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Spatial Resilience of Forested Landscapes Under Climate Change and Management

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RESEARCH ARTICLE

Spatial resilience of forested landscapes under climate change and management

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Abstract
Context Resilience, the ability to recover from disturbance, has risen to the forefront of scientific policy, but is difficult to quantify, particularly in large, forested landscapes subject to disturbances, management, and climate change.
Objectives Our objective was to determine which spatial drivers will control landscape resilience over the next century, given a range of plausible climate projections across north-central Minnesota.
Methods Using a simulation modelling approach, we simulated wind disturbance in a 4.3 million ha forested landscape in north-central Minnesota for 100 years under historic climate and five climate change scenarios, combined with four management scenarios: business as usual (BAU), maximizing economic returns ('EcoGoods'), maximizing carbon storage ('EcoServices'), and climate change adaption ('CCAdapt'). To estimate resilience, we examined sites where simulated windstorms removed >70% of the biomass and measured the difference in biomass and species composition after 50 years.
Results Climate change lowered resilience, though there was wide variation among climate change scenarios. Resilience was explained more by spatial variation in soils than climate. We found that BAU, EcoGoods and EcoServices harvest scenarios were very similar; CCAdapt was the only scenario that demonstrated consistently higher resilience under climate change. Although we expected spatial patterns of resilience to follow ownership patterns, it was contingent upon whether lands were actively managed.
Conclusions Our results demonstrate that resilience may be lower under climate change and that the effects of climate change could overwhelm current management practices. Only a substantial shift in simulated forest practices was successful in promoting resilience.

Keywords Carbon cycle · Century · Climate change adaptation · Forest simulation model · Forest management · Wind disturbance

Also, all input data associated with this paper have deposited in the LANDIS-II Foundation website: https://github.com/LANDIS-II-Foundation/Project-MN-Climate-Change-2017

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Introduction

Resilience has recently risen to the forefront of public policy. For example, the guiding principles of the US

Environmental Protection Agency currently state that "when relevant, adaptive [management for climate change] should take into account strategies to increase resilience" (EPA 2012). The US Forest Service Policy acknowledges that managing for genetic and species diversity promotes resilience and adaptive capacity (USDA Forest Service 2010). However, ecologists can't even agree on the best definition of resilience. It currently has at least 10 different definitions (Newton and Cantarello 2015), though they all focus on the ability of an ecosystem to recover from disturbance (Holling 1973). Controversy about its definition likely delayed its widespread application (Grimm and Calabrese 2011), as the term resilience was first applied to ecological systems nearly 40 years ago (Hollings 1973). The most accepted definition of ecological resilience is the amount of disturbance that a system can absorb while still remaining within the same state (Carpenter et al. 2001). Because measuring ecological resilience is fraught with difficulties (Grimm and Calabrese 2011), engineering resilience, or the capacity of a system to recover to a previous state after a disturbance event (Holling 1996), is more commonly measured and is what we mean by 'resilience' throughout this paper.

Forested landscapes present unique challenges to measuring, managing, or forecasting resilience (Seidl et al. 2016). Forest landscapes are subject to a broad range of disturbances with varying frequency, size, and intensity. This can potentially create large spatial variability in resilience (Cumming 2011), which can be difficult to quantify because areas with more severe disturbance events may appear less resilient than those with less severe disturbances. Also soil type, management strategies, forest fragmentation, and other factors may generate spatial variation in resilience. Quantifying forest resilience is also challenged by the long generation times of forests. Finally, forest landscapes are not—and likely never have been—in equilibrium, particularly at high latitudes (Minckley et al. 2012) and in areas with frequent disturbances (Turner et al. 2003). Therefore, the 'state' to which a forest returns following disturbance is not a fixed entity but is rather a broad community-level potential. Furthermore, these states have been substantially altered by land use change and forest management.

Scientists and managers alike are concerned that forest resilience may decline as the climate changes, as disturbance regimes shift, and as the regeneration of many extant tree species declines. In our study, we focused on the forests of north-central Minnesota that are located along a transition ('tension') zone between broadleaf and boreal forests and are expected to be vulnerable to climate change (Handler et al. 2014) and associated disturbances (e.g., White and Host 2008). Recent IPCC AR5 projections suggest that average annual temperatures in Minnesota will increase by 4.7 °C; precipitation will increase by 6% [averaged across 44 combinations of emissions and global circulation models (GCMs) over the next century].

Timber harvesting is the most prevalent disturbance in Minnesota with 29% of the landscape in active management with extensive early-successional forest managed for pulp production (MN Dept. of Natural Resources 2011). Windthrow is the most important natural disturbances in the northern temperate forests of north-central and northeastern North America (Frelich 2002). Windstorms have a return interval for severe disturbance (>70% overstory mortality) ranging from 500 to 1000+ years (White and Host 2008), but the interval is much shorter (closer to 50 years (Frelich 2002) when minor and moderate wind events are also taken into account.

Projecting resilience of forests under climate change is challenging but important, given their size and importance for people and wildlife. Forest landscape simulation models can serve as useful tools for projecting change, because they account for both spatial and non-spatial biotic and abiotic interactions that structure forested ecosystems (He 2008). They can simulate the timing and severity of disturbance events, forecast spatial patterns of forest composition, and quantify resilience both spatially and temporally. Simulation models that incorporate forest management activities can be used to test potential alternative management strategies (e.g., climate suitable planting) and to identify those activities that create more resilient landscapes. They can also identify areas that will be more or less resilient, enabling prioritization of effort at broad scales.

Our objective was to determine which spatial drivers will control landscape resilience over the next century, given a range of plausible climate projections across north-central Minnesota. To address our objective, we used a widely-used forest landscape simulation model (LANDIS-II) that includes the natural and anthropogenic disturbances that structure forests in north-central Minnesota.

Methods

Site description and landscape initialization

The study landscape occupies 3.4 million ha in north-central Minnesota and includes the Northern Minnesota Drift and Lake Plains Ecological Section (MDL or 212N), and the entirety of the Chippewa National Forest (CNF, Fig. 1). Multiple episodes of glaciation have left the region with hundreds of lakes and complex surficial geology and soils, which is reflected in the patchy distribution of vegetation. Mesic forests are widespread throughout the MDL, characterized by species such as aspen (*Populus tremuloides* and *P. grandidentata* Michx.), paper birch (*Betula papyrifera* Marshall), northern red oak (*Querus rubra* L.), basswood (*Tilia americana* L.), and sugar maple (*Acer saccharum* L.). The eastern part of the MDL is composed of glacial lake plains that have expansive bogs of black spruce (*Picea mariana* (Mill.) Britton, Stems and Poggenburg) and wetland forests of white cedar (*Thuja occidentalis* L.) and black ash (*Fraxinus nigra* Marshall). In the western part of the MDL, sandy and gravelly deposits atop moraines provide habitat for mixed forests of pine and boreal hardwood species, such as aspen and paper birch. Historically, forests of jack pine (*Pinus banksiana* Lam.) and red pine (*P. resinosa* Ait.) were very common in this landscape, but now these fire-dependent communities are often restricted to sandy outwash plains. The climate is humid, continental, and cold temperate with mean temperatures in January of −15 °C and in July of 20 °C; mean annual precipitation is 87 cm (PRISM Climate Group 2013).

We deployed a widely-used forest landscape simulation model, LANDIS-II v6.1 (Scheller et al. 2007) to simulate the effects of climate change, wind, and harvesting on forest succession, carbon and nitrogen cycling, and landscape resilience in the MDL. In LANDIS-II, the landscape is comprised of interconnecting grid cells with each cell assigned to an ecoregion (where climate and soil properties are assumed to be homogenous). Within each cell, trees are represented as species–age cohorts rather than individuals (Mladenoff 2004). Species–age cohorts are dynamic over time, and there may be multiple species and age cohorts within each cell. Disturbances in LANDIS-II are stochastic; each disturbance is encapsulated within an independent extension as detailed below. Species response to disturbance is dictated by life history attributes and competition (Roberts 1996).

To use LANDIS-II, we populated our landscape with cohorts representing 32 tree species (Table 1), by combining maps of forest types with Forest Inventory and Analysis data, and estimated the age distribution of all species using site index curves (full description of procedures outlined in Online Appendix 1). We divided our landscape into 25 ecoregions (regions with homogenous climate and soils) with 5 soil regions nested within each of the 5 climate regions. Our resolution was 4 ha and our landscape was 3.4 million ha.

Description of the Century Succession extension of LANDIS-II

We used the Century Succession extension (v4.0.2) of LANDIS-II to simulate forest succession (Scheller et al. 2015). The extension simulates aboveground (leaves and wood) and belowground (fine and coarse roots) growth of each cohort on each site on a monthly basis (Scheller et al. 2011, 2012). To calculate growth, it uses algorithms that consider species-specific life history attributes (e.g., longevity, shade tolerance), climate, age, ecoregion, competition (i.e., the biomass of other cohorts relative to the amount of maximum potential biomass), water availability, N availability and temperature to simulate growth and cohort competition. The Century Extension also simulates tree mortality caused by senescence (ongoing loss of trees and branches) and age (to account for the increase in mortality as a species approaches its life expectancy). In addition to growth, it also simulates regeneration via seeds or resprouting (vegetative reproduction) using life history attributes (e.g., age to sexual maturity and seed dispersal distances) and indices of light and water availability (Scheller et al. 2007). Spatial interactions during dispersal and disturbance events are represented, and they overlap in time and space.

The Century Succession extension also simulates C and N cycling through detritus (foliar, woody, fine roots and coarse root detritus), soil (fast, slow, and passive pools) and vegetation (leaf, wood, fine roots and coarse roots by species and age) (Scheller et al. 2011, 2012). Decomposition is assumed to be microbially mediated and is a function of litter

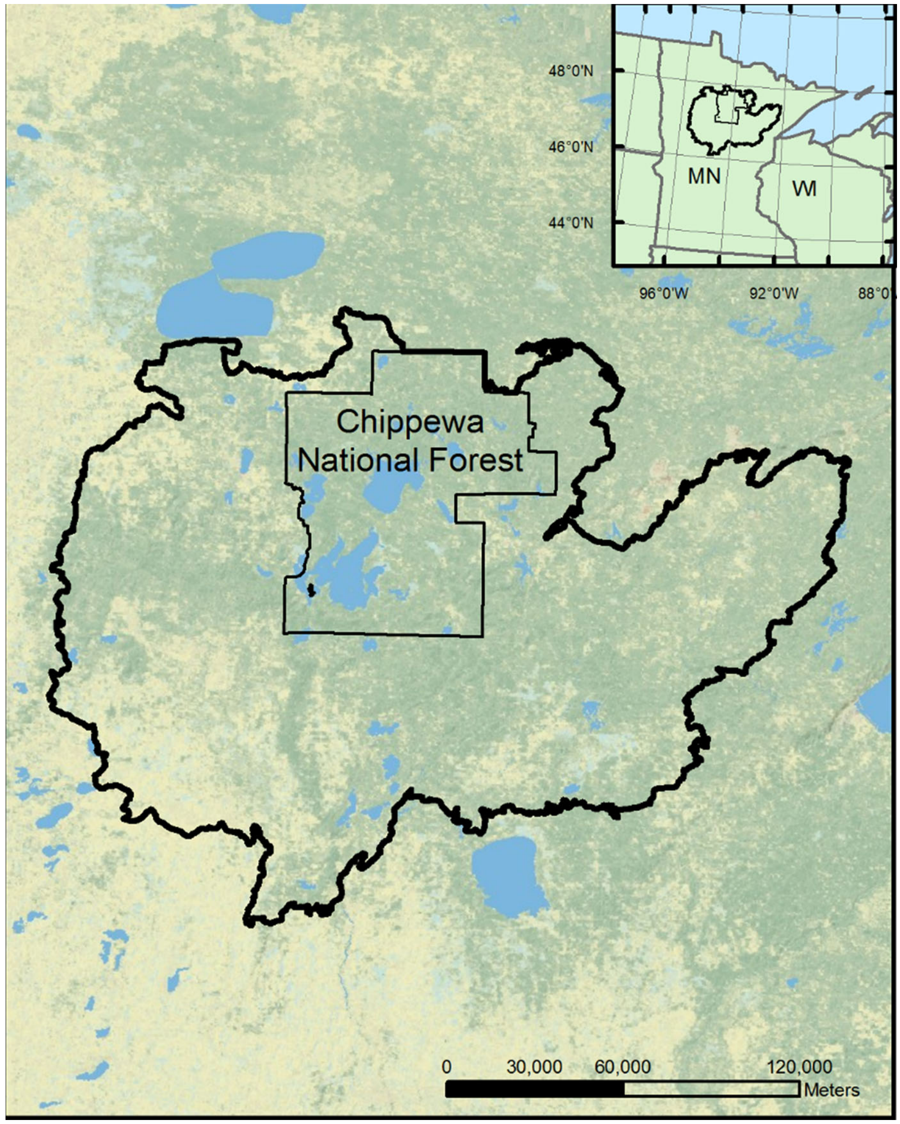


Fig. 1 Study landscape in north-central Minnesota, delineated by the state as the Northern Minnesota Drift and Lake Plains Ecological Section (MDL or 212N) and the entirety of the Chippewa National Forest

characteristics (e.g., leaf C/N ratios and lignin content) and soil conditions (e.g., soil moisture, temperature, and soil texture) using the algorithms specified in the extension's predecessor, the CENTURY soil model v 4.5 (Parton et al. 1983). The nitrogen cycle in the Century Succession extension is dynamic with a tightly coupled interaction between the atmosphere (wet and dry N deposition), vegetation (N uptake), and soil (N mineralization and leaching, Lucash et al. 2014). By simulating both aboveground (e.g., growth, mortality, regeneration) and belowground processes (e.g., decomposition and N mineralization) using a spatially-interactive framework, LANDIS-II is a powerful tool for simulating landscape-level changes in growth, species composition, and overall net ecosystem carbon balance (NECB or C sink strength) as a function of climate, succession and disturbance. Since previous versions of Century underestimated water availability in our landscape, we substantially revised the soil water algorithms, correcting errors in the timing of snowfall, snowmelt, runoff and available water. We modified retranslocation for conifers so that they could utilized the resorbed N throughout the year. In previous versions, conifers were restricted to using resorbed N in the spring (like hardwoods), but in this version, conifers are able to use this N source

Table 1 Species simulated in this study

Scientific names	Common names
Abies balsamea L. (Mill.)	Balsam fir
Acer negundo L.	Boxelder
Acer rubrum L.	Red maple
Acer saccharum L.	Sugar maple
Acer spicatum Lam.	Mountain maple
Betula alleghaniensis Britt.	Yellow birch
Betula papyrifera Marshall	Paper birch
Celtis spp. L.	Hackberry
Fraxinus americana L.	White ash
Fraxinus nigra Marshall	Black ash
Fraxinus pennsylvatica Marshall	Green ash
Larix laricina (Du Roi) K. Koch.	Black spruce
Ostra virginiana (Mill.) K.Koch.	Ironwood
Picea glauca (Moench) Voss.	White spruce
Picea mariana (Mill.) Britton, Sterns & Poggenburg.	Black spruce
Pinus banksiana Lam.	Jack pine
Pinus resinosa Ait.	Red pine
Pinus strobus L.	White pine
Populus balsamea (L.) Mill.	Balsam poplar
Populus deltoides W.Bartram ex Humphry Marshall	Black cottonwood
Populus grandidentata Michx.	Big-tooth aspen
Populus tremuloides Michx.	Trembling aspen
Prunus pensylvanica	Pin cherry
Prunus serotine Ehrh.	Black cherry
Prunus virginiana L.	Chokecherry
Quercus alba L.	White oak
Quercus ellipsoidalis E.J. Hill	Northern pin oak
Quercus macrocarpa Michx.	Bur oak
Quercus rubra L.	Red oak
Salix spp. L.	Willow
Thuja occidentalis L.	Northern white cedar
Tilia americana L.	Basswood
Ulmus americana L.	American elm
Ulmus rubra Muhl	Red elm

whenever tree growth is occurring. We also made several minor changes to the extension: (1) revised baseflow units to correct a previous error, (2) modified LAI so that it is set to zero in hardwoods when leaf drop occurs and (3) modified the BTOLAI and KLAI parameters to make them easier to calibrate.

Details of our Century Succession parameterization can be found in Online Appendix 2 and our calibration and validation of Century is detailed in Online Appendix 3.

Climate data

We created a climate library to reduce pre-processing time and create a common stream of climate data used by all climate-dependent LANDIS-II extensions (Lucash and Scheller 2015). The integrated climate library directly uses either monthly or daily climate data (minimum and maximum temperature, precipitation) directly from USGS Geo Data Portal (http://cida.usgs.gov/gdp/), and the climate library performs all pre-processing required by each climate-dependent LANDIS-II extension. In Century, the climate library provides the succession extension with monthly minimum and maximum temperatures which can positively (or negatively) affect monthly growth rates, based on the temperature response curves defined in the input file, as well as soil decomposition rates and tree cohort mortality (Scheller et al. 2011). Precipitation is added to each raster cell, and a simple bucket model is used to calculate water availability, which in turn affects cohort growth rates based on the pre-defined available water curves, decomposition rates, and mortality. Both temperature and water availability affect nitrogen cycling (e.g., N deposition, mineralization, uptake), which can affect growth rates (Lucash et al. 2014). Temperature and water availability also affect cohort regeneration rates (Scheller et al. 2011). The climate integration from the climate library allows LANDIS-II to respond to climate in a coordinated fashion across ecological processes (e.g., forest growth and decomposition, wildfire, and insect outbreaks) at each model time step and allows climate variability to produce realistic emergent properties of species composition, disturbance regimes, and ecosystem dynamics (e.g., carbon cycling).

During model spin-up, historic climate data are required to grow the trees and accumulate carbon up to the model start time (2010). For these spin-up data (and future projections under historic or 'baseline' climate), we used the University of Idaho meteorological data at a 4 km resolution (http://metdata.northwestknowledge.net/) over the period 1979–2010 from the USGS data portal (http://cida.usgs.gov/gdp/) using area-weighted averages. To simulate climate change, we used 12 km projections from the Bias Corrected Constructed Analogs V2 Daily Climate

Projections dataset available on the USGS data portal. We initially downloaded 44 climate scenarios (23 GCMs and 2 RCPs: 4.5 and 8.5 RCP) for the state of MN and graphed delta precipitation versus delta temperature for each of the 44 scenarios. Then we selected five GCMs to bracket the four corners of the graph (i.e., high change in temperature, low change in temperature, high change in precipitation, low change in precipitation) and the center of the graph (representing the mean), excluding major outliers using the methods developed by Vano et al. (2015). Therefore we bracketed much of the range of future climate projections by including GFDL-ESM2 RCP 8.5, MIROC ESM RCP 8.5, MIROC5 RCP 8.5, CCSIRO RCP 4.5, and ACCESS RCP 4.5

Description and parameterization of wind extensions

The Base Wind Extension v2.1.2 (Scheller and Domingo 2003) was used to simulate small (≥4 ha) and moderate (up to 1000 ha) patches of microburst wind disturbance with patches averaging 70 ha in size. Wind disturbance is age-dependent in this extension, and therefore the oldest cohorts have the highest mortality due to windstorms. The Linear Wind Extension v 1.0 (Gustafson 2016) was used to simulate large, linear wind events such as derechos and tornados. This extension is loosely based on the Base Wind extension, differing primarily in the shape of wind events and producing variability of damage within wind events. Each wind event is simulated by randomly choosing an orientation from a directionality distribution and placing a line segment on the landscape and damaging cells on and parallel to the line. The width of the disturbance is based on the type of event (i.e., derecho or tornado). Wind damage decreases linearly with distance from the line segment, with stochastic damage from an intensity variation parameter. Both wind extensions were calibrated together under historic climate to match wind event sizes from Frelich (2002) and the wind return interval derived from White and Host (2008). The wind regime did not vary by climate scenario. In our simulations, mean wind event size was 54 ha, maximum historical wind event was 2395 ha, and the mean wind return interval was 556 years.

Management scenarios

We used a collaborative, iterative approach (Gustafson et al. 2006) to enhance scientist-manager interactions, holding three workshops with forest managers from the CNF, the State Department of Natural Resources and other interested stakeholders at approximately 6-month intervals (Gustafson et al. 2016). As part of this process, we developed four scenarios that were of interest to the forest managers and described broad potential trends in management across our study area: business-as-usual (BAU), EcoGoods, EcoServices, and CCAdapt. BAU represents current practices across the landscape and varies by ownership and forest type, excluding areas set aside as forest reserves (e.g., wilderness areas) or left unmanaged by private landowners. The EcoGoods scenario was designed to emphasize economic return from the landscape by harvesting more land using shorter rotation lengths. Specifically, the scenario was the minimum stand age to harvest was reduced by 25% and amount of annual harvested land was increased by 30% compared to BAU. EcoServices focused on C storage and habitat for species that require old forests by harvesting 30% less land and increasing rotation lengths (i.e., doubling the minimum stand age to harvest in BAU). Finally, CCAdapt represents one possible strategy to manage for climate change (Millar and Stephenson 2015) that favors species adapted to expected future conditions, including planting of species not currently found in the region (Duveneck and Scheller 2015). The managers developed a complex set of rules whereby species that were projected to decline (i.e., aspen, black spruce, balsam fir, paper birch, ashes) were replaced with similar species that were projected to do well under climate change (e.g., white pine, oaks, yellow birch, basswood, sugar maple), based on simulations and vulnerability assessments in the region (Handler et al. 2014). Also stands were more frequently planted and with greater diversity than under current management, even adding *Carya ovata* (Mill.) K. Koch (shagbark hickory), *T. occidentalis* L. (eastern juniper), *Pinus contorta* Douglas ex Louden (lodgepole pine) and *Pinus ponderosa* Douglas ex Laws (ponderosa pine), which are not currently found in this region of MN. Full parameterization details can be found in Online Appendix 4.

The Biomass Harvest extension v. 2.2.2 (Scheller and Domingo 2015, 2016) was used to simulate the forest management activities associated with each scenario. This extension simulates harvesting of cohort biomass (including partial biomass of individual cohorts) and the planting of tree species following harvesting. Biomass removal is controlled by prescriptions targeted to specific forest types that specify how much biomass is removed from which species and cohorts within a forest stand. We calibrated acres harvested for each management area and prescription, based on current practices (USDA Forest Service 2007; D'Amato et al. 2008; Blinn pers. comm). Model run times across the 3.4 million ha landscape limited the number of replicates that could be completed, but each climate-management scenario was replicated three times to capture the spatial variation and stochasticity in windstorms, forest harvesting and regeneration after disturbance.

Measurement of resilience

To calculate resilience, we quantified the degree to which biomass and species composition on severely disturbed sites returned to the pre-disturbance state (Duveneck and Scheller 2016) for each climate ($n = 6$) and management ($n = 4$) scenario. We used the halfway point of our simulations (year 2050) as our reference point, so we could capture regeneration and recovery during the period of maximal climatic changes. For each simulation, we quantified resilience in only those cells that experienced at least a 70% reduction in aboveground biomass during a wind event (sample size for each simulation averaged 21,415 cells or 2.5% of the landscape). In those cells, we measured total aboveground biomass just prior to the windstorm (year 2040) and 50 years after the event (year 2100, the final year of our simulation), omitting cells that were disturbed multiple times by wind or harvest (Fig. 2). We also measured each species' biomass at year 2040 and year 2100 to calculate the Bray–Curtis index of dissimilarity (Eq. 1) as a dynamic index of overall changes in species composition over time,

$$BC_{jk} = \left(1 - \frac{2C_{jk}}{T_j + T_k}\right), \tag{1}$$

where BC_{jk} is the Bray–Curtis Index of dissimilarity between time j and k (calculated using the vegan-community ecology package in R Oksanen et al. 2013; R Development Core Team 2014), C_{jk} is the sum of minimum biomass between time j and time k for only those species in common at the two time periods, T_j is the total biomass at time j, T_k is the total biomass at time k. We relativized the changes in total biomass (Eq. 2) so they had the same range as the Bray–Curtis index (0–1, with 1 being the most dissimilar).

$$B_{jk} = \frac{B_k - B_j}{B_j}. \tag{2}$$

This allowed us to use the Euclidean distance (Eq. 3) between the initial and final time periods as a measure of landscape resilience for each scenario (Fig. 2).

$$R_{jk} = \sqrt{\left(B_{jk}^2\right) + \left(BC_{jk}^2\right)}, \tag{3}$$

where R_{jk} is the index of resilience between year j and k, B_{jk} is the relative total biomass between years j and k and BC_{jk} is the Bray–Curtis Index of dissimilarity between times j and k. We subtracted all our distances (R_{jk}) from the maximum Euclidean distance ($\sqrt{2}$) to create an index where 1.414 is the most resilient and both total biomass and species composition returned to the initial conditions. A value of zero is the least resilient and indicates that there was no regeneration after 50 years. Duveneck and Scheller (2016) used this novel technique to calculate mean resilience due to high severity fires across the entire landscape, but in this paper, we calculated resilience for every cell that was severely disturbed by wind. This allowed us to produce maps of resilience for each climate and soil region, management area, and forest type and examine spatial patterns of resilience.

To explain how forest composition differed among climate and management scenarios, we used nonmetric multidimensional scaling using the calculated using the vegan-community ecology package in R (Oksanen et al. 2013; R Development Core Team 2014). Using the approach outlined in Scheller and Mladenoff (2005), we created a species by ecoregion matrix of average aboveground live biomass for each ecoregion at the initial conditions (historic climate at year 2010) and for each climate and disturbance scenario at year 2110.

Results

Resilience was highest under historic climate using BAU management (Fig. 3). Climate change lowered

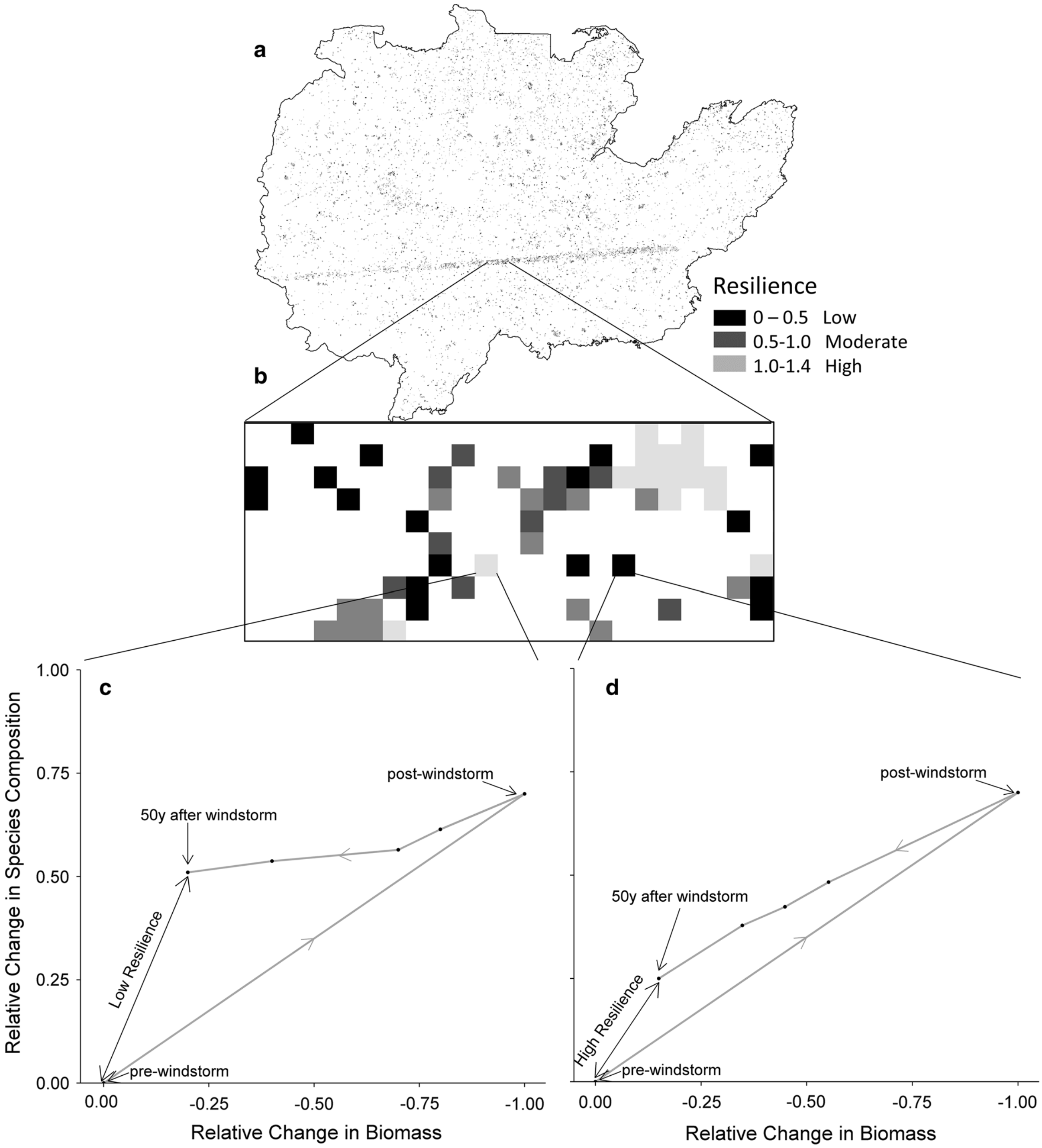


Fig. 2 Landscape map illustrating severe wind event, shown as a nearly horizontal band across the landscape (**a**) with a close-up of the disturbance (**b**). Using methods adapted from Duveneck and Scheller (2016), we calculated resilience in every raster cell that experience a severe event in our reference year (2050). In each of the graphs (**c**, **d**), "pre-wind" conditions are represented as the origin (0, 0) with zero change in aboveground biomass and zero change in species composition (as measured by the Bray–Curtis index of dissimilarity). Immediately after the wind event, there is a large reduction in biomass and a large change in species composition, reflected in a large relative change in both (labelled "post-windstorm"). In the years following the windstorm, biomass and composition move closer to pre-wind conditions. Resilience is quantified as the minimum Euclidean distance from the final point (year 2100) to the origin (*double arrow line*). A high Euclidean distance represents a scenario where resilience was low (**c**), which corresponds to the *black* raster in **b**. A short Euclidean distance indicates resilience was high (corresponds to the *light gray* raster in **b**)

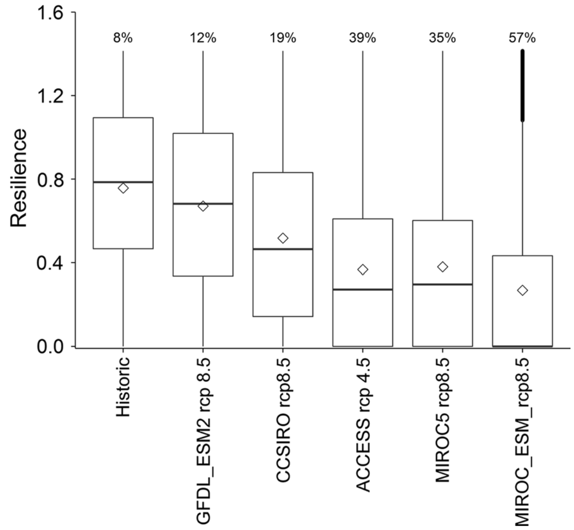


Fig. 3 Landscape resilience to severe wind events (≥70% removal of biomass) among six climate scenarios, which are ordered from lowest (Historic) to highest (MIROC ESM) change in temperature across the century (Table 2). Current management practices (BAU) were simulated in all climate scenarios. *Numbers above* the *boxes* indicate the percentage of the landscape without any regeneration. The year 2050 was used as the reference point, while year 2100 was chosen as the final point. Resilience was assessed using a Euclidean distance (see Fig. 2), so a distance of zero indicates that the system is highly resilient, and a distance of 1.4 denotes low resilience, where no species regenerated. In each *box*, *horizontal black lines* represent medians, while *diamonds* represent means; outliers are represented by *dots* (e.g., MIROC_ESM_RCP 8.5)

resilience, though there was wide variation among climate change scenarios. GFDL, the scenario with the greatest annual precipitation, had the highest resilience, while the scenario with highest mean annual temperature (MIROC_ESM) had the lowest resilience (Table 2).

The median resilience of MIROC_ESM was zero, reflecting the relatively high percentage of the landscape without regeneration following disturbance. Of all the climate scenarios we examined, MIROC5 had the largest amount of area without any tree regeneration (2.2% of the landscape or 57% of the disturbed area), while historic climate had the lowest (0.3% of landscape or 8% of the disturbed area). This reduction in regeneration was caused more by the decrease in soil water availability than rising temperatures associated with climate change. Because our resilience metric measured recovery of both biomass and species composition, we were able to decompose this result and determine that biomass was more resilient than species composition. In all the climate scenarios, relative changes in aboveground biomass recovered more quickly (to 85% of initial biomass) than the Bray–Curtis Index of dissimilarity (to only 67%).

Resilience was generally consistent across climatic zones (data not shown), with resilience more affected by soil conditions than climate. Resilience was higher as water holding capacity increased (Fig. 4) and clay content decreased (data not shown). The slope of the relationship was larger under historic climate; the slope declined under climate change, although with variation (Fig. 4).

We found that BAU, EcoGoods and EcoService harvest scenarios were very similar under historic and climate change (Fig. 5). CCAdapt was the only scenario that had consistently higher resilience under climate change.

Our ordination under BAU management illustrated that climate change caused a greater shift in species composition than historic climate (Fig. 6). Climate change increased the biomass of red maple, red oak, basswood, while reducing the biomass of black ash, red pine, aspen, and associates.

Of all the management scenarios, CCAdapt caused the largest shift in species composition, due to the addition of four new species not currently found in this region. This shift in species composition and therefore a reduction in the Bray–Curtis Index, was surpassed in magnitude by the increase in aboveground biomass, causing an overall increase in resilience compared to BAU (Fig. 5). White pine, red and sugar maple, larch, bur and red oak, and basswood had higher biomass under the CCAdapt scenario than under BAU. Under all management scenarios, historic climate was the most resilient and MIROC_ESM the least (Historic > GFDL_ESM > CCSIRO > ACCESS = MIROC5 > MIROC_ESM).

The sensitivity to forest type did not substantially differ among BAU, EcoGoods and EcoServices and therefore we only present results from BAU and CCAdapt scenarios (Fig. 7). There was little differentiation among forest types under BAU, except under climate scenarios with high mean annual temperatures (e.g., ACCESS and MIROC_ESM). For example, boreal species had high resilience under the current climate, but under ACCESS and MIROC_ESM, boreal species became much less resilient and had extremely low (or no) regeneration. The MIROC5 climate projection had the greatest differentiation

Table 2 Temperature and precipitation under historic climate (1950–2009) and climate change at the end of the century (2090–2100) for five climate change models with corresponding representative concentration pathways (RCPs)

Climate scenarios	Average annual temperature (°C)	Total annual precipitation (cm)
Historic	4	67
GFDL ESM2, RCP 8.5	8.0	89
CCSIRO, RCP 8.5	8.4	70
ACCESS, RCP 4.5	9.4	79
MIROC5, RCP 8.5	13.0	67
MIROC ESM2, RCP 8.5	14.1	61

These scenarios were chosen amongst the 44 possible climate scenarios to bracket changes in temperature and precipitation

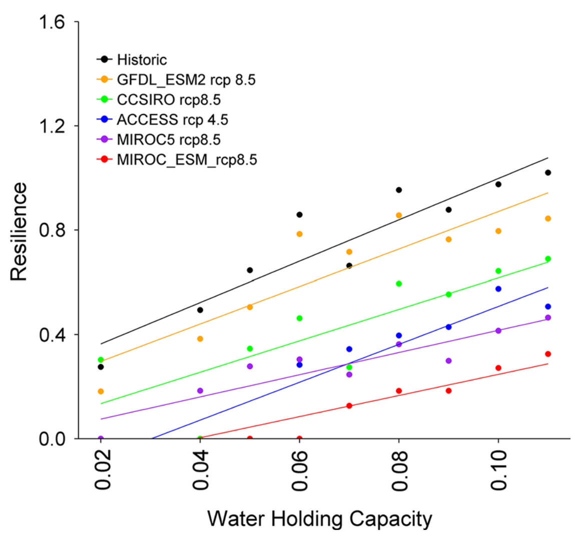


Fig. 4 Relationship between resilience and water holding capacity under six climate scenarios using current management practices (BAU management). Linear regression lines were fitted to each scenario with adjusted R^2 ranging from 0.59 to 0.84 and all $p \leq 0.002$

among forest types under BAU; conifers were the most resilient. All forest types, including boreal, had much higher resilience in the CCAdapt scenario than BAU, EcoGoods and EcoServices and greater differentiation among forest types. CCAdapt was most effective at increasing the resilience of the boreal forest type and least effective at increasing the resilience of hardwoods.

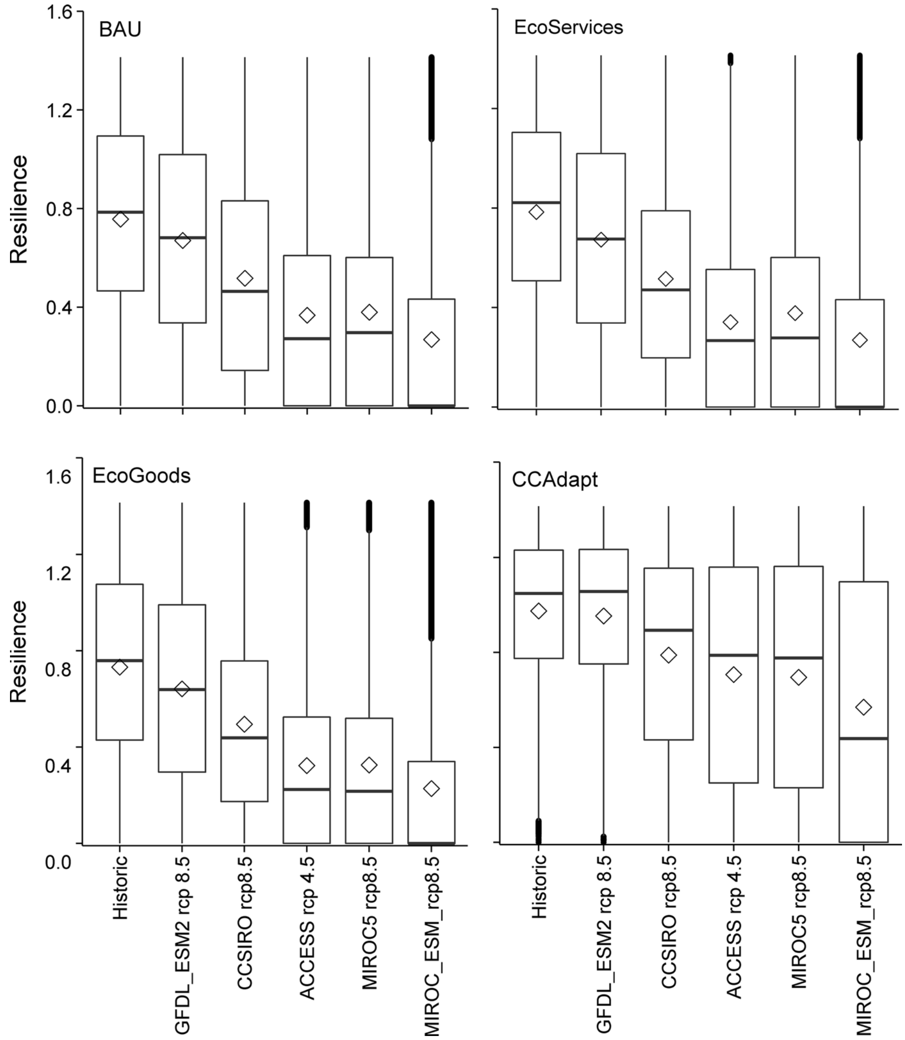
Among ownership types, there was a broad distinction between areas that were actively managed or without active management (Fig. 8). For example, on MN state DNR lands, harvested lands were generally more resilient than unharvested lands under both the historic and climate change scenarios under BAU. On federal land, managed lands were more resilient than unmanaged lands under historic climate, but results were mixed under climate change. Under some scenarios (e.g., CCSIRO and MIROC_ESM2), management lands were more resilient, but unmanaged lands were more resilient under GFDL, ACCESS and MIROC5. Under the CCAdapt scenario, actively managed state and federal lands were more resilient than unmanaged lands, except in the GFDL scenario. On private non-industrial lands (PNIF), the type of management had little impact on resilience under BAU, but with the CCAdapt scenario, the lands without active management emerged as more resilient with the warmer climate scenarios (e.g., ACCESS and MIROC_ESM). Resilience on private industrial lands (PIF) was similar to harvested non-industrial lands (PNIF) in all the management and climate scenarios.

Discussion

Climate change lowered the resilience of north-central Minnesota forests to major disturbance (in our case, windstorms with >70% mortality) under current management practices, with substantial differences among the climate change scenarios. Our results are similar to a previous study in northeastern MN that also found lower resilience under climate change, particularly under a high emissions scenario (Duveneck and Scheller 2016). We found that across all climate change scenarios, median resilience declined by about half, while they found a 5-fold decline using similar forest management practices. Differences in location (north-central vs. northeastern MN), succession extension (Century vs. Biomass Extension), and scale (1 ha cell vs. patch) may account for the differences in magnitude observed, but the overall declining trend of resilience was consistent between the studies.

Calculating resilience is particularly critical in areas at risk of a critical transition to an alternative state (Folke et al. 2004; Scheffer et al. 2012). Given the proximity of our landscape to the open parkland biome immediately to the west (Resources 1999), a shift from forestlands to savannas or grasslands has

Fig. 5 Landscape resilience to severe wind events (≥70% removal of biomass) under six climate scenarios and four management scenarios developed by stakeholders: BAU (current management), EcoGoods (economic yield), EcoServices (C storage) and CCAdapt (climate adaptation)



been hypothesized (Frelich and Reich 2009) and predicted using a Dynamic Global Vegetation Model for the region (Lenihan et al. 2008). In our hottest scenario (MIROC_ESM2), median resilience was extremely low, with ~57% of the disturbed area (averaging 31,000 ha across three replicates) showing no forest regeneration following windstorms. However, our data do not support widespread conversion to grassland because only a small proportion of the entire landscape lacked regeneration (2% in MIROC_ESM2). Although we didn't directly estimate ecological resilience (i.e., the amount of disturbance a system can absorb before changing to another state, Brand and Jax 2007), our results suggest that current levels of windstorms and management do not cause major declines in ecological resilience (i.e., shifts from forests to grasslands). Instead our results suggest that the forests of north-central MN will primarily undergo reorganization of their structure and composition in response to disturbance and climatic changes, and this will buffer them against more drastic changes in vegetation state, similar to what has been observed in the Rocky Mountains (Minckley et al. 2012). Nevertheless, the magnitude of climate changes may eventually overwhelm the buffering capacity of these forests and cause a regime shift from forests to savannas or grasslands. Our simulations suggest that such a shift would take more than a century to manifest. Last, Frelich (2002) suggests wind storm frequency may increase in this area under climate

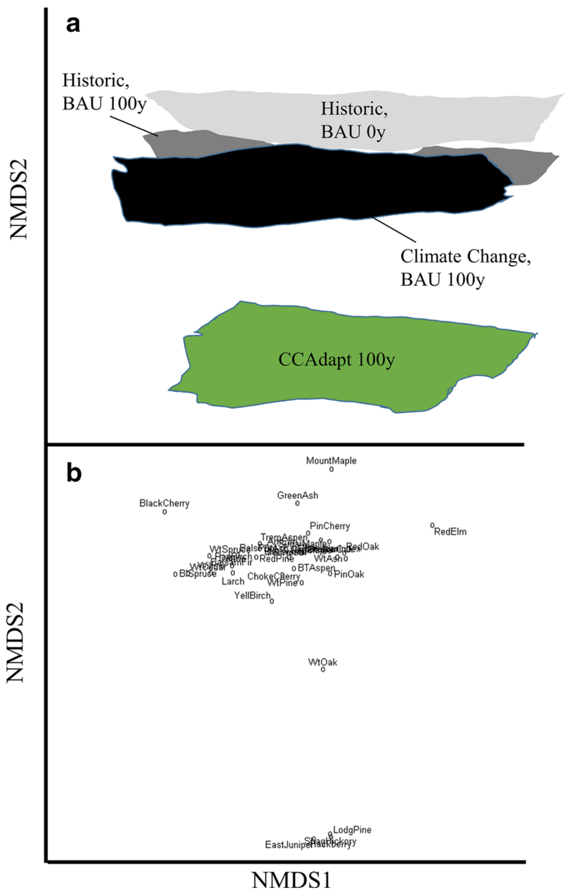


Fig. 6 Nonmetric dimensional scaling ordination of community aboveground biomass. **a** Distribution of 25 ecoregions where the range of communities is approximated by ellipses which approximate the community range of the six climate scenarios and two management scenarios (BAU and CCAdapt). The EcoGoods and EcoServices scenarios are not shown because their patterns mimicked the BAU scenario. **b** Distribution of 34 tree species in ordination space. Distance indicates dissimilarity between relative aboveground biomass distribution across ecoregions; *axes* are unitless

change. If this were to occur, then a transition to grasslands may be more likely than our results suggest, especially given the poor regeneration we observed.

Although the climate scenarios affected resilience, the spatial variation among climate zones was a poor predictor of resilience. Although climate exerts a strong influence on forest growth (Anderson et al. 2006) and regeneration (e.g., Anderson-Teixeira et al. 2013), particularly in boreal conifers (Fisichelli et al. 2014), the large climate zones we used in our simulations (only 5 in our study area since we were restricted by the GCM grid size) made it difficult to find any climatic patterns in resilience. Instead, at the scale of our study area, soil characteristics better explained spatial patterns of resilience; sites with higher soil water capacity and lower clay content had greater resilience than drier sites that had higher clay content (similar to (Pastor and Post 1988; Krishnan et al. 2006). This corresponds with a previous study that found that resilience in the tropics was primarily explained by soil texture heterogeneity and the length of the dry season (Levine et al. 2016). Together these studies highlight the importance of incorporating spatial variation in soil texture and water availability when simulating resilience to climate change (Gustafson et al. 2016).

Management practices between the EcoGoods and EcoServices scenarios had indistinguishable effects on resilience from the BAU scenario. These scenarios were designed by managers to simplistically represent divergent management strategies (economics vs. C storage) that might be politically feasible on this landscape. These caused differences in biomass and C stocks as expected (data not shown), but species regeneration after harvesting appeared to be fairly robust to modest changes in the timing and amount of harvested biomass.

Only the CCAdapt scenario, which represented a substantial divergence from the other management practices, increased resilience. This is because the CCAdapt scenario used a variety of forest management strategies developed by stakeholders (Online Appendix 4), including replacing climate-sensitive species with other species (e.g., aspen stands converted to white pine, oaks or other hardwoods, jack pine stands converted to lodgepole pine, red cedar and white pine, a greater focus on patch-cutting, larger proportion of planting than natural regeneration, and a greater diversity of species. Therefore, implementing a more comprehensive climate change-driven strategy may be more effective at increasing resilience over the long term than current practices or more modest changes in management practices. Our results differ from previous studies that found that management had limited ability (i.e., <10%) to increase resilience (Buma and Wessman 2013; Duveneck and Scheller 2016). Instead, our more aggressive CCAdapt scenario reveals a capacity for active management to increase resilience (as measured) by as much as 40%. Such 'managed resilience' may become essential if undesirable critical thresholds are to be avoided. This

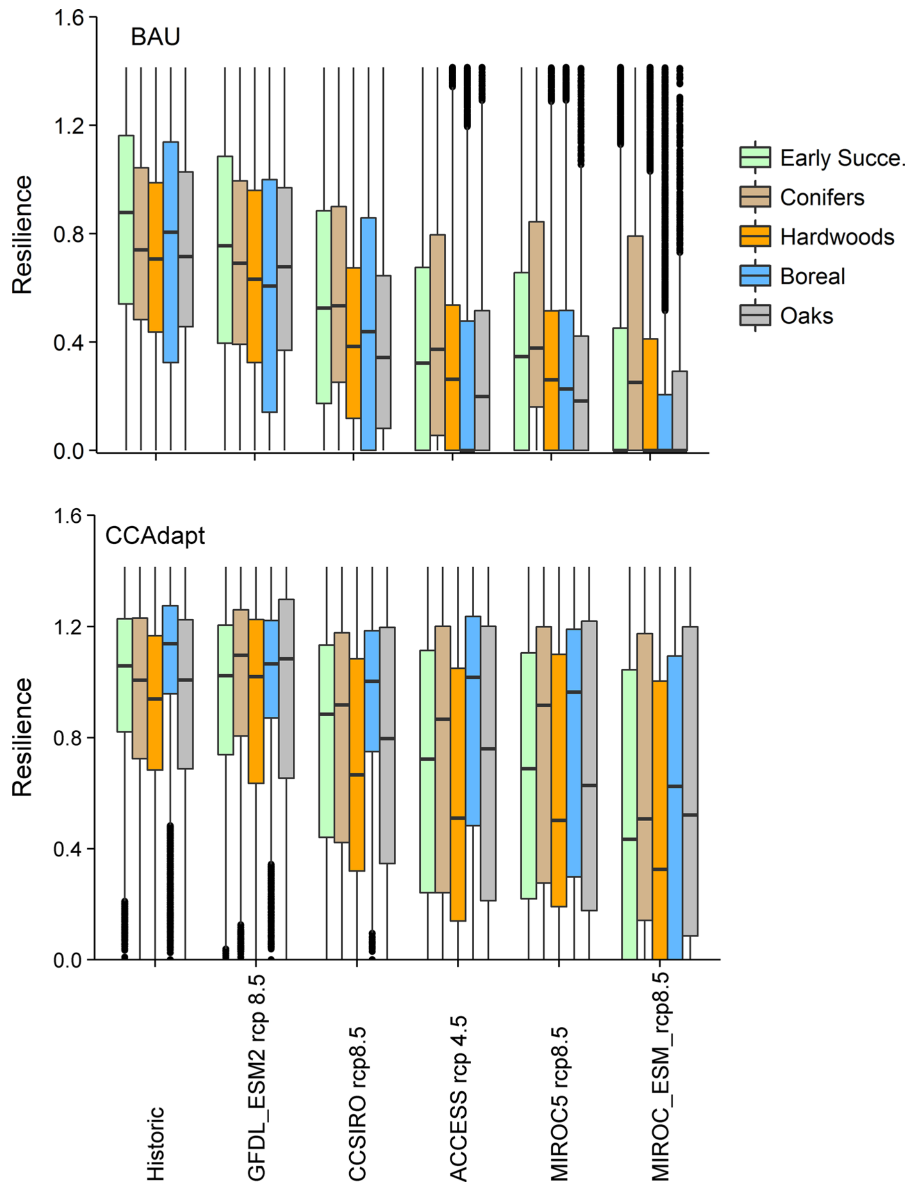


Fig. 7 Landscape resilience to severe wind events in selected forest types under the climate scenarios and two management scenarios (BAU and CCAdapt). The EcoGoods and EcoServices scenarios are not shown because their patterns mimicked the BAU scenario

would not be without economic ramifications however, because the extent of aspen, the area's primary timber species, was reduced and replaced by pines, oaks and hardwoods. As tree species composition and biomass shifts under climate change, the market will be forced to adapt to changes in timber supply and currently economically-unfeasible species may become profitable in the future. Our work provides support for the idea that land managers should adopt a portfolio of silvicultural strategies (Park et al. 2014) and incorporate climate research into their management practices to promote forest resilience under climate change.

Spatial patterns of resilience were less dependent on ownership and more dependent on whether the lands were actively managed or not. Ownership patterns in our study area are complex and our results reflect the diverse forest types and soils and land use

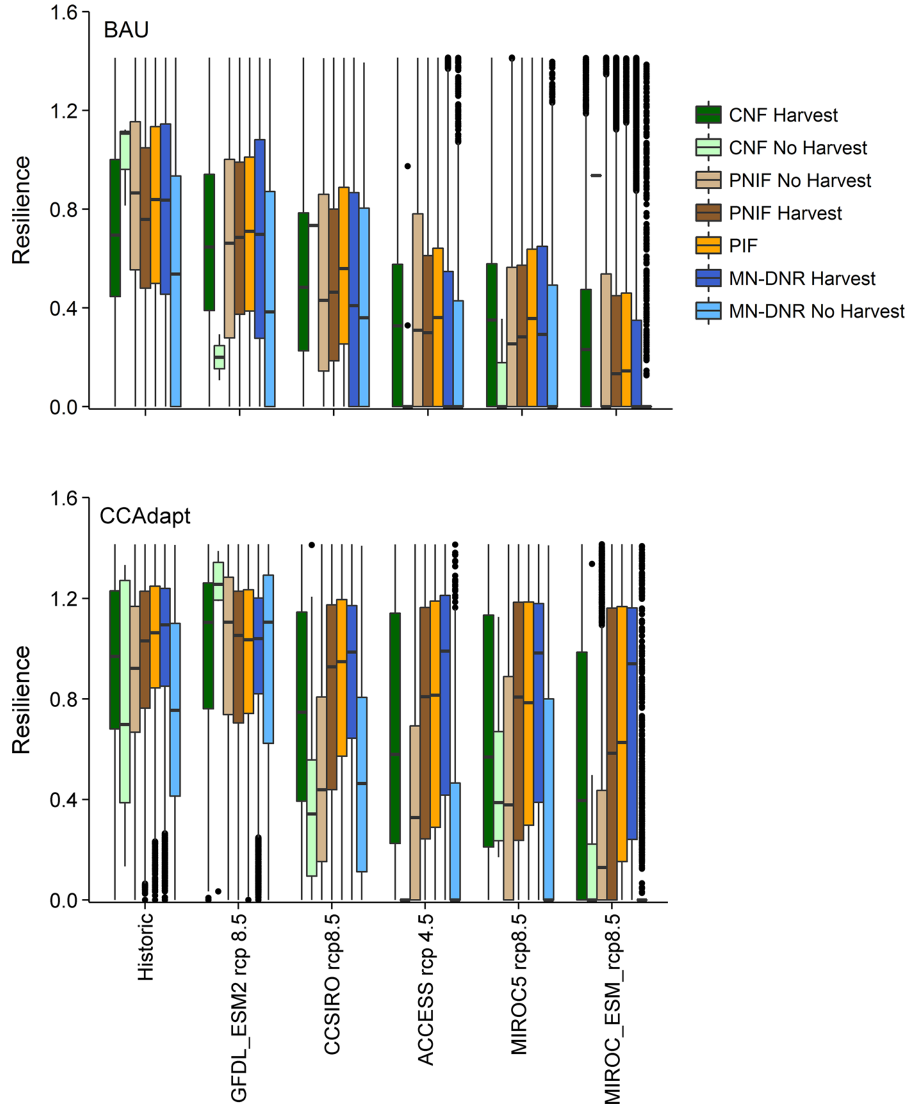


Fig. 8 Landscape resilience to severe wind events shown for federal (CNF, Chippewa National Forest), private non-industrial (PNIF) and state (MN DNR) unharvested and harvested lands under the climate scenarios and two management scenarios: BAU and CCAdapt. Resilience is also shown for private industrial forests (PIFs), but all the lands are considered for harvest (i.e., no unharvested lands). The EcoGoods and EcoServices scenarios are not shown because their patterns mimicked the BAU scenario

history within each ownership (e.g., Shinneman et al. 2010). For example, under all the management scenarios, state lands without active management were less resilient than those that are managed. This contradicts the commonly held belief that unmanaged natural systems are more resilient, because timber management is thought to simplify ecosystems (Haeussler and Kneeshaw 2003; Kimmins 2004). In these forests, active management has evolved over time to ensure the rapid recovery of forest stands to pre-harvest tree species composition. The effects of management on regeneration and recovery may have a ‘carry-over’ effect on resilience following wind disturbance. However, the importance of active management for some ownerships (e.g., federal, private) was dependent on the climate scenario. This complicates the manager’s task of selecting the best management strategy under climate uncertainty and underscores the importance of tools such as decision analytics, that allow assessment of trade-offs between management scenarios under high climate uncertainty (e.g., Garner et al. 2016).

Our results suggest that it is necessary to understand not just the landscape resilience of each system (e.g., Duveneck and Scheller 2016), but also the spatial pattern of resilience (sensu Cumming 2011; Allen et al. 2016) (i.e., the local context and connectivity of each patch within a broader region), since our resilience was highly dependent on soils, forest type, and management regime. Resilience is often quantified using a "conserve the stage approach", which assumes that complex topography and connected land cover are the primary determinants of resilience and its spatial pattern (Anderson and Ferree 2010). The biological underpinnings of resilience (e.g., species' growth rates and sensitivity to environmental change) are equally important and interconnected (Oliver et al. 2015), though they are, of course, mediated by landscape connectivity and topography. Finally, the stochastic and spatial nature of disturbances causes complex non-linear behaviors when spatial variation in topography, cover, fragmentation, and biotic processes, such as species-specific dispersal, play out across the landscape. These complex interacting effects are captured by our modeling framework and allowed us to estimate resilience at the species level, without assuming that topography and land cover are the only (and equal) determinants of resilience.

Our definition of resilience was very specific (i.e., recovery of biomass and species composition 50 years after a severe windstorm in 2050) and other definitions of engineering and ecological resilience may produce different conclusions. For example, our selection of a 50-year recovery window affected the magnitude of our resilience, though we expect that the differences among climate scenarios will persist over the long-term. Resilience tended to level off around 2080 and we expect rising temperatures will continue to limit growth and future regeneration. We did find that aboveground carbon pools recover from disturbance more quickly than species composition, which is in agreement with previous studies (Martin et al. 2013). In our study, neither biomass nor composition returned to initial conditions within 50 years, even under historic climate, but biomass recovered at a faster rate than species composition. These results suggest that carbon and species composition (or biodiversity) do not recover at the same rate after disturbance. Initiatives to enhance resilience must consider the temporal trends and potential time lags when selecting between metrics of resilience, though we conclude that a very quantitative approach to resilience is critical for subjective comparisons across climate and management scenarios.

All model forecasts provide limited inference. Although we attempted to minimize uncertainty by incorporating the major disturbances (harvesting and wind) and testing a broad spectrum of climate and management projections, considerable uncertainty remains. For example, access to downscaled projections of wind disturbance under climate change was not publically available, limiting our ability to directly link windstorms and climate. Also, there are key drivers shaping this landscape that were not considered in the study: deer browsing of young trees, insect pests, wildfire, and CO_2 fertilization. A forthcoming paper will address insects and wildfire in this study landscape and efforts are underway to incorporate CO_2 fertilization effect into the Century extension of LANDIS-II. Land use change and housing development also could cause substantial shifts away from forest (e.g., Thompson et al. 2011) or agricultural abandonment could result in additional early-successional forest (Miles et al. 2011). Our scenarios also do not capture the full suite of potential adaptations to climate change and, indeed, future unknown technologies could be brought to bear on the climate change challenge (Kolbert 2014).

Despite these limitations, our methodology provides a useful way to quantify spatial patterns of resilience, determine which factors drive these patterns, and improves our understanding of how the interactive effects of disturbances, management and climate may play out spatially across the landscape. Our results suggest that the effects of climate change may overwhelm current forest management practices and decrease resilience. Only markedly more aggressive forest management practices may be successful in sustaining resilience in the face of climate change. This points to the need for creative dialogue around adaptive forest management strategies that consider resilience under climate change as a management objective.

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