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# Climate-Suitable Planting as a Strategy for Maintaining Forest Productivity and Functional Diversity

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# Climate-suitable planting as a strategy for maintaining forest productivity and functional diversity

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*Abstract.* Within the time frame of the longevity of tree species, climate change will change faster than the ability of natural tree migration. Migration lags may result in reduced productivity and reduced diversity in forests under current management and climate change. We evaluated the efficacy of planting climate-suitable tree species (CSP), those tree species with current or historic distributions immediately south of a focal landscape, to maintain or increase aboveground biomass, productivity, and species and functional diversity. We modeled forest change with the LANDIS-II forest simulation model for 100 years (2000–2100) at a 2-ha cell resolution and five-year time steps within two landscapes in the Great Lakes region (northeastern Minnesota and northern lower Michigan, USA). We compared current climate to low- and high-emission futures. We simulated a low-emission climate future with the Intergovernmental Panel on Climate Change (IPCC) 2007 B1 emission scenario and the Parallel Climate Model Global Circulation Model (GCM). We simulated a high-emission climate future with the IPCC A1FI emission scenario and the Geophysical Fluid Dynamics Laboratory (GFDL) GCM. We compared current forest management practices (business-as-usual) to CSP management. In the CSP scenario, we simulated a target planting of 5.28% and 4.97% of forested area per five-year time step in the Minnesota and Michigan landscapes, respectively. We found that simulated CSP species successfully established in both landscapes under all climate scenarios. The presence of CSP species generally increased simulated aboveground biomass. Species diversity increased due to CSP; however, the effect on functional diversity was variable. Because the planted species were functionally similar to many native species, CSP did not result in a consistent increase nor decrease in functional diversity. These results provide an assessment of the potential efficacy and limitations of CSP management. These results have management implications for sites where diversity and productivity are expected to decline. Future efforts to restore a specific species or forest type may not be possible, but CSP may sustain a more general ecosystem service (e.g., aboveground biomass).

Key words: annual net primary productivity; assisted migration; carbon emission scenarios; climate-suitable planting; forest simulation modeling; functional diversity; Great Lakes region, USA; LANDIS-II model; managed relocation.

## Introduction

Forest management for future climate conditions must accept and use new paradigms for continued success in delivering ecosystem services (e.g., carbon sequestration, biodiversity, biomass, and wildlife habitat). Restoration of forest species composition to a historical range of variability (HRV; Landres et al. 1999, Wiens et al. 2012) may not be a realistic goal (Hobbs et al. 2011). Despite adaptation strategies to manage for resilience (Seidl et al. 2011, Duveneck et al. 2014*a*), extant tree species may not be suitable for future establishment, given their climate tolerances.

Within the next century, many tree species may not be capable of naturally migrating to more suitable sites at the rate of the changing climate (Scheller and Mladenoff

2008, Loarie et al. 2009, Bradshaw et al. 2010, Zhu et al. 2012, Diffenbaugh and Field 2013, Svenning and Sandel 2013). Even if suitable species are present or arrive in low abundance, a temporal lag is expected between arrival and expansion (Bradshaw and Lindbladh 2005, Wangen and Webster 2006, Birks and Birks 2008). Although this lag may not result in regional extirpation, the site or landscape may experience a decline in the density of extant species associated with a decline in ecosystem services. There is growing interest to explore climate suitable planting (CSP), also referred to as "assisted migration," "assisted colonization," or "managed relocation," whereby tree species are planted *beyond* their current range (Marris 2009, Richardson et al. 2009, Pedlar et al. 2012, Schwartz et al. 2012). This alternative management prescription is designed to facilitate migration while maintaining forest function, e.g., species diversity and carbon sequestration (Millar et al. 2007, O'Neill et al. 2008*b*). Given the lack of

experimental work focused on climate suitable planting, landscape modeling provides a suitable framework to assess the ability of CSP to overcome spatial and temporal migration barriers in forested ecosystems (Rehfeldt et al. 2006, Campbell et al. 2009).

### Climate-suitable planting

If future climate conditions reduce species and forest type diversity, the adaptive capacity of ecosystems will be compromised. Fewer species will reduce the response capability of forests to changing environmental conditions (Walker 1992, Walker et al. 1999). Low-diversity forests are also more susceptible to single-host insect or disease outbreaks (Naeem and Li 1997, Bentz et al. 2010). Increasing or maintaining diversity in these forests may create more climate-change-resilient forests (Chapin et al. 2007). This may be done by intensively planting a climate-suitable species following a disturbance when an undesirable condition such as lower productivity is otherwise expected (Spittlehouse and Stewart 2003).

Successful planting and establishment of a desired native species may become increasingly difficult as climate changes (Ledig and Kitzmiller 1992), making species from outside the range of a site more desirable (O'Neill et al. 2008b, Gray et al. 2010). In order to consider CSP management, it is vital to consider the biotic interactions of novel ecosystems, ecosystems composed of new species compositions (Blois et al. 2013). Assessing how these species might replace native niche spaces and/or expand their own niche space will provide a framework to evaluate the efficacy of CSP.

Rather than assisted migration for the refuge of a threatened species, maintaining a high level of function within a site or region requires new terminology and frameworks for success (Pedlar et al. 2012). A CSP prescription is designed to maintain or increase the ecosystem services of a site, e.g., biodiversity, carbon storage, timber products (Millar et al. 2007, O'Neill et al. 2008a). These objectives are different from the interest to protect or save an endangered species (Barlow and Martin 2004, Hoegh-Guldberg et al. 2008, Lunt et al. 2013). Assisted migration proposals for the protection of rare and endangered species are fraught with controversy, including a concern about negative effects if a species becomes invasive (Barlow and Martin 2004, McLachlan et al. 2007, Davidson and Simkanin 2008, Ricciardi and Simberloff 2009). Others however, have described potential benefits of nonnative species. These benefits include providing functional substitutes for declining or extinct native species (Schlaepfer et al. 2011). For example, within managed or degraded forests, CSP may be one of the only options for maintaining ecosystem services (Lunt et al. 2013).

The agriculture community has a growing recognition of species suitability shifts, as evidenced by the difference between the 1990 and 2012 plant hardiness maps (Daly et al. 2012). For silviculturists, this concept is familiar. Many commercial tree seedlings come from nursery stock grown in different regions of the country from where they are planted. Seedlings are selected based on the suitability matched to site conditions. Given the longevity of tree species, forest managers are seeking information about future suitability of seedlings. Online climate envelope models such as the "Seedlot Selection Tool," while not a simulation model, have been developed to assist managers to find seedlots for selected sites based on projected future conditions (available online).[2] In addition, this tool can select planting sites that are appropriate for particular seedlots. Because climate change uncertainty is high (IPCC 2013), simulation modeling of CSP is considered a vital component to understanding potential outcomes and choosing management alternatives regarding CSP (Pérez et al. 2012, Breed et al. 2013).

### Species and functional diversity

Species diversity is recognized as having a strong tie to potential ecosystem services (Tilman et al. 2006, Duveneck et al. 2014b). In addition, functional diversity (FD) based on functional traits has proven to be a useful measure of diversity. Rather than individual species, FD is based on the range of ecological functions provided by a community (Cornelissen et al. 2003, Laliberté and Legendre 2010). There is strong evidence that FD is a driver to ecosystem services (Díaz et al. 2007, Mokany et al. 2008) and ecosystem resilience (Folke et al. 2004), defined as "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function" (Folke et al. 2004:558).

Our objectives were to assess the efficacy of CSP to increase aboveground biomass (AGB), aboveground annual net primary productivity (ANPP), and species and functional diversity of forests expected to be substantially affected by climate change. Our previous work assessed business-as-usual (BAU) management under climate change (Duveneck et al. 2014b), and how modified forest management would compare to BAU (Duveneck et al. 2014a). In this work, we addressed the following questions. (1) As an alternative to business-as-usual (BAU) management, how might CSP under climate change affect AGB and ANPP? (2) How might CSP affect functional and species diversity under climate change as a surrogate for future ecosystem services?

We examined these questions within two landscapes in the upper Great Lakes of Minnesota and Michigan. These landscapes provided large variation in climate, soils, and forest management (Duveneck et al. 2014b). Northeastern Minnesota and northern lower Michigan landscapes provide island-like landscapes nearly surrounded by a combination of lakes, lowland conifer

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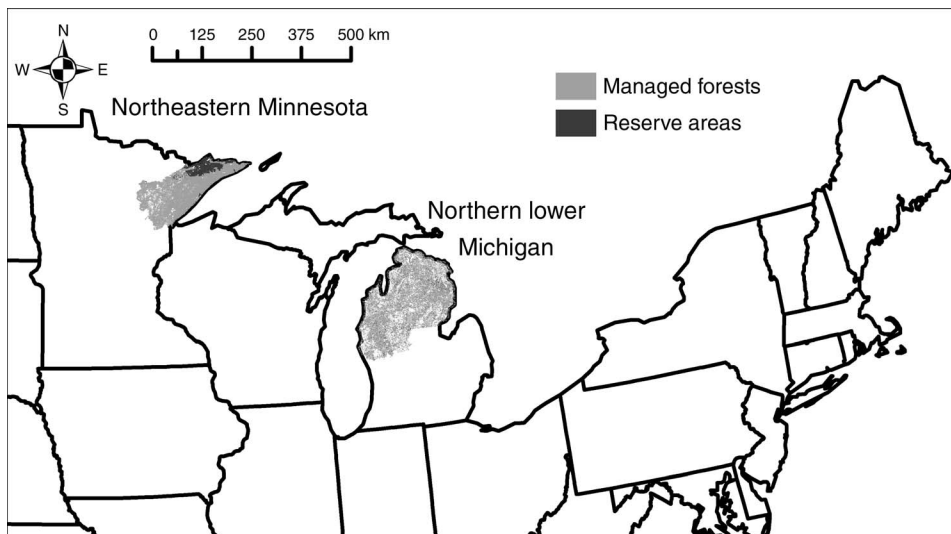[2] http://sst.forestry.oregonstate.edu/

FIG. 1. Landscape study areas in northeastern Minnesota and northern lower Michigan, USA.

forests, and agricultural development along the boreal–temperate forest ecotone (Curtis 1959).

## METHODS

### Study area

We selected two landscapes in the northern Great Lakes region within the boreal–temperate transition zone (i.e., northeastern Minnesota and northern lower Michigan; Fig. 1). Our landscapes encompass approximately 1.6 and 2.6 million ha of forest in the Minnesota and Michigan landscapes, respectively. We chose this region because the climate (IPCC 2013, Staudinger et al. 2013) and forests (Fisichelli et al. 2013, Duveneck et al. 2014b, Handler et al. 2014a, b) are expected to change substantially. By the end of the 21st century, temperatures in the region are expected to increase by 3–11°C (Andresen et al. 2012). In addition, these landscapes are naturally bounded by fragmentation, large bodies of water, and boreal–swamp forests (to the north of northeastern Minnesota), creating island-like conditions. For these reasons, we expect new species moving into these landscapes to be limited. We leveraged previous work in the region to parameterize natural disturbance regimes, initial species composition conditions, and BAU silviculture prescriptions (Duveneck et al. 2014b).

### Simulation model and experimental design

Our experimental design included both BAU and CSP management. For each management scenario, we assessed three climate scenarios. For all simulations, we used a 100-year time horizon starting at year 2000 and 2-ha cell resolution. We used a 2-ha cell size to balance forest composition precision with the computational processing time required of the simulations. In order to make our results more comparable to prior research in the region, whenever possible, we used

consistent methodology between this study and prior research (Duveneck et al. 2014a, b).

We modeled forest change using the LANDIS-II v6.0 forest landscape model at five-year time steps (Scheller et al. 2007). LANDIS-II is a spatially explicit landscape change model. Driven by ecological processes, LANDIS-II can be run at multiple temporal and spatial scales, and has been widely used (Gustafson et al. 2010, Ravenscroft et al. 2010, Thompson et al. 2011). Processes within the LANDIS-II modeling framework include tree species establishment, growth, mortality, and seed dispersal; fire; wind; and timber harvesting. These processes interact spatially and functionally across interconnected cells within climate and soil regions on a landscape.

We used the PnET-II tool for LANDIS-II (Xu et al. 2009) to calculate species-specific parameters, i.e., maximum aboveground net primary productivity per year ($ANPP_{max}$) and probability of establishment ($P_{est}$). These parameters are a function of climate (temperature, precipitation, and photosynthetic active radiation (PAR)) along with soil water-holding capacity (SWHC) and species-specific physiological parameters (e.g., foliar nitrogen content and maximum foliar mass area). We employed the PnET-II tool for each unique climate–soil region (Duveneck et al. 2014b).

LANDIS-II is built around a core modeling structure. The core interacts with user-chosen extensions of varying complexity. We used the LANDIS-II Biomass Succession extension (v3.1), which regulates the succession mechanisms of growth, reproductive maturity, and age-related mortality for species-cohorts (Scheller and Mladenoff 2004). Because Biomass Succession does not include density or diameter information, natural mortality due to stand development is a function of age, whereby cohort thinning leads to a decline in biomass and growth capacity over time. Although age is not a perfect proxy

for thinning, it sufficiently captures the general patterns over large landscapes (Scheller and Mladenoff 2004).

The PnET-II output parameters $ANPP_{max}$ and $P_{est}$ are utilized directly by the Biomass Succession extension. $ANPP_{max}$ regulates the maximum growth possible of aboveground biomass for a species-cohort (Scheller and Mladenoff 2004); $P_{est}$ determines the probability of a new cohort establishing, given a local seed source and adequate light (Xu et al. 2009).

We also simulated harvesting, fire, and wind disturbances. We used the Biomass Harvest extension (v2.1) to simulate harvest and planting prescriptions (Gustafson et al. 2000, Syphard et al. 2011). We applied specific prescriptions to unique management areas, described previously (Duveneck et al. 2014b). These management areas are based on ownership groups (i.e., state, county, U.S. Forest Service, private industrial, private non-industrial, and forest reserve areas). We delineated harvest stands within each management area to represent the range and variability of current stands within specific forest types. For each five-year time step, multiple unique prescriptions were implemented. First, the Biomass Harvest extension selected stands for treatment based on a stand ranking customized for each forest type. Next, biomass was harvested from cells within stands based on prescription-specific criteria. Prescription-specific rotation periods within each management area defined the proportion of the management area to be treated at each time step (Gustafson et al. 2000). Proportion to be treated within each management area was based on current proportion of forest types allowing for up to a 30% increase in area harvested if simulated future forest types matched harvest prescriptions. When CSP species matured to merchantable age, we harvested them with existing northern hardwood and oak prescriptions. We simulated natural fire and wind disturbance utilizing the Base Fire (v3.0; He and Mladenoff 1999) and Base Wind (v2.0; Scheller and Mladenoff 2004) extensions. Given uncertainty in future projections of natural disturbances (e.g., Butler et al. 2012) and the interest in reducing experimental variation, we simulated fire and wind disturbances based on recent trends rather than dynamic variation in future disturbance regimes. To quantify spatially explicit species aboveground biomass (AGB), we used the Biomass Output extension (v2.0). We utilized previously developed initial communities, fire and wind regimes, BAU timber harvest regimes, delineated ecoregions, and PnET-II parameters (Duveneck et al. 2014b).

### Climate data

For each unique climate region (described in Duveneck et al. 2014b), we accessed downscaled monthly climate data through the USGS data portal (Stoner et al. [2012]; *available online*).[3] We simulated current climate by randomly assigning observed monthly PRISM climate data (1969–1999) to future simulation years (Daly and Gibson 2002). We simulated climate change with future projections for years 2000–2100. We simulated a low-emission climate future with the IPCC B1 emission scenario (IPCC 2007) and the Parallel Climate Model (PCM) Global Circulation Model (GCM) (Washington et al. 2000). We simulated a high-emission climate future with the IPCC A1FI emission scenario (IPCC 2007) and the Geophysical Fluid Dynamics Laboratory (GFDL) GCM (Delworth et al. 2006). Climate projections from the PCM GCM are considered less sensitive to emissions than the GFDL GCM. The combination of carbon emission scenarios with GCM sensitivity will hereafter be referred to as low- and high-emission scenarios (Fig. 2). We bracketed a large range of plausible futures by coupling the separate emission scenarios to the more and less sensitive GCMs. In addition, these GCM emission scenario combinations are being used in other research in the region, providing model projection consistency (Peters et al. 2013, Handler et al. 2014a, b).

### Climate-suitable planting

We simulated planting tree species expected to respond well to a warmer climate. For each landscape, we selected three tree species that were present, according to range distribution maps (Burns and Honkala 1990), within 250 km south of each landscape boundary but were absent or in low abundance within each landscape; and whose habitat suitability are expected to increase with climate change (Iverson et al. 2008). For our CSP species selection, we leveraged previous habitat suitability analysis completed in northern Minnesota (Handler et al. 2014a) and northern lower Michigan (Handler et al. 2014b). Habitat suitability was assessed using a climate envelope approach where future temperature, future precipitation, topography, and soils were used to model future suitable habitat based on present species distribution (Iverson et al. 2008). In northeastern Minnesota, we selected bitternut hickory (*Carya cordiformis*), black oak (*Quercus velutina*), and northern pin oak (*Quercus ellipsoidalis*). In northern lower Michigan, we selected bitternut hickory, shagbark hickory (*Carya ovata*), and scarlet oak (*Quercus coccinea*).

In addition to the three selected species, we simulated planting American chestnut (*Castanea dentata*) in each landscape. American chestnut once was widespread throughout the mid-Atlantic United States (Russell 1987). The introduction of the chestnut blight (*Cryphonectria parasitica*) wiped out mature American chestnut throughout its range (Keever 1953, Lovett et al. 2006, Jacobs et al. 2013). Prior to the blight infection, American chestnut was considered a foundation species that had a strong role in structuring the forest community. Given the auspicious properties of Ameri-
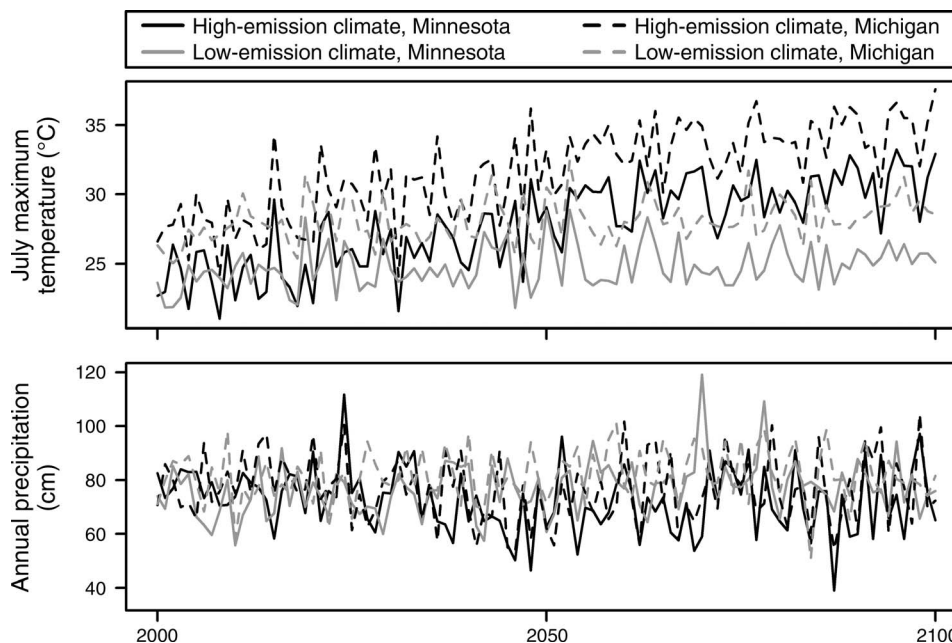
Fig. 2. Projected July maximum temperature and annual precipitation in each landscape and emission scenario for the years 2000 to 2100.

can chestnut, there has been considerable interest and investment in restoring the species with a blight-resistant hybrid (Smith 2000) that will likely be available in the near future (American Chestnut Foundation 2013). Although additional southern species are expected to have climate-suitable habitat in our landscapes (Iverson et al. 2008), we limited our experimental design to four species in each landscape.

The CSP prescriptions were implemented within existing harvesting regimes and management areas (Duveneck et al. 2014b). CSP prescriptions were only simulated in actively managed forests, excluding reserve areas such as the Boundary Waters Canoe Area Wilderness in Minnesota. Specifically, we simulated CSP wherever patch-cutting harvesting occurred in northern hardwood stands. Compared to BAU management, we simulated a fourfold frequency increase in implementing the northern hardwoods patch-cutting prescription for the first 50 simulation years. The planting intensity resulted in a target planting of 5.28% and 4.97% of forested area per five-year time step in the Minnesota and Michigan landscapes, respectively. This equates to planting ~17 111 and 22 180 ha/yr in the Minnesota and Michigan landscapes, respectively. We chose this planting intensity to balance a plausible management scenario (e.g., The Nature Conservancy planted 800 ha of climate-suitable seedlings in northeastern Minnesota in 2013 (M. White, *personal communication*), with a simulation experiment that was deliberately intensive. Because we simulated species-cohorts rather than individual seedlings, we did not simulate a specific planting density of seedlings within a site or stand.

*Species and functional diversity*

As a measure of species diversity, we calculated the Shannon Index of diversity, $H'$ (Gotelli and Ellison 2004). We calculated $H'$ within each landscape, utilizing species abundance (i.e., simulated AGB of individual tree species). We transformed $H'$ to the effective number of species ($e^{H'}$) as the number of species present if all species were equal in abundance. This transformation reduces inaccuracies when comparing diversity between scenarios (Jost 2006).

We calculated functional diversity within each landscape with the functional dispersion (FDis) index (Laliberté and Legendre 2010). Rather than counting species or groups of species, FDis is based on user-defined a priori traits (Villéger et al. 2008, Laliberté and Legendre 2010). For example, two separate species with identical user-defined traits would contribute the same FDis as one species. By definition, individual species are different from one another. Therefore, FDis is valuable when traits are considered that affect potential ecosystem functions of interest, e.g., nutrient cycling, carbon storage, carbon sequestration, and wildlife habitat (Cornelissen et al. 2003).

Specifically, FDis is the weighted (by abundance) mean distance of species traits in multidimensional space to the centroid of all species (Anderson et al. 2006). FDis is a flexible FD framework allowing both quantitative and qualitative traits, more traits than species, and the ability to weigh individual traits. FDis is not strongly influenced by outliers because it takes into account relative abundance (Laliberté and Legendre 2010). To calculate FDis, abundance was represented as simulated tree

TABLE 1. Some species traits used to calculate FDis (Paquette and Messier 2011).

| Species | H (m) | GR | LS | WD (g/m³) | WDR | SeM (mg) | LL (months) | LMA (g/m²) | N (%) |
|---|---|---|---|---|---|---|---|---|---|
| *Abies balsamea* | 25 | 1 | 1 | 0.34 | 1 | 2.15 | 4.70 | 151.00 | 1.66 |
| *Acer rubrum* | 25 | 3 | 3 | 0.49 | 1 | 3.04 | 1.72 | 71.09 | 1.91 |
| *Acer saccharum* | 35 | 1 | 3 | 0.56 | 1 | 4.19 | 1.71 | 70.63 | 1.83 |
| *Betula alleghaniensis* | 25 | 3 | 2 | 0.55 | 1 | 0.70 | 1.71 | 46.08 | 2.20 |
| *Betula papyrifera* | 25 | 3 | 2 | 0.48 | 1 | 0.29 | 1.28 | 77.88 | 2.31 |
| *Carya cordiformis* | 25 | 1 | 4 | 0.60 | 1 | 7.98 | 1.61 | 44.05 | 2.60 |
| *Carya ovata* | 35 | 1 | 4 | 0.64 | 1 | 8.39 | 1.61 | 75.00 | 1.76 |
| *Castanea dentate* | 30 | 3 | 3 | 0.40 | 3 | 8.15 | 1.61 | 100.00 | 2.30 |
| *Fagus grandifolia*† | 25 | 1 | 2 | 0.56 | 1 | 5.66 | 1.61 | 61.22 | 2.04 |
| *Fraxinus americana* | 30 | 2 | 4 | 0.55 | 1 | 3.83 | 1.74 | 76.75 | 2.12 |
| *Fraxinus nigra* | 20 | 2 | 4 | 0.45 | 1 | 4.08 | 1.61 | 71.94 | 2.10 |
| *Fraxinus pennsylvanica* | 25 | 3 | 4 | 0.53 | 1 | 3.50 | 1.61 | 87.72 | 1.80 |
| *Picea glauca* | 25 | 1 | 1 | 0.35 | 1 | 1.15 | 3.91 | 302.86 | 1.28 |
| *Picea mariana* | 20 | 1 | 1 | 0.41 | 1 | 0.74 | 3.81 | 294.12 | 1.12 |
| *Pinus banksiana* | 20 | 3 | 5 | 0.42 | 1 | 1.50 | 3.30 | 243.90 | 1.24 |
| *Pinus resinosa* | 25 | 3 | 5 | 0.39 | 1 | 2.27 | 3.58 | 294.12 | 1.17 |
| *Pinus strobus* | 30 | 3 | 5 | 0.36 | 2 | 2.89 | 3.00 | 121.92 | 1.42 |
| *Pinus sylvestris*† | 21 | 3 | 5 | 0.42 | 1 | 1.79 | 3.30 | 243.90 | 1.24 |
| *Populus balsamifera*† | 25 | 3 | 2 | 0.37 | 1 | 0.26 | 1.28 | 83.46 | 1.95 |
| *Populus grandidentata* | 20 | 3 | 2 | 0.39 | 1 | 0.17 | 1.61 | 70.45 | 2.50 |
| *Populus tremuloides* | 25 | 3 | 2 | 0.37 | 1 | 0.14 | 1.58 | 82.02 | 2.16 |
| *Prunus serotina* | 22 | 3 | 2 | 0.47 | 3 | 4.55 | 1.71 | 72.30 | 2.48 |
| *Quercus alba* | 35 | 1 | 3 | 0.60 | 3 | 8.17 | 1.61 | 81.21 | 2.39 |
| *Quercus coccinea* | 30 | 3 | 3 | 0.60 | 3 | 7.57 | 1.61 | 95.00 | 1.90 |
| *Quercus ellipsoidalis* | 22 | 1 | 3 | 0.56 | 3 | 8.50 | 1.79 | 88.00 | 2.29 |
| *Quercus macrocarpa*‡ | 15 | 1 | 3 | 0.58 | 3 | 8.71 | 1.79 | 92.74 | 2.27 |
| *Quercus rubra* | 25 | 2 | 3 | 0.56 | 2 | 8.20 | 1.79 | 84.20 | 2.06 |
| *Quercus velutina*† | 18 | 2 | 3 | 0.56 | 3 | 8.50 | 1.79 | 98.00 | 2.40 |
| *Thuja occidentalis* | 15 | 1 | 1 | 0.30 | 3 | 0.83 | 3.50 | 223.00 | 1.02 |
| *Tilia americana* | 35 | 2 | 3 | 0.32 | 1 | 2.77 | 1.61 | 60.81 | 2.94 |
| *Tsuga canadensis* | 30 | 1 | 1 | 0.40 | 1 | 2.31 | 4.09 | 122.55 | 0.99 |
| *Ulmus americana* | 35 | 3 | 3 | 0.46 | 1 | 2.00 | 1.78 | 79.47 | 2.07 |

*Note:* Terms are H, average maximum height; GR, growth rate (1, slow; 2, moderate; 3, rapid); LS, leaf size (1, needle/scale; 2, small <10 cm; 3, large; 4, compound); WD, wood density (specific gravity); WDR, wood decay resistance (1, not; 2, moderate; 3, resistant; 4, very resistant); SeM, seed mass; LL, leaf longevity; LMA, leaf mass per area; N, nitrogen content per leaf mass unit.

† Michigan landscape only.

‡ Minnesota landscape only.

species AGB. We utilized a species trait matrix used in previous research (Paquette and Messier 2011) and added species to the trait matrix that were unique to our study. Specific species traits included maximum height, growth rate, leaf size, longevity, foliar mass per area, foliar nitrogen content, wood density, decay resistance, vegetative reproduction, seed mass, pollination vector, mycorrhizal infection type, shade tolerance, drought tolerance, and water-logging tolerance (Tables 1 and 2).

### Analysis

We compared aboveground ANPP and diversity of BAU management to CSP management under each climate scenario. We calculated $e^{H'}$ and FDis diversity for every cell in a simulation and created raster files for each diversity index and scenario. We used these layers of diversity and LANDIS-II ANPP output raster layers for further spatial analysis. Of the actively managed cells, we separated sites where CSP species were present vs. absent to compare ANPP. We used the vegan-community ecology (Oksanen et al. 2012), FD function-al diversity (Laliberté and Legendre 2010), and raster (Hijmans and Etten 2013) libraries in R (R Core Team 2013) for all calculations and analysis.

We replicated each simulation five times in order to examine the stochastic variation within scenarios. The model stochastic behavior was largely driven by natural disturbances of fire and wind. The within-scenario variation was small due to the low stochastic variation of natural disturbance events relative to the large size of the landscapes. As an attempt to increase result variation, we bootstrapped the five replicates 1000 times under our three climate futures and two management scenarios. Given the low number of replicates (due to long computational time), the variance from the boot-strapping did not increase substantially. Compared to the total AGB replicate mean at year 2100, the maximum variance was less than 0.05% for every individual replicate. Therefore, we randomly selected one replicate from each simulation for additional analysis. Although strict validation of future simulation results is not possible, species-specific parameters used in PnET-II and the Biomass Succession extension to LANDIS-II have been evaluated in other northern Great Lakes landscapes (Scheller and Mladenoff 2004, Xu et al. 2007, Ravenscroft et al. 2010). Furthermore, we evaluated LANDIS-II simulated AGB to U.S. Forest Service Forest Inventory and Analysis field plot

TABLE 2. Additional species traits used to calculate FDis (Paquette and Messier 2011).

| Species | Veg | Pa | Pb | TolS | TolD | TolW | AM | EM |
|---|---|---|---|---|---|---|---|---|
| *Abies balsamea* | 1 | 1 | 0 | 5.0 | 1.0 | 2.0 | 0 | 1 |
| *Acer rubrum* | 1 | 1 | 1 | 3.4 | 1.8 | 3.1 | 1 | 0 |
| *Acer saccharum* | 1 | 1 | 1 | 4.8 | 2.3 | 1.1 | 1 | 0 |
| *Betula alleghaniensis* | 1 | 1 | 0 | 3.2 | 3.0 | 2.0 | 0 | 1 |
| *Betula papyrifera* | 1 | 1 | 0 | 1.5 | 2.0 | 1.3 | 0 | 1 |
| *Carya cordiformis* | 0 | 1 | 0 | 2.1 | 4.0 | 2.5 | 0 | 1 |
| *Carya ovata* | 2 | 1 | 0 | 3.4 | 3.0 | 1.4 | 0 | 1 |
| *Castanea dentata* | 2 | 1 | 0 | 3.1 | 3.0 | 1.0 | 0 | 1 |
| *Fagus grandifolia*† | 2 | 1 | 0 | 4.8 | 1.5 | 1.5 | 0 | 1 |
| *Fraxinus americana* | 1 | 1 | 0 | 2.5 | 2.4 | 2.6 | 1 | 0 |
| *Fraxinus nigra* | 1 | 1 | 0 | 3.0 | 2.0 | 3.5 | 1 | 0 |
| *Fraxinus pennsylvanica* | 1 | 1 | 0 | 3.1 | 3.9 | 3.0 | 1 | 0 |
| *Picea glauca* | 0 | 1 | 0 | 4.2 | 2.9 | 1.0 | 0 | 1 |
| *Picea mariana* | 2 | 1 | 0 | 4.1 | 2.0 | 2.0 | 0 | 1 |
| *Pinus banksiana* | 0 | 1 | 0 | 1.4 | 4.0 | 1.0 | 0 | 1 |
| *Pinus resinosa* | 0 | 1 | 0 | 1.9 | 3.0 | 1.0 | 0 | 1 |
| *Pinus strobus* | 0 | 1 | 0 | 3.2 | 2.3 | 1.0 | 0 | 1 |
| *Pinus sylvestris*† | 0 | 1 | 0 | 1.4 | 4.0 | 1.0 | 0 | 1 |
| *Populus balsamifera*† | 1 | 1 | 0 | 1.3 | 1.8 | 2.6 | 1 | 1 |
| *Populus grandidentata* | 1 | 1 | 0 | 1.2 | 2.5 | 2.0 | 1 | 1 |
| *Populus tremuloides* | 1 | 1 | 0 | 1.2 | 1.8 | 1.8 | 1 | 1 |
| *Prunus serotina* | 0 | 0 | 1 | 2.5 | 3.0 | 1.1 | 1 | 1 |
| *Quercus alba* | 0 | 1 | 0 | 2.9 | 3.6 | 1.4 | 0 | 1 |
| *Quercus coccinea* | 2 | 1 | 0 | 2.1 | 4.0 | 1.0 | 0 | 1 |
| *Quercus ellipsoidalis* | 2 | 1 | 0 | 2.9 | 2.9 | 1.2 | 0 | 1 |
| *Quercus macrocarpa*‡ | 0 | 1 | 0 | 2.7 | 3.9 | 1.8 | 0 | 1 |
| *Quercus rubra* | 1 | 1 | 0 | 2.8 | 2.9 | 1.1 | 0 | 1 |
| *Quercus velutina*† | 1 | 1 | 0 | 2.8 | 3.9 | 1.2 | 0 | 1 |
| *Thuja occidentalis* | 2 | 1 | 0 | 3.5 | 2.7 | 1.5 | 1 | 0 |
| *Tilia americana* | 1 | 0 | 1 | 4.0 | 2.9 | 1.3 | 0 | 1 |
| *Tsuga canadensis* | 0 | 1 | 0 | 4.8 | 1.0 | 1.3 | 0 | 1 |
| *Ulmus americana* | 1 | 1 | 0 | 3.1 | 2.9 | 2.5 | 1 | 0 |

*Note:* Terms are Veg, vegetative reproduction (0, never; 1, possible; 2, common); Pa, abiotic pollination (0, not possible; 1, possible); Pb, biotic pollination (0, not possible; 1, possible); TolS, shade tolerance (1, intolerant; 5, tolerant); TolD, drought tolerance (1, intolerant; 5, tolerant); TolW, waterlogging tolerance (1, intolerant; 5, tolerant); AM, arbuscular mycorrhiza (0, not possible; 1, possible); EM, ectomycorrhiza (0, not possible; 1, possible).

† Michigan landscape only.
‡ Minnesota landscape only.

estimates of AGB in northern lower Michigan (Pearson's correlation of 0.64, and RMSE of 44.3 Mg/ha). Details of our biomass evaluation are described in Duveneck et al. (2014b).

## RESULTS

### Aboveground biomass and annual net primary productivity

The high-emission climate scenario resulted in substantially less simulated total and harvested AGB compared to current and low-emission climate scenarios by year 2100 (Fig. 3). The large increase in simulated AGB under current and low emissions is a reflection of continued AGB recovery following large-scale logging across the region in the early 20th century. CSP management resulted in greater simulated total AGB compared to BAU management (Fig. 3). In the Minnesota landscape, simulated AGB at year 2100 increased under the CSP scenario by 18%, 19%, and 30% in the current, low-emission, and high-emission climate scenarios, respectively. In the Michigan landscape, where greater total AGB was simulated in general,

AGB at year 2100 increased less under the CSP scenario (3%, 3%, and 7% in the current, low-emission, and high-emission climate scenarios, respectively). In the Minnesota landscape, CSP under each climate scenario resulted in greater total AGB compared to BAU. In the Michigan landscape, larger AGB due to CSP was most pronounced under the high-emission climate scenario. Harvested AGB followed a pattern similar to that of total AGB. Harvested AGB was greater under CSP, but there was an overall declining trend in harvested AGB under the high-emission scenario. As simulated planted species matured to a merchantable age, more simulated biomass was harvested compared to BAU management (Fig. 3B). The initial larger harvested CSP biomass in the Minnesota landscape is due to an increase in implementation frequency of the northern hardwoods patch-cutting prescription necessary to implement the CSP treatment.

In each simulated landscape, CSP species established and increased in AGB through time (Fig. 4). The current and low-emission climate scenario generally resulted in greater CSP species AGB compared to the high-emission climate scenario. The Michigan landscape exhibited
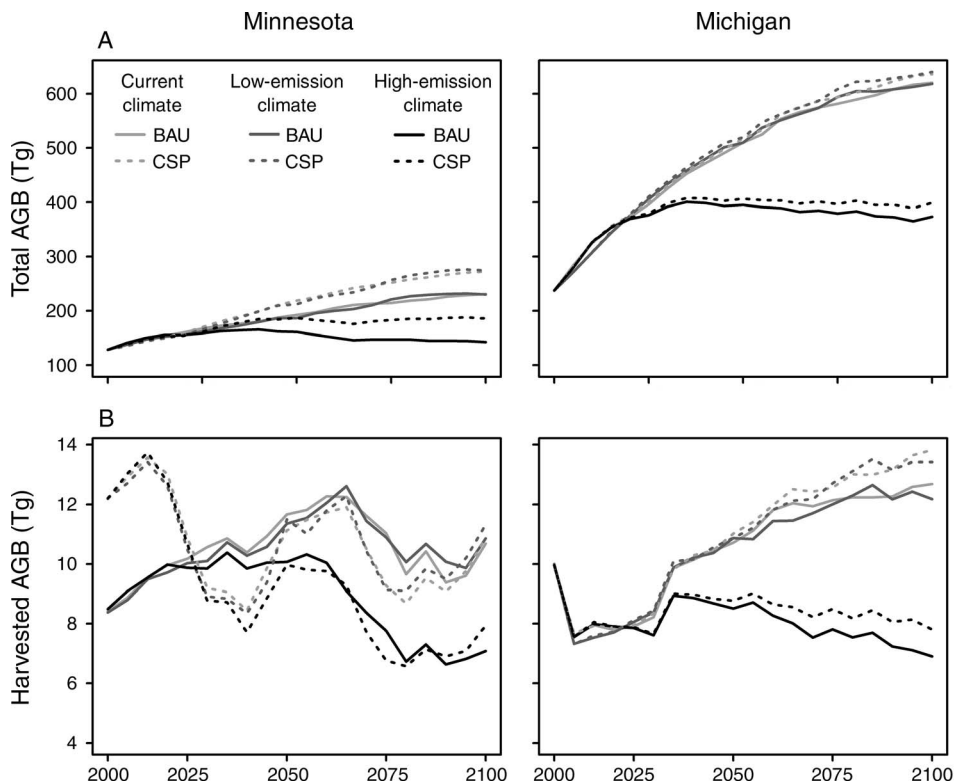
Fig. 3. Simulated (A) total aboveground biomass (AGB) and (B) harvested AGB over the years 2000 to 2100 for each landscape, climate, and management scenario. BAU is business-as-usual management; CSP is climate-suitable planting management.

larger climate scenario effects and larger increases in CSP species AGB compared to the Minnesota landscape. Of the planted species, American chestnut and bitternut hickory resulted in the largest increases in simulated AGB by year 2100.

Like AGB, aboveground ANPP was lower under the high-emission scenario compared to the current and low-emission scenario (Fig. 5). Although both landscapes resulted in similar ANPP at year 2100, the Minnesota landscape started with higher ANPP, and resulted in larger declines. Especially apparent in the Michigan landscape under the high-emission climate scenario, simulated ANPP resulted in a rapid decline before year 2050, followed by a relatively stable period. The stable period of ANPP may be due to the climate becoming more suitable for certain native species. In both landscapes, the effect of CSP resulted in limited differences in simulated ANPP as compared to BAU management. Specifically, simulated ANPP in the CSP management scenario under the high-emission climate scenario did not equal simulated ANPP under current climate and BAU management.

Although AGB of CSP species increased less in the high-emission scenario (Fig. 4), the proportion of cells occupied by CSP species was greatest in the high-emission scenario, followed by the low-emission and current climate (Fig. 6A). Compared to actively managed cells unoccupied by CSP species, actively managed cells occupied by CSP species resulted in similar simulated ANPP under the high-emission scenario (Fig. 6B). The results of the current and low-emission climate scenarios were mixed. Simulations in the Minnesota landscape resulted in generally less ANPP within CSP-occupied sites compared to unoccupied CSP sites within the current and low-emission climate scenario. After year 2070, the Michigan landscape resulted in greater simulated ANPP within CSP-occupied sites compared to unoccupied CSP sites within the current and low-emission climate scenario. The initial lower simulated aboveground ANPP in CSP species cells is expected due to the delayed growth in young cohorts. As the initial planted species mature, the effect of the growth lag in young cohort cells is reduced.

*Species and functional diversity*

The CSP scenario resulted in greater simulated species diversity ($e^{H'}$). Larger species diversity due to CSP was found in both landscapes under all climate scenarios and time steps (Fig. 7). In the Minnesota landscape, the CSP scenario also resulted in greater FDis in all climate scenarios. The CSP scenario however, reached an asymptote after 2050, while functional diversity under the BAU scenario continued to increase. In the Michigan landscape, where initial functional and species
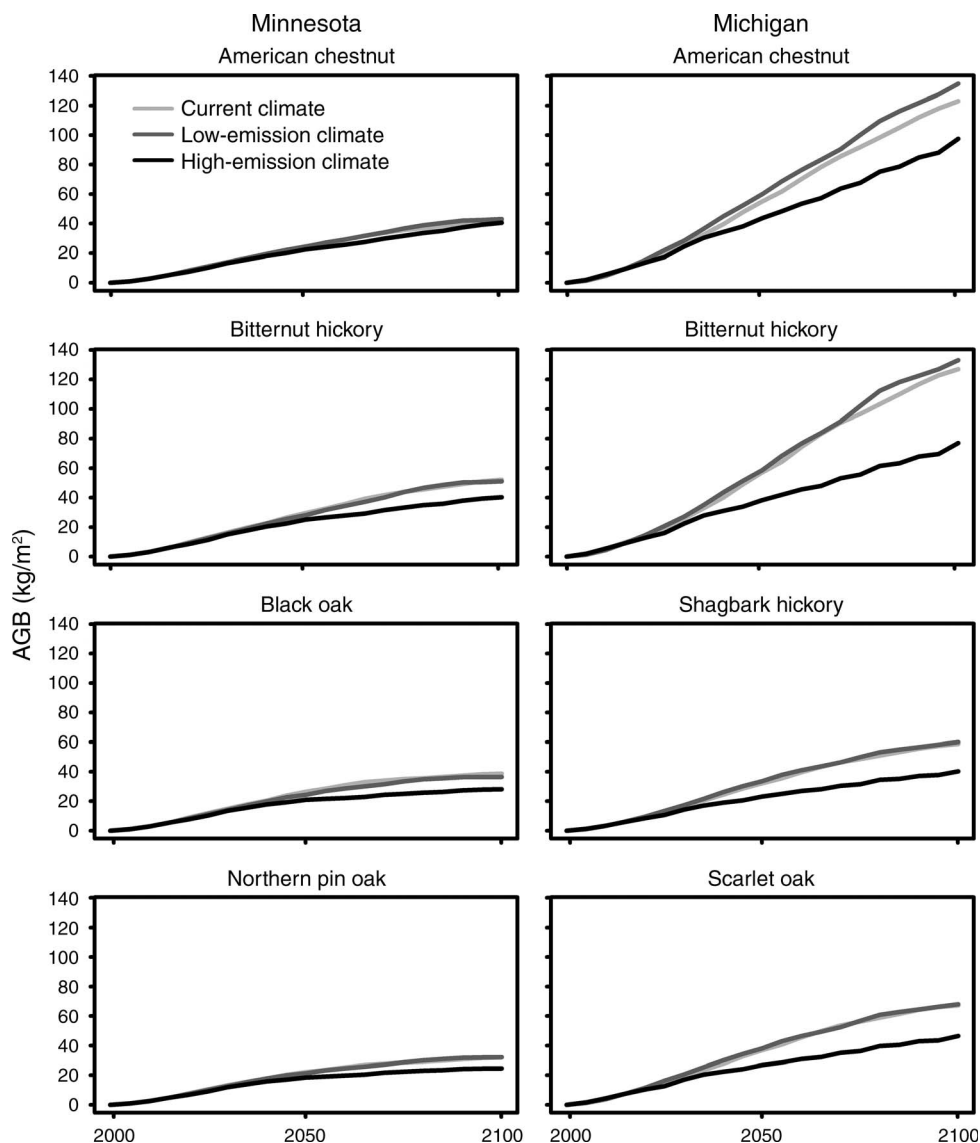
Fig. 4. Aboveground biomass (AGB) of climate-suitable planting species simulated in each landscape and climate scenario. American chestnut (*Castanea dentata*) and bitternut hickory (*Carya cordiformis*) were simulated in both landscapes. Other species were black oak (*Quercus velutina*), northern pin oak (*Q. ellipsoidalis*), scarlet oak (*Q. coccinea*), and shagbark hickory (*Carya obovata*).

diversity was higher, CSP resulted in less functional diversity in all climate scenarios after 2030.

In the Minnesota landscape, the high-emission climate scenario resulted in the largest increase in both species and functional diversity. These results are in contrast to the current and low-emission climate scenarios, which resulted in a consistent, although slower, increase in species diversity through time. The Michigan landscape exhibited greater initial diversity than Minnesota; over time, however, species diversity declined. The Michigan landscape exhibited relatively consistent FDis over time. The high- and low-emission climate scenarios resulted in less species diversity than current climate. The high-emission climate scenario,

however, resulted in the greatest functional diversity in the Michigan landscape.

## DISCUSSION

In some sites, CSP management may provide an opportunity to increase ecosystem services such as AGB, ANPP, and diversity under climate change. CSP may be most effective in sites or landscapes when otherwise large declines in productivity are expected (Stanturf et al. 2014). At timescales in the range of the longevity of many extant tree species (e.g., <200 years), climate is expected to change faster than species' ability to maintain equilibrium (Diffenbaugh and Field 2013, Svenning and Sandel 2013). However, forest manage-
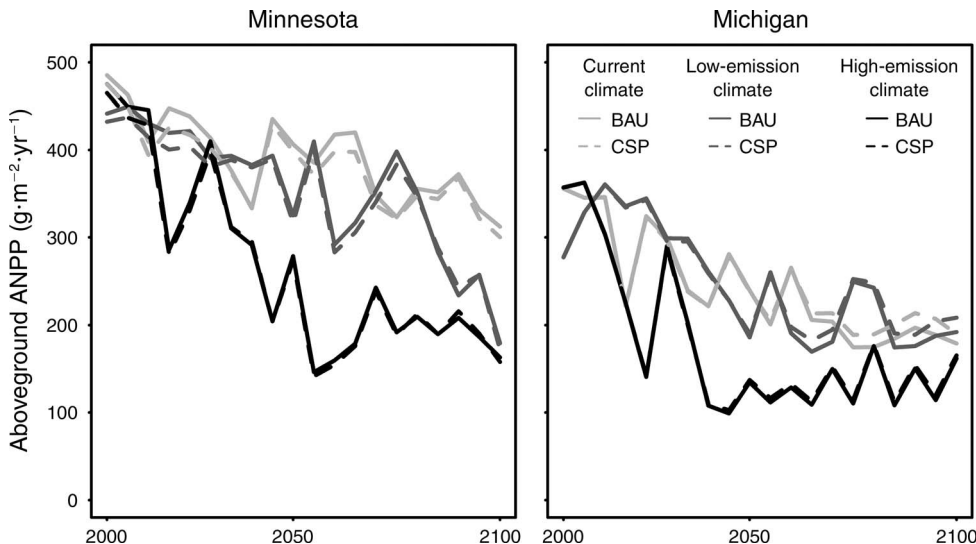
FIG. 5. Simulated average aboveground annual net primary productivity (ANPP) measured over time for each landscape, climate, and management scenario. BAU is business-as-usual management; CSP is climate-suitable planting management.

ment in our landscapes is often focused at rotation-period time scales (i.e., <100 years). The ability to maintain forest ecosystem services at those timescales is expected to be limited within traditional (Duveneck et al. 2014b) and even alternative management (without the use of CSP) (Duveneck et al. 2014a).

### Aboveground biomass and annual net primary productivity

As reported earlier (Duveneck et al. 2014b), under high-emission climate, BAU management suggests less simulated total and harvested AGB compared to current and low-emission climate scenarios. Greater simulated total and harvested ABG due to CSP suggests that planting climate-suitable species may increase the resilience of forests to the effects of climate change. The larger CSP AGB results are small in relation to the treatment intensity. Planting intensity was 5.28% and 4.97% of each landscape at each five-year time step in the Minnesota and Michigan landscapes, respectively. This suggests that the CSP scenario did not grossly contract the current niche space used by extant tree species. Although the species selected for planting are native to regions south of each
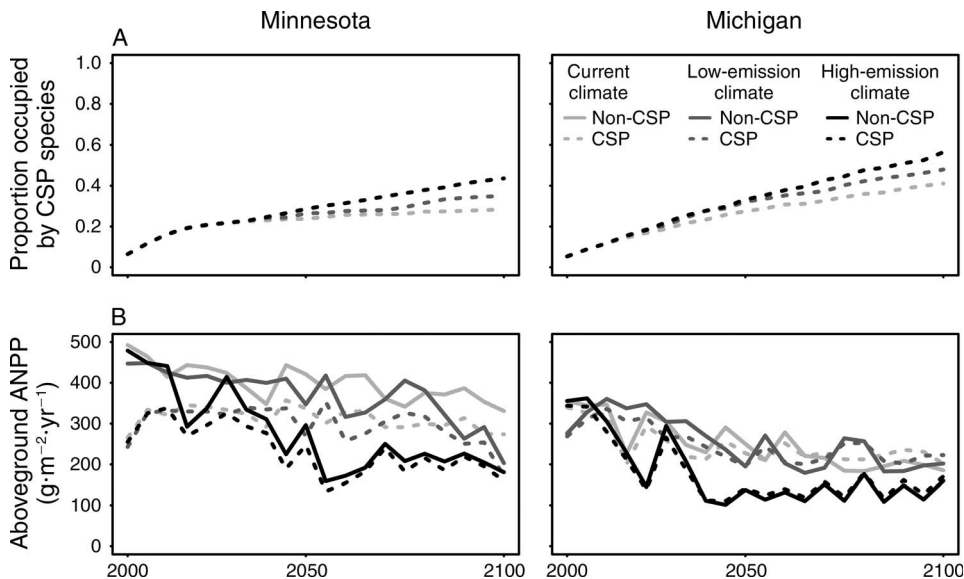


FIG. 6. (A) Within the climate-suitable planting (CSP) scenario, the proportion of landscapes occupied by at least one CSP species, and (B) average aboveground annual net primary productivity (ANPP) across actively managed sites where at least one CSP species was present compared to cells where CSP species were absent.
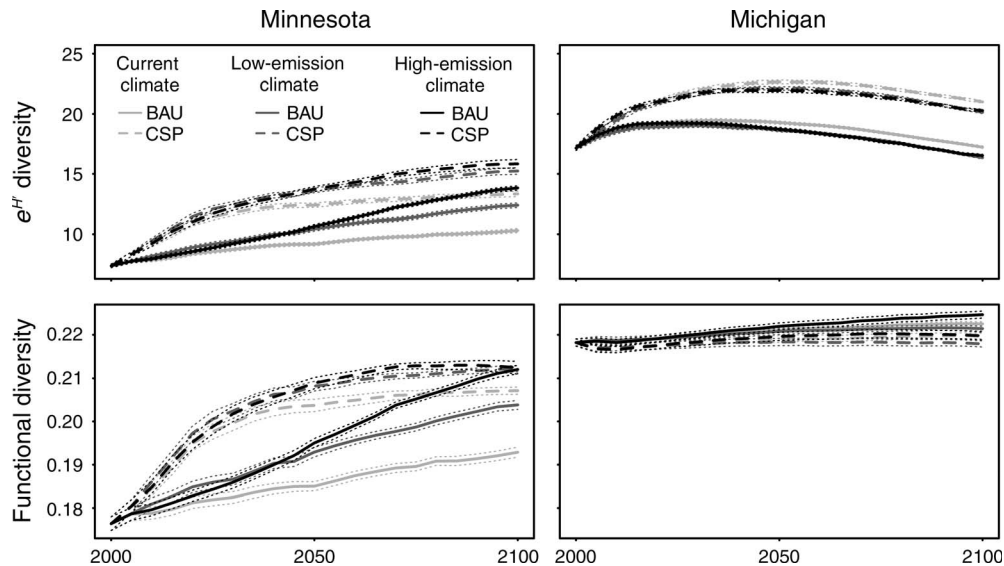
Fig. 7. Average species diversity ($e^{H'}$) and functional diversity (FDis) across cells for each landscape, climate, and management scenario over time. Light dotted lines represent standard error across cells for each scenario. BAU is business-as-usual management; CSP is climate-suitable planting management.

landscape, the high-emission climate scenario did not result in the most optimized climate selection for those species. The current and low-emission climate scenarios resulted in more optimal growth as measured by simulated AGB (Fig. 4). Had we simulated planting species from even farther south, we expect to have simulated more use of niche space, resulting in greater increases in AGB and ANPP under the high-emission climate.

The CSP treatment was implemented following simulated patch-cutting harvests. The initial decline in ANPP within CSP cells is due to the expected lag in growth response of young cohorts (Bowler et al. 2012). Compared to older stands, ANPP of recently harvested sites would lag behind before increasing. Although the non-CSP-occupied harvest areas (i.e., harvested stands that did not include any CSP species) were also vulnerable to disturbance, compared to the CSP sites, which all started with a disturbance, the non-CSP sites experienced less disturbance. Therefore, the majority of non-CSP sites were mature stands. Nevertheless, average ANPP within CSP sites was not substantially less than non-CSP-occupied sites, despite continual harvesting and new planting throughout the simulation. The CSP scenario in the Michigan landscape under the current and low-emission climate scenario resulted in greater simulated ANPP than BAU after 2075 (Fig. 5). As suggested in individual CSP species' response to climate (Fig. 4), the CSP species may have been best matched to the current and low-emission climate scenarios in the Michigan landscape.

In the Minnesota landscape, the net negative effect of CSP on ANPP was greater in the current and low-emission compared to the high-emission climate scenar-

io. Both the largest increase in proportion of sites occupied by CSP species and the largest decline in AGB and ANPP under BAU management were found under the high-emission climate scenario. Under the high-emission climate scenario, CSP species would have replaced species declining under climate change, e.g., balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*), that would otherwise be abundant under current climate (Duveneck et al. 2014*b*). This supports the suggestion that CSP may be most appropriate where large declines in productivity are expected (Lunt et al. 2013). Although the CSP scenario resulted in less of an increase in AGB under high-emission climate compared to current and low-emission climate, CSP did result in greater total and harvested AGB under the high-emission climate scenario where the largest BAU declines were simulated (Fig. 3). This suggests a net benefit in some ecosystem services under the CSP scenario.

As a restoration species, recent research suggests that American chestnut has the potential to fulfill much of its historical role as a foundation species (Gauthier et al. 2013, Jacobs et al. 2013). As climate has changed and will continue to change since American chestnut dominated the canopy of Eastern forests (Andresen et al. 2012), assessing landscape and site conditions for habitat suitability will be vital for reintroduction success. In the northern Great Lake region, disease-resistant chestnut seedlings have been successfully established within experimental plots (Jacobs and Severeid 2004). Our results suggest that introduced American chestnut has the potential to succeed within regions north of its historic range.

*Species and functional diversity*

In the Michigan landscape, simulated diversity remained relatively constant compared to the Minnesota landscape across all climate scenarios. This may be a result of greater initial species and functional diversity. In addition to inherent benefits of maintaining biodiversity (e.g., more species are less vulnerable to single host pathogens) (Wilson 2010), increasing diversity has the potential to enhance the range of environmental tolerances of the ecosystems providing ecosystem services (Walker 1992, Naeem and Li 1997). Within lower-productivity sites, the relationship between diversity and productivity may become more important (Loreau et al. 2001, Paquette and Messier 2011, Duveneck et al. 2014*b*). Furthermore, under a high-emission scenario, our results suggest productivity and AGB declines are expected.

CSP was more effective at increasing functional diversity in Minnesota than in Michigan. Where initial species diversity was lower and decline in productivity was higher (Minnesota), CSP initially resulted in greater functional diversity compared to BAU management. Following 100 simulation years of high emissions, however, FDis under the BAU scenario nearly surpassed FDis under the CSP scenario in the Minnesota landscape, where initial FDis was lower. This may be due to less initially dominant species (e.g., balsam fir and quaking aspen) under BAU because of a climate mismatch (Duveneck et al. 2014*b*). As these species declined, the simulated response of less dominant species became more equal, increasing FDis but decreasing AGB and ANPP. In addition, it is possible that the increase in functional diversity under BAU relative to CSP simulations can also be attributed to non-CSP species having unique functional roles that under CSP are being replaced by functionally similar CSP species.

Where initial species diversity was greater and the decline in productivity was lower (Michigan), CSP management resulted in less FDis compared to BAU management. In the Michigan landscape, the CSP scenario may have replaced functionally similar species, resulting in a landscape of less functionally dissimilar species. Therefore, landscapes expected to decline in productivity and diversity may provide more opportunity for effective climate management such as climate-suitable planting. Because our diversity results reflect a 2-ha grain size, our results are not necessarily scalable to finer grain sizes (Urban 2005). However, simulation results such as ours may help managers prioritize allocation of scarce resources to areas more critically vulnerable than others.

Given the novelty of assisted migration management (Lawler and Olden 2011) and the social limits to change (Adger et al. 2009), we chose CSP species based on close proximity (either current or historically) to our landscapes. This resulted in species that were functionally similar, i.e., functionally redundant (Walker 1992), to the species expected to persist under climate change (i.e., northern hardwoods and oaks). As such, CSP under the high-emission climate did not maintain greater functional diversity. Under BAU management and a high-emission climate future, we expect less spruce–fir species in these landscapes (Fisichelli et al. 2013, Duveneck et al. 2014*b*). Had we simulated planting central Appalachian conifers such as shortleaf pine (*Pinus echinata*), we would have likely seen a greater and sustained increase in functional diversity under climate change. Future work should consider exploring CSP treatments based on function replacement. Nevertheless, functional diversity generally increased through time and was greatest under the high-emission climate scenario in both landscapes (Fig. 7).

*Management challenges to climate-suitable planting*

The simulated benefits of CSP resulted from intensive planting prescriptions. We did not address CSP effects at varying management intensities to determine if equivalent benefits could be achieved at less (or more) intensive planting prescriptions. We do not expect the same benefits from an alternative planting intensity. Given economic constraints on managers, this is an area for future research.

Much discussion in the literature has centered on the debate for or against assisted migration (McLachlan et al. 2007, Hoegh-Guldberg et al. 2008, Ricciardi and Simberloff 2009, Lawler and Olden 2011). Most of this discussion has centered around movement for rare or endangered species protection (e.g., Barlow and Martin 2004). Less discussion has explored movement of species in order to maintain or increase ecosystem function of a site or region (Lunt et al. 2013). We recognize the risks of introduced species becoming invasive (Hoegh-Guldberg et al. 2008, Ricciardi and Simberloff 2009); however, the potential for novel ecosystems under climate change is unavoidable (Williams et al. 2007, Hobbs et al. 2009). In addition, benefits from ecosystem services from managed nonnative species are plausible (Lugo 2004, Schlaepfer et al. 2011). Restoring a specific species or forest type may not be obtainable, but maintaining a more general ecosystem service (e.g., AGB) may (Buma and Wessman 2013). Regardless of management planting decisions, our modeling results provide information critical to CSP decision support (Gray et al. 2010, Lawler and Olden 2011, Pérez et al. 2012).

Existing guidelines for genetic forest management minimize the movement of genetic material to avoid contamination of populations with poorly adapted genotypes (Millar et al. 2007, Breed et al. 2013). These guidelines were developed under the assumption that climate and the environment were stationary. Resampling common-garden experiments has demonstrated that native seed stock can be poorly adapted to changing climate (Millar and Brubaker 2006). Expanding guidelines for seed zone sizes based on the nonstatic and uncertain future has been implemented in British Columbia and other Canadian provinces (O'Neill et al. 2008*b*, Pedlar et al. 2012) and should be considered elsewhere (Breed et al. 2013).

## Model limitations

CSP represents a more radical climate change management strategy than previous work described (i.e., Ravenscroft et al. 2010, Duveneck et al. 2014a). Our CSP scenarios were not intended to be a "recipe book" for CSP, rather an introduction to understanding a management alternative. Our results should not be interpreted as predictions, but plausible futures with large uncertainty. There exists a large amount of variation across GCM and emission projections (IPCC 2007). Our low- and high-emission scenarios were designed to bracket GCM and emission uncertainty; however, carbon emissions have been observed at or above the high-emission scenario that we used (Jennings 2013, Peters et al. 2013), suggesting that our low-emission climate scenario is grossly underestimating the climate change trajectory. Although we used the most robust tree inventory data available, our imputation of initial conditions represents a simplification of current conditions (e.g., there does not exist an inventory plot for every simulated cell); initial diversity and or productivity may be greater than simulated. If so, the relative effect of CSP on diversity and/or productivity may be less than projected.

We modeled the realized niche (range of conditions that an organism occupies) of individual species. There is some likelihood that the actual realized niche will be smaller or larger than simulated. If on a given site, for example, a species expected to decline under climate change persists (larger realized niche than simulated), more species utilizing resources more completely may result in increased productivity. Alternatively, a species with a smaller realized niche than modeled may result in less site productivity than simulated.

In addition to climate and model uncertainty, there exist ecological processes that we did not include in our modeling framework. We did not include the fertilization effect of rising $CO_2$ concentration. Although we recognize that increasing $CO_2$ will positively affect photosynthesis (Norby et al. 2005), limits to growth such as nitrogen (Luo et al. 2004) or ozone (Ainsworth et al. 2012) may diminish these effects. We did not consider browse damage by white-tailed deer (*Odocoileus virginianus*), which can severely limit regeneration and growth of seedlings (Fisichelli et al. 2012, Nuttle et al. 2013). We also did not directly model effects of insects such as spruce budworm *Choristoneura fumiferana* (MacLean and Ostaff 1989). Because many forest-damaging insects are single-host specific, the interaction of management on diversity, combined with insect damage, represent important opportunities for future research. We did not incorporate future alternations to natural disturbance regimes. Fire and wind regimes were assumed to be constant through each simulation. Finally, BAU forest management represents our best guess at current silviculture practices (Duveneck et al. 2014b). Future management will depend on difficult-to-predict landowner objectives, market fluctuations, and changing ecosystem service priorities. Finally, model parameters were based on the best available input data. Future empirical research will reduce parameter uncertainty.

## CONCLUSIONS

For forests and other landscapes that are substantially degraded or disturbed, restoration treatments are often implemented with an objective to restore conditions to pre-disturbance conditions within a historical range of variability, HRV (Landres et al. 1999). Hobbs et al. (2011) suggest "intervention" ecology as a more direct and meaningful strategy than restoration. Rather than considering restoration to a historical range of variability, intervention ecology can consider expected future ranges of variability (Harris et al. 2006). Trade-offs exist, however, between preserving (to what once was) and adapting (to what is possible) (Marris 2009, Buma and Wessman 2013). HRV continues to contain important information, as many organisms still depend on habitats represented by the HRV. For example, CSP may increase the adaptive capacity of a forest's ANPP, but may outcompete or reduce habitat for a vulnerable native species (Ackerly 2003). Ideally, trade-offs can be managed through CSP treatment intensity, allowing some areas reserved for historic processes and species (e.g., Duveneck et al. 2014a).

As pressures for increased agriculture develop (Wheeler and von Braun 2013), further fragmentation of forest land (due to agriculture) may further limit seed dispersal (Scheller and Mladenoff 2005, Iverson et al. 2008). In more fragmented landscapes, interest in CSP may increase. Finally, a future increase in the value of carbon sequestration to mitigate climate change may provide more impetus to manage forests to maximize ANPP.

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## SUPPLEMENTAL MATERIAL

### Data Availability

Data associated with this paper have been deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.18ng6