed lakes and lowland forest throughout (Sturtevant et al., 2009). Mesic forests are dominated by northern hardwood species (e.g., sugar maple, American basswood, yellow birch; see Table 1 for scientific names), while xeric forests contain significant areas of pine and oak forests (i.e., jack pine, red pine, red oak, and pin oak). Boreal species (e.g., quaking and big tooth aspen, balsam fir, and paper birch) are common throughout the landscape, while lowlands contain species such as black spruce, tamarack, black ash, and white cedar. This landscape has a mix of private and federal owners, but for the objective of our controlled experiment, we assumed that the entire landscape was under a single management regime for each simulation run.

Our experiment was designed to detect response of aboveground woody biomass of trees (hereafter, biomass) to two treatment factors –

(1) silvicultural strategy and (2) climate scenario. The silvicultural strategies represent generic components of realistic silvicultural practices. The purpose was to conduct an experiment to produce insight rather than to predict the outcome of specific practices on this landscape. Three strategies formed the levels of the “silvicultural” treatment factor: business as usual or “BAU” (i.e., current sustained yield practices), diversification for resilience (DIV), and climate change adaptation (CCA).

BAU cutting practices were designed to sustain productivity and composition diversity and reflect conventional practices (e.g., USDA Forest Service, 2004, Wisconsin Department of Natural Resources, 2013) such that the entire stand is harvested (i.e., no uncut patches) in the eligible age classes at the defined rotation length. DIV cutting practices were designed to increase stand heterogeneity (e.g., cut and uncut patches), maintain elements of the previous stand (i.e., retention of some trees at final harvest), and provide longer periods of recovery (after harvest), such that some biomass is left at harvest as retention trees and uncut patches, and rotations were extended reflecting regional guidance (e.g., USDA Forest Service, 2004, Wisconsin Department of Natural Resources, 2013). CCA cutting practices were designed to maintain some elements of DIV to support ecosystem resilience coupled with the higher cutting rates of BAU to take advantage of anticipated higher growth rates under climate change, and to reduce competition for light, water and nutrients. The total area of the stands selected for harvesting was held constant among treatment combinations, but the altered retention practices of the treatment levels resulted in varying amounts of timber volume (biomass) being harvested.

Table 1
Species used in the simulations. Non-endemic species (indicated by *) appear in the CCA treatment only.

| Scientific name | Common name | Abbreviation | Initial mean biomass (kg/m ²) |
|-------------------------------|------------------------------|--------------|---|
| <i>Abies balsamea</i> | Balsam fir | B. fir | 0.883 |
| <i>Acer rubrum</i> | Red maple | R. maple | 2.505 |
| <i>Acer saccharum</i> | Sugar maple | Su. maple | 4.003 |
| <i>Acer saccharinum*</i> | Silver maple | Sil. maple | 0.00 |
| <i>Betula alleghaniensis</i> | Yellow birch | Y. birch | 0.730 |
| <i>Betula papyrifera</i> | Paper birch | P. birch | 1.169 |
| <i>Carya cordiformis</i> | Pignut hickory | P. hickory | 0.034 |
| <i>Fagus grandifolia</i> | American beech | A. beech | 0.133 |
| <i>Fraxinus americana</i> | White ash | W. ash | 0.385 |
| <i>Fraxinus nigra</i> | Black ash | B. ash | 1.389 |
| <i>Fraxinus pennsylvanica</i> | Green ash | G. ash | 0.106 |
| <i>Larix laricina</i> | Tamarack (American larch) | A. larch | 1.588 |
| <i>Picea glauca</i> | White spruce | W. spruce | 0.489 |
| <i>Picea mariana</i> | Black spruce | B. spruce | 1.015 |
| <i>Pinus banksiana</i> | Jack pine | J. pine | 0.126 |
| <i>Pinus resinosa</i> | Red pine | R. pine | 1.002 |
| <i>Pinus strobus</i> | Eastern white pine | W. pine | 0.923 |
| <i>Populus balsamifera</i> | Balsam poplar | B. poplar | 0.012 |
| <i>Populus grandidentata</i> | Bigtooth aspen | BT aspen | 1.735 |
| <i>Populus tremuloides</i> | Quaking aspen | Q. aspen | 2.128 |
| <i>Prunus serotina</i> | Black cherry | B. cherry | 0.513 |
| <i>Quercus alba</i> | White oak | W. oak | 0.018 |
| <i>Quercus coccinea*</i> | Scarlet oak | Sc. oak | 0.000 |
| <i>Quercus ellipsoidalis</i> | Northern pin oak | Pin oak | 0.402 |
| <i>Quercus macrocarpa</i> | Bur oak | Bur oak | 0.002 |
| <i>Quercus rubra</i> | Northern red oak | R. oak | 0.888 |
| <i>Quercus velutina</i> | Black oak | Bl. oak | 0.001 |
| <i>Taxodium distichum*</i> | Baldcypress | B. cypress | 0.000 |
| <i>Thuja occidentalis</i> | Northern white cedar | W. cedar | 0.388 |
| <i>Tilia americana</i> | American basswood | Basswd | 2.765 |
| <i>Tsuga canadensis</i> | Eastern hemlock | Hemlock | 0.816 |
| <i>Ulmus americana*</i> | American elm | A. elm | 0.000 |

The silviculture strategies (Table 2) were modeled using specific silvicultural prescriptions that included (1) regeneration method, (2) cutting cycle interval (uneven-aged methods) or rotation length (even-aged methods), (3) the biomass retained after each entry, and (4) the proportion of the stand area harvested. The prescriptions were assigned to stands according to forest types defined by the dominant species in the stand (Table S1), and in each time step, eligible stands were

Table 2
Components of the silvicultural prescriptions by silvicultural strategy. See harvest input file in the Supplement for greater detail.

| Silvicultural strategy | Cutting cycle or rotation length (yr) ¹ | Retention after each harvest entry (%) biomass remaining) ² | Harvested area (% of stand)) | Regeneration sources ³ |
|------------------------|--|---|------------------------------|---|
| Selection | BAU 15 | 75/75/0 ⁴ | 100 | Natural regeneration only |
| | DIV 20 | 75/85/5 | 85 | Natural regen. plus enrichment ⁵ planting |
| | CCA 20 | 70/70/5 | 95 | Natural regen. plus assistance ⁶ planting |
| Shelterwood (2-cut) | BAU 60–90 | Initial removal: 30–60 Final removal: 0–2 | 100 | Natural and artificial regen |
| | DIV 80–130 | Initial removal: 30–60 Final removal: 0–50 | 85 | Natural and artificial plus enrichment planting |
| | CCA 80–300 | Initial removal: 20–60 Final removal: 0–40 | 95 | Natural and artificial regen. plus enrichment and assistance planting |
| Clearcut | BAU 40–120 | 0–10 | 100 | Natural and artificial regen. |
| | DIV 60–200 | 0–15 | 85 | Natural and artificial regen plus enrichment planting |
| | CCA 60–200 | 0–5 | 95 | Natural and artificial regen. plus enrichment and assistance planting |

¹ Actual value is forest type-dependent.

² Ranges reflect forest type-dependent differences.

³ Species planted are listed by forest type and strategy in Table 3.

⁴ Approximately pole-, small sawlog-, and large sawlog-sized trees.

⁵ Planting to restore local, native tree composition and diversity.

⁶ Planting to enhance the capacity of the forest communities to respond to climate change.

harvested in order of decreasing age until cutting targets for the time step were reached or until all eligible stands were harvested. In general, stands dominated by shade-tolerant tree species were harvested using selection cutting, shade mid-tolerant species were harvested using shelterwood (two-entry) methods, and intolerant species such as poplars and conifers were harvested using clearcut prescriptions (Table S1).

Silvicultural strategies were further defined by planting practices (Table 3). BAU followed conventional practices to naturally and artificially regenerate conifer stands. DIV aimed to restore native species composition through enrichment planting interspersed among other natural and artificial regeneration. CCA retained the diversification elements of DIV (including planting of endemic species), but in areas dominated by boreal species or species likely to be extirpated (e.g., ash species killed by EAB), moderate-warm temperate, non-endemic species (silver maple, scarlet oak, bald cypress and American elm) were planted to offset expected losses of other species under future climates (Swanston et al., 2011) (see Table 1 for scientific names). For elm, we assumed that Dutch elm disease resistant genotypes would be planted and did not simulate disease-induced mortality or decline. (Knight et al., 2017). The model includes species-specific cold tolerance (Table 4), and all non-endemic species survived the winters under the RCP 8.5 climate scenario. The cutting practices and planting practices were merged to form the three levels of the silviculture treatment.

The climate scenario treatment also had 3 levels based on standard CO₂ Representative Concentration Pathways (IPCC, 2013): 1) RCP 2.6 (little change in CO₂), 2) RCP 6.0 (intermediate change in CO₂), 3) RCP 8.5 (dramatic increase in CO₂) (Fig. 2). The monthly climate projections for the climate treatment were generated by the General Fluid Dynamics Laboratory earth system model (GFDL-ESM2G, r1i1p1) (Dunne et al., 2012). We used the temporal extensions of the RCP CO₂ scenarios as estimated to 2200 by Meinshausen et al. (2011), holding the final concentration constant after that. Climate (i.e., temperature and precipitation) projections provided by the GFDL Global Circulation Model end at the year 2100, but it is expected that temperatures will continue to rise even if CO₂ concentrations plateau (Meehl et al., 2012). We extended the RCP 6.0 and 8.5 temperature projections by continually repeating the variability of the final 30 years (2071–2100) of projected temperatures by incrementing values according to the trend of the first 100 years for an additional 100yrs, and then using a flat trend thereafter (Fig. 2). Precipitation had a negligible increasing trend under all climate scenarios, so we did not extrapolate any trend beyond year

Table 3
Species planted by silvicultural strategy and forest type.

| Prescription/forest type | Business as usual (BAU) | Diversify (DIV) | Climate change adaptive (CCA) |
|--------------------------------------|-------------------------|----------------------|--|
| Selection-Northern Hdwd ¹ | None | W. pine | W. oak + R. pine + W. oak + R. pine |
| Clearcut-Aspen | None | W. spruce | R. pine + R. oak + W. oak |
| Clearcut-Jack pine | J. pine | J. pine + R. pine | Sc. oak |
| Clearcut-Spruce-Fir | W. spruce | W. spruce + B. fir | R. pine + R. oak + W. oak |
| Clearcut-White pine | W. pine | W. pine + R. pine | W. pine + R. pine + A. elm + R. oak + W. oak |
| Clearcut-Red pine | R. pine | R. pine + W. pine | R. pine + W. pine + R. oak + W. oak |
| Shelterwood-Oaks | R. oak | R. oak + R. pine | R. oak + R. pine + W. oak |
| Shelterwood-Birch | None | W. spruce | R. pine + R. oak + W. oak |
| Shelterwood-MxdHwd ² | None | W. pine | A. elm R. pine + R. oak + W. oak |
| Lowland conifers | No cutting or planting | B. spruce + A. larch | B. cypress |
| Lowland hardwood | No cutting or planting | R. maple + Y. birch | Sil. maple |

¹ Shade-tolerant hardwoods.

² Intermediate shade-tolerant hardwoods.

2100, simply repeating the last 30 years of the projected values (not shown).

2.1. Model description

The modeling platform was LANDIS-II v7.0 (Scheller et al., 2007), a forest landscape model that simulates forest development (seed dispersal; tree establishment, growth, competition, and degeneration; senescence; and disturbance) over long time periods. LANDIS is built as a collection of modules (extensions) that can be activated to simulate

specific ecological processes. Within LANDIS, landscapes are represented as a grid of spatially interacting cells (typically 0.1–6.25 ha) on which species composition and canopy layering are assumed to be homogeneous, and these cells are spatially aggregated into ecological land types with homogeneous climate and soils. On each cell, forest composition is represented as age cohorts of one or more tree species that compete via a suite of vital attributes (e.g., longevity, growth capacity, shade tolerance, drought tolerance, seed dispersal, ability to sprout vegetatively) to generate nondeterministic successional pathways driven by competition, and by disturbance type and severity

Table 4

Selected species life history parameters used as input to the model, derived from various empirical studies and syntheses as described in Gustafson et al. (2016). Complete PnET-Succession input files are available in the online Supplement.

| Species | Amax ($\mu\text{mol/g}$ fol./s) ^a | HalfSat ($\mu\text{mol/m}^2/\text{s}$) ^b | Water-logging Toler. (%) ^c | Drought Toler. (MPa) ^d | Leaf-On MinT ($^{\circ}\text{C}$) ^e | Psn MinT ($^{\circ}\text{C}$) ^e | Psn OptT ($^{\circ}\text{C}$) ^e | Psn MaxT ($^{\circ}\text{C}$) ^e | Lethal Cold Temp. ($^{\circ}\text{C}$) |
|------------|---|---|---------------------------------------|-----------------------------------|--|--|--|--|--|
| B. fir | 35.4 | 150 | 20 | -1.37 | 1.9 | 5.7 | 20.5 | 29 | -65 |
| R. maple | 119.4 | 150 | 41 | -1.49 | 2.5 | 6.5 | 28.5 | 38 | -50 |
| Su. maple | 119.4 | 100 | 0 | -1.42 | 2.5 | 6.5 | 26.1 | 33 | -55 |
| Sil. maple | 126.6 | 250 | 62 | -1.42 | 2.8 | 6.8 | 28.5 | 36.4 | -45 |
| Y. birch | 112.2 | 150 | 35 | -1.42 | 2.5 | 6.5 | 23.5 | 34 | -55 |
| P. birch | 133.8 | 250 | 20 | -1.49 | 1.8 | 5.8 | 21.5 | 30 | -65 |
| P. hickory | 126.6 | 250 | 20 | -1.57 | 3 | 7 | 28.3 | 36.3 | -51 |
| A. beech | 119.4 | 97 | 0 | -1.37 | 2.7 | 6.7 | 28.4 | 36.5 | -50 |
| W. ash | 126.6 | 200 | 20 | -1.42 | 2.8 | 6.8 | 28.5 | 36.5 | -50 |
| B. ash | 126.6 | 250 | 62 | -1.42 | 2 | 6 | 23.6 | 33.3 | -60 |
| G. ash | 126.6 | 200 | 35 | -1.57 | 2.5 | 6.5 | 28.5 | 36.5 | -51 |
| A. larch | 140.9 | 300 | 62 | -1.42 | 1.7 | 5.7 | 19.5 | 30 | -65 |
| W. spruce | 35.4 | 200 | 0 | -1.49 | 1.6 | 5.7 | 19.5 | 30 | -66 |
| B. spruce | 31.1 | 200 | 62 | -1.42 | 1.6 | 5.6 | 19.5 | 29 | -66 |
| J. pine | 39.7 | 300 | 0 | -1.57 | 1.7 | 5.7 | 19.5 | 30 | -61 |
| R. pine | 39.7 | 250 | 0 | -1.49 | 2.2 | 6.2 | 22.1 | 32 | -55 |
| W. pine | 41.9 | 200 | 20 | -1.49 | 2.2 | 6.2 | 25 | 33.3 | -53 |
| B. poplar | 133.8 | 300 | 11 | -1.42 | 2 | 5.7 | 20.5 | 29 | -65 |
| BT aspen | 133.8 | 300 | 11 | -1.49 | 2.5 | 6.1 | 23 | 32 | -55 |
| Q. aspen | 133.8 | 300 | 0 | -1.49 | 2 | 6 | 22 | 31.4 | -65 |
| B. cherry | 140.9 | 250 | 0 | -1.49 | 2.8 | 6.8 | 28.5 | 36.5 | -43 |
| W. oak | 133.8 | 250 | 0 | -1.57 | 3 | 7 | 28.5 | 36.5 | -41 |
| Sc. oak | 140.9 | 300 | 0 | -1.57 | 4.3 | 8.3 | 28.5 | 36 | -35 |
| Pin oak | 133.8 | 250 | 0 | -1.57 | 2.5 | 6.5 | 26 | 34.5 | -50 |
| Bur oak | 133.8 | 200 | 0 | -1.57 | 2.3 | 6.3 | 26 | 34.6 | -53 |
| R. oak | 133.8 | 200 | 0 | -1.49 | 2.7 | 6.7 | 28.5 | 36 | -50 |
| Bl. oak | 126.6 | 200 | 0 | -1.49 | 3.1 | 7.1 | 28.5 | 36.3 | -41 |
| B. cypress | 126.6 | 200 | 83 | -1.35 | 4.5 | 8.5 | 30 | 38.5 | -34 |
| W. cedar | 35.4 | 200 | 62 | -1.49 | 2 | 6 | 22.8 | 32 | -60 |
| Basswd | 119.4 | 150 | 0 | -1.42 | 2.4 | 6.4 | 26 | 34.5 | -51 |
| Hemlock | 41.9 | 95 | 0 | -1.37 | 2.7 | 6.7 | 26 | 34.2 | -65 |
| A. elm | 119.4 | 200 | 41 | -1.42 | 2 | 6 | 28.3 | 36.5 | -40 |

^a Amax; maximum photosynthesis rate under optimal conditions, proportional to foliar nitrogen content.

^b Half saturation; light intensity at which photosynthesis is half that under full light saturation.

^c Waterlogging tolerance given as percentage of Amax when soil is over-saturated (Niinemets and Valladares, 2006).

^d Drought tolerance; water potential below which photosynthesis does not occur (Niinemets and Valladares, 2006).

^e Parameters defining temperature controls on photosynthesis rate. Values represent mean daytime temperature.

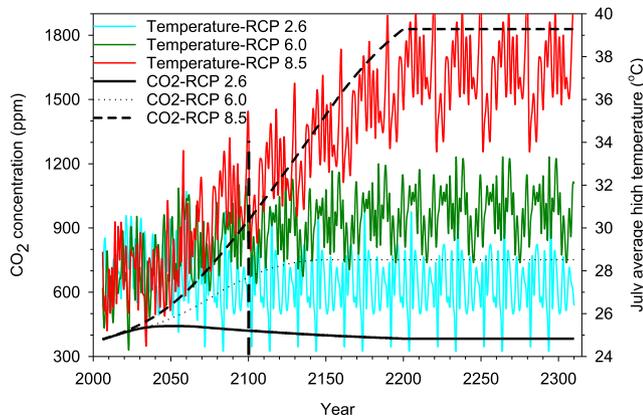


Fig. 2. Projected future atmospheric CO₂ concentration and temperature trends under the three RCP scenarios. CO₂ concentrations estimated to 2200 by Meinshausen et al. (2011). The vertical dashed line at year 2100 indicates the transition from GFDL temperature projections to extrapolated values.

(Mladenoff, 2004). Independent disturbance extensions (including timber harvest) simulate processes that kill cohorts or remove some of their biomass. The LANDIS framework robustly scales site-level physiological mechanisms to the landscape scale through process-based simulation of growth and competition and the interaction of grid cells via dispersal and spatial disturbance processes.

The experiment was implemented using the PnET-Succession v4.0 (De Bruijn et al., 2014) succession (growth and competition) extension within the LANDIS-II modeling framework, because PnET-Succession has direct links between climate drivers (CO₂ concentration, temperature and precipitation) and tree species cohort net primary productivity are based on physiological first principles (Aber et al., 1995). Such a mechanistic approach is important when studying climate change effects because phenomenological modeling approaches use the past to predict the future, and future climates are expected to fall well outside the domain of the scientifically studied past (Gustafson, 2013). Forest dynamics emerge from the competition of tree cohorts for light and water on each grid cell, interacting with the disturbances that alter successional trajectories.

PnET-Succession scales leaf-level processes such as photosynthesis, respiration and transpiration to the grid cell by integrating light extinction and water consumption in stacked canopy layers and computing a dynamic soil water balance. Growth capacity (species-cohort photosynthetic capacity under optimal conditions) is a function of foliar nitrogen concentration, and actual photosynthesis in each month is computed by applying multiple reduction multipliers (0.0–1.0) reflecting departure from optimal conditions (stress). Cohort stress is dynamically calculated relative to shade, drought, waterlogging and temperature tolerance parameters. Grid-cell soil water is tracked using a “bucket” hydrology model based on precipitation, runoff, loss to evaporation and percolation out of the rooting zone, and transpiration by the cohorts (Gustafson and Miranda, 2019). Response (and acclimation) to elevated CO₂ concentrations is modeled according to Franks et al. (2013). PnET-Succession accounts for growth and maintenance respiration using a Q10 relationship (Atkins, 1978), and acclimation of respiration to elevated temperature is simulated as in Wythers et al. (2013). Net primary productivity is allocated to biomass pools of foliage, wood, root and reserves (non-structural carbon) according to allocation parameters. New cohorts are stochastically established throughout the growing season with species-specific establishment probabilities calculated monthly based on soil water and sub-canopy light relative to drought, waterlogging and shade tolerance.

2.2. Modeling details

The study area was a gridded representation (cell size = 30 m) of the study area. The abiotic environment was categorized using SSURGO (Soil Survey Staff, 2013) soil map polygons, simplifying the abiotic environment to six major soil types (Fig. 1) with homogeneous climate across the study area. We used initial forest conditions (species and age classes) produced for Janowiak et al. (2014b), which were created using the imputation methods of Wilson et al. (2012) to assign Forest Inventory and Analysis (FIA) plot attributes to each 250-m cell based on MODIS satellite imagery. The original raster maps indicating presence of tree species in ten-year age cohorts were resampled to 30-m resolution to match other simulation input layers. Experiment simulations were run for 300 years (2006–2305) to allow legacies and ecological inertia to be overcome by the treatment effects. Variability among model runs at the landscape scale was relatively low, so each experimental combination was replicated 5 times.

For calibration of PnET-Succession, we required strictly comparable empirical growth data to ensure comparable parameters among species to accurately simulate competitive behavior, including non-endemics. We generated such growth curves generated using the Lakes States variant of the FVS model (Dixon and Keyser, 2008), which uses local FIA (US Forest Service Forest Inventory and Analysis) data to predict stand growth as a function of site conditions. For each species we projected tree biomass growth curves for the 5th, 50th, and 95th percentiles of site index values. For those rare tree species having insufficient FIA samples (including assisted migration species), we used the growth curves of a similar species with which it is commonly found. For bald cypress, we used the growth curves of tamarack growing in a lowland environment. PnET-Succession assumes optimum photosynthesis when a cohort is not stressed, so we calibrated PnET-Succession parameters (Table 4) to produce growth curves approaching those on the best sites.

The silvicultural strategies were simulated using the LANDIS-II Biomass harvest extension (v4.2 Gustafson et al., 2000). We simulated wildfires and windstorms, the two natural disturbances that have important structuring effects on landscapes in this region. Wildfire was simulated using Base Fire (v3.1 Scheller and Domingo, 2017), calibrated against records of wildfires in the region compiled by the Wisconsin Department of Natural Resources (Miranda et al., 2012) using the RCP 2.6 climate projection. The probability of fire ignitions was modified for the other two climate scenarios after year 2050 compared to RCP 2.6 and in inverse proportion to the (modest) change in the average Palmer Drought Severity Index (PDSI, Palmer, 1965), estimated from temperature and precipitation values in the climate projections. Cohort damage caused by microburst wind events was simulated using Base Wind (v2.2 Scheller and Domingo, 2011), parameterized based on data in Rich et al. (2007). Tornadoes and derechos were simulated using Linear Wind (v2.0, Gustafson et al., 2018a), calibrated to data in Hjelmfelt (2007). Although little empirical evidence has accumulated relating wind disturbance over land to climate change, there is theoretical and other evidence suggesting that increased temperatures will produce tropical oceanic storms of greater intensity while storm frequency is expected to decline or be unchanged (Emanuel, 2005, Knutson et al., 2010). We therefore decreased storm frequency by 6% compared to the historical baseline under the RCP 6.0 climate scenario and by 34% under RCP 8.5, and increased storm intensity by 2% under RCP 6.0 and 11% under RCP 8.5 (Knutson et al., 2010).

Finally, we assumed that emerald ash borer (EAB) would move into the area as anticipated, and rapidly deplete the standing biomass of all ash species, including black ash, which dominates many of the lowland forests of the study area. EAB was simulated using the Base Biological Disturbance Agent extension (v4.0, Sturtevant et al., 2019). We followed the methods of Gustafson et al. (2018c), but decreased the likelihood of disturbance from 1.0 to 0.5, applied every 10 years, to simulate mortality of all ash cohorts as an exponential decline that

reduced ash occupancy to about 15% of its initial abundance by 20 years, with complete extirpation by 100 years.

PnET-Succession uses a hydrologic “bucket” model to simulate competition for water. Soil texture and rooting depth parameters define the water capacity of the “bucket” for each cell, and the leakage parameter determines the ability of the soil to drain to field capacity. The amount of water in the “bucket” of each cell is used to compute monthly soil water potential. Lowland forest hydrologic dynamics were simulated using recent modifications described by Gustafson et al. (in review) that allow soil water to exceed field capacity and saturation (i.e., flooded) when runoff is impeded by topography and/or drainage is reduced by an impermeable or semi-impermeable soil layer. Waterlogging occurs when cumulative precipitation inputs exceed the cumulative removal of water by runoff, leakage and transpiration, and consequently the growth of species with higher waterlogging tolerance is favored. For forested wetland sites we parameterized a muck soil with high water capacity by setting runoff to zero and calibrating water leakage using actual assemblages on wetland sites, finding a value that generally maintained supersaturated soils without a continually increasing excess water.

2.3. Analysis

We chose response variables to reflect aspects of forest productivity and ecological characteristics function. Total landscape aboveground tree biomass was used to represent cumulative forest productivity and carbon storage, and the areal extent of forest type groups to represent forest composition change through time. Individual species biomass was used to assess species turnover in response to treatments. Commercial productivity was represented by the biomass removed by harvest activities by species and forest type groups. Forest diversity (a proxy for resilience) was measured by mean cell-level species and (5-year) age class richness across the landscape. Ecological role was represented by the total biomass of functional groups (i.e., habitat) defined by mast or ecological value, and economic value by classes defined by historical economic value (Table 5). Landscape pattern was quantified by aggregation index (He et al., 2000) computed from maps of forest type, where higher values represent more aggregation of pixels of the same class. We used the mean of the last 100 years of the time series (200–300) to compute response variables, to reduce the influence of initial conditions (demographics) and maximize the signal from a gradually changing climate.

We visualized treatment effects through simulated time by comparing plots (with uncertainty estimates) of mean biomass for selected species of each treatment combination. We calculated 95% confidence intervals in R from the standard errors of the means and the 0.975 quantile from the Student t distribution, and evaluated significance based on overlapping confidence intervals. We did not compute significance tests for this modeling experiment as advocated by White et al. (2014). The two treatment factors were (a) silviculture strategy (built from fixed combinations of cutting and planting practices shown in Tables 2 and 3), and (b) climate scenario.

3. Results

3.1. Climate effects

The general effect of climate change (CO₂ fertilization and growing season effect) was to increase the biomass of all species (Fig. 3), although the most cold-adapted eventually declined under warming climate scenarios (Figs. 4a and 4b). For several species (B. fir, W. spruce, B. spruce, J. pine, R. pine, Q. aspen, BT aspen, B. poplar, Pin oak, W. cedar), temperatures exceeded their photosynthetic tolerance range sufficiently to almost extirpate them from the landscape under the warmest climate scenario (RCP 8.5). Total landscape biomass was clearly driven by climate (i.e., CO₂), although the effect of disturbances

Table 5

Assignment of species to functional groups for analysis.

| Species | Drought Tolerance | Economic Value | Ecologic Value | Mast Value |
|------------|-------------------|----------------|----------------|------------|
| B. fir | SomewhIntol | Medium | Low | Low |
| R. maple | WaterlogTol | Low | High | Medium |
| Su. maple | SomewhIntol | High | Medium | Medium |
| Sil. maple | WaterlogTol | Low | Medium | Medium |
| Y. birch | SomewhTol | High | Low | Low |
| P. birch | SomewhIntol | Medium | Medium | Low |
| P. hickory | SomewhIntol | Medium | High | High |
| A. beech | SomewhTol | Low | Low | Medium |
| W. ash | SomewhTol | High | Medium | Medium |
| B. ash | WaterlogTol | Medium | High | Medium |
| G. ash | WaterlogTol | Low | Low | Medium |
| A. larch | WaterlogTol | Medium | Medium | Low |
| W. spruce | SomewhTol | High | Medium | Low |
| B. spruce | WaterlogTol | Medium | Low | Water |
| J. pine | Tolerant | High | Medium | Low |
| R. pine | Tolerant | Medium | Medium | Low |
| W. pine | SomewhTol | High | Medium | Low |
| B. poplar | Intolerant | Medium | Medium | Low |
| BT aspen | Intolerant | Medium | Medium | Low |
| Q. aspen | Intolerant | Medium | Medium | Low |
| B. cherry | SomewhTol | High | High | Medium |
| W. oak | Tolerant | High | High | High |
| Sc. oak | Tolerant | High | High | High |
| Pin oak | Tolerant | High | High | High |
| Bur oak | Tolerant | Medium | High | High |
| R. oak | SomewhTol | High | High | High |
| Bl. oak | SomewhTol | High | High | High |
| B. cypress | WaterlogTol | Medium | Medium | Low |
| W. cedar | WaterlogTol | High | High | Low |
| Basswd | SomewhTol | Medium | Medium | Medium |
| Hemlock | SomewhIntol | Low | Medium | Low |
| A. elm | WaterlogTol | Medium | Medium | Medium |

can be seen in the ups and down of the trajectories and widening error bars (Figs. 4a and 4b).

The effect of climate on other biomass response variables was similar (Table 6), with CO₂ fertilization and longer growing seasons generally increasing biomass. The effect on biomass harvested (Fig. 5) was less straightforward, with the RCP 8.5 climate reducing harvest outputs compared to the RCP 6.0, except under the CCA silviculture strategy.

3.2. Silviculture effects

Using the BAU silvicultural scenario as a comparison baseline, the alternative silvicultural strategies resulted in clearly different outcomes, although the difference in landscape-scale outcomes between the two alternatives (Table 6, Figs. 4a and 4b) was not as great as the stand-scale differences in harvest tactics (Table 2) might suggest. Simulated total landscape biomass was least under BAU, reflecting relatively high biomass removal rates, and greatest under CCA. Harvested biomass was always much higher under the BAU strategy, reflecting its low retention practices, and CCA always produced more harvested biomass than DIV (Fig. 5). A climate by silviculture interaction existed for all response variables in that confidence intervals for every treatment combination were distinct from all the others, likely reflecting the fact that the silvicultural treatments were coarsely designed for specific climate futures.

The abundance of forest types is a mapped landscape attribute based on the importance (biomass) of the species cohorts found on a site, and this attribute was also affected by the treatments. Most forest types declined in abundance with warmer climate except oaks and mixed hardwoods (Fig. 6). Forest types responded to silvicultural strategy according to their dependence on disturbance (e.g., Aspen-birch) or how intentional a strategy was toward maintaining that type. For example, the DIV and CCA strategies aggressively favored oaks and pines,

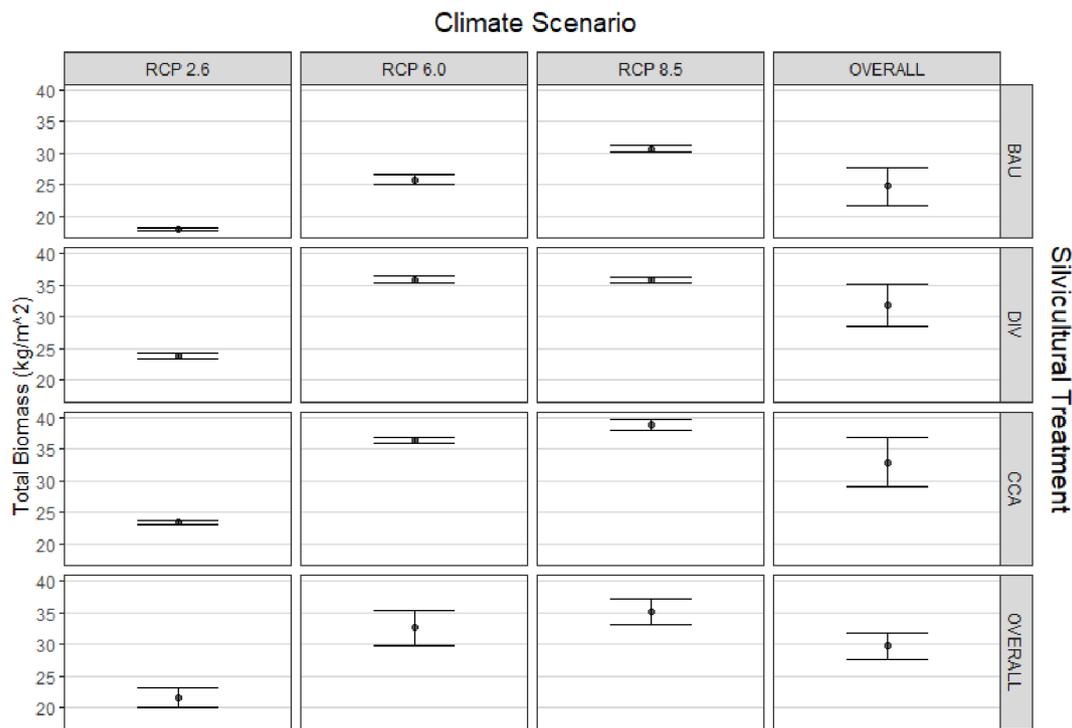


Fig. 3. Assessment of relative effect of the treatment factors on mean (final 100 years) total landscape aboveground woody biomass (kg/m^2). Error bars show 95% confidence intervals.

and also favored northern hardwoods over mixed hardwoods. In some cases, the RCP 8.5 climate reduced the abundance of a forest type in spite of management efforts to sustain it (e.g., northern hardwoods). Lowland hardwoods survived only under the CCA silvicultural strategy because it replaced ash species with planted silver maple, a warm-adapted species; under other silvicultural strategies ash was replaced by lowland conifers by natural regeneration. The patchiness of the forest type maps (Aggregation Index, Table 6) was affected by the silviculture treatments because of variation in gap size and rotation lengths (Table 2), and by the gain and loss of species under warming climates. Under the DIV strategy, site-scale species richness (mean number of species on a site) was not high compared to the CCA strategy, but site age class richness was (Fig. 7).

4. Discussion

4.1. Insights

Hypothesis 1, that CO_2 fertilization and longer growing seasons will cause the climate factor to have a greater effect than the silviculture factor, was clearly supported. An ad hoc Type 3 test of fixed effects on total landscape biomass showed an F-value for the climate effect over two times larger than that for the silviculture effect (3668 v. 1392, $p < 0.001$ for each effect). Although CO_2 and temperature effects were confounded in our climate treatments, it is evident in Fig. 4b that species that eventually decline from heat stress under RCP 8.5 (e.g., P. birch) have elevated biomass prior to their decline, compared to other RCP scenarios. Hypothesis 2, that ecosystem goods and services will be highest under the CCA treatment under both RCP 6.0 and 8.5, was mostly supported. The biomass of species of high economic, ecologic, and mast production values under CCA were always greater than the other silviculture treatments (Table 6). However, harvested biomass was by far the highest under the BAU treatment because of the more intensive cutting of BAU (Fig. 5). Note that BAU harvest outputs increased with moderate warming, but decreased to historical levels under extreme warming, likely due to heat stress. DIV followed a

similar pattern, but harvest outputs declined less under extreme warming. CCA produced a steady increase in harvest outputs as climate warmed, likely driven mostly by CO_2 fertilization and longer growing seasons, and partly by addition of more heat-adapted species. Hypothesis 3, that site-scale species richness will be highest for CCA under RCP 8.5 was supported (Fig. 7). It was also clear that RCP 8.5 dramatically reduced both species and age-class richness. Hypothesis 4, that coniferous forest types would decline for all silvicultural treatments under RCP 8.5, but would decline the least under DIV, was supported. Mean conifer biomass was 5.5, 6.3, and 4.7 kg/m^2 for RCP 2.6, 6.0 and 8.5, respectively, with no range overlap between any two climate scenarios. Note that conifer biomass was greater under the RCP 6.0 climate scenario than for climate scenario RCP 2.6. Hypothesis 5, that all response variables except the quantity of biomass harvested will respond most favorably to CCA under RCP 8.5 and least favorably to BAU, and that the DIV strategy will respond most favorably to the intermediate RCP 6.0 climate scenario, was not supported (Figs. 3 and 5, Tables S2–S4). The expectation was met for some variables (including total biomass), but not for others. Hypothesis 6, that CCA will best maintain harvested biomass and species diversity under both RCP 6.0 and 8.5, was not supported. The intense harvest rates of BAU could not be matched by CCA, even with the increased growth produced by CO_2 fertilization. Note that harvested biomass under BAU was highest under RCP 6.0 and lowest under RCP 8.5, demonstrating that temperature stress can eventually overwhelm the growth effects of CO_2 and longer growing seasons to reduce the biomass supply, providing additional insight to the results of Gustafson et al. (2018b) that showed less of a negative temperature effect under lower CO_2 concentrations.

There are five general insights from our modeled results. First, our results suggest that novel forest management strategies can produce significant improvements in outcomes compared to BAU under all CO_2 scenarios (Figs. 4a, 4b, 7, Table 6). The alternative management strategies increased landscape biomass to a greater extent than BAU under higher CO_2 scenarios, and generally produced more favorable outcomes for all variables except biomass harvested. Our methods evaluated only two generic adaptive silviculture alternatives, but the results suggest

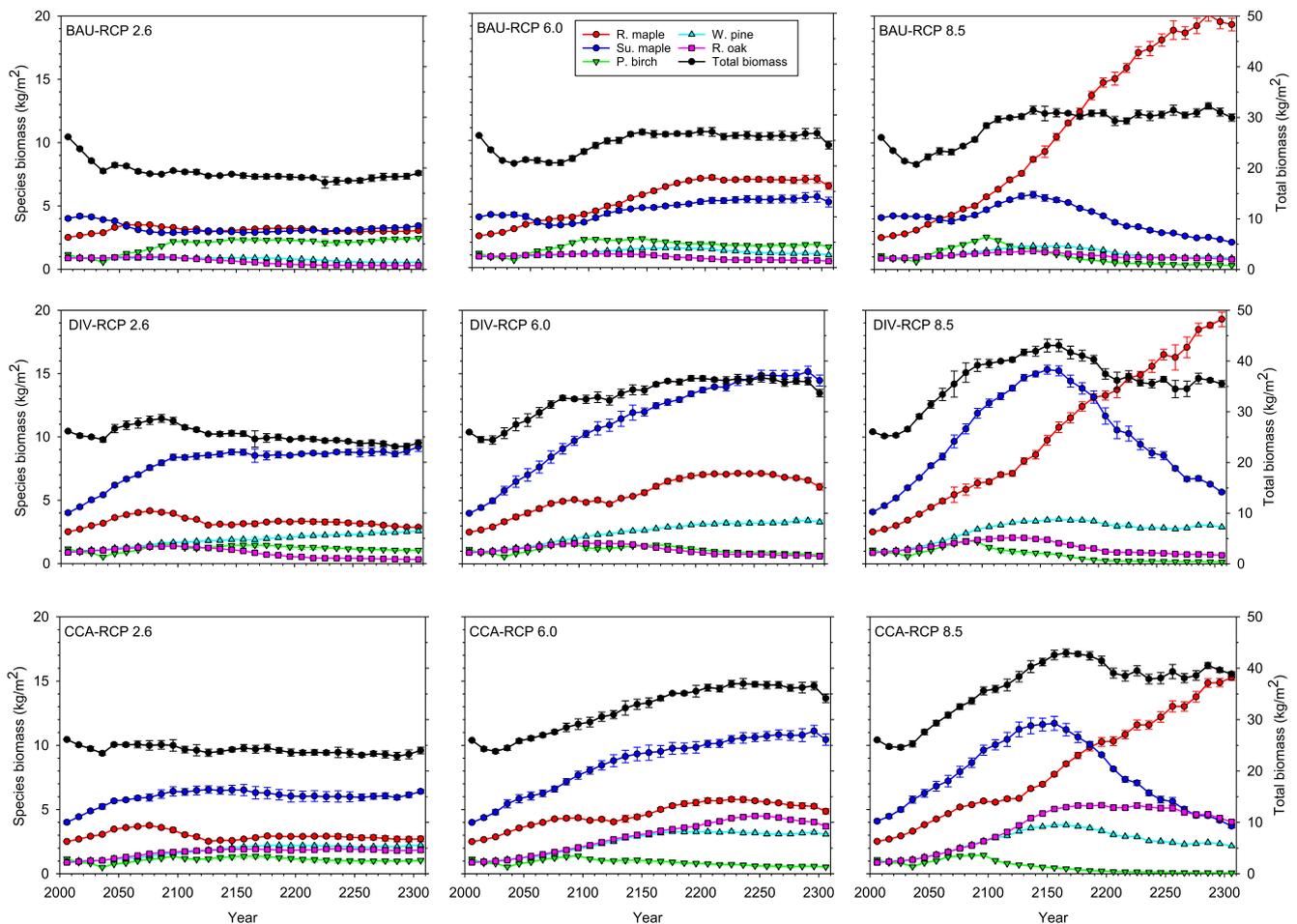


Fig. 4a. Mean biomass through time of the five most abundant species by treatment combination. The y-axis is landscape aboveground biomass for each species (left y-axis) and for all species combined (right y-axis, black curve). Error bars show 95% confidence intervals.

that other more specific and more creative alternatives could be screened using our methods for landscape-level effectiveness prior to conducting expensive field studies of stand-level effectiveness.

Second, the longevity of trees results in considerable inertia against climate change because weather itself rarely kills individuals. This gives management strategies considerable time to be implemented and produce desired species composition before the existing forest completely dies off. Our study area has tree demographics that reflect a landscape-wide cutover approximately 100 years ago, but that type of historical harvest disturbance is representative of many forests in the central and eastern United States. There is some concern that even the most aggressive climate adaptive strategies will be unable to maintain ecosystem goods and services provided by forests (e.g., [Chmura et al., 2011](#), [Ledig et al., 2012](#)), but our study that evaluates forest outcomes after regeneration, harvest, and mortality of many tree cohorts over 300 years of management suggests that there is a path to discovering effective options.

Third, CO₂ and temperature were linked in our abiotic model inputs, and our results clearly show that these two factors create a tension in forest response. CO₂ fertilization, especially under the extremely high levels of the RCP 8.5 scenario, provides a powerful stimulant to tree growth that can mitigate heat stress to some degree ([Gustafson et al., 2018b](#)). However, temperatures increase greatly with such elevated CO₂ levels, with some temporal lag. While this can lengthen growing seasons considerably, for some endemic species, heat stress can eventually dampen photosynthesis for enough of the growing season to reduce their competitiveness such that they are extirpated from the

landscape. This causes niches to be vacated and filled by either other endemic species that may not provide similar ecosystem goods and services, or by introduced non-endemic species that have characteristics similar to the extirpated ones.

Fourth, our results suggest that a CCA approach may provide enough versatility to produce desirable outcomes regardless of what the future climate is. CCA was related to high ecological and economic value and also resulted in high residual biomass on the landscape. CCA can provide recoverable volume, or wood volume potentially available for harvest if objectives warrant (*sensu* [Hanson et al., 2012](#)), providing options for adaptive management over time. Our CCA strategy retained some elements of DIV such that this CCA strategy was based on regional ecological research and management recommendations. In contrast, CCA strategies could be inspired by high intensity plantation management to facilitate rapid change in forest structure and composition to create forests resilient to changing climatic conditions. A high intensity management approach could increase harvested biomass and support economic values, but the effects of rapid forest structure and composition changes on ecological values are not clear and would require additional study ([Pawson et al., 2013](#)).

Lastly, it is obvious from our results that the forests of today (at least in the ecosystem studied) cannot be maintained over the next three centuries in their current state under likely climate futures, but diverse and productive forests can nevertheless be produced to continue to provide ecosystem goods and services, made possible by a combination of thoughtful forest management, the fertilization effect of elevated CO₂ and lengthened growing seasons. More focused study is needed to

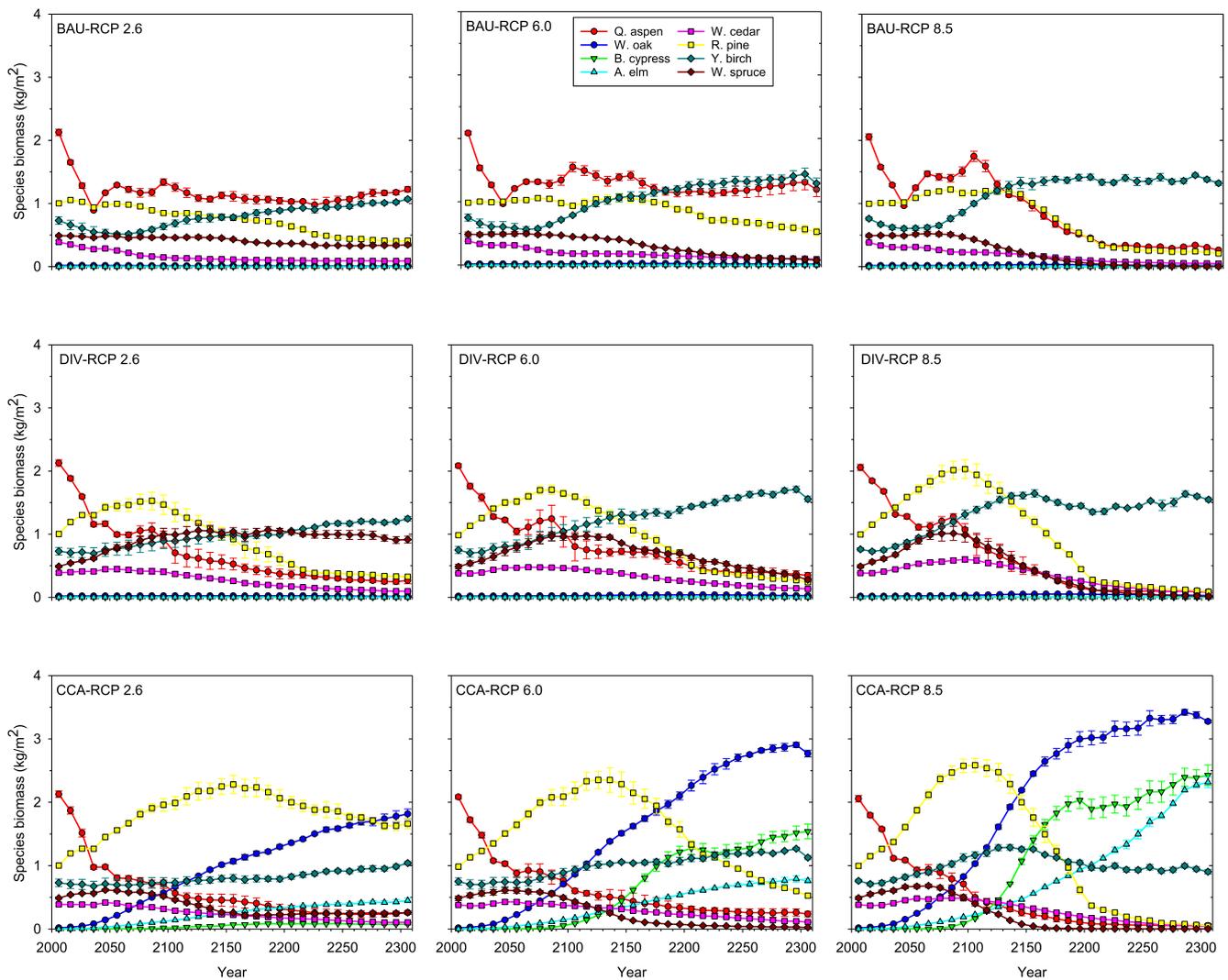


Fig. 4b. Mean biomass through time of eight additional species by treatment combination. Note that y-axis scaling differs from Fig. 4a. Error bars show 95% confidence intervals.

Table 6

Mean and 2 × standard error (95% confidence interval) of the biomass (final 100 years) of the species in groups categorized as ‘High’ in economic, ecologic, and mast value, and of aggregation index values of forest type maps, by silviculture treatment and future climate scenario. Mean values that are not significantly different are indicated with the same letter. Means for each treatment combination can be found in Tables S2–S4.

| Treatment | High economic value species | High ecologic value species | High mast value species ¹ | Forest type aggregation index |
|------------------------------|-----------------------------|-----------------------------|--------------------------------------|-------------------------------|
| <i>Silviculture strategy</i> | (kg/m ²) | (kg/m ²) | (kg/m ²) | (%) |
| BAU | 6.6 (0.14) | 11.0 (0.16) | 0.9 (0.06)A | 53.6 (0.62)B |
| Diversify | 13.7 (0.14) | 10.1 (0.16) | 0.9 (0.06)A | 54.0 (0.62)B |
| CC Adaptive | 15.2 (0.14) | 13.9 (0.16) | 6.5 (0.06) | 46.5 (0.62) |
| <i>Climate scenario</i> | | | | |
| RCP 2.6 | 9.4 (0.14) | 4.8 (0.16) | 1.6 (0.06) | 55.3 (0.62) |
| RCP 6.0 | 15.3 (0.14) | 9.9 (0.16) | 3.1 (0.06) | 51.4 (0.62) |
| RCP 8.5 | 10.8 (0.14) | 20.2 (0.16) | 3.6 (0.06) | 47.3 (0.62) |

¹ Species that produce acorns and nuts, but not winged seeds or cones.

determine what specific ecosystem goods and services may require more intentional management to sustain.

A more specific result is that the diversity of tree species appears quite sensitive to climate change such that several dominant broadleaf species essentially take over at the expense of other, largely needle-leaved species. This shift in leaf habit diversity represents change in many ecosystem processes. For instance, broadleaves tend to have higher photosynthesis efficiency than needles, affecting forest

productivity (Reich et al., 1995). Tree species diversity, particularly the mixture of broadleaved (deciduous) and evergreen, needle-leaved (coniferous) species, is a key characteristic of the Laurentian mixed forests (Niemi et al., 2016, Fisichelli et al., 2014). Increased broadleaf and decreased needle foliage may increase forage quality for browsers; yet, important winter thermal cover that conifers provide will diminish (Schmitz, 1991). Overstory tree diversity also affects belowground processes: mycorrhizal fungi diversity is higher in mixedwood forests

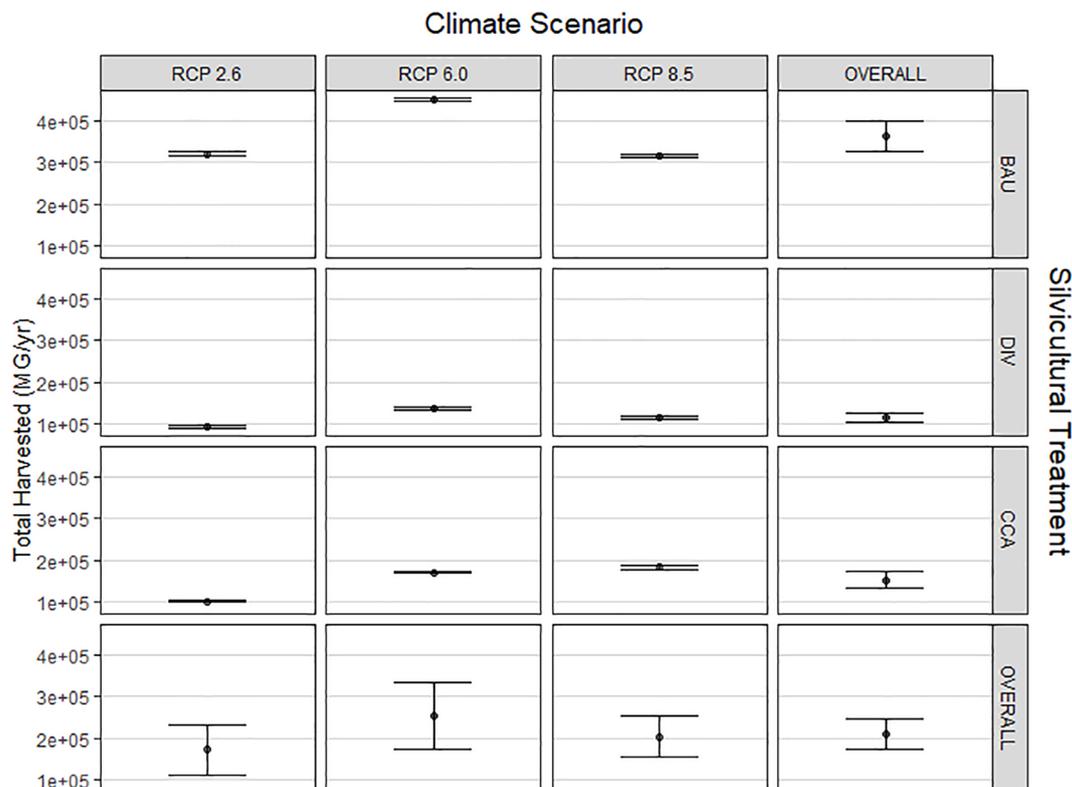


Fig. 5. Assessment of the effect (final 100 years) of the treatment factors on total biomass harvested across the study area. Error bars show 95% confidence intervals.

than monotypic forests of broadleaved or needle-leaved species (DeBellis et al., 2006).

Other studies, such as Crookston et al. (2010), use modeling to investigate the processes underlying the relative efficacy of climate change adaptation strategies. Their application of Climate-FVS (not yet available for eastern forests of the conterminous United States), includes some processes analogous to those simulated here, such as the effects of climate change on non-spatial factors underlying competitive interactions among tree species (e.g., growth, reproductive success, and mortality as a function of climatic drivers). As demonstrated here, factors not accounted for in empirical approaches such as FVS (i.e., atmospheric CO₂ concentrations) can have very strong influence over biomass accumulation and competitive interactions (e.g., Gustafson et al., 2018d). Other processes not accounted for in our study, such as tree species provenance, might have similarly important implications for the efficacy of CCA strategies (Crookston et al., 2010), and might be accommodated in future applications of our approach. We did not specifically investigate the sensitivity of our results to spatial processes included in our landscape modeling approach, but not addressed by non-spatial models such as FVS. However, past studies have shown that spatial processes such as seed dispersal, disturbance patterns, and their interactions introduce additional system inertia via “ecological memory” (Peterson, 2002).

4.2. Effect of disturbances

Natural disturbances were modelled in the background of each treatment scenario. In all scenarios, we simulated the emerald ash borer (EAB) insect pest, which killed over 80% of the cohorts of the three ash species within 20 years, and extirpated all ash species by 2100 (not shown). Under DIV and CCA, we simulated an aggressive attempt to conserve lowland hardwoods by doubling the normal cutting rate of stands dominated by black ash and establishing either red maple or silver maple (depending on silviculture treatment) in them. However,

even with this ambitious cutting schedule, the model was unable to convert all black ash stands before they were killed off by EAB and replaced by natural recolonization of lowland conifers and other flood-tolerant species such as red maple.

The area burned annually was small and was not affected by either the climate or the silvicultural treatments (not shown) in spite of modestly altered ignition probabilities across climate scenarios. Although there is some potential for exacerbated fire disturbance under warmer and drier conditions (Miranda et al., 2012), fires in this region are strongly suppressed, and consequently affect a small proportion of the landscape (Sturtevant and Cleland, 2007). Wind disturbance is currently far more prevalent. Indeed, in 2007 the study area was impacted by a severe tornado damaging a swath of vegetation nearly a kilometer in length, while the entire study area was impacted by back-to-back derecho events in summer of 2019 (J. Lampereur, *pers. comm*). In our simulations, area damaged by microburst wind events was not affected by silvicultural treatments, but the area damaged declined modestly with warmer climate treatments (not shown), reflecting the increased wind rotation lengths coupled with increased wind intensity thought to be associated with warming climate (Knutson et al., 2010). The area damaged by derechos and tornadoes was highly variable through time and among replicates, and did not differ by either the climate or the silvicultural treatments (not shown). We simulated these natural disturbances as background disturbances that, while consistently applied across all treatments, created some variability across replicates representing uncertainty reflective of this region.

4.3. Major assumptions

Our study implies some important assumptions that should be noted. First, we assumed that simplistic timber management rules adequately mimic the landscape consequences of decisions made by multiple foresters based on specific stand and market conditions and landowner goals. This assumption is required by landscape models

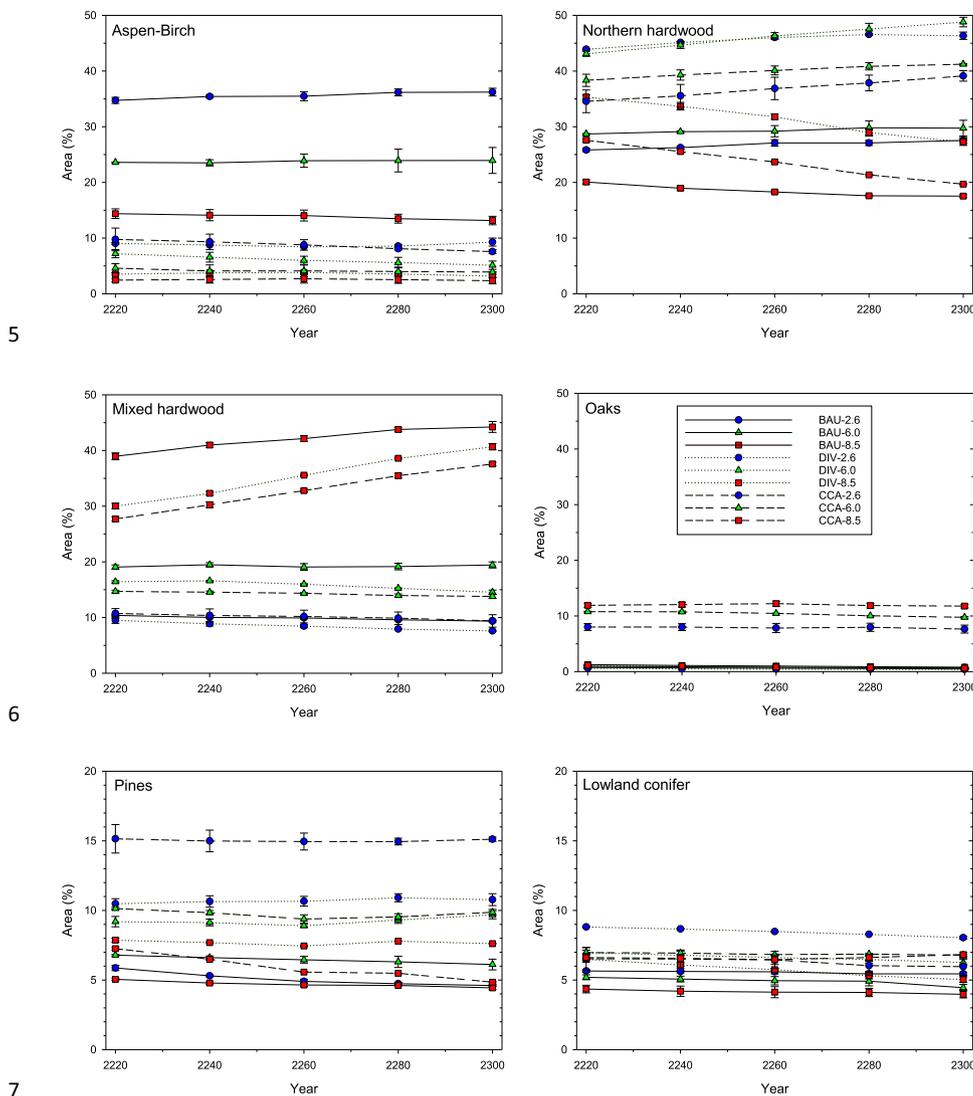


Fig. 6. Effect of the treatment factors on the proportion of the landscape occupied by forest types. Symbols indicate climate scenario and lines indicate silvicultural strategy. Error bars show 95% confidence intervals. Note that y-axis is scaled differently for each graph.

because a more mechanistic simulation of economic cycles and the decisions of multiple agents is computationally prohibitive and highly uncertain. Second, we assumed that climate effects on forest successional dynamics were limited to CO₂ fertilization, temperature effects on photosynthesis (including lengthened growing seasons), soil water stress, and disturbance regime effects. There is evidence that climate can also affect disease virulence and tree susceptibility, insect outbreak dynamics (e.g., Régnière et al., 2012), invasive species dynamics (Logan et al., 2003), and produce some acclimation to chronically altered abiotic conditions. PnET-Succession does account for acclimation to CO₂ concentrations as high as those used in this study according to Franks et al. (2013), but it does not include acclimation to temperature. Warming climate is also expected to increase the incidence of extreme weather events that can have important effects on forest structure and succession. PnET-Succession does model those events that produce a signal at a monthly time step (e.g., drought, heat waves), but is unable to account for events that occur at a daily temporal scale (e.g., late spring frost or concentrated precipitation). Finally, we assumed that the RCP 8.5 climate scenario would continue the increases in CO₂ and temperature beyond the year 2100 and stabilizing thereafter. This is consistent with the scenario description (IPCC, 2013) and the non-declining trends through 2100 (Fig. 2).

4.4. Caveats

Our study examines generic forest management strategies, and does not account for all the many site-level and local market conditions that drive on-the-ground stand management decisions. Further, forest management systems are often based on adaptive management cycles (Walters, 1986). Our study did not attempt to simulate adaptive management, but instead showed the long-term consequences of specific climate-adaptive strategies implemented in perpetuity. Our study is therefore a proof-of-concept evaluation of the ability of a mechanistic forest landscape model to conduct experiments to reduce uncertainty surrounding the ability of climate adaptive silvicultural strategies to achieve their stated objectives. We also did not include new pests (except EAB, which is already present within < 100 miles) or diseases and changing timber markets. Important trophic interactions such as deer browse were also not included. Nevertheless, our results provide critical insights into the long-term, landscape-level effects of the generic forest management strategies that we evaluated.

Some of the variability of tree species biomass through time reflects the demographics of the specific study area we used. Rounded peaks in species biomass trends followed by declines (Figs. 4a, 4b) were often the result of simulated growth and senescence of many similar-aged

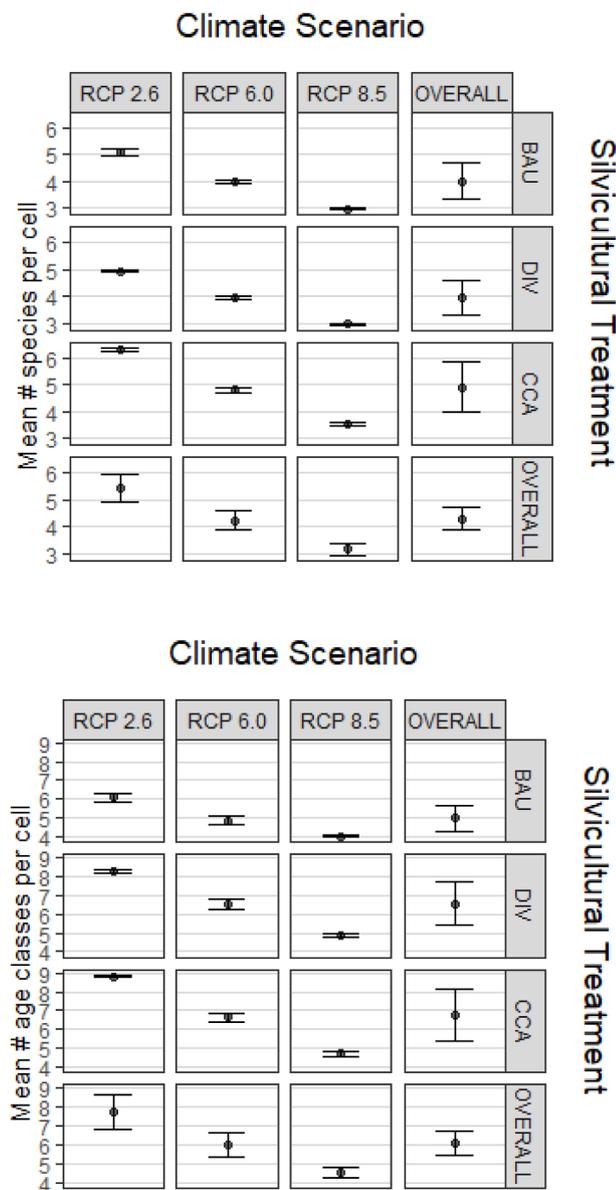


Fig. 7. Mean site-scale richness (species and 5-year age class) by treatment combination. Error bars show 95% confidence intervals. Plots reflect an average of all climate scenarios in each management scenario and an average of all management scenarios in each climate scenario.

cohorts across the landscape. Simulated abrupt declines were usually caused by large-scale disturbances, such as derechos. Additionally, each climate model has unique sensitivities, and we used a single climate model. Therefore, the generality and uncertainty of our results should be assessed by replicating our methods with other climate models and for other ecosystems with alternative initial species demographics and initial forest age diversity.

Species temperature parameters (Table 4) are not well established empirically. We estimated them by assuming that optimal temperatures were related to the July isotherm at the center of each species' range, minimum temperature to the northern range boundary, and maximum temperature to the southern range boundary. Absolute values for temperature parameters were generated for species for which we had the greatest empirical confidence, and the other species were set relative to those species based on range map comparisons. This results in some uncertainty because range boundaries can be determined by factors other than temperature, such as land use, land form, precipitation and disturbance regimes, but we believe that the error in relative

differences in temperature parameters is low. Thus, the absolute response of species to the climate inputs is likely to be more uncertain than the relative response. Consequently, we focus our analyses on relative changes in response to silviculture and climate effects rather than on absolute responses for any individual treatment combination. Empirical research to establish species photosynthetic response to temperature (including acclimation to temperature) is needed to improve our ability to accurately simulate climate change effects at landscape scales. It is also possible that one or more limiting factors will limit the ability of forests to take advantage of such high CO₂ concentrations. It is uncertain what those factors might be for our study area, and our model does not track soil nutrients (e.g., nitrogen), which are among the most likely candidates.

We used overlap of 95% confidence intervals to assess significance of treatment effects. It must be noted that the variability among replicate simulations was low because we intentionally minimized stochasticity of the inputs to maximize the signal from the treatments. Specifically, a consistent climate/weather stream for each of the three climate scenarios was applied across replicates and silvicultural treatments to eliminate the effects of climate and weather uncertainty on treatment responses. Furthermore, the response variables were mean values across a large landscape. Because there is a danger of inflating impressions of significance by excessive replication of modeling experiments (White et al., 2014), we limited the number of replicates to five. We believe that this approach provides a realistic picture of the effect of the treatment effects.

4.5. Management implications

Our results raise questions of the appropriate trade-off between sustained yield and other ecosystem services of interest (i.e., economic value, ecological value, and wildlife value). In our simulations, sustained yield (BAU) produced the most wood under all climate scenarios, although it also appeared to be the most sensitive to extreme climate. The implication of this result is that the DIV and CCA strategies leave a lot of residual biomass on the landscape, which creates recoverable biomass and options for managers. We did not simulate adaptive management, which is the most likely response to such options. Managers re-evaluate stand and landscape conditions before implementing any harvest activities (Alexander, 2013), and almost certainly will not be doing the same thing for 300 years. The large difference between BAU and the other strategies suggests that there may be some flexibility in the details of DIV- and CCA-like strategies to achieve a similar improvement over a BAU approach. However, these flexibilities would need to be constrained by the goals of the alternative approaches. For example, adjustments to rotation, retention, and harvest area should be weighed against other ecological and social goals to remain consistent with overall DIV- and CCA-like strategies.

Moreover, the shifts in the abundance of individual species lead to shifts in forest types. Boreal and conifer types decreased in area with increasing climate scenario, while oaks and mixed hardwoods showed the opposite trend. Some silvicultural strategies were more effective at increasing or maintaining certain forest types (e.g., BAU and Aspen-Birch), but no forest type was lost from the landscape due to silvicultural strategy or climate scenario. In other words, drastic forest type-wide mortality events due to management or climate may not be likely, suggesting a temporal window for managers to implement a combination of adaptive strategies in the context of the forest condition and the threats it faces over time (Rissman et al., 2018). Our study does not provide guidance on the best mix of adaptive strategies, but provides the outcomes of the general strategies we simulated.

On the other hand, homogenization of forest landscapes through the expansion and dominance of individual species or forest types there is a considerable concern for the future of eastern U.S. forests (e.g., Schulte et al., 2007), such as expansion of 'super-generalist' red maple (Abrams, 1998). Our simulations suggest that red maple expansion is exacerbated

by climate change under BAU management, but the DIV and CCA management strategies were able to mitigate this trend to some degree (Fig. 4a). Future simulation studies will be conducted to explore targeted strategies to address specific management issues such as this.

4.6. Conclusions

Our results demonstrate the competing effects on vegetation of CO₂ fertilization (and longer growing seasons) and heat stress that can result in the replacement of some species by non-endemic species that may or may not provide similar ecosystem goods and services. It seems clear that Laurentian forests of today cannot be maintained in their current state under likely climate futures, but our study suggests that creative silvicultural practices can be developed to maintain productive and ecological healthy forests. Our study provides proof-of-concept for the utility of mechanistic forest landscape modeling to assess the effectiveness of proposed climate adaptive silvicultural strategies in achieving their stated objectives. Of the silvicultural strategies we studied, our results suggest that climate adaptation practices may result in high productivity, diversity, and economic value, providing options for adaptive management over time. Future studies can refine the details of such strategies for specific ecosystems and management objectives, and used to inform more expensive field studies.

CRedit authorship contribution statement

Eric J. Gustafson: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing - original draft. **Christel C. Kern:** Methodology, Validation, Writing - review & editing. **Brian R. Miranda:** Software, Writing - review & editing. **Brian R. Sturtevant:** Methodology, Formal analysis, Investigation, Visualization, Writing - review & editing. **Dustin R. Bronson:** Methodology, Validation, Writing - review & editing. **John M. Kabrick:** Methodology, Validation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118208>.

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