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RESEARCH ARTICLE

Complex interactions among successional trajectories and climate govern spatial resilience after severe windstorms in central Wisconsin, USA

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Abstract

Context Resilience is a concept central to the field of ecology, but our understanding of resilience is not sufficient to predict when and where large changes in species composition might occur following disturbances, particularly under climate change.

Objectives Our objective was to estimate how wind disturbance shapes landscape-level patterns of engineering resilience, defined as the recovery of total biomass and species composition after a windstorm, under climate change in central Wisconsin.

Methods We used a spatially-explicit, forest simulation model (LANDIS-II) to simulate how windstorms and climate change affect forest succession and used boosted regression tree analysis to isolate the important drivers of resilience.

Results At mid-century, biomass fully recovered to current conditions, but neither biomass nor species composition completely recovered at the end of the century. As expected, resilience was lower in the south, but by the end of the century, resilience was low throughout the landscape. Disturbance and species' characteristics (e.g., the amount of area disturbed and the number of species) explained half of the variation in resilience, while temperature and soil moisture comprised only 17% collectively.

Conclusions Our results illustrate substantial spatial patterns of resilience at landscape scales, while documenting the potential for overall declines in resilience through time. Species diversity and windstorm size were far more important than temperature and soil moisture in driving long term trends in resilience. Finally, our research highlights the utility of using machine learning (e.g., boosted regression trees) to discern the underlying mechanisms of landscape-scale processes when using complex spatially-interactive and non-deterministic simulation models.

Keywords Climate change · Windstorms · Resilience · Forest simulation model · LANDIS-II

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Introduction

Natural disturbances, such as windstorms, wildfire and insect outbreaks, cause pulses of mortality that can have lasting effects on forest dynamics and succession (Carpenter and Turner 2000). Forest management has historically tried to suppress or prevent natural disturbances to provide a consistent supply of ecosystem services such as pulpwood and water supply (Holling and Meffe 1996). Now recognizing the futility of this approach, especially with impending changes in climate, managers and scientists have turned to resilience as a guiding theme of natural resource management (e.g., Scheffer et al. 2001; Folke et al. 2004; Rist and Moen 2013; Bone et al. 2016). By definition, resilience encompasses both stability and dynamism, recognizing that the ability of an ecosystem to recover from disturbance is influenced by the characteristics of the disturbance regime, climate, and ecosystem structure (Gunderson 2000), as well as human activities (Preise et al. 2018). Fostering resilience, especially within a value-explicit framework (Higuera et al. 2019), has the potential to promote adaptive management, help prioritize management efforts, and treat disturbances as a management opportunity rather than something to be avoided (Seidl et al. 2016).

Applying the concept of resilience in natural resources, however, has proven difficult because there is still not agreement within the ecological community about how to define resilience (Folke et al. 2004; Brand and Jax 2007; Grimm and Calabrese 2011; Newton and Cantarello 2015; Quinlan et al. 2016). Based on the framework outlined in (Newton and Cantarello 2015), resilience can be divided into engineering resilience (i.e. time required for a system to return to an equilibrium point following a disturbance event, e.g., Pimm 1984; Holling and Meffe 1996) or ecological resilience, which is defined as the amount of disturbance that a system can absorb before changing to another stable state (e.g., transitioning from hardwood to conifer-dominated forests, Gunderson 2000; Holling and Gunderson 2002; Brand and Jax 2007). In the Upper Midwest, engineering resilience, hereafter referred to as resilience, is an appropriate lens, given this is a region where we expect species reorganization (Scheller and Mladenoff 2005; Scheller et al. 2011; Swanston et al. 2018) more than shifts in ecological states (for exception see Lenihan et al. 2008; Frelich and Reich 2009).

Resilience is often quantified by measuring tree regeneration several decades after a disturbance, however, these limited field measurements cannot account for the nonlinear temporal dynamics in recovery. Chronosequence approaches are better able to capture temporal variation in resilience by substituting time for space, (e.g., Letcher and Chazdon 2009; Bhaskar et al. 2018), but capturing the full range of disturbance frequency, size, and intensity is challenging with field sampling. By comparison, spatially explicit, forest landscape simulation models can project both the timing and severity of disturbance events (He 2008) and identify areas where a lack of resilience may hinder re-establishment of forest communities across large areas and long time scales (Serra-Diaz et al. 2018). Models have the added advantage of being able to incorporate how climate change may affect resilience (Duveneck and Scheller 2016; Lucash et al. 2017), either directly (e.g., temperature effects on growth and regeneration) or indirectly via climate-mediated disturbances.

Resilience is often quantified after wildfire (e.g., Stevens-Rumann et al. 2018) or deforestation (e.g., Zemp et al. 2017), but it is less often quantified following other types of disturbances. Windthrow is the most important natural disturbance in the upper Midwest (i.e. Minnesota, Wisconsin, Michigan, USA, Frelich 2002). Wind events range in size from small-scale patches (< 1 ha) to large, intense events, like tornados and derechos, which are widespread and fast-moving windstorms. Severe windstorms (≥ 70% overstory mortality) have a return interval ranging from 500 to 1200 years in the upper Midwest (Canham and Loucks 1984; White and Host 2008), but return intervals are closer to 50 years if all wind events are considered (Frelich 2002). Although wind events are common throughout the region, resilience after windstorms is most often quantified after a specific mortality event, e.g., a particularly notable and/or large storm, such as the 1999 blowdown in the Boundary Waters Canoe Area (Nelson et al. 2009), without considering landscape context and the nonlinear patterns of recovery.

Forests undergo substantial reorganization after a wind event, a time when changes in successional trajectories and growth rates are mediated by temporal trends in site conditions (Everham and Brokaw 1996).

Shade intolerant and disturbance-adapted species often have a competitive advantage because of increases in light availability following canopy removal (Curtis 1959). However, the establishment of these species may be limited by seed production, dispersal and/or edaphic conditions (Bazzaz 1979), especially after large wind events or in areas that are already fragmented due to large clear-cuts or large areas of agricultural production. As trees establish following disturbance, biomass accumulates and competition for light intensifies. Even though these overall trends after disturbance appear straightforward, the spatial pattern and timing of forest recovery are often difficult to predict over time. Interactions among edaphic (e.g., soil moisture, nitrogen availability), climatic (e.g., temperature), life history strategies (e.g., shade tolerance, seed production and dispersal), disturbance history (e.g., frequency, severity and size), legacy effects, and competition among tree species create many possible successional trajectories (Frelich 2002), especially when overlain with temporal trends in temperature and precipitation. Forests in northern Minnesota, for example, are currently well-buffered against shifts in species composition, but resilience may decline as temperatures rise under climate change (Duveneck and Scheller 2016), especially in areas with low soil moisture (Lucash et al. 2017). The severity and extent of disturbances may hinder recovery after windstorms by increasing distance to seed source, as has been shown with severe wildfires (e.g., Donato et al. 2016; Tepley et al. 2017). Currently our understanding of the factors conferring resilience is not sufficient to project when and where large changes in species composition might occur following disturbances and where biomass recovery might be altered by climate change.

Quantifying the spatial pattern of resilience, by its very definition, assumes that the goal is to return a landscape to an equilibrium state following a disturbance event. However, forests are dynamic across time and space. The upper Midwest has a long history of logging and attempted agricultural production, which resulted in the current patchwork of public, private and tribal lands, with unproductive agricultural areas often reverting to the state and federal governments and more productive land remaining in private ownership (Dickmann and Leefers 2016). Because of fire suppression policies coupled with extensive pine planting efforts of Civilian Conservation Corps, and the current focus on timber production, this region is now a spatially-heterogeneous landscape of young (median age = 53 years) mixed hardwoods and boreal conifers across multiple ownerships with different goals and objectives. The northern and central portions of the landscape are mostly forested under federal or tribal ownership, while the southern portion is highly fragmented with a mix of forested and agricultural lands, mostly under private ownership. This landscape context sets the stage and is not necessarily an "equilibrium point", but rather a reference point of current conditions by which we can quantify where forests may remain resilient under a changing climate.

We focused on forest resilience in central Wisconsin, since there are concerns about how rising temperatures will affect forest sustainability and economics, recreation and water quality in this region (Janowiak et al. 2014). Recent IPCC AR5 projections suggest that average annual temperatures in WI will increase by 5 °C while precipitation will increase by 5%, averaged across 44 global circulation models and RCPs over the next hundred years (http://cida.usgs.gov/gdp/). Temperatures are projected to increase more in the winter than the rest of the season and the growing season is projected to lengthen (Janowiak et al. 2014). Rising temperatures and longer growing seasons may increase evapotranspiration and result in lower soil water availability or the projected increases in precipitation may compensate and soil moisture may increase or be unaffected (Seneviratne et al. 2010). Changes in soil moisture may drive changes in species composition in this landscape, given that this region is dominated by drought-sensitive hardwoods. Also, boreal species, including paper birch, trembling aspen, and black spruce, are projected to decline in this region under climate change since they are near their southern temperature and moisture-driven range (Iverson et al. 1999; Scheller and Mladenoff 2005; Frelich and Reich 2010). These boreal species are critical for maintaining wildlife habitat and timber harvesting, and have strong cultural meaning to indigenous communities in the region (Dockry et al. 2016).

Our overarching objective was to estimate how disturbance shapes landscape-level patterns of resilience under climate change. Few studies have quantified the spatial pattern of resilience (see Lucash et al. 2017 for an exception) despite its importance (Cumming 2011; Allen et al. 2016). We focused on metrics reflecting engineering resilience, quantifying how close the biomass and species composition of a site recovered to a pre-disturbance conditions following wind disturbance (Duveneck and Scheller 2016). To do so, we used a spatially-explicit, forest simulation model (LANDIS-II) that simulates how windstorms and climate change affect forest growth, mortality, regeneration, and above- and belowground cycling of water, carbon, and nitrogen. We hypothesized that (1) resilience will decline over time (i.e. lower resilience at 2100 than 2050), especially under climate change, based on previous studies in Minnesota and Michigan (Duveneck and Scheller 2016; Lucash et al. 2017), (2) resilience will vary spatially, with lower resilience in the southern, more highly-fragmented area of the landscape due to higher distance to seed source, and (3) landscape-level characteristics (i.e. area of windstorm, distance-to-seed source) will be important predictors of resilience by mid-century, but climatic and edaphic factors (i.e. air temperature, soil moisture) will become increasingly important and drive resilience under climate change by the end of the century.

Methods

Site description

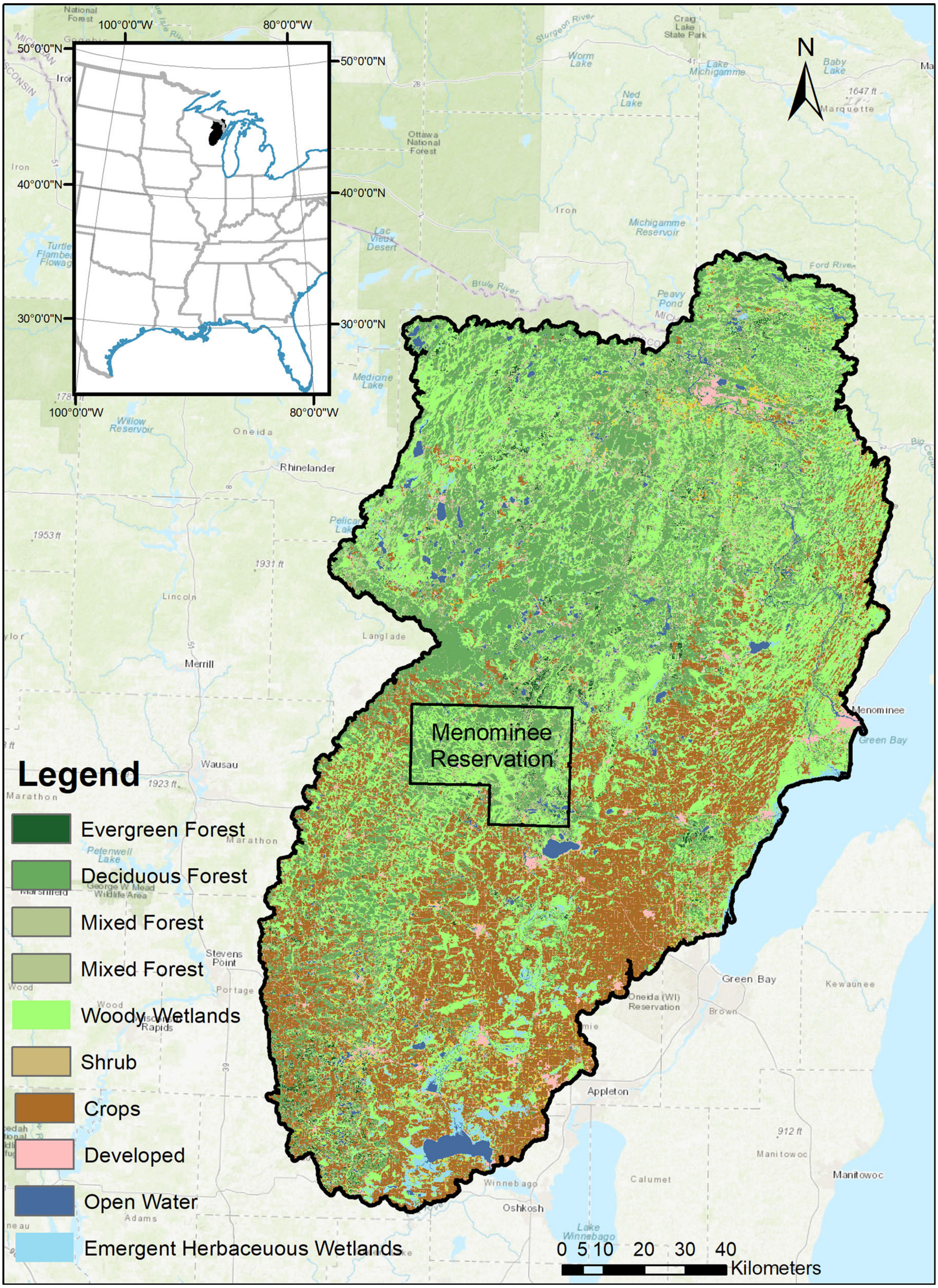
Our study landscape contains ~ 2 million hectares of land in central Wisconsin, about forty-five miles northwest of Green Bay, Wisconsin (Fig. 1). This landscape is an ideal location to explore the ecological impacts of climate change for three reasons. First, the "tension zone" falls within our landscape (Kucharik et al. 2010), characterized by steep climatic gradients and ecotonal boundaries, wherein small changes in temperature and precipitation are expected to drive sizeable shifts in species composition (Curtis 1959). Second, Wisconsin has already experienced warming of 0.3–1.2 °C and a 10–15% increase in precipitation over the past century (Janowiak et al. 2014), and an additional 5 °C rise in temperature and 5% increase in precipitation are predicted over the next 100 years (http://cida.usgs.gov/gdp/). Finally, the study area includes the Menominee Reservation, home to a tribal nation widely recognized for their sustainable forest management (Dockry et al. 2016).

This landscape is located at the nexus between northern hardwoods and boreal forest, with forests occupying approximately 42% of the area (220,000 ha). The most common forest type is maple/beech/birch, which comprises about 50% of the forested landscape, and includes species such as sugar maple (*Acer saccharum* L.), red maple, (*Acer rubrum* L.), American beech (*Fagus grandifolia*), and paper birch (*Betula papyrifera* Marshall). The northern part of the landscape is dominated by aspen (*Populus tremuloides* and *P. grandidentata* Michx.), paper birch, black spruce (*Picea glauca* (Moench) Voss), white spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg), and balsam fir (*Abies balsamea* L. (Mill.)). Oak (*Quercus spp.*) and hickory (*Carya spp.*) forests dominate in the southern portion. The western portion of the landscape is primarily aspen/birch, while the eastern is a mix of elm (*Ulmus spp.*), ash (*Fraxinus spp.*) and black cottonwood (*Populus deltoides* W.Bartram ex Humphry Marshall). White (*Pinus strobus* L.), red (*Pinus resinosa* Ait.), and jack (*Pinus banksiana* Lam.) pines are scattered throughout the landscape. Soil parent materials are glacially-derived and range from sandy outwash of Valders age in the southeastern portion of the county to silt-capped Cary drumlins in the west and northwest (Milfred et al. 1967). The study region has a humid, continental climate with warm summers and cold, snowy winters (Kottek et al. 2006). Average monthly temperature ranges from − 10 °C in January to 20 °C in July, and mean annual precipitation is 79 cm, based on our analysis of gridded weather observations (Abatzoglou 2013).

Fig. 1 Study landscape in north-central Minnesota as delineated by the Menominee Nation and surrounding watersheds, encompassing an area of 2.2 million hectares ▶

Simulation modeling

In our study, we used LANDIS-II v6.2 (Scheller et al. 2007), a spatially explicit, mechanistic simulation model that simulates the effects of climate on species dynamics and disturbance regimes. In LANDIS-II, the landscape is comprised of interconnecting grid cells. Each raster cell is assigned to a climate region (within which climate is assumed to be homogenous) and within each cell, trees are represented as species-age cohorts, not individuals (Mladenoff 2004). There may be multiple species and age cohorts within each cell,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30°0'0"N
100°0'0"W
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N
Menominee Reservation
Legend
Evergreen Forest
Deciduous Forest
Mixed Forest
Mixed Forest
Woody Wetlands
Shrub
Crops
Developed
Open Water
Emergent Herbaceuous Wetlands
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Kilometers
Rhinelander
Langlade
Merrill
Wausau
Green Bay
Appleton
Oshkosh
Menominee
Marquette
Lake Winnebago
Stevens Point

though the exact location is not determined (i.e. LANDIS-II is non-spatial within a cell); species-age cohorts are dynamic over time. Successional dynamics are projected by simulating cohort growth, competition, establishment and mortality, as dictated by life history attributes (Roberts 1996).

We created an initial map of species composition and species' age at a resolution of 1 ha, by imputing USDA Forest Inventory and Analysis data onto maps of forest types and stand age (Online Appendix 1). We included 36 tree species in our map, choosing the species with the largest biomass in the FIA database. Several less-common species, such as butternut (*Jugans cinerea* L.) and serviceberries (*Amelanchier* spp.) were included based on their cultural importance (Dockry et al. 2016).

Forest succession and C dynamics

We used the Net Ecosystem Carbon and Nitrogen Succession extension (v6.0) of LANDIS-II (hereafter referred to as 'NECN') to simulate forest succession (Scheller et al. 2011; Lucash et al. 2017). This extension simulates aboveground (leaves and wood) and belowground (fine roots and coarse roots) growth of each cohort on each site on a monthly basis (Scheller et al. 2011). It calculates growth using algorithms that integrate cohort age, species-specific life history attributes (e.g., longevity, shade tolerance), competition (i.e. the biomass of other cohorts relative to the amount of maximum potential biomass), climate (e.g., air temperature, precipitation), and soils (e.g., drainage, soil water, and N availability). The NECN extension simulates tree mortality caused by senescence (continuous loss of leaves and branches) and age (which accounts for the higher levels of mortality as a cohort approaches its life expectancy). It also simulates water availability within each cell using a simple water bucket model. Finally, it simulates regeneration via seeds or resprouting using species' life history attributes (e.g., age to sexual maturity, effective and maximum seed dispersal distances), water availability, and competition (Scheller et al. 2007). A double exponential algorithm with effective distance and maximum distance is used to determine the probability that the parent cohort's seeds will reach another cell on the landscape, assuming that the cohort has reached sexual maturity (He and Mladenoff 1999). If the grid cell exceeds the effective dispersal distance, then the probability of the effective seeding distance effectively becomes one.

The NECN extension simulates C and N cycling in the vegetation (leaf, wood, fine roots, and coarse roots by species and age), detritus (foliar, woody, fine root, and coarse root detritus), and soils (fast, slow, and passive soil pools) (Scheller et al. 2011, 2012). Decomposition rates are a function of litter quantity, quality (e.g., leaf C/N ratios and lignin content), and soil conditions (e.g., soil moisture, temperature, and soil texture), as specified by the algorithms from the CENTURY soil model v 4.5 (Parton et al. 1983, 1994). The N released via decomposition or added to the soil via N deposition can either be taken up by the vegetation or leached out of the system (Lucash et al. 2014).

Previous versions of NECN used large, homogeneous soil regions; these are not included in NECN version 5, allowing soil characteristics to vary at the site-scale (1 ha). In simulating both aboveground (e.g., growth, mortality, regeneration) and belowground processes (e.g., decomposition and N mineralization) using a spatially-interactive framework, LANDIS-II can simulate landscape-level changes in species composition and resilience as a property of climate, succession, and disturbance. Details of NECN parameterization, calibration, and validation are outlined in Online Appendix 2.

Climate data

For the sake of computational efficiency, LANDIS-II uses areas of homogenous climate, typically referred to as "ecoregions" or "climate regions" (Scheller et al. 2007), rather than assimilating standard gridded climate data. Determining an appropriate number, shape and size of climate regions can be somewhat subjective and often depends on the research objectives, data availability, and topographic variation. To provide an objective basis for the aggregation of weather data into climate regions, we performed two separate analyses. First, we performed a geostatistical analysis of the historical (1979–2010) weather data over the modeling domain to identify the optimal scale required to capture the main spatial variability in the landscape's climate. Using variograms to estimate the spatial correlation structure and spatial dependence of gridMET temperature and precipitation observations (Hengl 2006), we found an optimal spatial resolution of 25 km, i.e. each region should cover an area of approximately 625 km^2. Next, we performed a spatial cluster analysis on the historical weather data to determine an optimal spatial configuration for the climate regions of this size. The resulting map of climate regions, within each of which the climate is considered to be homogenous, contains 38 climate regions, such that the average area of the clusters was the target 625 km^2 (Online Appendix 3).

For climatic conditions representative of the recent historical period, we calculated daily temperature and precipitation from the University of Idaho gridMET 4-km daily gridded observational analysis (Abatzoglou 2013) for each climate region. Weather data for the "historical" climate scenario were randomly selected, one calendar year at a time, from this dataset for the full length of the 100-year LANDIS-II run.

To simulate future climate change, we used projections from the Multivariate Adapted Constructed Analogs product (MACA) (Abatzoglou and Brown 2012), a suite of 40 high resolution (4-km) daily gridded climate projections to year 2099 that have been generated by statistically downscaling global climate model projections from Phase 5 of the Coupled Model Intercomparison Project (CMIP5, Taylor et al. 2012). For this study we selected five future climate scenarios to roughly span the range of projected growing season average temperature and precipitation over the study region. The selected models and emissions scenarios—CCSM4 RCP4.5 (less warming + drier), bcc-csm1-1 RCP4.5 (less warming + wetter), HadGEM2-ES365 RCP8.5 (more warming + drier), CSIRO-Mk3-6-0 RCP8.5 (more warming + wetter), and MIROC-ESM RCP4.5 (near ensemble mean)—were chosen using methods developed by (Vano et al. 2015) and are shown in Online Appendix 4.

Description and parameterization of wind extensions

The Base Wind Extension v2.1.2 (Scheller and Domingo 2003) was used to simulate small-moderate (4–1000 ha) patches of microburst wind disturbance with patches averaging 70 ha in size. In this extension, wind disturbance is age-dependent, with the highest mortality in the oldest cohorts. The Linear Wind Extension v1.0 (Gustafson 2016) was used to simulate large wind events (i.e. derechos and tornados). Each wind event is simulated by randomly choosing an orientation from a directionality distribution and placing a line segment on the landscape; cells are damaged 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 stochasticity introduced by an intensity variation parameter that controls the relative variability within a wind event. Both wind extensions were run and calibrated simultaneously under historic climate to match the mean annual area disturbed by high severity wind events (3000 ha, Zhang et al. 1999; Frelich 2002; White and Host 2008) using the procedures outlined in Online Appendix 2. Our annual high severity disturbance rate was 0.15%/year, which was similar to the literature mean (0.12) and fell within the range of reported values (0.05 to 0.18, Zhang et al. 1999; Frelich 2002; White and Host 2008). In our simulations, the mean wind event size was 154 ha, the maximum historical wind event was 52,633 ha (similar to the observed value of 43,915 in the Chequamegon-Nicolet, Linda Parker pers comm), and the mean wind rotation period was 207 years. The wind regime did not vary by climate scenario, wind projections under future climate regimes were not publicly available at the time the study was initiated.

Measurement of engineering resilience

To calculate engineering resilience, we quantified the degree to which total biomass and species composition returned to the pre-disturbance state after a severe windstorm using the methods developed by Duveneck and Scheller (2016) and later revised by Lucash et al. (2017). For each simulation, we quantified resilience for only those cells that experienced at least a 70% reduction in live aboveground biomass during a wind event (Lucash et al. 2017); the sample size for each simulation averaged 2267 ha. In those cells, we calculated resilience in ~ 2050 and ~ 2100 to get an estimate of how mid-century and end-of-century landscape change might differ. Since a small number of cells were disturbed in any given simulation year and we wanted to capture the stochasticity of wind events and reproduction, we calculated resilience at 2041–2050 (i.e. 2050 or mid-century) and 2091–2100 (2100 or late century). Specifically, we measured wind-disturbed cells 1 year before the windstorm (in year 2000–2009 and 2040–2049), immediately following the wind event (years 2001–2010 and 2041–2050), and ~ 50 years after the event (years 2051–2060, 2091–2100), omitting cells that were disturbed multiple times by wind (Fig. 2). We did consider including cells that experienced repeated windstorms, but these events were extremely rare given the short duration of our recovery period (50 years) and the age dependence of wind mortality (i.e. older cohorts are most vulnerable to wind mortality).

In these wind-disturbed cells, we quantified the degree to which total biomass and species composition recovered to the initial conditions in the cell. We calculated the Bray–Curtis index of dissimilarity (Eq. 1) as an index of changes in species composition over time,

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

where BC_{jk} = Bray–Curtis index of dissimilarity between time j and k (calculated using the vegan-community ecology package in R (Oksanen et al. 2013) (Team 2014), C_{jk} = sum of minimum biomass between time j and time k for only those species in common at the two time periods, T_j = total biomass at time j, T_k = 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 to 1, with 1 being the most dissimilar).

$$Bjk = \frac{B_{k-B_j}}{B_j} \tag{2}$$

This allowed us to use the Euclidean distance (Eq. 3) between the initial and final time periods as a

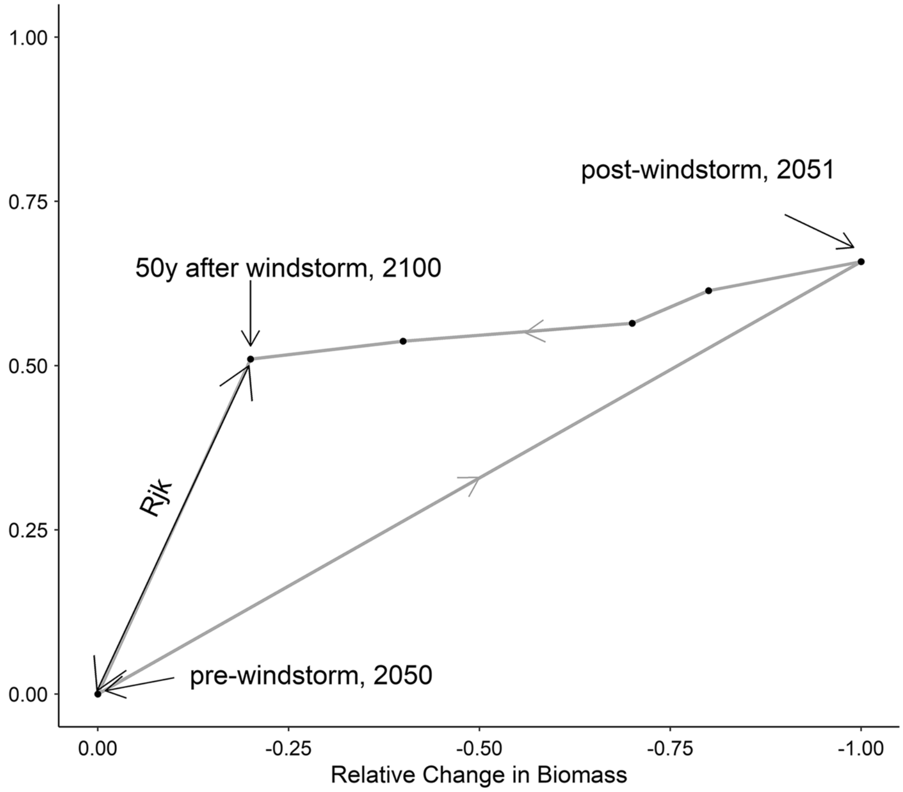

Fig. 2 Immediately after the wind event, there is a large reduction in biomass and a large change in species composition (labelled "post-windstorm"). In the years following the windstorm, biomass and species composition move closer to pre-wind conditions. In the final year, the minimum Euclidean distance from the final point (year 2050 or 2100) to the origin (2000 or 2050) is calculate, represented as a double arrow line (R_{jk}). Resilience is quantified by subtracting each distance from the maximum Euclidean distance ($\sqrt{2}$) to create an index where 1.414 is the most resilient (both total biomass and species composition returned to the initial conditions) and zero is the least resilient (indicates that there was no regeneration after 50 years)

measure of resilience for each disturbed raster cell (Fig. 2).

$$Rjk = \sqrt{\left(B_{jk}^{2}\right) + \left(BC_{jk}^{2}\right)} \qquad (3)$$

where Rjk = index of resilience between year j and k, Bjk = relative total biomass between years j and k and BCjk = Bray–Curtis index of dissimilarity between times j and k. We subtracted all our distances (Rjk) from the maximum Euclidean distance to create an index where 1.414 is the most resilient (both total biomass and species composition returned to the initial conditions) and zero is the least resilient (indicates that there was no regeneration after 50 years). This methodology allowed us to produce maps of average resilience (using ten replicates to capture the stochasticity in wind events and plant dispersal and vegetative reproduction) for two time frames (2050 and 2010) and five climate change scenarios.

Boosted regression tree model

A boosted regression tree model (BRT) was used to determine the relative importance of different drivers of resilience spatially across the landscape using the ‘gbm’ package in R (Greenwell et al. 2018). We selected twenty metrics which represented climatic, biotic, and edaphic factors, as well as metrics of the disturbance. The metrics of the disturbance (i.e. area and perimeter) were calculated at the patch scale using the ‘landscapemetrics’ R package (Hesselbarth et al. 2018). Shannon’s diversity index was calculated using the ‘vegan’ package (Oksanen et al. 2013). Boosted regression grows a large number of simple regression trees, with each successive tree built to reduce the residual variance in the predictor. Resilience and its associated covariates were first split into a training (80%) and testing (20%) dataset and the optimal number of boosting iterations was calculated for each climate scenario using the gbm.perf function in R gbm (Greenwell et al. 2018). In our final boosted regression function, the number of regression trees, interaction depth, and cv.folds differed among the scenarios. Since we had a large number of drivers (20), we decided to group variables into six categories—(1) species (N and ANPP), (2) disturbance characteristics (area and perimeter), (3) distance-to-seed sources of all species, (4) temperature (mean, spring, summer and winter), (5) % sand and (6) soil moisture- to gain a more complete picture of how climate change may alter the drivers of resilience.

Results

Hypothesis 1 Resilience will decline over time

Surprisingly, wind-disturbed sites did not fully recover from severe windstorms even under historical climate scenarios (Fig. 3a) At mid-century (2050), median resilience (1.0) was 28% lower than the maximum resilience of 1.414 (Fig. 4). This was due to relatively large shifts in species’ biomass distribution; the Bray–Curtis index indicated a recovery of only 10% relative to potential (Fig. 4). Bigtooth aspen, quaking aspen cottonwood, and black cherry had higher relative biomass than initial conditions, while sugar maple, red pine, pin oak, hemlock, and red maple were lower (Appendix 5). These large shifts in species composition occurred in the severely disturbed cells, but when species composition was examined over the entire landscape at the end of the century, there were only subtle changes in species composition. Black cherry, white cedar, and basswood increased only slightly compared to initial biomass (Online Appendix 6).

Keeping the duration of the simulation constant at 50 years, we found that our results supported our hypothesis that *resilience was higher at mid-century (2050) than at the end of the century (2100)* (Fig. 3). Median resilience at 2050 (1.0) was 28% lower than the maximum resilience (1.414) because of shifts in species composition, but changes in both total aboveground biomass and species composition caused an additional 32% decline in resilience at 2100 (median = 0.76, Fig. 4). At mid-century, aboveground biomass fully recovered, but by the end of the century, biomass only recovered to 80% of initial biomass (Fig. 4). Biomass recovery was possible after only 50 years, because the mean age of the trees at the start of the simulation was 53 years.

Resilience was similar among all the climate scenarios at mid-century, but by 2100, climate scenarios were significantly different from one another (Fig. 3b, Kruskallis p value = 0.004, all Dunn tests p values < 0.05), likely because of the large sample size (167,567 disturbed cells across all scenarios). Resilience was especially low for the hot-dry scenario (HADGEM2), with a median of only 0.63, 55% less

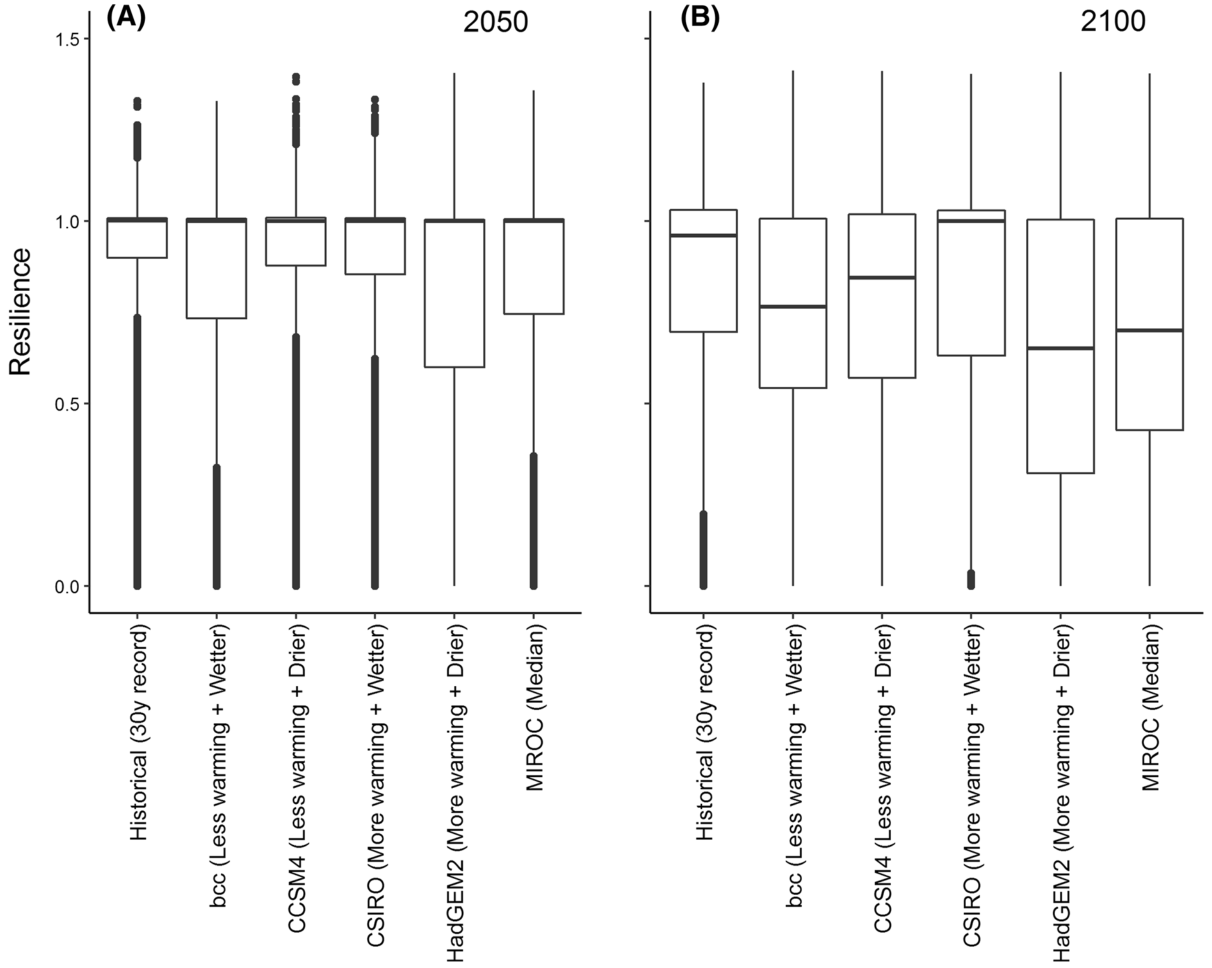

Fig. 3 Resilience was measured in: **a** ~ 2050 (2041–2050), 50 years after a severe wind event in 2000–2009 and **b** ~ 2100 (2091–2100), 50 years after a severe wind event in 2041–2050 under historical climate (no climate change) and five climate change scenarios: historical 30 years period, bcc-csm1-1 RCP4.5 (less warming + wetter), CCSM4 (less warming + drier), CSIRO-Mk3-6-0 RCP8.5 (more warming + wetter), HadGEM2-ES365 RCP8.5 (more warming + drier), and MIROC-ESM RCP4.5 (near ensemble mean)

than maximum resilience of 1.414. The climate scenario which represented median changes in climate (MIROC-ESM) also had low resilience (mean = 0.62), similar to the hot-dry climate scenario. Under climate change, bigtooth aspen and black cherry increased, and overall the landscape became more homogenous (Online Appendix 5). At the end of the century, Shannon's diversity index was 1.5 under historical climate and only 1.1 under climate change (averaged across all scenarios) with the average number of species per hectare declining from 8.6 to 5.8; Shannon's diversity index was 1.2 under historical climate and 1.1 under climate change with the average number of species declining only from 7.7 to 6.3.

Hypothesis 2 Resilience will vary spatially, with lower resilience in the southern portion of the landscape.

As expected, resilience was not uniform across the landscape By mid-century, resilience was lower in the southern portion of the landscape (Fig. 5) with differences in climate, growth rates, and disturbed area. For example, under the "warm-wet" scenario (bcc), the southern portion of the landscape had 30% more area disturbed by wind. Also, the south was 1.7 °C higher, growth rates were 70% lower and distance-to-seed-source across all ten species was 30% higher than the rest of the landscape. Variance between replicates was

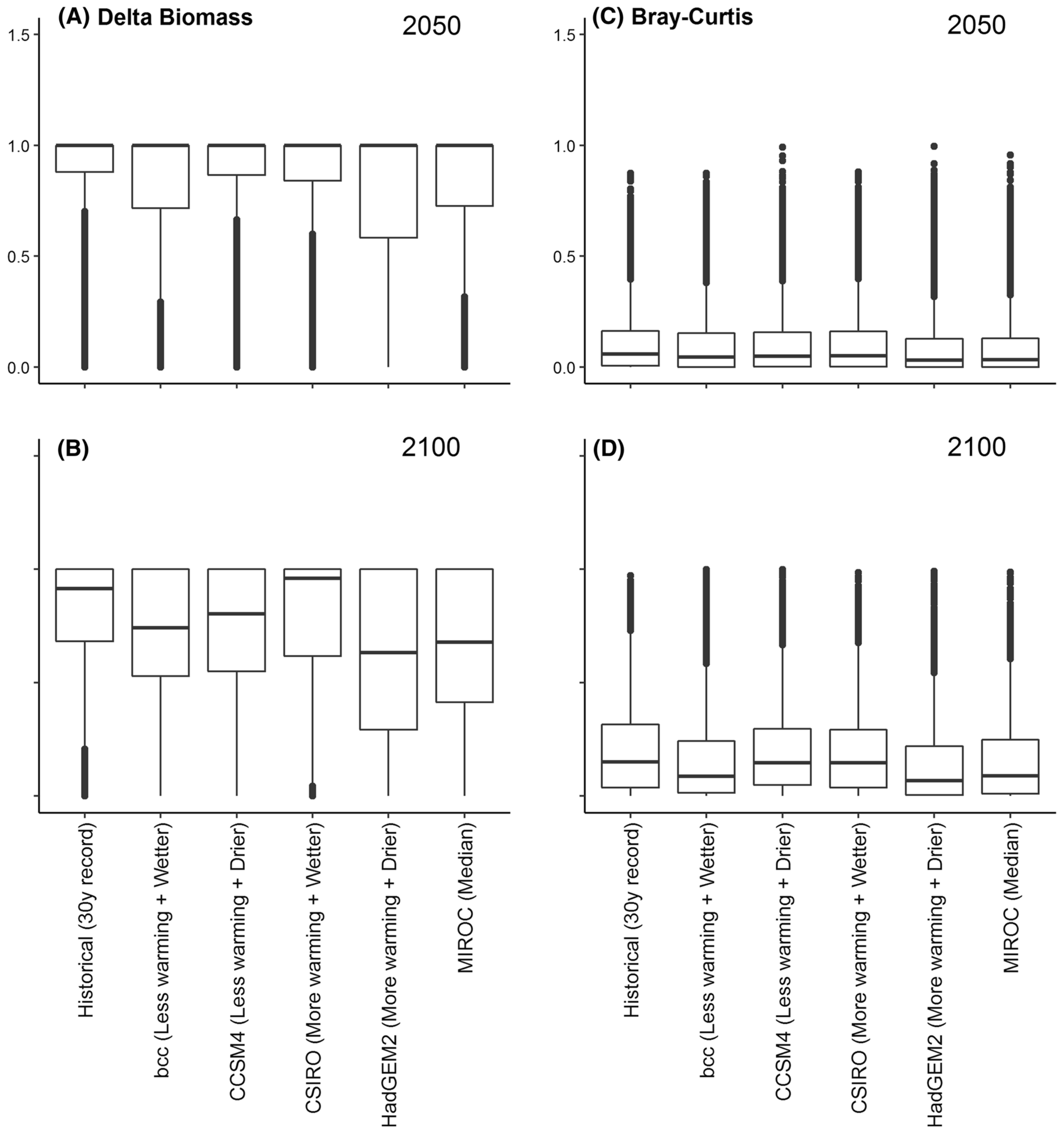

Fig. 4 Deconstructing the resilience measure into its components: **a** change in total biomass and **b** Bray–Curtis index of dissimilarity under historical climate (no climate change) and five climate change scenarios: bcc-csm1-1 RCP4.5 (less warming + wetter), CCSM4 (less warming + drier), CSIRO-Mk3-6-0 RCP8.5 (more warming + wetter), HadGEM2-ES365 RCP8.5 (more warming + drier), and MIROC-ESM RCP4.5 (near ensemble mean). These metrics have been normalized to go from zero to one, where one indicates complete recovery to pre-wind conditions

also highest in the southeastern region of the landscape (Online Appendix 7). This corresponded with higher variance in area disturbed (+ 20%), windstorm perimeter (+ 33%), soil moisture (+ 33%) and distance-to-seed-source (+ 27%), but lower variance in temperature (− 22%) and growth rates (− 10%) in the southern region. Variance between replicates was

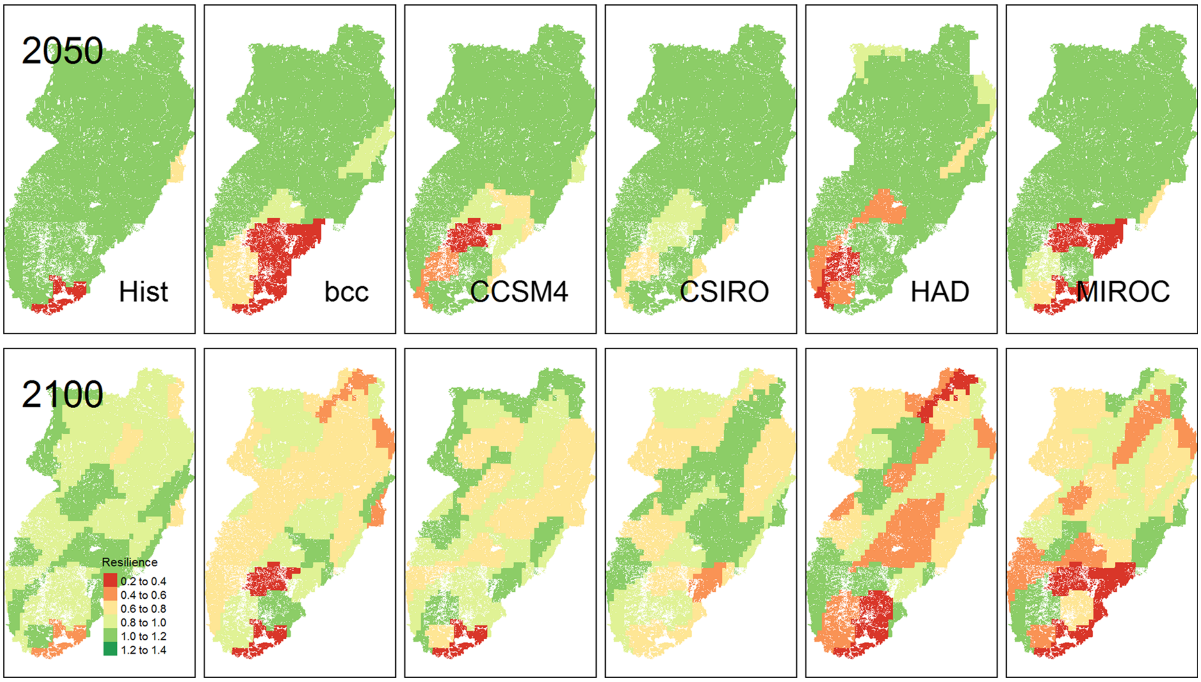

Fig. 5 Median resilience for each of the 38 climate regions under historical climate (no climate change) and five climate change scenarios at 2050 and 2100. Climate change scenarios included bcc-csm1-1 RCP4.5 (less warming + wetter), CCSM4 (less warming + drier), CSIRO-Mk3-6-0 RCP8.5 (more warming + wetter), HadGEM2-ES365 RCP8.5 (more warming + drier), and MIROC-ESM RCP4.5 (near ensemble mean)

lower at the end of the century than mid-century, especially in the southeast.

By the end of the century, low values of resilience were evident throughout a greater portion of the landscape (*Fig.* 5) This occurred even under historical climate, but was exacerbated under climate change. Instead of only 5% of the landscape designated as low resilience (resilience ≤ 0.4) at 2050, 9% of the landscape was categorized as low resilience under climate change. The hot-dry scenario (HAD) had the largest percentage of area classified as low resilience (20%) with hot-spots of resilience in the southern and northern portions of the landscape (Fig. 5).

Hypothesis 3 Landscape-level factors (i.e. disturbed area and distance to seed source) will be important predictors of resilience by mid-century, but climatic and edaphic factors will become increasingly important by the end of the century, especially under climate change.

In comparing the relative importance of different factors in explaining resilience using BRT, we found that our hypothesis was not well supported. Species' characteristics (number of species and growth rates) were the most important factor in driving resilience at mid-century (Fig. 6, Online Appendix 8). Species' characteristics explained over half (60%) of the variation in resilience under historical climate and about 30% under climate change.

Partial dependencies from the fitted model indicate that, when other variables were held constant, resilience was most likely to be higher (not lower) when there were fewer species (Online Appendix 9). As expected, the amount of disturbed area was important at mid-century, explaining between 10 (historical) to 25% (climate change) of the variation in resilience (Fig. 6). Resilience tended to be highest in medium-sized wind patches but declined in larger patch sizes (Online Appendix 9).

Contrary to our hypothesis, distance-to-seed-source became more (not less) important over time. Distance-to-seed-source explained 17% of the variation mid-century and increased to 37% by the end of the century (35% under historical, 38% under climate change, Fig. 6). Also, distance-to-seed-source of hardwoods was a more important factor in driving resilience

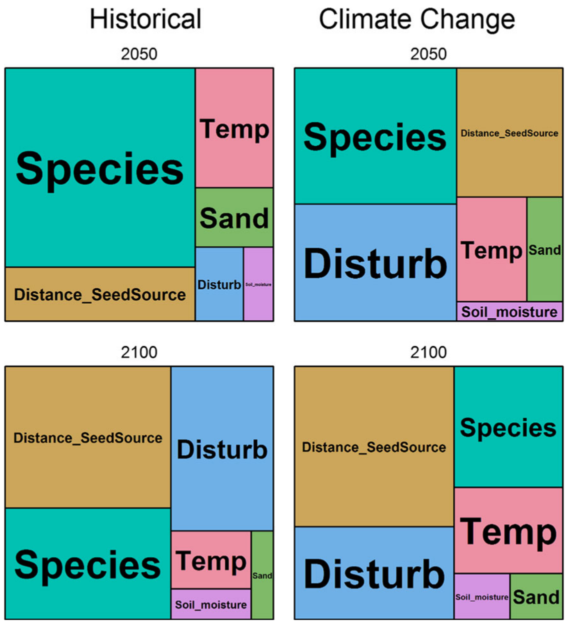

Fig. 6 The relative importance of different drivers of resilience under historical climate (no climate change) and the average of five climate change scenarios at 2050 and 2100 as determined by boosted regression tree analysis. Drivers from Online Appendix 8 were classified into six bins: species characteristics (number of species and ANPP), disturbance characteristics (area and perimeter), distance to seed source of all species, temperature (mean, spring, summer, winter), percent sand, and soil moisture

(26%) compared to conifers (11%, Online Appendix 8). Basswood, white cedar, paper birch, and red oak were particularly important at the end of the century in explaining the variation in the distance-to-seed-source.

Several drivers became more important under climate change by the end of the century. As expected, temperature became more important under climate change; it explained only 7% of the variation in resilience under historical climate, but it explained 14% of the variation in resilience under climate change (Fig. 6). Resilience tended to be higher at higher temperatures, especially at the end of the century, though not always (Appendix 9). Soil moisture played a small and consistent role in explaining variation in resilience (3–4%, Fig. 6), with resilience associated with higher soil moisture (Online Appendix 9). Since temperature and soil moisture played much less of a role than expected in resilience, we looked at the climatic constraints on establishment only (as opposed to both growth and establishment combined). The limitations to tree establishment by temperature and soil moisture were higher (12% and 8% respectively) across all climate change scenarios than under historical climate, as assessed by the probability of establishment limitation factors (0–1) in LANDIS-II.

The most important factor in driving resilience differed among climate scenarios. At mid-century, the number of species was the most important factor for the "wet" climate scenarios (bcc and CSIRO), but the area of the windstorm was the most important factor in the remaining climate scenarios (CCSM4, HAD, MIROC), explaining between 29 and 55% of the variation in resilience (Online Appendix). At the end of the century, windstorm characteristics explained most of the variation in the "wet" scenarios (19–22% for bcc and CSIRO) and "median" scenario (29% in MIROC). Growth rates (ANPP) were the dominant driver under historical (26%) and the "hot-dry" (HAD) scenario (14%), respectively. Under the "warm-dry" scenario (CCSM4), the distance-to-seed-source of paper birch was the most important driver, explaining 17% of the variation in resilience, though resilience was higher when distance-to-seed-source was higher.

In all the climate scenarios, there was a single factor (either disturbance area or the number of tree species prior to disturbance) that explained about half of the variation at mid-century, but two (ANPP plus disturbance area or perimeter) factors explained variation at the end of the century. For example, under the "hot-dry" climate scenario (HAD), the most important factor (area) explained 30% of the variation at mid-century, but at the end of the century, the most important factor (ANPP) explained only 14% (Online Appendix).

Discussion

Our results suggest that the resilience of central Wisconsin's forests will decline by the end of the century, especially under the hotter and drier scenarios of climate change. However, our initial supposition of the landscape-level characteristics (i.e. distance-to-seed source and soil moisture) driving resilience was too simplistic and discounted the importance of species and disturbance (e.g., number of species, disturbed area and perimeter) interactions in shaping resilience. Our research also highlights the utility of using machine learning (e.g., boosted regression trees or Random Forest) to discern the underlying mechanisms of landscape-scale processes when using complex spatially-interactive and non-deterministic simulation models like LANDIS-II.

Declines in resilience over time

Our simulations projected that resilience will decline over the next 50-100 years even under a "no climate change" scenario (historical climate, Fig. 3). At the start of the simulation, these forests were generally young (mean tree age = 53 years) and had relatively low biomass (6200 g/m^2) and therefore we should not be surprised to see successional momentum drive landscape change and cause shifts in species composition. These forests are in transition from the relatively simple communities that emerged from extensive logging and fire that characterized the late 19th and early 20th centuries (Rhemtulla et al. 2009b) to more complex, higher-diversity, and multi-age forests more typical of older forests in the region (Rhemtulla et al. 2009a).

By quantifying resilience, which by its very definition necessitates looking at only disturbed sites, species composition appeared substantially different at the end of the century under all our climate scenarios. For example, severe disturbance promoted the growth of disturbance-adapted species, like aspen and black cherry, especially under climate change, and it appears as if large shifts in species composition are projected under climate change. However, when the entire landscape is examined (both disturbed and undisturbed cells), species composition was relatively unchanged among the climate scenarios, remaining dominated by maples and oaks. Studies which focus on resilience, especially of severely disturbed sites, may overestimate landscape-scale change under climate change.

The differences in resilience between climate scenarios were not predictable based solely on the climate trends, even at the end of the century. Some climate scenarios had lower resilience than historical conditions (e.g., "less warming and wetter) and others showed no effect (e.g., "more warming and wetter"). This conflicts with other studies showing a strong correlation between rising temperatures and declining resilience. In a previous study, resilience declined monotonically as the average temperature of the scenario increased in central Minnesota (Lucash et al. 2017). Another study found that a low emissions scenario had no impact on resilience, but a high emissions scenario (i.e. greater increase in temperature) reduced resilience in Minnesota and Michigan (Duveneck and Scheller 2016). In our study, warming tended to reduce resilience under "dry" scenarios as expected. However, under the "wet" scenarios, some warming ("less warming", bcc) lowered resilience compared to historical climate, but "more warming" increased resilience (CSIRO) due to higher biomass recovery rates. At first glance, this might seem like model error, since we wouldn't expect biomass recovery to decrease under "less warming", when it increases under "more warming". However, in this case, species trajectories likely played an indirect role in explaining biomass recovery after severe disturbance. For example, the "less warming" scenario favored the growth of aspen, which achieves lower maximum biomass (15,000 g/m^2) than many of the other dominant species (e.g., white pine and red maple can attain biomass of 33,000 g/m^2). This serves as a reminder that changes in climate interact with successional trajectories in LANDIS-II and produce emergent behavior not easily predicted based on simple relationships between temperature and biomass.

Given that management promotes resilience in this region through harvesting and replanting, we expected our simulations—that did not include responsive management strategies- to generate lower resilience than previous studies which included management. Forest management practices play an important role in maintaining species composition in this region. This landscape is heavily managed, with coppice-cutting to maintain aspen and clear-cutting followed by replanting to maintain pines (i.e. red, white, and jack pine) and spruce-fir on federal lands (USDA 2004). Without management shaping forest recovery, engineering resilience declines as species trajectories become less predictable and driven more by climate and soils than human activity. Instead, our estimate of resilience was higher than a previous study in Minnesota using the same methodology. Resilience averaged only 0.8 under historical climate and business-as-usual management (Lucash et al. 2017), while ours was 1.0, with both studies using a maximum resilience of 1.414. The Wisconsin landscape is 50 years younger on average and is dominated more by hardwoods, which are expected to be more resilient under climate change than the boreal species of central MN (Handler et al.

2014). However, our landscape was less resilient than northern MN and MI (Duveneck and Scheller 2016), though they computed resilience at the landscape-level ($\sim$ 1.3 for the entire landscape under historical climate and management) and not uniquely for each raster cell (as in our study).

Spatial patterns of resilience

The southern end of the landscape had low resilience and was most vulnerable to species shifts. Many factors could have contributed to its low resilience, including warmer temperatures, lower growth rates, larger wind patches and greater fragmentation due to the patchwork of forested and agricultural lands. Fragmentation is often an obstacle to species' regeneration, preventing establishment in suitable climate habitat and constraining migration in response to climatic shifts (Collingham and Huntley 2000; Bertrand et al. 2011; Meier et al. 2012). Low values of resilience spread northward by 2100. This suggests that low resilience might be detected first in the southern portion of the landscape, but that the entire landscape is subject to declines in resilience over the next century due to large shifts in species composition.

We observed a negative correlation between resilience and variance spatially, but not temporally within the climate regions. At mid-century, we observed spatial correspondence between low resilience (Fig. 5) and high variance (Online Appendix 7), suggesting that as resilience declines, variability may increase in concert. However, this was not the case with time, since resilience tended to decrease throughout the landscape by the end of the century without a concomitant change in variance. If variation varies spatially and increases with climate change, as in this study, it may become increasingly difficult to project changes in successional trajectories. More quantitative field studies on rates of seed and vegetative production across a range of climate, soil and disturbance conditions will help inform models which rely on species life history strategies to simulate successional trajectories.

Drivers of resilience

We found little support for our hypothesis that landscape factors (i.e. distance-to-seed source and area of windstorm) would be the most important predictor of resilience initially, but would decline in importance over time as climate became more important. Instead the relationships were far more complicated. The number of tree species was the most important factor at mid-century (Fig. 6). However, higher diversity led to lower resilience, likely because our metric relied on recovery of species composition, which is achieved more easily when there are fewer species. It is important to recognize that the choice of metric biases the interpretation of resilience. For example, a system may be considered resilient if the number of species is chosen as the metric, as compared to species biomass distribution (in this study) or the percentage of late successional species (Seidl et al. 2016).

As expected, the size and pattern of wind events (i.e., area and perimeter) was a critical factor in explaining resilience. The annual frequency of tornados has increased in the upper Midwest over the past 40 years (Gensini and Brooks 2018) and if this trend continues as some projections suggest (Diffenbaugh et al. 2013; Gensini et al. 2014; Tippett et al. 2015), then windstorms may become an even more important driver of long-term changes in these forests. Our study would have been strengthened by downscaled projections of wind disturbance under climate change, but they are not yet publicly available.

Distance-to-seed-source was more important in explaining resilience at the end of the century than mid-century. Long distances from seed sources are commonly associated with larger or more severe disturbances, which can limit post-disturbance recruitment and extend the time it takes for the forest to recover (e.g., Donato et al. 2009; Harvey et al. 2016; Tepley et al. 2017), but in our study, the wind rotation period of high severity events was kept constant. Instead, our landscape became less resilient by the end of the century due to successional momentum, rather than an increase in the size or severity of windstorms. As disturbance-adapted species became established after the wind event, the distance to the closest tree of the same species increased, limiting post-wind recruitment.

Climate played a much smaller role in driving resilience at the end of the century than expected based on field studies illustrating the importance of warming and low soil moisture (or low climate water deficit) on post-disturbance tree regeneration (Donato et al. 2016, Kueppers et al. 2017, Davis et al. 2019). Although the model captured the limitations to seedling growth due to temperature and soil moisture at the cell-scale, disturbance and species' characteristics were far more important at the landscape scale in driving long-term changes than climate. Climatic signals often appear strong at smaller spatial scales, but may be harder to discern at the landscape scale, given the potential for interactions among successional dynamics, N supply, water availability, and disturbances and their associated uncertainties (Reyer et al. 2015). Other factors, not explored here, such as deer browsing, insect pests, wildfire, or CO_2 fertilization, are likely to further influence resilience and the direction and magnitude of species recovery to windthrow.

Using machine learning to improve simulation modeling

Machine learning is commonly used to improve parameterization of simulation models (e.g., PECAN, LeBauer et al. 2013) and used in sensitivity analysis to isolate the most important parameters in the model. Machine learning techniques (e.g., boosted regression trees or Random Forest) could also be used, as in this study, to analyze output from simulation models by extracting patterns from data and helping to identify underlying mechanisms from complex spatial models like LANDIS-II. This approach can help determine which processes dominate in the model output, isolate model errors, and potentially improve the credibility of the model (Reichstein et al. 2019). Complex models like LANDIS-II contain spatio-temporal, nonlinear dynamics and the underlying mechanisms are difficult to discern using simple regression or correlative techniques, which remain the norm for analyzing simulation model output (Duveneck and Scheller 2016; Duveneck and Thompson 2017; Lucash et al. 2017, for exception see Perry et al. 2015).

In our study, careful consideration was given to the model inputs and outputs included in our boosted regression tree, recognizing that previous time steps contain "memory effects" and neighboring grid cells influence the output. For example, we used an average temperature of the 50-year period, along with the average spring, summer and winter temperatures, recognizing that these will differ among the climate change scenarios. The challenges to isolating mechanisms may not be completely solved by machine learning, however. For example, the importance of distance-to-seed-source may encapsulate the temperature and soil moisture limitation to establishment and obscure the role of these variables in driving resilience. While recognizing they are not a panacea, we suggest that adoption of machine learning techniques in concert with simulation modeling output are a vast improvement over simple correlative metrics and will help determine which factors are driving temporal and spatial patterns, help eliminating model errors and ultimately make models better and make the mechanisms more transparent.

Conclusions

Our work highlights the important role of disturbance and dispersal in shaping the temporal and spatial pattern of forest succession and resilience under climate change. We also recommend the more widespread use of machine learning, especially boosted regression tree and Random Forest, to discern the relative importance of underlying mechanisms in complex simulation models.

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