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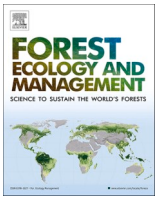

Can assisted tree migration today sustain forest ecosystem goods and services for the future?

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ABSTRACT

Forest managers are exploring options to proactively facilitate forest adaptation to climate change (resistance or resilience) or to introduce species (transition) that are better suited to future climates. Forest managers must have confidence that implementing an assisted migration (AM) transition strategy will maintain a more reliable stream of goods and services than strategies emphasizing resistance or resilience. The outcome of transition strategies can be evaluated with forest landscape models having direct links to climate and atmospheric drivers. We used the LANDIS-II forest landscape model to conduct a simulation experiment in northern Wisconsin (USA) with climate scenarios and AM strategies as treatment factors, and metrics of ecosystem goods and services as response variables. We found that major forest functional types were maintained under some climate change with AM strategies that selected species having similar silvics and site adaptations as existing species but sourced from different climate regions. We also found that AM alone was increasingly unable to maintain ecosystem goods and services (e.g., productivity, wildlife food) with increasing severity of climate change. For instance, total woody biomass, total harvested biomass, and species and age class richness were largely determined by the climate scenario and not AM strategy. Our results suggest that modest changes in climate are likely to enhance species diversity and increase biomass production through longer growing seasons and CO_2 fertilization, but that under extreme climate change even the most aggressive AM strategies fail to mitigate the deleterious effects of moisture stress and increased respiration on overall productivity. Where AM strategies were successful, there were subtle and unintended changes in the extent of available landscape goods and services. Additional research is needed to further refine AM strategies to conserve a complete range of goods and services under changing climate.

1. Introduction

Resilience of forest ecosystems to stressors is critical to support a sustainable flow of goods and services to societies around the world. Although most forest ecosystems are inherently resilient because of their diversity of plant species, climate projections indicate that sustained changes in precipitation and temperature patterns are likely to compromise tree regeneration and migration patterns (Gulev et al. 2021, Zhu et al. 2012, Thompson et al. 2009). Therefore, forest managers will need to be increasingly aware of how precipitation and temperature patterns are likely to change in their location and understand how management options might impact forest resilience and sustainable ecosystem goods and services for centuries to come.

The discipline of silviculture provides a toolbox of management actions to produce desired forest stand conditions, and modification of those actions is thought necessary to create forests today that will be resilient and adapted to future conditions (Nagel et al. 2017). Such adaptation strategies generally include silvicultural practices that proactively increase a forest's resistance or resilience to climate change or help forests transition to species compositions and age structures better suited to anticipated future climates (Millar et al. 2007). Resistance and resilience strategies include the application of regeneration and thinning methods to enhance the vigor and growth of present or endemic tree species that are deemed better adapted to future conditions. Transition strategies employ similar regeneration and thinning methods but also seek to alter the existing species composition through supplemental or "enrichment" planting to enhance compatibility with future climates (Swanston et al. 2016).

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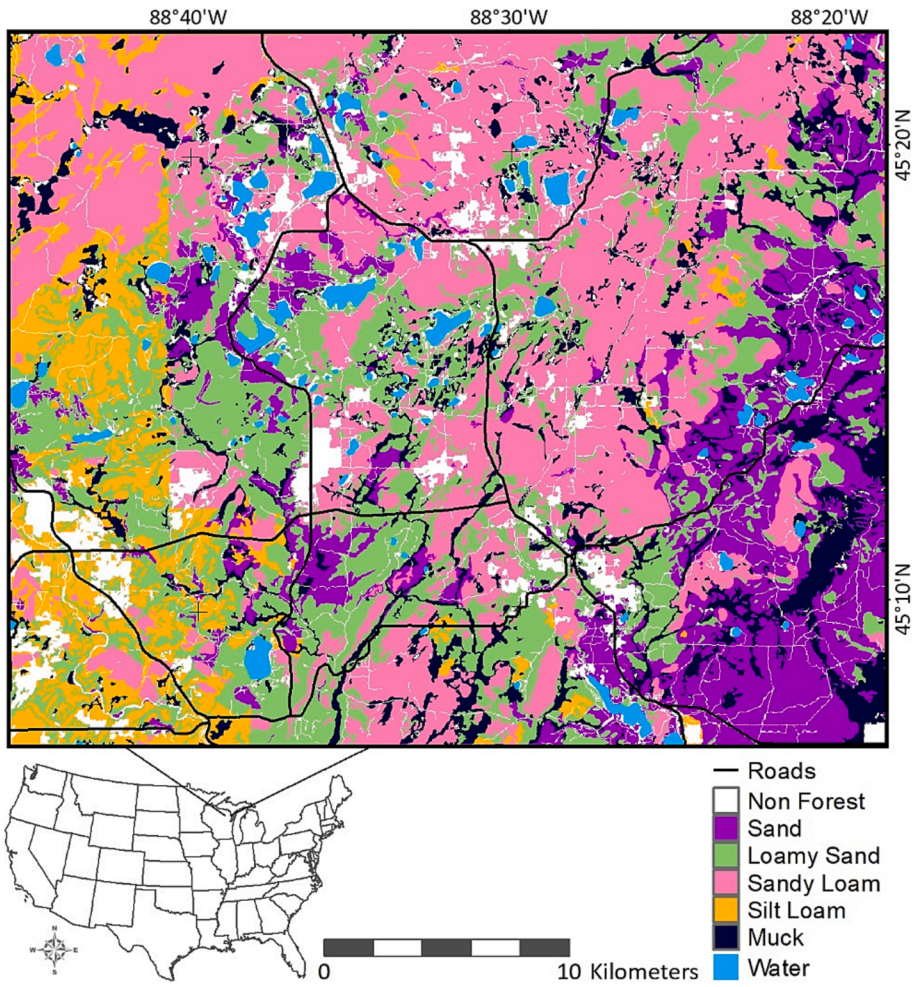

Fig. 1. Study area (104,471 ha) location in Oconto County (Wisconsin, USA), showing the general soil types affecting soil water availability and dominant forest community types.

Of the adaptation strategies, transition strategies, including those described as "assisted migration" (AM), are the most aggressive because they seek to fundamentally alter the composition and genetic diversity of forests (Williams and Dumroese 2013). However, forest managers must have confidence that implementing an AM strategy will maintain a more reliable stream of goods and services than strategies that retain only the species present or endemic on the current landscape. Modeling studies have indicated that continued planting of species already present, but low in abundance, may not ensure indefinite persistence, resulting in lower landscape aboveground forest biomass than in current conditions (Duveneck et al. 2014). Early results for a few species indicate that provenances from warm northern hemisphere climates can survive in experimental out-plantings to cooler, more northerly settings where the climate is anticipated to warm in the future (Etterson et al. 2020). However, seedlings of other species planted to mimic AM have not always survived under the current climate conditions (Tíscar et al., 2018). Results from silvicultural trials and literature review show that local and regional factors (e.g., browse, competing vegetation) may reduce the ability of AM to successfully adjust future forest composition (Clark et al. 2022; Champagne et al. 2021). The urgency of climate change calls for the implementation of novel silviculture strategies now to sustain forest ecosystem goods and services in the distant future. Therefore, there is a need for studies, beyond long-term field experiments, to evaluate the efficacy of various transition strategies so that they can be applied with an acceptable level of confidence.

Evaluating the efficacy of transition strategies (such as AM) for uncertain climatic forecasts is challenging because forests developed from AM are unlikely to have natural analogs in their biome and thus represent novel ecosystems. The outcome of transition strategies can be evaluated with forest landscape models having direct links to climate and atmospheric drivers to fully capture the interactions among plants, soils, climate factors, and natural and management disturbances over long time periods. For example, in a modeling study of the effects of climate and adaptive forest management on forest composition in Vermont (USA), inertia from the initial forest landscape condition was predicted to be more important than climate over the first 100 years while climate had the greatest effect in the subsequent century (Nevins et al. 2021). In northern temperate forests, modeled AM strategies of trees sourced just south of study landscapes showed low success after 150 years under high emission climate scenarios and the authors speculated that species sourced from farther south might have greater success (Duveneck and Scheller 2015). Modeled AM also produced greater resilience (e.g., biomass) than business-as-usual strategies, although extreme climate change may overwhelm silvicultural strategy after 200 years (Duveneck and Scheller 2015). Other forest landscape modeling studies predict that AM strategies can increase functional diversity but may also increase vulnerability to disturbance. For example, a simulated transition of a landscape from a cool boreal-temperate to warm temperate forest composed largely of central/southern hardwoods resulted in more vulnerability to generalist non-native insect outbreaks than the initial mixedwood landscape (Mina et al. 2022). Evaluating transition strategies is necessary to understand the economic and ecologic costs of implementing approaches that attempt to provide the expected ecosystem goods (commodities) and services, and

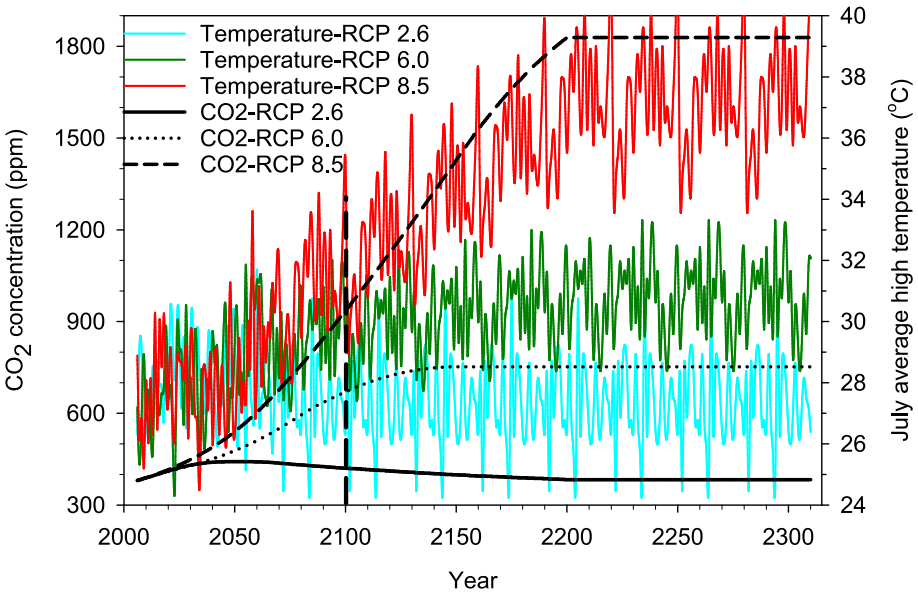

Fig. 2. Projected future atmospheric CO_2 concentration and temperature trends under the three climate scenarios for our study landscape. CO_2 concentrations estimated to 2200 by Meinshausen et al. (2011). The vertical dashed line at year 2100 indicates the transition from GFDL temperature projections to extrapolated values. .
Adapted from Gustafson et al. (2020a)

comprehensive studies using landscape models could fill this knowledge gap.

In a previous study, our group used the LANDIS-II forest landscape model to project the impacts of contrasting generic silviculture strategies on forest productivity and composition (Gustafson et al. 2020a). A "business as usual" scenario representing current sustained yield practices was compared to two climate-adaptive silvicultural strategies; 1) a "diversify for resilience" scenario designed to increase multiple aspects of stand heterogeneity to make stands more resilient to disturbance, and 2) a "climate change adaptation" scenario designed to incorporate transition strategies into the "diversify for resilience" approach. Each scenario included planting to achieve its goals, but only the "climate change adaptation" scenario used AM, involving a very limited number of species. That study suggested that climate-adaptive silvicultural practices could be developed (and tested) to maintain forest productivity under climate change, but the tested AM strategy was limited in scope and failed to maintain all forest functional types needed to broadly sustain ecosystem goods and services. The current study uses the same modeling framework but focuses on climate-adaptive transition scenarios explicitly designed to broadly maintain the ecological function, extent and diversity of existing forest types and to clarify the role that AM must play to make such climate-adaptive transition strategies successful under various climate futures.

The objectives of our study were to 1) assess how increasingly aggressive AM strategies (i.e., increasingly dissimilar climate between seed source and out-planting site) affect the maintenance of the ecosystem goods and services currently provided by upper Great Lakes (USA) forests, 2) assess how increasing severity of climate change impacts the ability of silvicultural strategies to sustain ecosystem goods and services, and 3) understand the interaction between AM strategies and climate change to provide insight into how aggressive (i.e., plant species mix and migration distance) AM must be to sustain ecosystem services under various potential climate projections. To achieve these objectives, we conducted a simulation experiment using a physiologically mechanistic module of LANDIS-II (PnET-Succession), which robustly simulates the competition of tree cohorts for light and water to support photosynthesis while accounting for dynamic CO_2 concentration and climate (De Bruijn et al. 2014). Specifically, based on our last study (Gustafson et al. 2020a), we anticipated that higher emission scenarios would increase productivity (i.e., CO_2 fertilization effect) compared to current climate; consequently, transition harvest prescriptions could be increased in frequency, intensity, and extent to sustainably capitalize on available merchantable timber and provide increased growing space for new tree cohorts established through AM (compared to our previous study which used extended rotations and higher retention after harvest, producing less growing space for new cohorts). With this climate-adaptive approach to forest transition, AM would be implemented to change forest composition for the purpose of maintaining the areal extent of forest functional types to sustain forest resilience, thereby potentially sustaining the availability of ecosystem goods and services for existing infrastructure, systems and communities on the landscape. We hypothesized 1) that greater levels of climate change would require more aggressive AM (taxa moved greater distances) to maintain ecosystem goods and services and 2) that AM alone would be increasingly unable to maintain ecosystem function as the degree of climate change increased.

2. Methods

2.1. Study area

Our simulation experiment was conducted on a 104,471 ha Laurentian mixed forest ecosystem in northeast Wisconsin (USA) (Fig. 1). Forest types in the study area are strongly shaped by glacial landforms that create a sharp soil moisture gradient from mesic (west) to xeric (east), with interspersed lakes and lowland forest throughout (Sturtevant et al. 2009). Mesic forests are dominated by northern hardwood species (e.g., sugar maple, yellow birch, American basswood; see Table A1 for scientific names), while xeric forests are dominated by oak and pine forests (i.e., red oak, pin oak, jack pine, and red pine). Boreal species (e.g., quaking and big tooth aspen, paper birch, and balsam fir) are common throughout the landscape, while lowlands contain species such as black ash, white cedar, tamarack and black spruce. This landscape has a mix of federal and private 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.

Table 1
Climate-adaptive silvicultural prescriptions for forest transition with climate change. The harvest timing, intensity, and extent of silviculture prescriptions were determined by forest type and stand age. Silvicultural prescriptions were constant across AM strategies; only planting differed (Table 2). See harvest input file in the Supplement for full details.

Silvicultural prescription	Rotation or cutting cycle (yr)	Retention after each harvest entry (% biomass remaining)[1]	Harvested area (% of stand)	Types targeted[2]
Selection	15	100 (age 1–60), 70 (age 61–105), 2 (age > 105)	100	Northern Hdwd
Shelterwood (2-entries)[3]	65–90	Initial entry: 20–60 (age > rotation length) Final entry: 0–50 (age > rotation length + 10)	100	MxdHdwd, Birch, Oak, Lowlnd Hdwd, CentHdwd, SouthHdwd
Clearcut	50–135	0–5	100[4]	Aspen, J pine, Spruce-Fir, W pine, R pine, Lowlnd Conif, Pine-oak

[1] Ranges reflect forest type-dependent differences.
[2] Forest types in which silvicultural strategy is used.
[3] Second entry 10 years after first entry.
[4] Complete cutting of clearcuts, except when not planting cut 96%, to allow for reserve trees.

2.2. Experimental design

The simulation experiment was designed with two main factors (climate scenario and AM strategy), each with three treatment levels. The climate factor levels were based on standard CO_2 Representative Concentration Pathways (IPCC 2013): 1) RCP 2.6 (minimal change in CO_2, "Limited climate change"), 2) RCP 6.0 (intermediate increase in CO_2, "Moderate climate change"), and 3) RCP 8.5 (dramatic increase in CO_2, "Extreme climate change") (Fig. 2). The monthly climate projections for the climate treatments were generated by the General Fluid Dynamics Laboratory earth system model (GFDL-ESM2G, r1i1p1) (Dunne et al 2012). To include increases in CO_2 beyond the year 2100, we used extrapolations of CO_2 concentration (Extended Concentration Pathways) to 2200 for each RCP scenario (Meinshausen et al. 2011), holding the final concentration constant after that to mitigate the massive uncertainty around projections of CO_2 concentration in excess of 2000 ppm and the uncertainty about the acclimation of plants to such elevated CO_2 levels (Moore et al. 1999). These climate scenarios were used in our prior paper (Gustafson et al. 2020a), allowing comparisons with those results. Climate (i.e., temperature and precipitation) projections provided by the GFDL Earth System Model have not been extrapolated beyond the year 2100, but temperature rise is expected to continue even if CO_2 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 but incrementing those values for an additional 100 years using the trend of the first 100 years, with a flat trend thereafter (Fig. 2). Because precipitation had a negligible trend under all climate scenarios, we did not extrapolate any trend beyond year 2100, but repeated the last 30 years of the projected values (not shown).

The AM strategy factor also had three levels and each level increased the distance between the study area (out-planting site) and the source of the taxa that were planted. Each of the three strategies were embedded within a standard silvicultural prescription that was designed for a climate-adaptive approach to forest transition with climate change (Table 1). That is, the harvest frequency, intensity, and extent varied by forest type in the same way across AM strategies, with only planting differing by AM strategy. The aggressiveness of AM strategies was considered to be proportional to the distance between the source and out-planting sites. New cohorts were established by planting after every harvest event during the first rotation, with species planted (Table 2) tailored to the forest type of the stand harvested and AM strategy (Table 1). The "Short-range" migration strategy used the AM of native species with provenances south of (warmer than) the study area. Because there are few empirical data on the temperature drivers of photosynthetic output of different provenances, we altered existing model parameters (Short-Range AM species only) in a simplistic way to cause the photosynthetic output of the southerly provenances of endemic species to be optimal under slightly warmer temperature regimes. This was achieved by adding 1 degree (C) to LeafOnMinT and PsnTMin, and 2 degrees to the PsnOptT, PsnMaxT and ColdTol values of the native provenances, while leaving all other life history parameters unchanged (Table A2). The "Medium-range" migration strategy used the AM of non-endemic species whose native ranges are south of and warmer than the study area. The "Long-range" migration strategy assisted the migration of species whose native ranges are considerably south of and warmer than the study area; Long-range AM species overlapped with or were farther south than species used in the Medium-range migration strategy. The species selected in Medium- and Long-range AM strategies have familiar approaches to artificial regeneration, where the site condition (e.g., soil nutrient and water supply,

Table 2
Species planted by AM strategy and forest type. Planting was implemented for the first rotation (see Table 1) of shelterwood and clearcutting; four cutting cycles (60 years total) with selection cutting. Species codes are defined in Table A1.

Prescription/ forest type	Short-range	Medium-range	Long-range
Selection-Northern Hdwd [1]	Su. maple-S, Y. birch-S, Basswd-S	B. hickory-M, W. oak, Bl. maple	Sw. gum-L, B. birch-L
Shelterwood-MxdHwd [2]	R, maple-S, B. cherry-S, N.R. oak-S	B. hickory-M, W. oak, Bl. oak-M	Y. poplar-L, Sw. gum-L, W. basswd-L
Clearcut-Aspen	Q. aspen-S, BT aspen-S,	E. cottnwd-M,	N. poplar-L
Clearcut-Jack pine	J. pine-S	Pit. pine-M, Bl. oak-M	Sh. pine-L, S. R. oak,-L Ch. oak-L
Clearcut-Spruce-Fir	W. oak	B. tupelo-M, R. spruce-M	S.R. oak-L, F. fir-L
Clearcut-White pine	W. pine-S	Pon. pine-M, Bl. oak-M	L. pine-L, Sc. pine-L, B. hickory-M
Clearcut-Red pine	R. pine-S	Pon. pine-M, Bl. oak-M	L. pine-L, Sh. pine-L, Sc. oak-L
Shelterwood-Oaks	N.R. oak-S, Pin oak-S	W. oak, S.W. oak-M, Bur oak-M	Sh. oak-L, S.R. oak-L
Shelterwood-Birch	P. birch-S	R. birch-M	B. birch-L
Lowland conifers	Tamrck-S	Atl. cedar-M, Silv. maple-M, S.W. oak-M	B. cypress-L
Lowland hardwood	R. maple-S, Y. birch-S, Am. Elm-S	Silv. maple-M, S.W. oak-M, Bl. willow-M	Ov. oak-L, Ch. oak-L
Central hardwood [3]	NA	B. hickory-M, W. oak, B. maple-M	Sw. gum-L, B. birch-L
Pine-oak [3]	NA	Pit. pine-M, Bl. oak-M	Sh. pine-L, S.R. oak-L, Ch. oak-L
Southern hardwood [3]	NA	B. hickory-M, W. oak, Bl. oak-M	Y. poplar-L, Sw. gum-L, W. basswd-L

[1] Shade-tolerant hardwoods.
[2] Intermediate shade-tolerant hardwoods.
[3] New forest types produced by assisted migration.

natural drainage) and management goals (e.g., commercial and ecological value) guide decisions, but are integrated within a climate adaptation (i.e., transition) framework (Williams and Dumroese 2013). For example, southern oak species adapted to site conditions similar to those of current oak sites were selected as similar functional types to plant and eventually replace northern oak species, with the goal of maintaining a similar functional type on the landscape (*sensu* Nagel et al. 2017). We also simulated a "No-Harvest" scenario under each climate to gauge the importance of timber harvest (and planting) as a disturbance type and to show the effect of climate in the absence of the AM treatments.

2.3. Model description

We used LANDIS-II v7.0 (Scheller et al. 2007), a forest landscape model that simulates forest succession using the processes of forest development (seed dispersal, tree establishment, growth) and degeneration (disturbance, competition and senescence) over time. LANDIS consists of a collection of extensions (modules) that can be activated to simulate specific ecological processes. In LANDIS, landscapes are represented as a grid of spatially interacting cells (typically 0.1–2.5 ha) on which species composition and vertical structure are assumed to be homogeneous, and these cells are spatially aggregated into biophysical units (ecoregions) having homogeneous soils and climate. On each cell, forest composition is represented as age cohorts of one or more tree species whose competition is a function of their vital attributes (e.g., growth capacity, shade tolerance, drought tolerance, longevity, seed dispersal, ability to sprout vegetatively) and conditions on the cell. This produces nondeterministic successional pathways driven by abiotic conditions, competition and disturbance (Mladenoff 2004). Independent disturbance extensions (including silvicultural activity) simulate processes that remove some or all of their biomass as a function of disturbance type and severity. The LANDIS framework robustly scales site-level mechanisms to the landscape scale through process-based simulation of growth and competition, and the interaction of grid cells via spatial processes (dispersal and disturbances).

The experiment was implemented using the PnET-Succession v5.0b18 (De Bruijn et al. 2014; Gustafson and Miranda, 2022) succession (growth and competition) extension of LANDIS-II, because PnET-Succession has direct links between climate drivers (CO_2 concentration, temperature and precipitation) and tree species cohort net primary productivity, which are based on physiological first principles (Aber et al. 1995). PnET-Succession also accounts for life history traits that are necessary for this study (e.g., waterlogging tolerance, temperature tolerances). A mechanistic approach is critical when evaluating climate change effects because phenomenological modeling approaches use the past to predict the future, and future climate is expected to fall well outside the domain of the scientifically studied past (Gustafson 2013). Tree cohorts (and their propagules) compete for light and water on each grid cell, with their competitiveness determined as their life-history traits interact with the abiotic environment, and this competition interacts with disturbances to determine 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 photosynthetic capacity under optimal conditions) is a function of foliar nitrogen concentration, and actual photosynthesis in each month is computed by applying several reduction multipliers (0.0–1.0) that reflect departure from optimal conditions (stress). Cohort stress is calculated monthly relative to shade, drought, waterlogging and temperature tolerance parameters. Grid-cell soil water is tracked based on precipitation input, and losses to runoff, evaporation, percolation out of the rooting zone, and transpiration (Gustafson and Miranda, 2022). Response (and acclimation) to elevated CO_2 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 wood, roots, foliage, and reserves (non-structural carbon) according to allocation parameters. New cohorts establish stochastically 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.

PnET-Succession uses a hydrologic "leaky 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 availability 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. (2020b) that allow soil water to exceed field capacity (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 allowing standing water up to 30 cm deep and calibrating water leakage using actual assemblages on wetland sites, finding a value that generally maintained supersaturated soils without continually increasing excess water.

2.4. Modeling details

The input maps were gridded representations (cell width = 30 m) of the study area. The abiotic environment was represented as biophysical units based on soil types found in SSURGO (Soil Survey Staff 2013) soil map polygons, simplifying the abiotic environment to six major biophysical units (Fig. 1). Climate was assumed to be homogeneous across the study area. Initial forest conditions (species and age classes) were based on maps produced by Janowiak et al. (2014) 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. These 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 (2010–2309) 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 four times ($n = 4$).

We calibrated PnET-Succession species parameters (Table A2) to 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. The AM strategies (and associated silvicultural practices) were simulated using the LANDIS-II Biomass Harvest extension (v4.5.1, Gustafson et al. 2000).

To conduct the experiment in the context of realistic natural disturbance regimes, we included wildfires, windstorms, and insect pests as background disturbances in all treatment combinations. Wildfire is rare in this landscape and was simulated using Base Fire (v3.1 Scheller and Domingo 2017), calibrated against records of wildfires in the region as described in Gustafson et al. (2020a). 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), and adjusted for climate change based on findings of Emanuel (2005) and Knutson et al. (2010) as described in Gustafson et al. (2020a). The major insect pests of the study area include defoliators, budworms and borers. Defoliators (Forest Tent Caterpillar, Gypsy Moth) were simulated

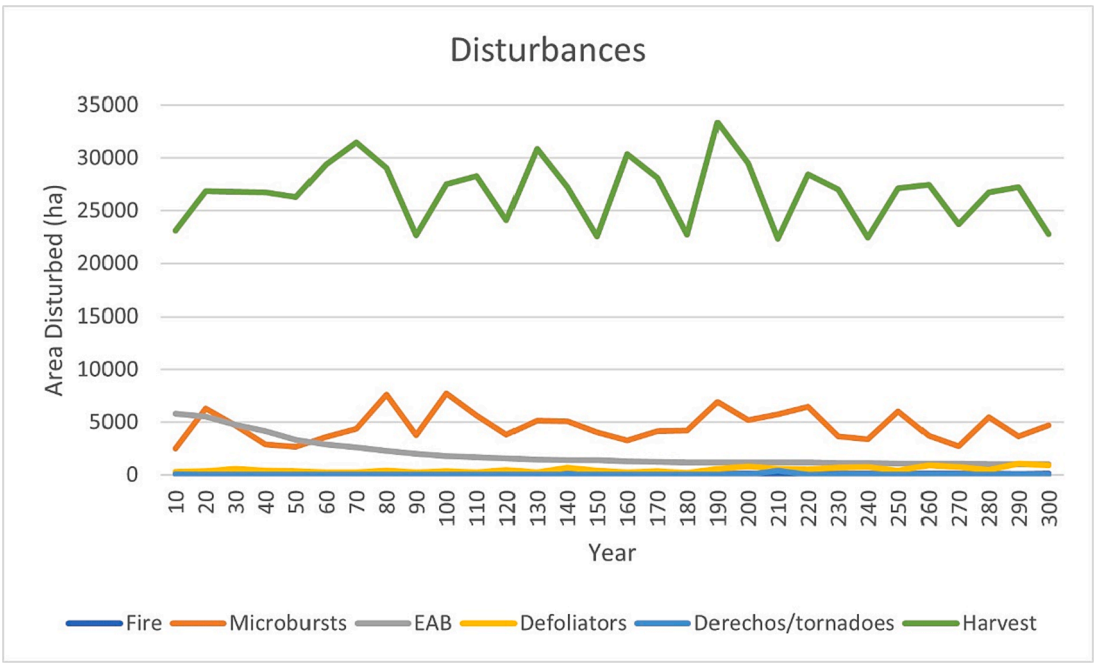

Fig. 3. Area disturbed each decade by natural disturbances and timber harvest (including AM planting) under the Short-Range / RCP 2.6 scenario.

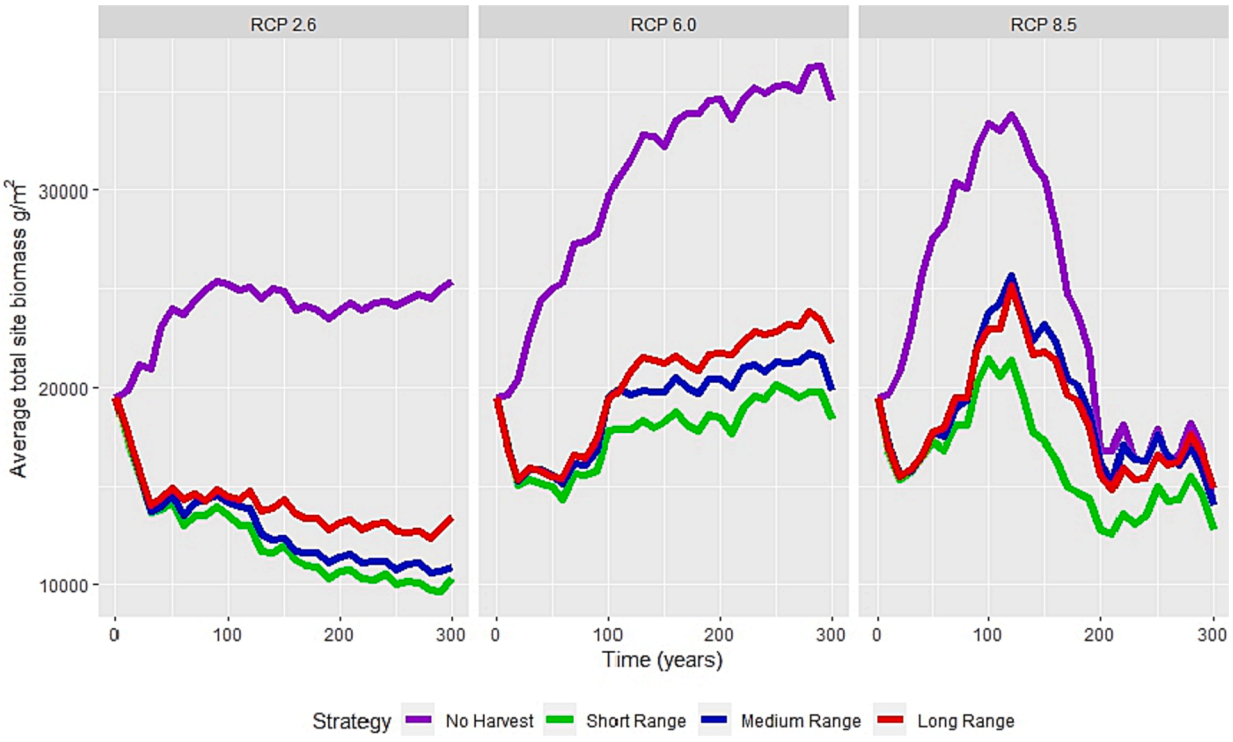

Fig. 4. Effect of climate and AM strategy on total above-ground biomass. Variation among four replicates is not shown, generally being less than the thickness of the curves.

using Biomass Insects v. 3.0 (Foster 2011) and calibrated for the study area by Lucash et al. (2018). Emerald ash borer (EAB) was simulated using the Base Biological Disturbance Agent extension (v4.0, Sturtevant et al. 2019). We assumed that EAB will move into the area as anticipated, rapidly depleting the standing biomass of all ash species, including black ash, which dominates many of the lowland forests of the study area. We followed the methods of Gustafson et al. (2018b) 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. Harvest (and replanting) of lowland hardwood stands (dominated by black ash) was accelerated (doubled) in the first 20 years in an attempt to convert some such stands to non-ash types before EAB killed the ash.

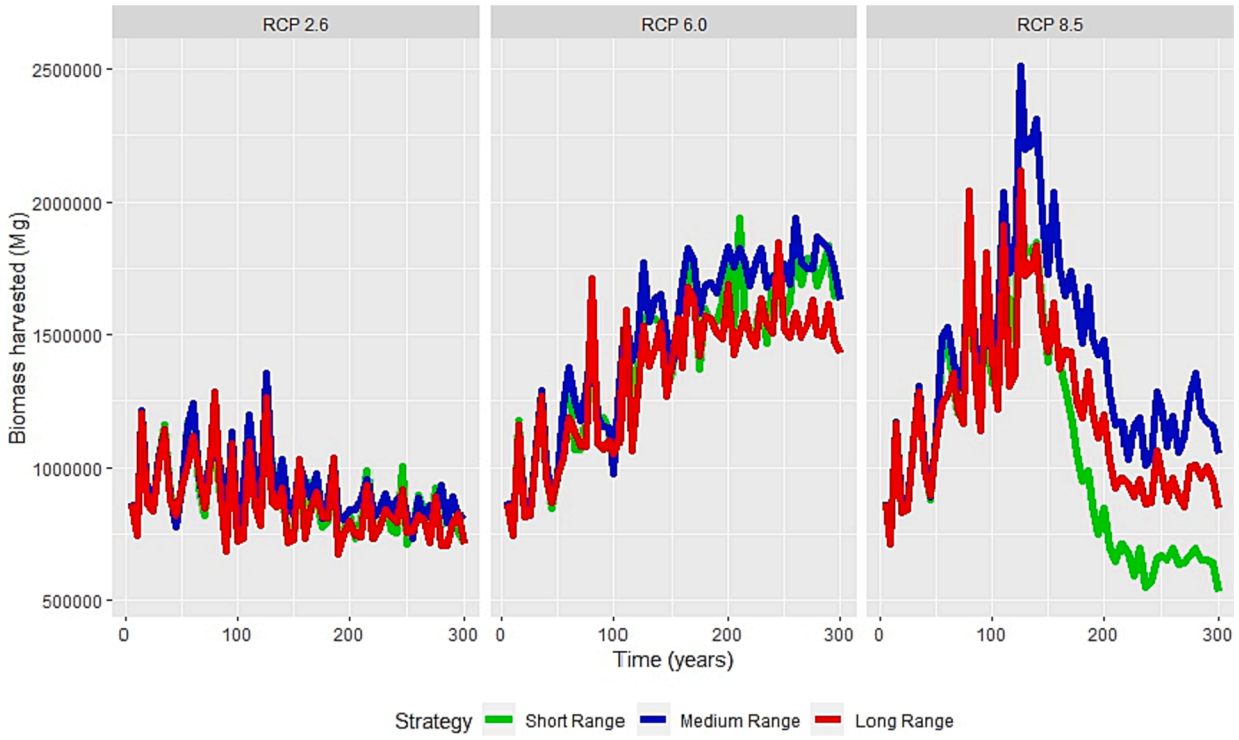

Fig. 5. Effect of climate and AM strategy on the total biomass harvested (all prescriptions) from the landscape in each 5-year time step. Amount harvested reflects rotational limits in the first rotation (Table 1) and number of eligible stands available thereafter. Variation among four replicates is not shown, generally being less than the thickness of the curves.

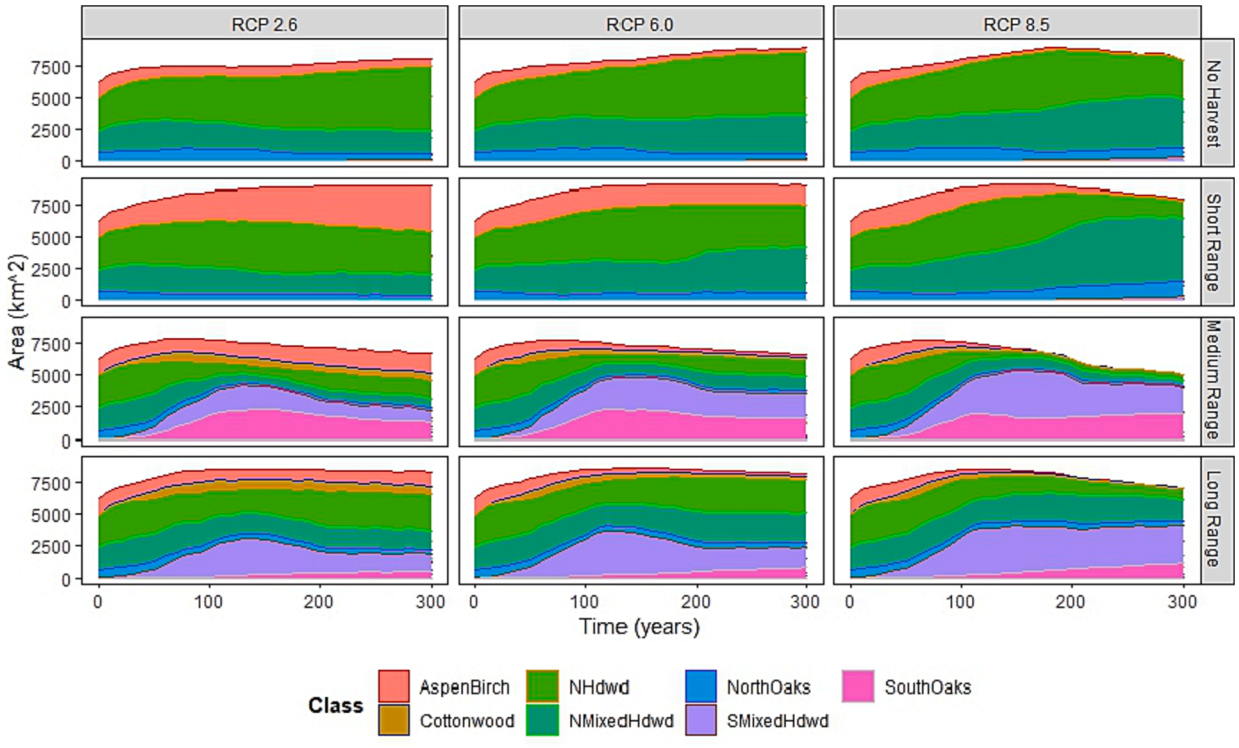

Fig. 6. Effect of climate (columns) and AM strategy (rows) on the abundance of a subset of forest types. One standard deviation of four replicates is shown, although values were less than the thickness of the curves. Species composition of the forest types are listed in Table A3.

2.5. Analysis

We evaluated the sustainability of the standard silvicultural prescription by expecting aboveground biomass to remain approximately steady and for year 300 biomass to be similar or greater than initial (year 0) biomass, coupled with an approximately steady supply of

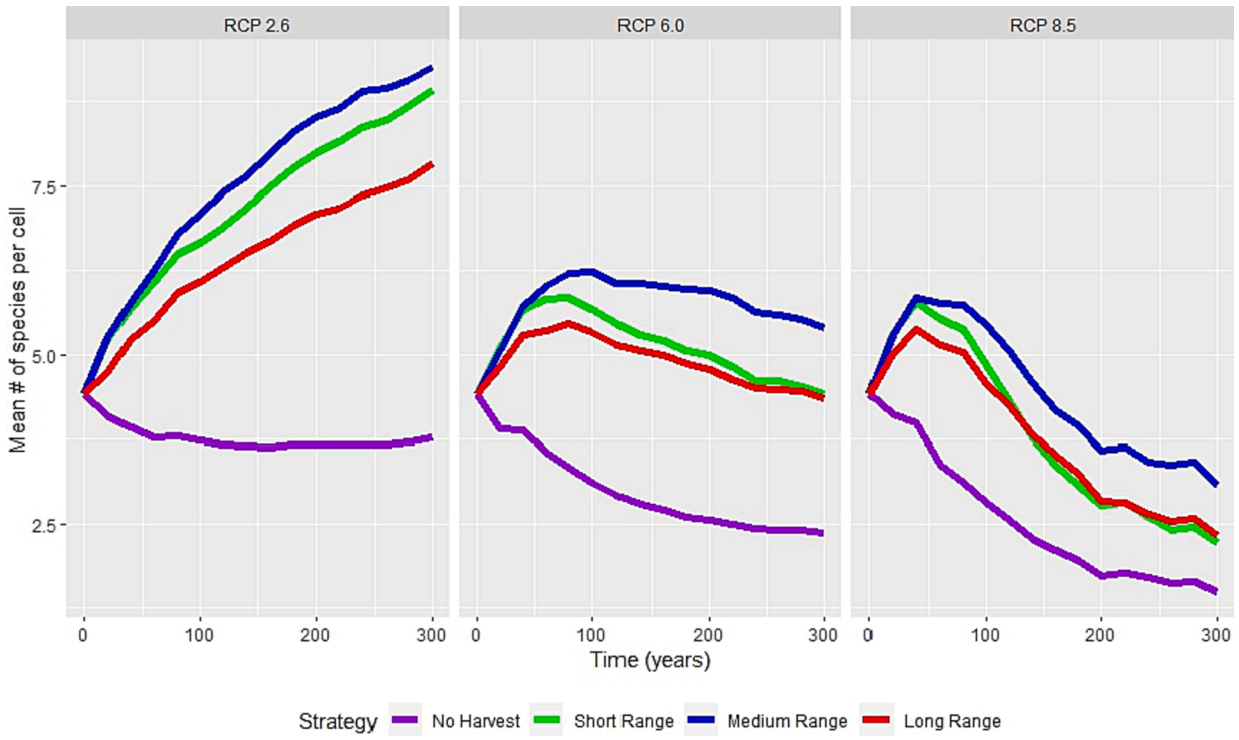

Fig. 7. Effect of climate and AM strategy on the mean number of species (richness) on a cell. Variation among four replicates is not shown, generally being less than the thickness of the curves.

harvested biomass.

To test the effects of the silvicultural treatments on ecosystem resilience, goods, and services, we evaluated the areal extent of various combinations of species providing specific ecosystem goods and services (Table A3). Ecosystem goods were evaluated with the areal extent (i.e., potential availability) of tree species used for commercial forest products and non-timber maple syrup production (Table A3). Ecosystem services were represented by the area of the landscape by classes of non-extractive forest benefits for wildlife and aesthetics: potential availability of mast/food type and fall foliage colors (Table A3). We assumed that if forest functional type extent was maintained during the simulation of our experimental treatments, then the associated ecosystem goods and services would also be maintained for existing biota and human systems on the landscape.

We relied on visual comparison of confidence intervals and temporal trends rather than on significance tests in this study as advocated for modeling experiments by White et al. (2014). We visualized treatment effects through simulated time by comparing plots (with uncertainty estimates) of mean values of response variables for 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's t distribution.

3. Results

Variability among replicates was quite low (generally less than the width of lines in the results presented here) and reflected stochasticity in the disturbance processes (Fig. 3) and in the competition of cohorts for light and water.

3.1. Sustainability of landscape productivity

Total above-ground biomass (AGB; average total biomass density on active landscape cells) was greater in the No Harvest compared to all AM strategies that included harvesting and planting (Fig. 4). Within a climate change scenario, AM strategy displayed very little difference in AGB at any given point in time during the 300-year simulation period. We observed that the AGB response to the AM strategy varied by climate change scenario, increasing during the simulation period under Limited (RCP 2.6) climate change, substantially increasing under Moderate (RCP 6.0) climate change and decreasing under Extreme climate change (RCP 8.5) scenarios. This suggested that there was an important interaction among climate change scenarios and AM strategies.

The residual total aboveground biomass of the AM strategy in Fig. 4 is the living biomass that remained after harvested AGB was removed (Fig. 5). Under Limited climate change (RCP 2.6), total biomass harvested was maintained over time, regardless of AM strategy. Under Moderate climate change (RCP 6.0), harvested biomass increased over time for all AM strategies. Similarly, under Extreme climate change (RCP 8.5), all AM strategies displayed a similar pattern, harvested biomass increased during the first 100 years of simulation and then decreased the second 100 years. However, AM strategies did show some differences in the final 100 years (years 200–300 of the simulation) of Extreme climate change (RCP 8.5), where Short-, Medium-, and Long-range AM had lower, similar, and higher levels (respectively) relative to the initial harvested biomass (Fig. 5). This suggested that AM strategy had negligible overall effects, particularly compared to climate change.

3.2. Sustainability of ecosystem resilience

The extent of forest types through time reflects the dynamics of growth, competition and mortality as individual species responded to the climate and AM scenarios (Fig. 6). In the No Harvest strategy, northern hardwoods were the dominant forest type through time except during the later years under Extreme climate change (RCP 8.5). Generally, AM strategy altered the forest types that dominated the landscape, but not with a clear one-to-one substitution. Short-range AM largely did not change the forest types present, because endemic species with southern provenances were planted. However, climate change did affect the extent of current forest types managed with Short-range AM.

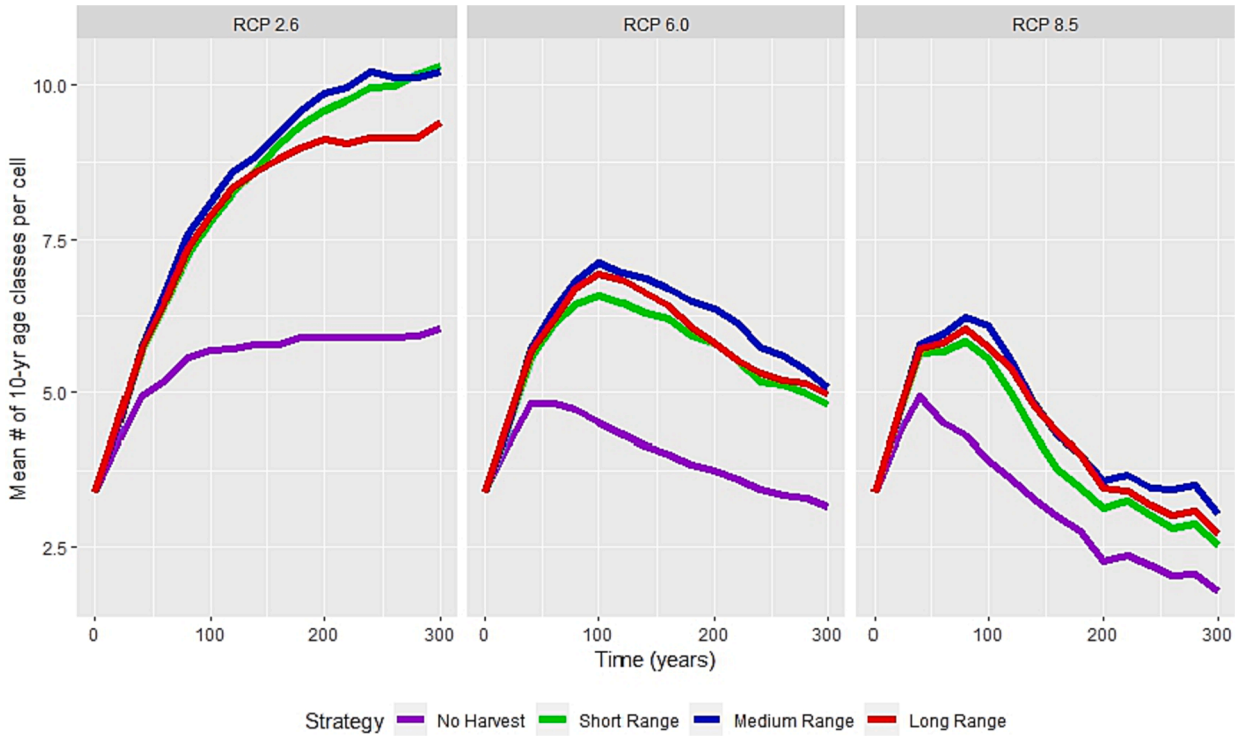

Fig. 8. Effect of climate and AM strategy on the mean number of 10-yr age classes (richness) on a cell. Variation among four replicates is not shown, generally being less than the thickness of the curves.

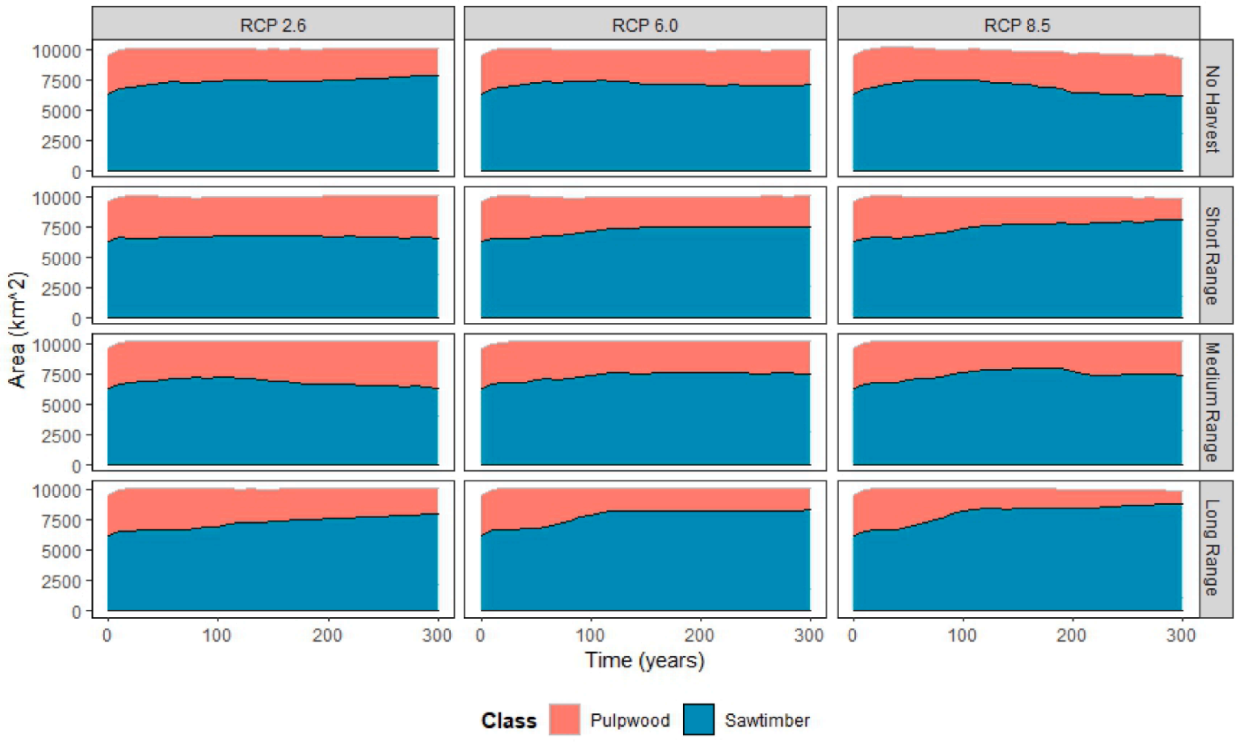

Fig. 9. Effect of climate (columns) and AM strategy (rows) on the areal abundance on the landscape of species providing the ecosystem good of timber products. Variation among four replicates is not shown, generally being less than the thickness of the curves. The species composition is defined in Table A3.

For instance, the boreal aspen-birch forest type expanded, maintained, or diminished in extent under RCP 2.6, RCP 6.0, and RCP 8.5 scenarios, respectively, while temperate northern mixed hardwood and oak forest types increased. Medium- and Long-range AM strategies, which used non-endemic, warm-adapted species, shifted landscape dominance away from northern hardwoods to northern and southern mixed

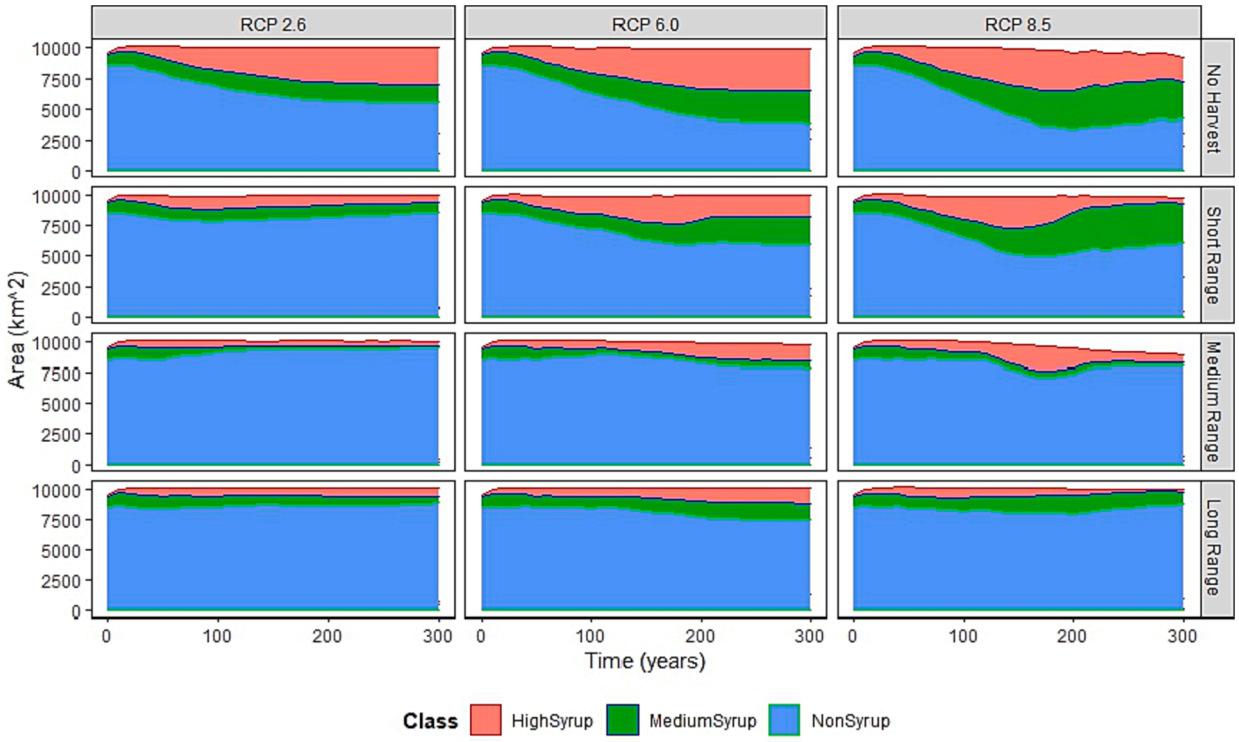

Fig. 10. Effect of climate (columns) and AM strategy (rows) on the areal abundance on the landscape of species providing the ecosystem good of maple syrup. Variation among four replicates is not shown, generally being less than the thickness of the curves. The species composition is defined in Table A3.

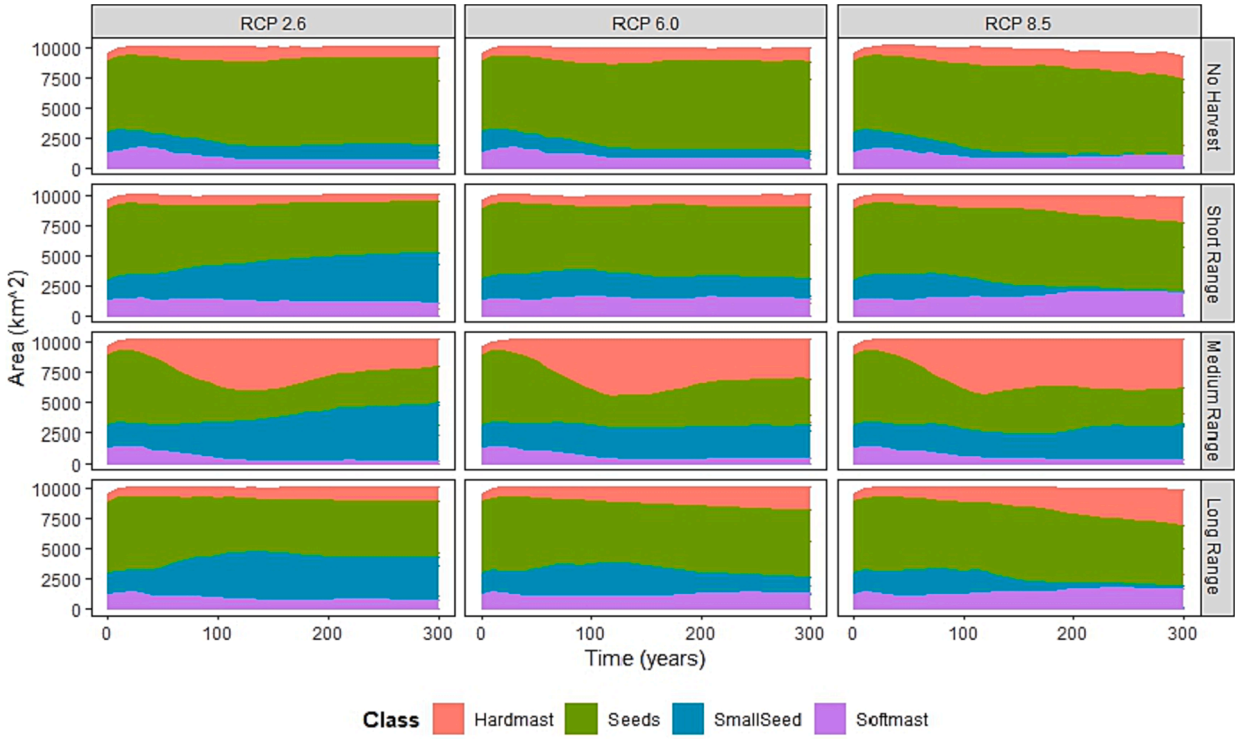

Fig. 11. Effect of climate (columns) and AM strategy (rows) on the areal abundance on the landscape of species providing the ecosystem service of wildlife mast. One standard deviation of four replicates is shown, which generally was less than the thickness of the curves. The species composition of classes are defined in Table A3.

hardwood and southern oak forest types with Limited, Moderate, and Extreme climate change (RCP 2.6, 6.0, and 8.5), respectively. Replacement of Aspen-Birch with Cottonwood in the Medium- or Long-range AM strategies did not result in new cottonwood forests of similar extent as the initial Aspen-Birch extent in the landscape.

Under the No Harvest strategy, species richness was generally low and increasing climate change reduced it further (Fig. 7). Under Limited climate change (RCP 2.6), AM strategies increased richness over time.

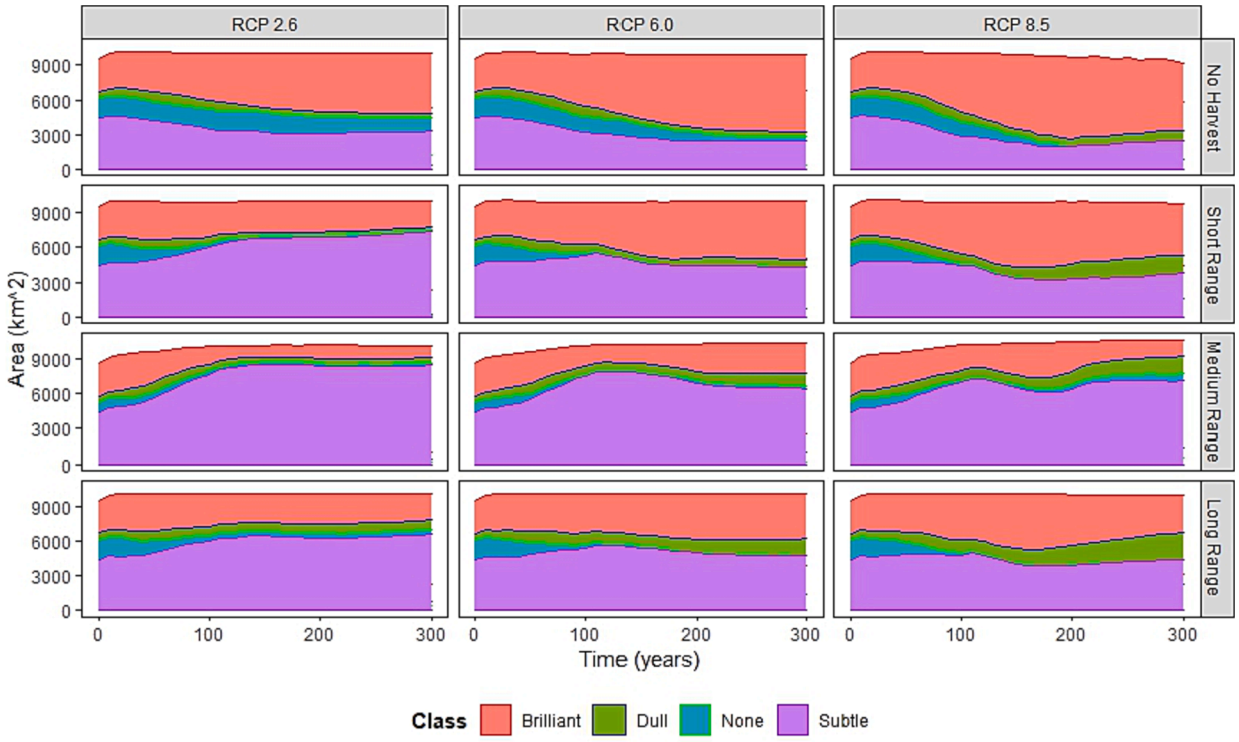

Fig. 12. Effect of climate (columns) and AM strategy (rows) on the areal abundance on the landscape of species providing the ecosystem service of fall color by color category. One standard deviation of four replicates is shown, which generally was less than the thickness of the curves. The species composition of classes is defined in Table A3.

Richness decreased under Moderate (RCP 6.0) and Extreme (RCP 8.5) climate change, but AM strategies reduced species losses compared to the No Harvest strategy. AM strategy had negligible effects on species richness despite our expectation that Medium- and Long-range AM strategies would increase species richness. Age-class richness (Fig. 8) generally followed the same patterns as did species richness, demonstrating the benefits of management or harvesting, regardless of AM strategy, for maintaining or increasing age-class diversity under the different climate scenarios.

3.3. Sustainability of ecosystem goods

Sawtimber species were dominant across the landscape regardless of climate scenario or AM strategy (Fig. 9). In the No Harvest strategy, land area for potential sawlog and pulpwood production remained steady. Among AM strategies, increasing climate change increased the gap between the extent of species used for timber products, i.e. more and less area available for potential sawlog and pulpwood production, respectively. This trend was most pronounced in the Long-range AM strategy. Overall, climate scenario was a minor influence and Long-range AM strategy was the most influential on potential availability of commercial forest products over 300 years.

In the No Harvest strategy, increasing climate change increased the land area suited for syrup production (Fig. 10). The No Harvest strategy had more potential area for maple syrup production than AM Harvest strategies. Among AM strategies, the Short-range AM strategy using endemic species maintained more potential land area in maple production than Medium- and Long-range AM strategies, regardless of climate scenario.

3.4. Sustainability of ecosystem services

Ecosystem services for wildlife food type availability were influenced by both climate and AM strategy. In the No Harvest strategy, the landscape was dominated by tree species producing seeds as a mast type (Fig. 11). Increasing climate change decreased small seed and increased hard mast extent in the landscape over time; this trend was accentuated under the AM strategies. The abundance of wildlife mast was affected more by AM strategy than climate because specific tree species were introduced or maintained on the landscape by each AM strategy. For example, the Medium-range AM strategy was the only simulation where hard mast species were often more abundant than seed-producing species, because more hard mast species were planted under this AM strategy (Table 2).

Fall color, an ecosystem service with aesthetic benefits, always exhibited an increase of colorful species, because the area of “no color” tree species declined over time in all treatment combinations. Under the No Harvest strategy, climate change increased land area in brilliant fall colors, while other color categories stayed the same or decreased (Fig. 12). The AM scenarios increased the areal extent of trees with subtle coloration, but the land area in subtle fall colors declined with increasing climate change. Among the AM strategies, the most colorful fall landscapes were produced by the Short-range AM strategy that maintained existing endemic species, with area in brilliant fall colors increasing with increasing climate change. Overall, AM strategy was more influential than climate on fall color extent.

4. Discussion

4.1. Insights

Resilient forest landscapes that provide a reliable flow of ecosystem goods and services are critical as global climate change develops in unprecedented ways. Given the accelerating pace of climate change, the assisted migration of climate-suitable species may be necessary to sustain indefinitely the full complement of goods and services provided by forest ecosystems. The science of assisted tree migration for climate change is emerging, including a limited suite of species studied with

short-term results (Nagel et al. 2017). Landscape forest modeling is an approach to test much longer-term outcomes of AM strategies (Duveneck and Scheller 2015, Gustafson et al. 2020a). In this study, we used landscape modeling to test outcomes of three AM strategies under three climate change scenarios. AM strategies were used to transition current northern forest types to mixed and southern types over 300 years. However, this change in species and their mixtures had both intended and unintended effects on the production of ecosystem goods and services. Climate was indeed the major factor in overall landscape productivity (biomass) and contributed to the success of warm-adapted species over multiple centuries.

5. Sustainability of managed landscape productivity

A critical assumption for the design of our AM strategies was that productivity would increase with climate change because of CO_2 fertilization. Thus, our climate-adaptive prescriptions for forest transition had harvest rates consistent with increased productivity, but varied the AM species planted. The outcomes suggested that the harvest rates were accommodated by increased productivity; Moderate climate change (RCP 6.0) increased AGB over three centuries, but this pattern did not extend to the Extreme climate change (RCP 8.5) scenario because of extreme water and heat stress induced by very warm temperatures. Our harvest targets assumed that CO_2 fertilization would greatly increase the availability of timber. Thus, too much AGB was harvested when climate did not change, causing a decline in AGB under the Limited climate change (RCP 2.6) scenario, while harvest rates did indeed go up dramatically under the medium climate change (RCP 6.0) scenario. But, when climate change was Extreme (RCP 8.5), water and heat stressors overwhelmed the CO_2 fertilization, causing a decline in timber harvest in the last 150 years. The model includes a CO_2 acclimation response based on Franks et al. (2013), so the extremely high CO_2 concentrations of the RCP 8.5 scenario do not provide much more fertilization than the RCP 6.0 scenario. The growth inhibition seen in the last 150 years of the RCP 8.5 scenario is likely due to temperature, through both elevated vapor pressure deficit (water stress) and direct heat stress on photosynthesis rate. Similarly in a forest landscape model of southeastern Canada, harvest levels were not sustainable after 100 years, due to high tree mortality (through fire or drought) (Brecka et al. 2020).

A number of AM species did not thrive under any climate. Because of the number of interacting factors in the model, it is difficult to determine the specific limiting factor(s). Poor performance seems to be related to one or more of three characteristics: intolerance to shade (W spruce-S, J. pine-S, R. pine-S, W. pine-S, Sc. pine-L, N. poplar-L), relatively low maximum temperature for photosynthesis (e.g., R. spruce-M, W spruce-S, J. pine-S, R. pine-S, W. pine-S) or low cold tolerance (e.g., P. hickory-L, L. pine-L, Sh. pine-L, Sc. oak-L, Sh. oak-L, R. birch-M, B. tupelo-M). It should be noted that some AM species with these characteristics did thrive, but they typically had just one of these limiting characteristics. It does not appear to be simply cold-tolerance because the least cold-tolerant species (B. cypress-L) was able to eventually survive under the Limited-change climate scenario (RCP 2.6). These non-thriving species were also not all one life form (deciduous/evergreen), not all low vagility species (e.g., cottonwood was included), nor slow growing. Conversely, there were some native species that were able to maintain their status as a dominant member of altered ecosystems under climate change. Examples include Su. maple, R. maple, A. beech, B. cherry, R. oak and Am. elm. These species generally have a relatively high maximum temperature for photosynthesis (Table A2) and this temperature is quite high ($\geq$34.5C) if they are also somewhat shade intolerant (B. cherry, Am. elm). We also suspect that regeneration failure played a role, resulting from our decision to simulate only natural regeneration (no site preparation or competitor control) after one rotation. Further study is needed to identify combinations of characteristics that lead a species to poor performance as an AM species.

Generally, most temperate species growing in our study area are likely to find several growing season months close to their optimal temperature (likely in spring and fall for northern species under a warm climate), but species with higher optimal temperatures are likely to have fewer months in which they are heat-stressed, which gives them an advantage, even when their growing season is shorter. The main disadvantage for long-distance migrants would be less resistance to cold-killing (e.g., Montwé et al. 2018) and simulated cold-killing was indeed more common under cooler climates and during early decades under warming climates. However, Long-range AM species produced the greatest AGB under all climate scenarios, suggesting that even Limited climate change (RCP 2.6) is sufficient to allow them to survive north of their current range. It is possible that our parameters did not accurately limit their growth under climates other than Extreme climate change (RCP 8.5), although as indicated above, species with relatively high optimal temperature can thrive under a wide range of climates.

Despite the unknowns underlying AGB patterns, climate was clearly a major influence, regardless of AM species planted. In another landscape model study, utilizing trees sourced from a great distance south of the landscape were suggested for AM strategies (i.e. Long-range AM), because trees sourced just south of the landscape did not survive over time under extreme climate change (Duveneck and Scheller 2015). Our study indicates Long-range AM was not able to override effects of Extreme climate change on AGB. A sustainably managed landscape (as measured by AGB) was only produced under the Moderate climate change scenario using any of the AM strategies. This highlights the importance of aligning climate-adaptive harvest prescriptions with anticipated climate change.

5.1. Sustainability of ecosystem resilience

Another critical approach of our study was designing AM strategies to sustain forest functional types across the landscape. Our aim was to maintain the land area of the various forest functional types through AM to ensure diversity and some of level of functional redundancy (Díaz and Cabido 2001, Messier et al. 2019). This was accomplished by planting either the same species from more southerly locations or by introducing similar species presently located in dissimilar and warmer climates. Introduced species were matched to edaphic conditions, e.g., bottomland species were selected for planting in lowlands and drought-tolerant trees selected for planting in dry uplands. Out-planting AM strategies were generally more influential than climate and successful as a climate-adaptive approach to transition forest composition in the available landscape area. For instance, while boreal and north temperate species declined, central and southern species increased, maintaining or expanding the areal extent of most forest functional types.

The resilience of forest types to disturbance was also measured by species and age class richness. High species and age class diversity was expected to produce a greater capacity to recover after disturbance and maintain the forest functional types than low diversity. Here the effects of AM strategy were less strong, and climate had greater effects. Limited climate change had the greatest species richness (per cell), which may be due to the large number of species that can survive in this type of climate (discussed above). Species richness was maintained and declined in the Moderate and Extreme climate change scenarios, respectively, over the 300-year simulation. Additional measures of diversity should be considered in future studies of AM strategies and ecosystem resilience because species richness alone does not account for structural aspects of diversity such as the spatial arrangement, density, or size class distribution of trees (McElhinny et al., 2005). One additional measure of diversity examined here was age-class richness. Simulation showed that AM strategies increased the age-class diversity relative to the No-Harvest alternative for each of the climate change scenarios, indicating greater structural diversity or resilience to disturbance on the landscape with AM strategies.

Table A1
Species used in the simulations. Southerly provenances (Short-range migration strategy) are indicated by the suffix *"-S,"* species planted in the "Medium-range migration strategy" are indicated by "-M," and species planted in the "Long-range migration strategy" are indicated by "L". (For planted species details, see Table 2). Initial biomass is the mean across all active cells on the landscape and reflects the initial abundance of the species on the study landscape. NA indicates the species was not present in the initial landscape.

Scientific name	Common name	Abbreviation	Initial mean biomass (kg/m^2)
Abies balsamea	Balsam fir	B. fir	0.500
Abies fraseri-L	Fraser fir	F. fir-L	NA
Acer nigrum-M	Black maple	B. maple-M	NA
Acer rubrum	Red maple	R. maple	2.937
Acer rubrum-S	Red maple-south	R. maple-S	NA
Acer saccharum	Sugar maple	Su. maple	2.2974
Acer saccharum-S	Sugar maple-south	Su. maple-S	NA
Acer saccharinum-M	Silver maple	Silv. maple-M	NA
Betula alleghaniensis	Yellow birch	Y. birch	0.881
Betula alleghaniensis-S	Yellow birch-south	Y. birch-S	NA
Betula lenta-L	Black birch	B. birch-L	NA
Betula nigra-M	River birch	R. birch-M	NA
Betula papyrifera	Paper birch	P. birch	0.168
Betula papyrifera-S	Paper birch-south	P. birch-S	NA
Carya cordiformis-M	Bitternut hickory	B. hickory-M	0.528
Carya glabra-L	Pignut hickory	P. hickory-L	NA
Chamaecyparis thyoides-M	Atlantic white cedar	Atl. cedar-M	NA
Fagus grandifolia	American beech	A. beech	0.117
Fraxinus americana	White ash	W. ash	0.927
Fraxinus nigra	Black ash	B. ash	0.798
Fraxinus pennsylvanica	Green ash	G. ash	0.107
Larix laricina	Tamarack (American larch)	Tamrck	0.492
Larix laricina-S	Tamarack-south	Tamrck-S	NA
Liquidambar styraciflua-L	Sweet gum	Sw. gum-L	NA
Liriodendron tulipifera-L	Yellow poplar	Y. poplar-L	NA
Nyssa sylvatica-M	Black tupelo	B. tupelo-M	NA
Picea glauca	White spruce	W. spruce	0.035
Picea glauca-S	White spruce-south	W. spruce-S	NA
Picea mariana	Black spruce	B. spruce	0.236
Picea rubens-M	Red spruce	R. spruce-M	NA
Pinus banksiana	Jack pine	J. pine	0.0234
Pinus banksiana-S	Jack pine-south	J. pine-S	NA
Pinus echinate-L	Shortleaf pine	Sh. pine-L	NA
Pinus ponderosa-M	Ponderosa pine	Pon. pine-M	NA
Pinus resinosa	Red pine	R. pine	0.064
Pinus resinosa-S	Red pine-south	R. pine-S	NA
Pinus rigida-M	Pitch pine	Pit. pine-M	NA
Pinus strobus	Eastern white pine	W. pine	1.095
Pinus strobus-S	Eastern white pine-south	W. pine-S	NA
Pinus sylvestris-L	Scots pine	Sc. pine-L	NA
Pinus taeda-L	Loblolly pine	L. pine-L	NA
Populus balsamifera	Balsam poplar	B. poplar	0.0001
Populus deltoides v. deltoides-M	Eastern cottonwood	E. cottnwd-M	NA
Populus deltoides v. occidentalis-L	Necklace poplar	N. poplar-L	NA
Populus grandidentata	Bigtooth aspen	BT aspen	1.300
Populus grandidentata-S	Bigtooth aspen-south	BT aspen-S	NA
Populus tremuloides	Quaking aspen	Q. aspen	0.946
Populus tremuloides-S	Quaking aspen-south	Q. aspen-S	NA
Prunus serotina	Black cherry	B. cherry	0.658
Prunus serotina-S	Black cherry-south	B. cherry-S	NA
Quercus alba	White oak	W. oak	0.017
Quercus bicolor-M	Swamp white oak	S.W. oak-M	NA
Quercus coccinea-L	Scarlet oak	Sc. oak-L	NA
Quercus ellipsoidalis	Northern pin oak	Pin oak	0.332
Quercus ellipsoidalis-S	Northern pin oak-south	Pin oak-S	NA
Quercus falcata-L	Southern red oak	S.R. oak-L	NA
Quercus lyrata-L	Overcup oak	Ov. oak-L	NA
Quercus michauxii-L	Swamp chestnut oak	S.Ch. oak-L	NA
Quercus macrocarpa-M	Bur oak-M	Bur oak-M	0.002
Quercus prinus-L	Chestnut oak	Ch. oak-L	NA
Quercus rubra	Northern red oak	N.R. oak	0.986
Quercus shumardii-L	Shumard oak	Sh. oak-L	NA
Quercus velutina-M	Black oak	Bl. oak-M	0.001
Salix nigra-M	Black willow	Bl. willow-M	NA
Taxodium distichum-L	Baldcypress	B. cypress-L	NA
Thuja occidentalis	Northern white cedar	W. cedar	0.365
Tilia americana	American basswood	Basswd	2.924
Tilia americana-S	American basswood-south	Basswd-S	NA
Tilia heterophylla-L	White basswood	W. basswd-L	NA
Tsuga canadensis	Eastern hemlock	Hemlock	0.379
Ulmus americana	American elm	Am. elm	0.240
Ulmus americana-S	American elm-south	Am. elm-S	NA

5.2. Sustainability of ecosystem goods and services

The hypothesis that greater levels of climate change would require more aggressive AM strategies to maintain ecosystem goods and services was only partially supported by the simulation outcomes. AM strategies altered species assemblages and maintained a diverse forested landscape area over three centuries, but the effectiveness of AM strategy varied by ecosystem good or service and sometimes interacted with climate.

Forest goods were measured by sustained land area in timber and non-timber products. Generally, conventional timber products were maintained across the landscape over the centuries, except in the Long-range AM strategy where pulpwood slightly decreased and sawlog slightly increased in areal extent. Sustained forest products may be attributed to the AM species selection process, because AM replacement species were purposely selected for similar traits as existing species and for commercial value. Maintaining availability of timber products in a landscape is important to sustain supply to existing economies into the future. Existing infrastructure is also built around the availability of non-timber products, such as maple syrup, in a landscape. In our results, Short- and Medium-range AM strategies maintained the areal extent of syrup producing species. Overall, the areal extent of forest ecosystem goods was sustained with AM strategies and the effect of climate was negligible.

The ecosystem service variables largely revealed unintended outcomes from AM species selections, because we did not explicitly include criteria for wildlife or aesthetics in our selection of AM species. The selected species resulted in changes in masting type from those that produce medium-sized seeds to a more diversified landscape that also included hardmast-, softmast- and small seed-producing trees. The Medium-range AM strategy in particular appeared to provide the most diverse mixture of native and introduced species, producing the greatest diversity of wildlife food. Climate appeared to have some influence on ecosystem services results, but no clear interaction with AM emerged. Similarly, choice of AM species seemed to be a stronger influence than climate on the areal extent of fall color categories. Tree species producing brilliant fall color such as sugar maple and red maple decreased under aggressive AM strategies and were partially replaced by hickories, oaks, willows, sweetgum, bald cypress, and other species that are more subtle in color.

Table A2
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, 2020a). Complete PnET-Succession input files are available in the online Supplement. Species codes are defined in Table A1.

Species	Amax (μmol/ g fol. /s)[1]	HalfSat (μmol/ m2/s)[2]	Water-logging Toler. (%)[3]	Drought Toler. (MPa)[4]	Leaf-On MinT (°C)[5]	Psn MinT (°C)[6]	Psn OptT (°C) [6]	Psn MaxT (°C) [6]	Lethal Cold Temp. (°C)
A. beech	83.4	148	0 %	−1.37	2.2	1.7	26.7	34.2	−50
Am. elm	97.8	212.5	70 %	−1.42	2.3	1.3	26.3	35.0	−40
Am. elm-S	97.8	212.5	70 %	−1.42	3.3	2.3	28.3	37.0	−38
Atl. cedar-M	26.8	197	75 %	−1.49	3.2	2.5	26.5	34.2	−38
B. ash	90.6	244	75 %	−1.33	2.1	1.0	21.0	29.5	−60
B. birch-L	97.8	244	0 %	−1.42	3.1	2.5	24.0	32.0	−50
B. cherry	112.2	244	0 %	−1.49	2.8	2.2	26.0	34.5	−43
B. cherry-S	112.2	244	0 %	−1.49	3.8	3.2	28.0	36.5	−41
B. cypress-L	90.6	212.5	91 %	−1.37	4.5	1.3	28.5	35.0	−34
B. fir	26.8	134	33 %	−1.37	1.9	0.8	16.8	27.0	−65
B. hickory-M	105.0	244	20 %	−1.57	3.0	1.3	26.7	34.0	−51
B. maple-M	83.4	149	0 %	−1.49	3.2	2.5	26.5	33.0	−55
B. poplar	112.2	275	11 %	−1.42	1.6	0.3	15.1	29.0	−65
B. spruce	29.0	197	75 %	−1.35	1.5	0.2	15.1	26.6	−66
B. tupelo-M	90.6	181	20 %	−1.42	3.3	2.7	26.5	34.5	−41
Basswd	90.6	181	0 %	−1.49	2.4	1.7	24.0	32.2	−51
Basswd-S	90.6	181	0 %	−1.49	3.4	2.7	26.0	34.2	−49
Bl. oak-M	105.0	212.5	0 %	−1.49	3.2	2.6	27.0	34.4	−41
Bl. willow-M	112.2	275	83 %	−1.35	3.1	2.5	27.5	36.0	−35
BT aspen	112.2	275	11 %	−1.49	2.3	1.4	23.5	31.0	−55
BT aspen-S	112.2	275	11 %	−1.49	3.3	2.4	25.5	33.0	−53
Bur oak-M	90.6	212.5	20 %	−1.57	2.5	1.3	24.7	34.0	−53
Ch. oak-L	90.6	244	0 %	−1.57	3.2	2.6	25.7	33.3	−41
E. cottnwd-M	112.2	275	75 %	−1.42	2.6	1.3	20.5	31.8	−55
F. fir-L	26.8	134	33 %	−1.37	2.9	1.8	18.8	29.0	−65
G. ash	90.6	244	62 %	−1.49	2.5	1.8	25.5	34.2	−51
Hemlock	29.0	133	0 %	−1.37	2.5	1.8	21.0	29.5	−65
J. pine	39.7	250	0 %	−1.57	1.8	0.5	16.0	28.1	−61
J. pine-S	39.7	250	0 %	−1.57	2.8	1.5	18.0	30.1	−59
L. pine-L	33.3	228	0 %	−1.49	4.3	3.7	28.7	35.0	−35
N. poplar-L	112.2	275	57 %	−1.49	2.6	1.3	20.5	31.8	−55
N.R. oak	105.0	212.5	0 %	−1.49	2.5	1.3	25.6	34.1	−50
N.R. oak-S	105.0	212.5	0 %	−1.49	3.5	2.3	27.6	36.1	−48
Ov. oak-L	105.0	212.5	62 %	−1.49	4.5	1.3	27.8	34.8	−35
P. birch	97.8	244	0 %	−1.42	1.8	0.5	16.5	28.5	−65
P. birch-S	97.8	244	0 %	−1.42	2.8	1.5	18.5	30.5	−63
P. hickory-L	97.8	244	20 %	−1.57	3.3	1.3	25.5	34.2	−41
Pin oak	105.0	244	0 %	−1.57	2.5	1.8	25.0	33.0	−50
Pin oak-S	105.0	244	0 %	−1.57	3.5	2.8	25.5	35.0	−48
Pit. pine-M	39.7	250	0 %	−1.57	3.1	2.4	24.1	32.0	−50
Pon. pine-M	33.3	228	0 %	−1.49	2.9	2.3	21.9	31.2	−55
Q. aspen	112.2	275	0 %	−1.42	1.6	0.3	18.5	29.8	−65
Q. aspen-S	112.2	275	0 %	−1.42	2.6	1.3	20.5	31.8	−63
R. birch-M	97.8	244	40 %	−1.42	3.5	2.9	26.5	35.0	−40
R. maple	90.6	181	50 %	−1.42	2.4	1.8	26.5	34.5	−50
R. maple-S	90.6	181	50 %	−1.42	3.4	2.8	28.5	36.5	−48
R. pine	33.3	228	0 %	−1.49	2.3	1.3	18.6	28.2	−55
R. pine-S	33.3	228	0 %	−1.49	3.3	2.3	20.6	30.2	−53
R. spruce-M	26.8	134	33 %	−1.37	2.5	1.8	21.5	29.0	−55
Ch. oak-L	112.2	275	40 %	−1.57	4.5	4.0	28.0	34.3	−35
S.R. oak-L	105.0	212.5	0 %	−1.57	4.5	1.3	27.3	34.2	−35
S.W. oak-M	105.0	212.5	62 %	−1.49	3.2	2.6	25.0	32.4	−53
Sc. oak-L	112.2	275	0 %	−1.57	3.5	2.9	25.5	33.0	−35
Sc. pine-L	38.6	250	0 %	−1.57	2.0	1.3	24.5	33.0	−59
Sh. oak-L	105.0	275	40 %	−1.57	4.2	3.5	27.3	34.0	−36
Sh. pine-L	39.7	250	0 %	−1.57	4.1	3.3	25.5	34.0	−35
Silv. maple-M	105.0	244	61 %	−1.42	2.8	2.1	26.8	34.8	−45
Su. maple	83.4	149	0 %	−1.40	2.5	1.8	25.5	31.0	−55
Su. maple-S	83.4	149	0 %	−1.40	3.5	2.8	27.5	33.0	−53
Sw. gum-L	112.2	275	62 %	−1.42	4.2	3.6	28.0	34.2	−35
Tamrck	97.8	275	70 %	−1.42	1.5	0.2	18.5	29.9	−65
Tamrck-S	97.8	275	70 %	−1.42	2.5	1.2	20.5	31.9	−63
W. ash	90.6	212.5	20 %	−1.42	2.3	1.2	26.5	34.1	−50
	90.6	181	0 %	−1.49	3.8	3.1	26.9	34.3	−35

(continued on next page)

Table A2 (*continued*)

Species	Amax (μmol/ g fol. /s)[1]	HalfSat (μmol/ m2/s)[2]	Water-logging Toler. (%)[3]	Drought Toler. (MPa)[4]	Leaf-On MinT (°C)[5]	Psn MinT (°C)[6]	Psn OptT (°C) [6]	Psn MaxT (°C) [6]	Lethal Cold Temp. (°C)
W. basswd-L									
W. cedar	26.8	197	75 %	−1.49	2.2	1.3	21.3	29.9	−60
W. oak	105.0	244	0 %	−1.57	3.0	1.3	26.7	34.0	−41
W. pine	31.1	197	20 %	−1.49	2.3	1.4	21.5	30.0	−53
W. pine-S	31.1	197	20 %	−1.49	3.3	2.4	23.5	32.0	−51
W. spruce	31.1	197	0 %	−1.49	1.5	0.2	15.1	26.6	−66
W. spruce-S	31.1	197	0 %	−1.49	2.5	1.2	17.1	28.6	−64
Y. birch	83.4	181	20 %	−1.49	2.5	1.8	21.7	30.5	−55
Y. birch-S	83.4	181	20 %	−1.49	3.5	2.8	23.7	32.5	−53
Y. poplar-L	112.2	275	11 %	−1.49	3.3	2.7	26.5	34.2	−41

[1] Amax; maximum photosynthesis rate under optimal conditions, proportional to foliar nitrogen content.
[2] Half saturation; light intensity at which photosynthesis is half that under full light saturation.
[3] Waterlogging tolerance given as percentage of Amax when soil is over-saturated (Niinemets and Valladares 2006).
[4] Drought tolerance; water potential below which photosynthesis does not occur (Niinemets and Valladares 2006).
[5] Determines growing season length. Values are monthly mean nighttime low temperature, above which growing season is active.
[6] Parameters defining temperature controls on photosynthesis rate. Values represent monthly mean temperature during daylight hours.

5.3. Caveats

In practice, adaptive management is used for course correction of management plans as needed to maintain forest sustainability. This would include monitoring growth, mortality, and yield for sustainable forest management. For experimental reasons, our study used the same harvest prescriptions and AM strategies without modification for three centuries. In practice, unsuccessful attempts at AM (e.g., cottonwood planting failures to replace aspen/birch types) would be recognized and a revised planting scheme would be attempted within decades. Therefore, our study should be interpreted as an experiment, not a projection.

Another aspect of adaptive management is sustained yield, where harvested biomass is continually adjusted to be less than or equal to growth. Our results indicated overcutting for some climate scenarios; AGB declined under the Limited climate change (RCP 2.6) and Extreme climate change (RCP 8.5) scenarios. Harvest rates were initially set according to typical rotation lengths for each forest type, and after the first rotation the model cut stands according to their availability (i.e., meeting age and composition constraints). In practice, managers would use more specific information, such as forest inventory data, to monitor growth, mortality, and yield and adjust harvest prescriptions such that AGB and species composition would be maintained or altered to meet management goals.

Current range limits reflect historical climate interacting with other drivers such as soils, land use, forest management, ice-age legacies, etc. We assumed that the temperature regime found within the current range of a species is an indicator of its temperature-related physiology parameters. Our approach features mechanistic simulation of ecophysiology that allows future survival of a translocated species to be an emergent property of a potential future climate and the temperature-related physiology parameters of each species.

Our results are focused on the effects of climate and the AM treatments on forest composition and the abundance of forest functional types. We assessed these effects in terms of potential availability of ecosystem goods and services as measured by species biomass or areal extent across the landscape, but we did not assess related production issues such as altered freeze–thaw dynamics that might affect maple syrup production (Duchesne et al. 2009) or reduced winter timber harvest operations that require frozen soils.

We evaluated our hypotheses by visualizing the trajectories and variability of specific response variables with respect to overlap in uncertainty envelopes. Uncertainty caused by stochastic process simulated by the model was extremely low, even with four replicates. However, there are other sources of uncertainty (primarily parameter and model uncertainty) that were not estimated by our model and study design, so we assumed that actual uncertainty was considerably greater than shown in our visualizations.

5.4. Management implications

In this study, AM maintained most forest types needed for general commercial function. We considered common site conditions and commercial value of the current landscape forest types and selected AM species from warmer geographic areas with similar silvics. The goal was to maintain commercial viability so the landscape would provide harvest opportunities and sustain general forest ecosystem goods and services. A one-to-one replacement was not feasible, so we chose AM of species with approximate similarities. For example, the regional forest industry may be set up for oak veneer, so replacing the areal extent of northern red oak with southern red oak would maintain commercial viability and likely provide other services (e.g., wildlife habitat and mast). However, by focusing on the site and commercial value of species for AM, the effects on other ecosystem goods and services were unplanned. This oversight resulted in positive or negative outcomes that were sometimes significant. For example, the change in the mast type availability could affect bird populations, which could be positive for some species and a boost to the local economy (e.g., bird watching). Or, while the extent of a forest functional type might be maintained with AM, the specific changes in species could have serious effects on the existing infrastructure and economy, such as the non-timber products (e.g., syrup, fall color tourism). In practice, an integrated approach to AM strategies considers key ecological and societal factors in addition to conventional site and commercial value criteria when selecting species for AM. AM decisions might also include interactions with micro and macro biota, cultural and spiritual needs and uses (e.g., tribal ceremonies), and local and regional infrastructure and economy (e.g., recreation, forest industry, non-timber industries, tourism). In any case, there will be tradeoffs with AM decisions and those should be purposefully evaluated.

If climate is always changing, the window of opportunity to establish species through AM may be limited and adaptive management might evaluate when an AM strategy should be adjusted or changed. For example, the Moderate climate change (RCP 6.0) resulted in AGB gains and increasing harvested biomass over the centuries, because the standard climate-adaptive harvest prescription that was used in all AM strategies turned out to be best suited for that climate scenario. This suggests that the success of AM may require first developing a climate-adaptive harvest prescription aligned with climate and then using appropriate criteria to select species for AM planting. Given the caveats and potential opportunities with AM, strategies to implement AM will likely depend on careful adaptive management to identify climate windows and suitable actions for forest transition practices.

Table A3
Assignment of species to forest functional types for analysis. Species codes are defined in Table A1.

Species	Forest Type	Timber Product	Climate Trait[a]	Fall Color[b]	Mast Type[c]
A. beech	NorthHdwd	Sawtimber	TempMid	Brilliant	Hard
Am. elm	NLowlHdwd	Sawtimber	TempMid	Subtle	Seed
Atl. cedar-M	SLowlConif	Sawtimber	TempMid	None	Seed
B. ash	NLowlHdwd	Sawtimber	TempNorth	Brilliant	Seed
B. birch-L	SMixedHdwd	Sawtimber	TempMid	Subtle	Small seed
B. cherry	NMixedHdwd	Sawtimber	TempMid	Dull	Soft
B. cypress-L	SLowlConif	Sawtimber	TempSouth	Subtle	Seed
B. fir	SpruceFir	Pulpwood	Boreal	None	Seed
B. hickory-M	SMixedHdwd	Sawtimber	TempMid	Subtle	Hard
B. maple-M **	SMixedHdwd	Sawtimber	TempMid	Brilliant	Seed
B. poplar	AspenBirch	Pulpwood	Boreal	Dull	Seed
B. spruce	NLowlConif	Pulpwood	Boreal	None	Seed
B. tupelo-M	SMixedHdwd	Sawtimber	TempSouth	Brilliant	Soft
Basswd	NorthHdwd	Sawtimber	TempMid	Subtle	Soft
Bl. oak-M	SouthOaks	Sawtimber	TempMid	Dull	Hard
Bl. willow-M	SLowlHdwd	Pulpwood	TempSouth	Subtle	Small seed
BT aspen	AspenBirch	Pulpwood	Boreal	Subtle	Small seed
Bur oak-M	NorthOaks	Sawtimber	TempMid	Dull	Hard
Ch. oak-L	SouthOaks	Sawtimber	TempSouth	Dull	Hard
E. cottnwd-M	Cottonwood	Pulpwood	TempSouth	Subtle	Small seed
F. fir-L	SpruceFir	Pulpwood	TempNorth	None	Seed
G. ash	NLowlHdwd	Sawtimber	TempMid	Brilliant	Seed
Hemlock	NorthConif	Sawtimber	TempNorth	None	Seed
J. pine	NorthConif	Pulpwood	Boreal	None	Seed
L. pine-L	SouthPine	Sawtimber	TempSouth	None	Seed
N. poplar-L	Cottonwood	Pulpwood	TempSouth	Subtle	Small seed
N.R. oak	NorthOaks	Sawtimber	TempMid	Subtle	Hard
Ov. oak-L	SLowlHdwd	Sawtimber	TempSouth	Dull	Hard
P. birch	AspenBirch	Pulpwood	Boreal	Subtle	Small seed
P. hickory-L	SMixedHdwd	Sawtimber	TempSouth	Subtle	Hard
Pin oak	NorthOaks	Sawtimber	TempMid	Dull	Hard
Pit. pine-M	SouthPine	Sawtimber	TempSouth	None	Seed
Pon. pine-M	SouthPine	Sawtimber	TempMid	None	Seed
Q. aspen	AspenBirch	Pulpwood	Boreal	Subtle	Small seed
R. birch-M	SMixedHdwd	Sawtimber	TempMid	Subtle	Small seed
R. maple *	NMixedHdwd	Pulpwood	TempMid	Brilliant	Seed
R. pine	NorthConif	Sawtimber	TempNorth	None	Seed
R. spruce-M	SpruceFir	Sawtimber	TempNorth	None	Seed
Ch. oak-L	LowlHdwd	Sawtimber	TempSouth	Dull	Hard
S.R. oak-L	SouthOaks	Sawtimber	TempSouth	Dull	Hard
S.W. oak-M	SLowlHdwd	Sawtimber	TempMid	Dull	Hard
Sc. oak-L	SouthOaks	Sawtimber	TempMid	Subtle	Hard
Sc. pine-L	SouthPine	Pulpwood	TempNorth	None	Seed
Sh. oak-L	SouthOaks	Sawtimber	TempSouth	Subtle	Hard
Sh. pine-L	SouthPine	Sawtimber	TempSouth	None	Seed
Silv. maple-M *	SLowlHdwd	Sawtimber	TempMid	Subtle	Seed
Su. maple**	NorthHdwd	Sawtimber	TempMid	Brilliant	Seed
Sw. gum-L	SMixedHdwd	Sawtimber	TempSouth	Brilliant	Seed
Tamrck	NLowlConif	Pulpwood	Boreal	Subtle	Seed
W. ash	NMixedHdwd	Sawtimber	TempMid	Brilliant	Seed
W. basswd-L	SMixedHdwd	Sawtimber	TempSouth	Subtle	Soft
W. cedar	NLowlConif	Sawtimber	TempNorth	None	Seed
W. oak	SouthOaks	Sawtimber	TempMid	Subtle	Hard
W. pine	NorthConif	Sawtimber	TempNorth	None	Seed
W. spruce	SpruceFir	Pulpwood	Boreal	None	Seed
Y. birch	NorthHdwd	Sawtimber	TempNorth	Subtle	Small seed
Y. poplar-L	SMixedHdwd	Sawtimber	TempSouth	Subtle	Small seed

[a] Categories are Boreal, Temperate North (sub-boreal temperate zone), Temperate Mid (middle temperate zone) and Temperate South (southern temperate zone).
[b] Species whose fall foliage is considered: Brilliant (bright reds, oranges, yellows), Subtle (light yellows, purples), Dull (browns, greens), and None (no color change at the end of the growing season).
[c] Food type for wildlife.
** High sugar content for maple syrup production.
* Medium sugar content for maple syrup production.

5.5. Conclusions

Four general conclusions can be drawn from our results. First, AM strategies can successfully be implemented for climate-adaptive forest transition and maintain functionally similar forest types on the landscape. Second, these altered species assemblages can help forests maintain resilience, goods, and services, but important landscape ecosystem goods and services should be considered when selecting species for AM to avoid unintended outcomes. Third, total residual and harvested biomass are strongly influenced by climate, regardless of AM strategy, and the specifics of the climate-adaptive harvest prescriptions linked to AM largely determine their success. Fourth, productivity may decrease over time under Extreme climate change and many species may struggle to survive, thereby jeopardizing their associated goods and services.

Our study illustrates how a mechanistic forest landscape model can

be used to conduct controlled experiments at landscape spatial and temporal scales that are impossible to conduct empirically. The results are useful to objectively compare the temporal dynamics of the supply of multiple goods and services for specific landscapes under alternative climate and management scenarios. It also appears that while our specific AM strategies achieved their primary objectives, they had some unintended consequences and could therefore be improved. Many AM species did not thrive under any climate or AM strategy for reasons that are not entirely clear. There are multiple processes (senescence, dispersal, establishment, competition, disturbances, climate effects) acting simultaneously on all cohorts. This suggests that further iterations of simulation experiments are needed to discover optimal AM strategies that can fully conserve ecosystem goods and services under a range of climate futures while minimizing planting efforts. Alternatively, recruitment failure may represent parameter errors for species that were planted in locations and in assemblages that were different than where they are currently found. Simulations in other landscapes are certainly needed to confirm the generality of our results prior to implementing any such AM strategy in the field. Our results can also be used to identify specific needs for empirical research to find the best silvicultural practices to allow AM species to thrive and regenerate in specific regions.

CRediT authorship contribution statement

Eric J. Gustafson: Conceptualization, Methodology, Software, Writing – original draft. **Christel C. Kern:** Conceptualization, Methodology, Writing – original draft. **John M. Kabrick:** Methodology, 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.

Data availability

Data will be made available on request.

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Appendix

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