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RESEARCH ARTICLE

Measuring and managing resistance and resilience under climate change in northern Great Lake forests (USA)

Matthew J. Duveneck · Robert M. Scheller

Abstract

Context Climate change will have diverse and interacting effects on forests over the next century. One of the most pronounced effects may be a decline in resistance to chronic change and resilience to acute disturbances. The capacity for forests to persist and/or adapt to climate change remains largely unknown, in part because there is not broad agreement how to measure and apply resilience concepts.

Objectives We assessed the interactions of climate change, resistance, resilience, diversity, and alternative management of northern Great Lake forests.

Methods We simulated two landscapes (northern Minnesota and northern lower Michigan), three climate futures (current climate, a low emissions trajectory, and a high emissions trajectory), and four management regimes [business as usual, expanded forest reserves, modified silviculture, and climate suitable planting (CSP)]. We simulated each scenario with a forest landscape simulation model. We assessed resistance as the change in species composition over time. We assessed resilience and calculated an index of resilience that incorporated both recovery of pre-fire tree species composition and aboveground biomass within simulated burned areas.

Results Results indicate a positive relationship between diversity and resistance within low diversity areas. Simulations of the high emission climate future resulted in a decline in both resistance and resilience.

Conclusions Of the management regimes, the CSP regime resulted in some of the greatest resilience under climate change although our results suggest that differences in forest management are largely outweighed by the effects of climate change. Our results provide a framework for assessing resistance and resilience relevant and valuable to a broad array of ecological systems.

Keywords Alternative forest management · Climate change · LANDIS-II · Michigan (USA) · Minnesota (USA) · Resistance · Resilience

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Introduction

Climate change effects to forests

Climate change is expected to alter forest succession across landscapes (Svenning and Sandel 2013) including recovery following disturbance (Anderson-Teixeira et al. 2013). A substantial shift in tree species composition, a decline in annual net primary productivity, a decline in biomass, and other ecosystem function changes have been forecast (e.g., (Duveneck et al. 2014a). There is

however large variation in ecosystem functioning within and between landscapes and this variation may be magnified by climate change (Scheller et al. 2012). Some communities (plant assemblages) may continue to persist providing similar function while others may decline in function or perish and novel assemblages emerge (Williams and Jackson 2007). Understanding the mechanisms that maintain function will help managers plan future actions and priorities. Some landscapes may naturally adapt to change while continuing to provide ecosystem function; others may require more active management to maintain or enhance ecosystem function (Duveneck et al. 2014b, Duveneck and Scheller 2015).

Forests are affected by both press and pulse disturbances. Press disturbances can be defined as chronic long term exogenous forcing; while pulse disturbances can be defined as acute short term disturbances (Bender et al. 1984). We consider climate change a press disturbance that may, for example, directly affect species growth and regeneration potential through long term changes in environmental conditions (Fisichelli et al. 2012, 2013). Climate change will also cause alternations in pulse disturbance regimes (Dale et al. 2001), for example insect outbreaks (Bentz et al. 2010). In addition, we expect the magnitude of the direct effects of climate change to vary over time (e.g., temperature projections in 2020 compared to 2100).

Resistance to climate change effects

Although resistance can be used to describe acute expressions of environmental drivers (e.g. resistance of a forest to a specific insect outbreak), we use resistance of a system to describe its ability to persist through chronic change (Landres et al. 1999; Minckley et al. 2012). The degree to which a system changes in response to a press disturbance, such as climate change, is therefore a measure of its resistance. As an example, the resistance of a site or landscape to climate change may be represented by the shifts in species composition during a period of climatic change (Bradt et al. 1999; Rydgren et al. 2004; Thrush et al. 2008).

Ecologists have long theorized (Elton 1958), tested (Tilman and Downing 1994; Tilman et al. 2006; Moore et al. 2011), and debated (McCann 2000) the diversity-stability hypothesis whereby higher diversity results in

greater stability. As a stabilizing (resistance generating) mechanism, diversity can provide both complementarity and identity effects (Eisenhauer et al. 2013). Resistance can also be regarded as synonymous with stability and initial diversity of a site or landscape may affect resistance (represented by the conceptual diagram (Fig. 1).

Functional diversity based on species traits rather than species themselves (Laliberté and Legendre 2010; Duveneck and Scheller 2015) may provide additional information about the resistance of future ecosystem function. The relationship between functional diversity and resistance, however, has been largely unexplored. The loss of a single foundational species (Ellison et al. 2005) could result in a large decline in resistance of that community. As compared to lower diversity ecosystems, greater functional diversity ecosystems are expected to be more resistant to climate change induced declines in ecosystem function (Millar et al. 2007; Spies et al. 2010; Swanston and Janowiak 2012; Duveneck et al. 2014a). However, this relationship may not hold under all conditions. For example, the relationship between functional diversity and productivity may be
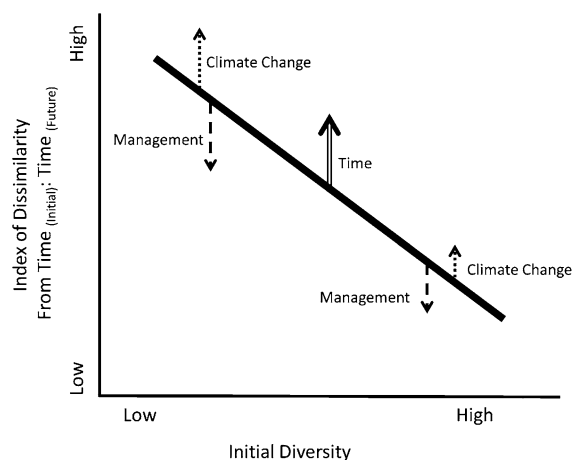

Fig. 1 Conceptual representation of diversity and dissimilarity supporting the hypothesis that as initial diversity increases, dissimilarity decreases (*solid line*). As time period increases, dissimilarity increases (*double arrow*). An exogenous threat (e.g., climate change) may increase the dissimilarity between two time periods (*dotted lines*). Adaptive management may decrease (or inadvertently increase) dissimilarity between two time periods (*dashed lines*). Climate change and management may affect dissimilarity in non-linear ways in respect to diversity (length of *dotted* and *dashed lines*)

positive under low productivity or negative under high productivity (Paquette and Messier 2011).

Forest resilience

An assessment of forest resilience under climate change is equally important. The resilience of a system can be defined as the ability to recover from a disturbance back to a similar initial state (Gunderson 2000; Anderson-Teixeira et al. 2013). Resilience can be used to measure the indirect effects of pulse disturbances under climate change. Because recovery from a pulse disturbance (e.g., fire) is affected by the press disturbance (e.g., climate change), resilience is a good measure of the interacting effects of both pulse and press disturbances. Any discussion of resilience must include a description of: "what system" (system identity) and "to what disturbance" given that the identity and disturbance of a system can be measured along multiple dimensions (Carpenter et al. 2001; Cumming 2011).

A system's identity can be defined in multiple ways (Cumming 2011) (e.g., species composition or total abundance). With species composition as a measure of a system's identity, community dissimilarity can be used in a definition of resilience as the recovery of a system's initial conditions. Alternatively, total abundance [e.g., aboveground biomass (AGB)] irrespective of species composition can be used as a measure of identity, and resilience measured by the recovery of initial abundance.

Indicators of resilience should include multiple measures of identity. In multidimensional space, resilience can be measured with multiple definitions of the identity of a system. As expressed in the conceptual diagram (Fig. 2), resilience of a forest could be measured as the distance from initial conditions on both a species composition axis (dissimilarity) and a total abundance axis (AGB).

Managing for forest resistance and resilience

Previous studies have explored the ability of management to steer the trajectory of forests subject to climate change (e.g., Lawler 2009; Spies et al. 2010). Under a high emission future, reduced abundance of range-limited species is expected over the next century (e.g., balsam fir *(Abies Balsamea)* in the boreal-temperate ecotone) compared to a current climate future

(Scheller and Mladenoff 2008; Xu et al. 2009; Fisichelli et al. 2012, 2013; Duveneck et al. 2014a). Management regimes designed to counter climate change effects, including expanded reserves, modified silviculture, and climate suitable planting, may have a limited ability to maintain ecosystem services (Ravenscroft et al. 2010; Duveneck et al. 2014b; Duveneck and Scheller 2015). Although these studies describe landscape-scale dynamics under climate change, they did not explicitly examine the effects of climate change and management on resistance and resilience. To date few studies (e.g., Anderson-Teixeira et al. 2013; Buma and Wessman 2013) have measured resistance and resilience in the context of managing forests for climate change. Managing forests for resistance and resilience, however has been identified as a priority for managers interested in maintaining and/or increasing adaptive capacity under climate change (Millar et al. 2007; Puettmann 2011).

Understanding landscape ecological processes that incorporate dispersal, disturbance, and intrinsic limits have been identified as important research priorities
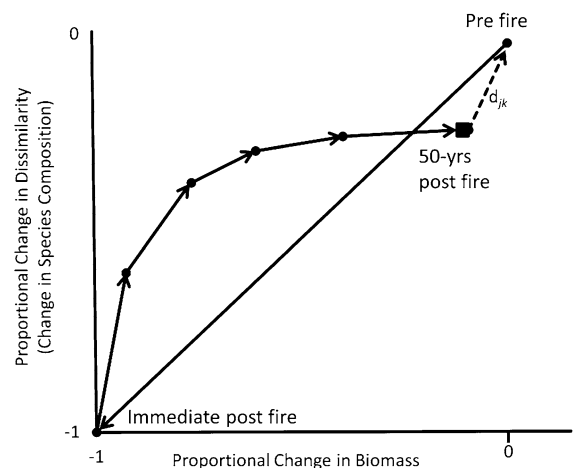

Fig. 2 Conceptual diagram of resilience following a fire measured along two axes. Pre-fire conditions represent zero change in biomass and zero dissimilarity. Immediately post-fire represents a reduction in biomass and an increase in dissimilarity. The years following the fire represent recovery of biomass (slower at first) and dissimilarity (faster at first) towards pre-fire conditions. The *dashed line* d_{ij} represents the minimum distance from any successive time step (k) to the origin (j). Climate change and management may result in a change in d_{ij} representing changes to resilience. It is possible to fully recover (if not exceed) pre-fire biomass. Due to successional trajectories, it is unlikely that a system will recover exactly to pre-fire species composition
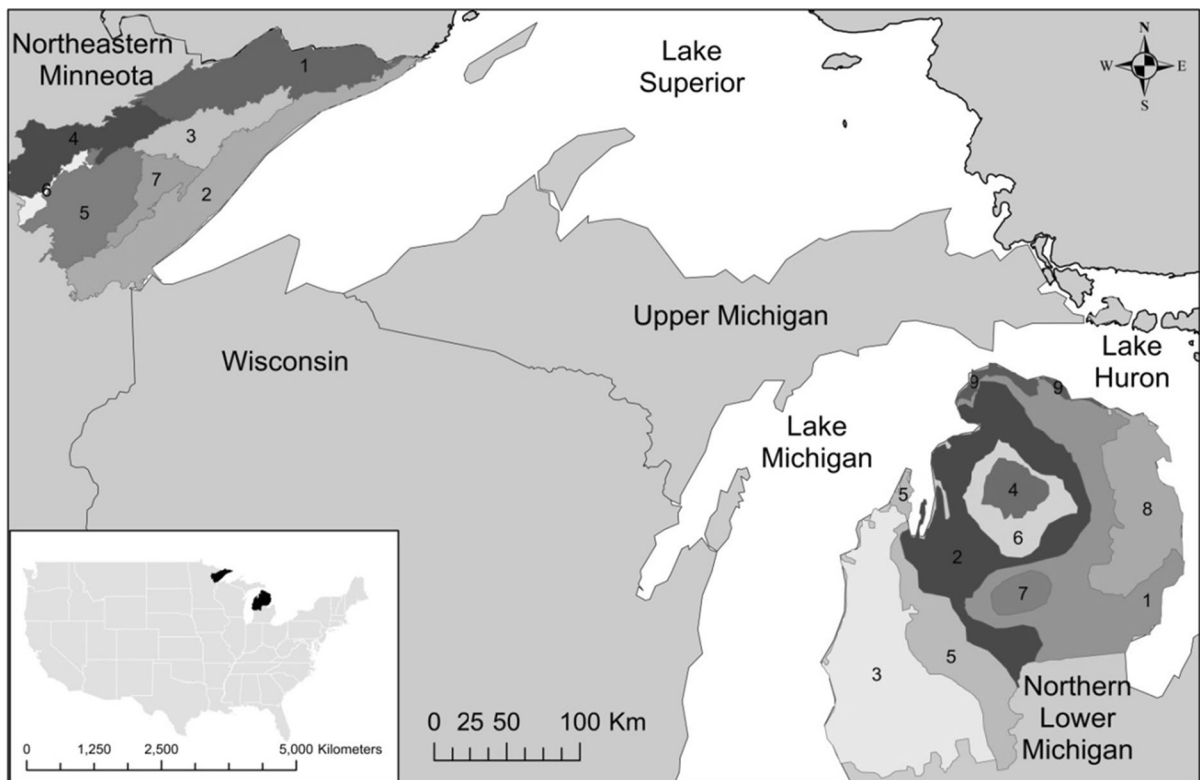
Fig. 3 Northeastern Minnesota and northern lower Michigan study regions. *Numbers* represent unique climate regions within each landscape. *Inset* study regions within continental United States

for understanding species and ecosystem response to climate change (Moritz and Agudo 2013). Spatially explicit models are useful for evaluating multiple interacting spatial processes on landscapes. We explored the effect of climate change, and management on resistance and resilience of forests via simulation modeling. We explored alternative forest management scenarios that could increase resistance and resilience. Specifically, we addressed the following hypotheses (Fig. 1): (1) Initial species and functional diversity will increase resistance as measured by dissimilarity. (2) Climate change will reduce resistance over time. (3) Management has the capacity to increase resistance to change. (4) Following acute disturbance, climate change will reduce resilience and management will increase resilience (sensu, Fig. 2). We explored these hypotheses by comparing two distinct landscapes within the Great Lakes region (northeastern MN and upper-lower MI). By incorporating two landscapes, we were able to broaden our

inferences beyond a single case study and expand the range of conditions explored.

Methods

Site descriptions and experimental design

Our study includes a landscape in Northeastern Minnesota and another in northern lower Michigan that, together, encompass a broad gradient of conditions in Great Lake Forests (Fig. 3). Forest distribution shifts are expected to be slow due in part to the geographic isolation (i.e. discontinuity with large forested areas to the south) pattern of the landscapes (McLachlan et al. 2005; Vanderwel and Purves 2013). Great Lakes forests are situated within the boreal-temperate forest transition ecotone. These forests are largely managed for forest products by a range of public and private landowners (Duveneck et al.

2014a). In each landscape, we delineated unique climate regions that represent relatively homogenous climate (White and Host 2000; Duveneck et al. 2014a).

The Minnesota landscape has more contiguous forest than the Michigan landscape, which includes large forest reserves not present in northern lower Michigan. The Michigan landscape is further south with warmer projected temperatures than Minnesota (Andresen et al. 2012; Duveneck et al. 2014a). The Minnesota landscape is managed intensively; is dominated by a matrix of aspen forests (D' Amato et al. 2009); and is closer to the boreal forest ecotone (Curtis 1959). The Michigan landscape has greater tree diversity, has less aspen, and is further from the boreal forest ecotone (Duveneck et al. 2014b). Together, these two landscapes encompass much of the broad range of social and ecological forests dynamics found immediately adjacent to the Great Lakes. In the northern Great Lake forests, fire events occur with large variability in severity and frequency. Infrequent fires in the Great Lakes Region, along with more frequent smaller fires, result in a mixed severity fire regime (Frelich 2002). White and Host (2008) estimate percent area burned annually in Northeastern Minnesota to be between 0.1 and 0.6 % of the landscape. In northern lower Michigan, Cleland et al. (2004) estimate the percent area burned annually to be between 0.09 and 0.13 %.

Our experimental design encompassed both landscapes, four management regimes (described below), multiple climate regions (Fig. 3), and three climate futures (current climate, low emission future, and high emissions futures described below). Our simulations had a two-hectare resolution and a 150 year simulation horizon starting at year 2000. Within each scenario, we examined the effect of simulated fires at years 2050 and 2100. To assess resistance, we measured the dissimilarity of initial species composition to the effects of climate change over time. To measure resilience, we assessed the recovery of ecosystem structure (AGB) and initial species composition over time to the effect of simulated fires.

Simulation model

We used the LANDIS-II (v6.0) forest landscape model (Scheller et al. 2007) to simulate forest change. LANDIS-II is a successional process model that emphasizes disturbance interactions on a landscape of interconnected grid cells. Within cells, species-by-age cohort combinations are tracked. LANDIS-II incorporates successional processes of seed dispersal, regeneration, competition, growth, and mortality. At every 5-year time step, we utilized the following extensions to the LANDIS-II core framework: Biomass Succession (v3.1) (Scheller and Mladenoff 2004) which implements succession in LANDIS-II using tree species AGB as its primary currency, Biomass Harvest (v2.1) (Gustafson et al. 2000) which implements the harvest prescriptions, Base Fire (v3.0) (He and Mladenoff 1999), and Base Wind (v2.0) (Scheller and Mladenoff 2004) which implements fire and wind disturbances, respectively. LANDIS-II and the extensions described have been validated against empirical data from these study landscapes (Duveneck et al. 2014a) as well as other landscapes from the northeastern region (Scheller and Mladenoff 2004; Ravenscroft et al. 2010; Thompson et al. 2011). We validated simulated AGB at year 2000 to measured AGB in USDA Forest Service Inventory and Analysis field plots used in the imputation of initial conditions (Root Mean Square Error $= 44.3$ Mg ha^{-1} and Pearson's Correlation Coefficient $= 0.64$) (Duveneck et al. 2014a).

Climate change was incorporated into Biomass Succession through variation in annual estimates of maximum aboveground annual net primary productivity (ANPP$_{max}$), and probability of establishment (P$_{est}$) for each species. Species parameters are provided in previous work (Duveneck et al. 2014a). To calculate ANPP$_{max}$ and P$_{est}$, we used the PnET-II for LANDIS-II tool which incorporates monthly climate data (maximum and minimum temperature, precipitation, and photosynthetic active radiation) (Xu et al. 2009). To incorporate variation in growth and establishment, we ran PnET for unique tree species within unique soil and climate regions in each landscape. Percent foliar nitrogen content, maximum foliar mass area, and soil water holding capacity are required PnET parameters previously described (Duveneck et al. 2014a). In addition, we calculated AGB$_{max}$ for each species, climate and soil region based on the species specific relationships between AGB$_{max}$ and ANPP$_{max}$ (Thompson et al. 2011).

Biomass Succession uses AGB$_{max}$, ANPP$_{max}$, and P$_{est}$, to simulate establishment, growth, reproduction, and age-related mortality of species cohorts. The

establishment of a new cohort is determined by P_{est} (provided a seed source and sufficient available light) based on a climate envelope model (Xu et al. 2009). $ANPP_{max}$ determines the growth potential of a species given no competition. ANPP is limited by a species specific growth curve parameter that regulates how fast ANPP reaches $ANPP_{max}$. Competition further reduces growth through utilization of finite growing space (Scheller and Mladenoff 2004). Input parameters and soil and climate region delineations for each landscape are provided in Duveneck et al. (2014a).

We initialized each simulation with an initial community map with species-age cohorts in every forested cell. The initial community maps were based on spatial imputations of plot inventory data. We utilized previously developed initial community data for Minnesota (Ravenscroft et al. 2010) and Michigan (Duveneck et al. 2014a).

Climate futures

Our objectives were not to create the most accurate and precise prediction of future forests under climate change. Rather, our objectives were to broadly bound potential future forests based on a range of emission projections. We simulated a 'current climate' future by randomly selecting historic years (1969–1999) monthly PRISM climate data (Daly and Gibson 2002) to represent future years. We simulated a low emissions climate future based on the Parallel Climate Model (PCM) Global Climate Model (GCM) (Washington et al. 2000) and the B1 emission scenario (Intergovernmental Panel on Climate Change 2007). We simulated a high emission climate future based on the Geophysical Fluid Dynamics Laboratory (GFDL) GCM (Delworth et al. 2006) and the A1FI emission scenario (Intergovernmental Panel on Climate Change 2007). The B1 and A1FI emission scenarios represent the least and most fossil fuel intensive future described by IPCC, respectively and are comparable to the new IPCC scenarios of carbon dioxide concentration projections (IPCC 2013). We accessed monthly downscaled temperature and precipitation projections through the USGS data portal http://cida.usgs.gov/climate/gdp/ (Stoner et al. 2012) averaged within each climate region (Duveneck et al. 2014a). The IPCC climate projections provide climate data to year 2100 (Intergovernmental Panel on Climate Change 2007). In order to simulate forest change to year 2150, we extrapolated climate data (temperature and precipitation) from 2100 to 2150 based on the variability within the initial 100 years of IPCC projections (Duveneck et al. 2014a, b). We extrapolated climate data in order to explore interactions (including those of long lived tree species) recognizing the increase in uncertainty. For temperature extrapolations, we included a linear regression component with variation based on the increasing trend in temperature from 2000 to 2100.

Disturbance regimes

To simulate fire, we used the Base Fire extension (He and Mladenoff 1999) to simulate fires on a five-year time step. We varied fire regimes spatially throughout each landscape based on historical fire regimes delineated in Minnesota (White and Host 2008) and Michigan (Cleland et al. 2004). We did not, however, modify the fire regime based on the changing future climate.

We used the Biomass Harvest extension to simulate forest management regimes (Gustafson et al. 2000; Syphard et al. 2011). Stands were selected for harvest based on user-defined criteria (e.g., when cohorts reach merchantable age). At each time-step, AGB was removed within stands based on user-defined prescriptions regulating patch size, percent biomass by species removed, and planting. Rotation periods were incorporated by defining the proportion of each prescription implemented within each management area (ownership group) and time-step (Gustafson et al. 2000).

We developed four separate management regimes in each landscape; these were designed to encapsulate a plausible envelope of future management actions as a full management space was not possible (Thompson et al. 2012). (1) We implemented a BAU regime based current management in Minnesota and Michigan (Potter-Witter 2005; D' Amato et al. 2009; Ravenscroft et al. 2010). This regime represents intensive even-aged management. We simulated a range of common silviculture prescriptions that varied from 0.1 to 7 % of the landscape every five-year timestep. Details of this regime are provided in Duveneck et al. (2014a). (2) We implemented an expanded reserve scenario where forest reserve areas were expanded along river corridors. This resulted in 18 % of each landscape in reserve areas. Within these reserves, disturbances were limited to natural disturbances of

infrequent wind and fire events. In this scenario, timber harvesting was limited to the non-reserve areas allowing long-lived tree species to mature with a less frequent disturbance regime. 3) We implemented a modified silviculture management regime where individual prescriptions were adjusted to include smaller patches and longer rotation periods. This scenario is based on the premise that the ecosystem service value of forest biomass left on site will increase in relation to the value of harvested biomass. Therefore, this scenario represents a less intensive disturbance regime compared to BAU. Generally, we reduced the rotation frequency of the even-aged management prescriptions by 45 %, increased northern hardwood patch cutting by 25 %, and reduced other prescriptions by 15 %. Details of the expanded reserve and modified silviculture regimes are available in Duveneck et al. (2014b). (4) We implemented a climate suitable planting (CSP) regime where species from outside the landscapes were planted within existing northern hardwood patch cutting prescriptions. With the exception of American chestnut (*Castanea dentata*), we choose species present directly south of each landscape. We simulated planting approximately 5 % of forested area per five-year timestep in each landscape. This regime was meant to increase the suite of species that may not be able to naturally migrate under climate change (Iverson et al. 2008) while accepting the tradeoff that these species may not be present in the initial conditions; details of the CSP regime are available in Duveneck and Scheller (2015).

Spatial analysis

We replicated each combination of climate future and management regime (a 'scenario') five times to assess the stochastic variation in AGB within scenarios as arises from disturbance events and dispersal. Individual disturbances vary spatially due to differences in soils, climate, and tree species. Due to the low stochastic variation in relation to the size of our landscapes, maximum variance of total AGB of each replicate at the end of the simulation was <2 % of the mean of replicates. Therefore, we randomly selected one replicate for the remaining analysis. For each landscape cell, we calculated initial species and functional diversity.

In order to address the hypotheses associated with diversity and resistance (Fig. 1), we assessed the relationship between initial mean alpha diversity and dissimilarity at simulation years 2050, 2100, and 2150 within each climate region. In addition, at simulation year 2100, we assessed the relationship between dissimilarity and mean alpha species and functional diversity within aggregated cells in each landscape. We aggregated raster layers from 2 hectares to 50, 100, and 200 hectares and within each aggregated cell, calculated mean species and functional diversity. Few differences emerged among the larger spatial resolutions (Duveneck 2014), therefore we presented only the 50 hectare results. We calculated the Shannon index (H′) as a measure of species diversity (Gotelli and Ellison 2004), and then exponentially transformed Shannon index ($e^{H'}$) to represent the equivalent number of species (Jost 2006).

We used the functional dispersion (FDis) measure of functional diversity in the FD functional diversity package in R (Laliberté and Legendre 2010; R Core Team 2013). FDis is a measure of the range of predefined functional traits that describe the functions of a community of species (Laliberté and Legendre 2010). FDis uses relative abundance thus is not sensitive to outliers. We selected functional traits used in previous work expected to have ecological importance (Paquette and Messier 2011; Duveneck and Scheller 2015). Specific species traits included: maximum height, growth rate, leaf size, longevity, foliar mass per area, foliar nitrogen content, wood density, decay resistance, vegetative reproduction, seed mass, pollination vector, mycorrhizal infection type, shade tolerance, drought tolerance, and water-logging tolerance. Species-specific trait parameters are available in previous work (Duveneck and Scheller 2015).

We calculated Bray–Curtis community dissimilarity at the cell level to assess community change over time using the vegan-community ecology package in R (Oksanen et al. 2012; R Core Team 2013). (Eq. 1)

$$B_{jk} = \left(1 - \frac{2w_{jk}}{T_j + T_k}\right) \qquad (1)$$

where B_{jk} Bray–Curtis's Index of Dissimilarity between time (j) and time (k), W_{jk} = Sum of minimum simulated abundance from time (j) and time (k), T_j = Sum of total simulated abundance at time (j), T_k = Sum of total simulated abundance at time (k)
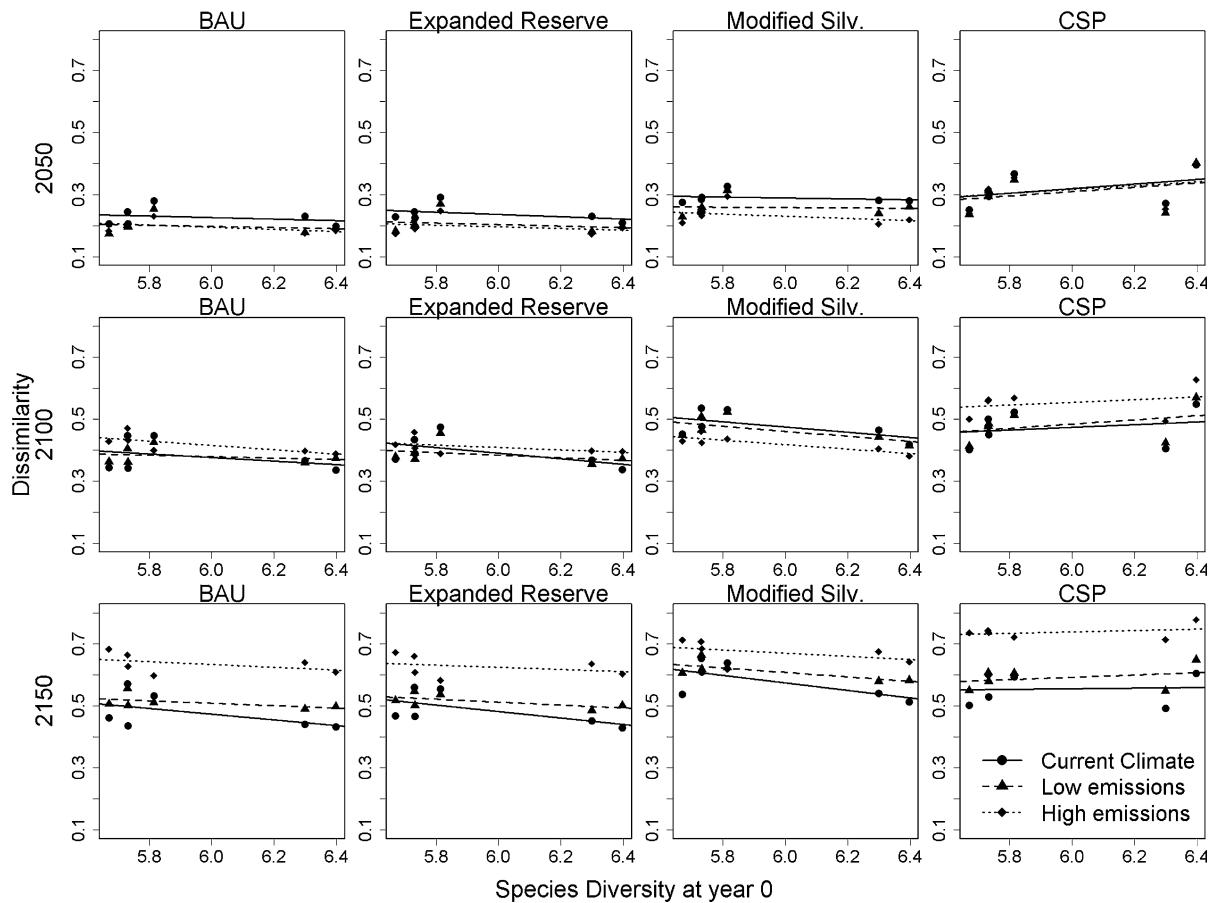
Fig. 4 The interacting effects of management, climate, and duration (simulation years 2050, 2100, and 2150) on dissimilarity and initial diversity across climate regions in the Minnesota landscape

The Bray–Curtis index has been used to measure dissimilarity between sites in space (e.g., Scheller and Mladenoff 2002; Moore et al. 2011; Thompson et al. 2013) and time (Rydgren et al. 2004; Thrush et al. 2008). Bray–Curtis values range between 0 and 1 with 1 being the most dissimilar. We used simulated species AGB within cells as a measure of abundance between time periods.

To assess resilience, we measured the simulated response following wildfire. We chose fire as an example disturbance that can result in large shifts in forest structure. We selected cells within simulated fire patches at years 2050, and 2100 from each landscape, climate future, and management regime with the raster package in R (Hijmans and Etten 2013; R Core Team 2013). We calculated B_{jk} and the change in total AGB within burned patches from the time-step prior to the

fire year to 50 successive simulation years. We plotted both change in total AGB and change in species composition as measured by B_{jk} for all time-steps prior to and following simulated fires (Fig. 2). This allows two measures of resilience plotted together for each landscape, climate, and management scenario combination. In order to normalize the axes, we calculated the proportional change in AGB and B_{jk} immediately following disturbance. Using the proportional change in recovery from both AGB, and B_{jk}, we calculated an index of resilience (r_{jk}) in a novel approach based on the minimum multidimensional distance to recovery within a time period. r_{jk} ranges from 1 to 0 with 1 being the most resilient, and 0 being the least resilient.

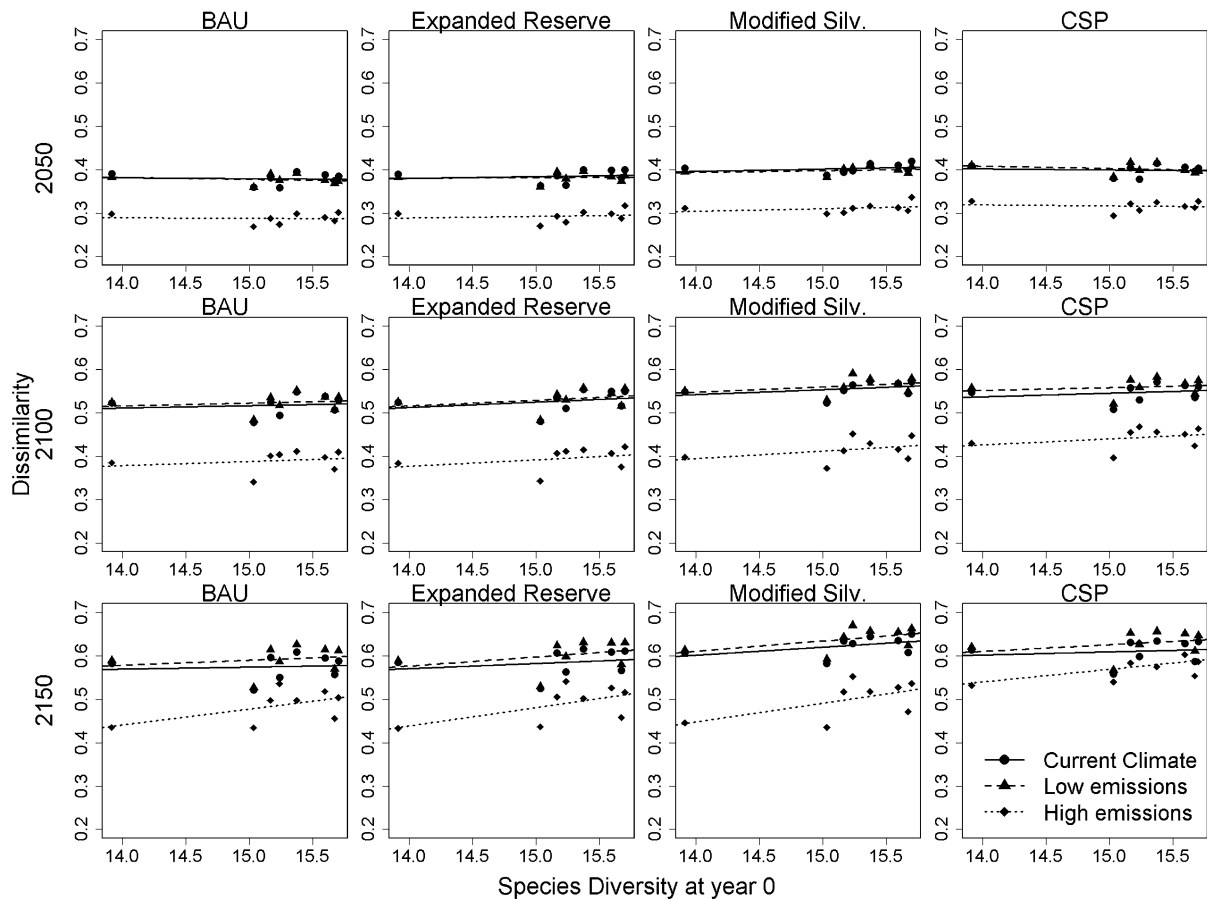$$r_{jk} = \frac{\sqrt{2} - d_{jk}}{\sqrt{2}} \tag{2}$$

Fig. 5 The interacting effects of management, climate, and duration (simulation years 2050, 2100, and 2150) on dissimilarity and initial diversity across climate regions in the Michigan landscape

where, r_{jk} = Index of resilience between time (j) and time (k) assuming time (j) is at time of disturbance, d_{jk} = Minimum multi-dimensional Euclidean distance between time (j) and (k), $\sqrt{2}$ = Maximum possible d_{jk}.

Results

Effect of diversity on dissimilarity

Across climate regions, (i.e., regions of relatively consistent climate (Fig. 3)), resistance from initial conditions decreased (i.e., dissimilarity increased) with time. In each scenario, dissimilarity between simulation years 2000 and 2050 was less than between 2000 and 2100, and 2000 and 2150 (Figs. 4, 5). The effect of management on dissimilarity was

minimal. In the Minnesota landscape, the CSP regime and the high emissions climate future at simulation years 2100 and 2150 resulted in the largest dissimilarity compared to the BAU, modified silviculture, and expanded reserves regimes (Fig. 4). Generally, however, variation in management did not generate differences in dissimilarity.

The effect of simulated diversity on resistance was more pronounced in the Minnesota landscape (Figs. 4, 6) as compared to the Michigan landscape (Figs. 5, 6) however the variability in species diversity across climate regions was low in both landscapes. In the Minnesota landscape, lower simulated functional and species diversity resulted in less resistance to change (greater dissimilarity following 100 years of BAU management) and a stronger negative relationship between diversity and dissimilarity. In contrast, simulations in the Michigan landscape resulted in larger
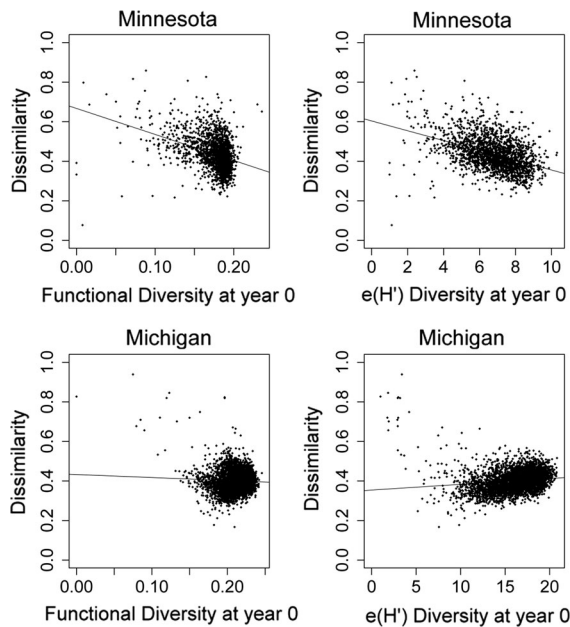
Fig. 6 Species and functional diversity effect on dissimilarity at year 2100 under BAU management and high emissions climate. Dissimilarity represents resistance to change between simulation years 2000 and 2100. Each point represents a 50 ha aggregated cell. *Lines* represent significant (p < 0.05) linear fit.

species diversity and to some extent, functional diversity. With the exception of lower diversity sites (Fig. 6), simulations in Michigan did not result in a diversity-dissimilarity effect.

Effect of climate change on resilience of forests following fires

The simulated response of forests to fire disturbances resulted in progressively less resilient forests under the high emissions climate future compared to the low emissions and current climate futures. Current and low emissions climate futures resulted in greater resilience to simulated fires compared to high emissions climate future at year 2050 and 2100 (Fig. 7, 8). While none of the scenarios resulted in recovery to an identical pre-fire species and biomass composition ($r_{jk} = 1$), the current climate future resulted in the fastest recovery to the inflection point before additional successional departure. Furthermore, we did not expect recovery to an identical species and biomass composition.

Compared to simulated fires in 2050 (Fig. 7), the climate change effect following fires in year 2100 was

more pronounced (Fig. 8). Successional changes resulted in larger pre-fire AGB in 2100 than 2050. Under current and low emission climate futures, simulations resulted in complete or near complete AGB recovery at 2150. Under the high emissions climate future, simulations following fires in 2100 resulted in less resilience indicated by less AGB and less species composition recovery (Fig. 8).

Although the Minnesota and Michigan landscapes differed in latitude, management, and diversity, the variation between landscapes in response to fires was minimal compared to the variation due to climate. Compared to Minnesota, the more diverse and larger total AGB Michigan landscape resulted in less dissimilarity and more AGB recovery in both year 2050 and year 2100 fires (Fig. 7, 8).

Management differences resulted in small variation in resilience to simulated fires (Fig. 7, 8). Following fires in the high emission climate futures in 2100, for example, the CSP management regime resulted in the greatest resilience in Michigan but not in Minnesota (Fig. 8) (Table 1). High resilience resulting from CSP management was likely due to more climate suitable species recovering more biomass than the current species mix. From simulation years 2000 to 2050, CSP species were planted into the landscapes and established. As resilience of species composition was measured from immediately pre-disturbance conditions, the initial species composition of fires later in the simulation would have included CSP species. For this reason, resilience of both AGB and dissimilarity had the potential to be greater in the CSP management regime.

Table 1 Management effect on resilience after 50 years following simulated fires at year 2100 under the high emissions climate future

Management	Minnesota		Michigan	
	N	r_{50}	N	r_{50}
Business as usual	148	0.63	187	0.68
Expanded reserved	141	0.66	191	0.68
Modified silviculture	156	0.71	171	0.67
Climate suitable planting	142	0.69	223	0.741

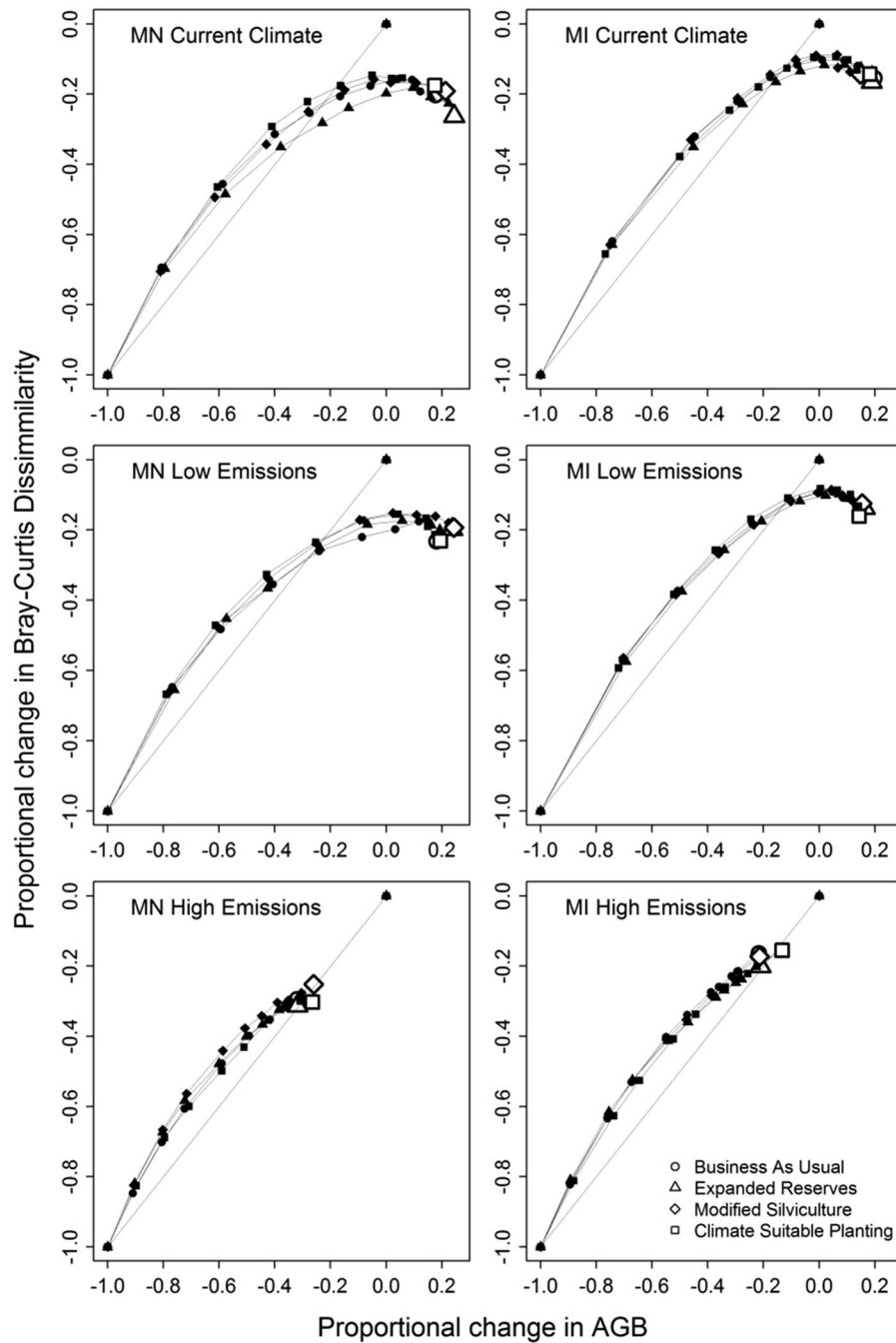*N* number of fires within each scenario, r_{50} average resilience index

Fig. 7 Resilience of proportional change in forest AGB and species dissimilarity to the effect of simulated fires and climate change at year 2050 under alternative management regimes. Pre-fire conditions are represented by coordinates (0,0) in graph. Successive time steps following fires at coordinates (−1,−1) are represented by *line segments* between *small closed symbols*. Conditions after 50 years are represented by *larger open symbols*
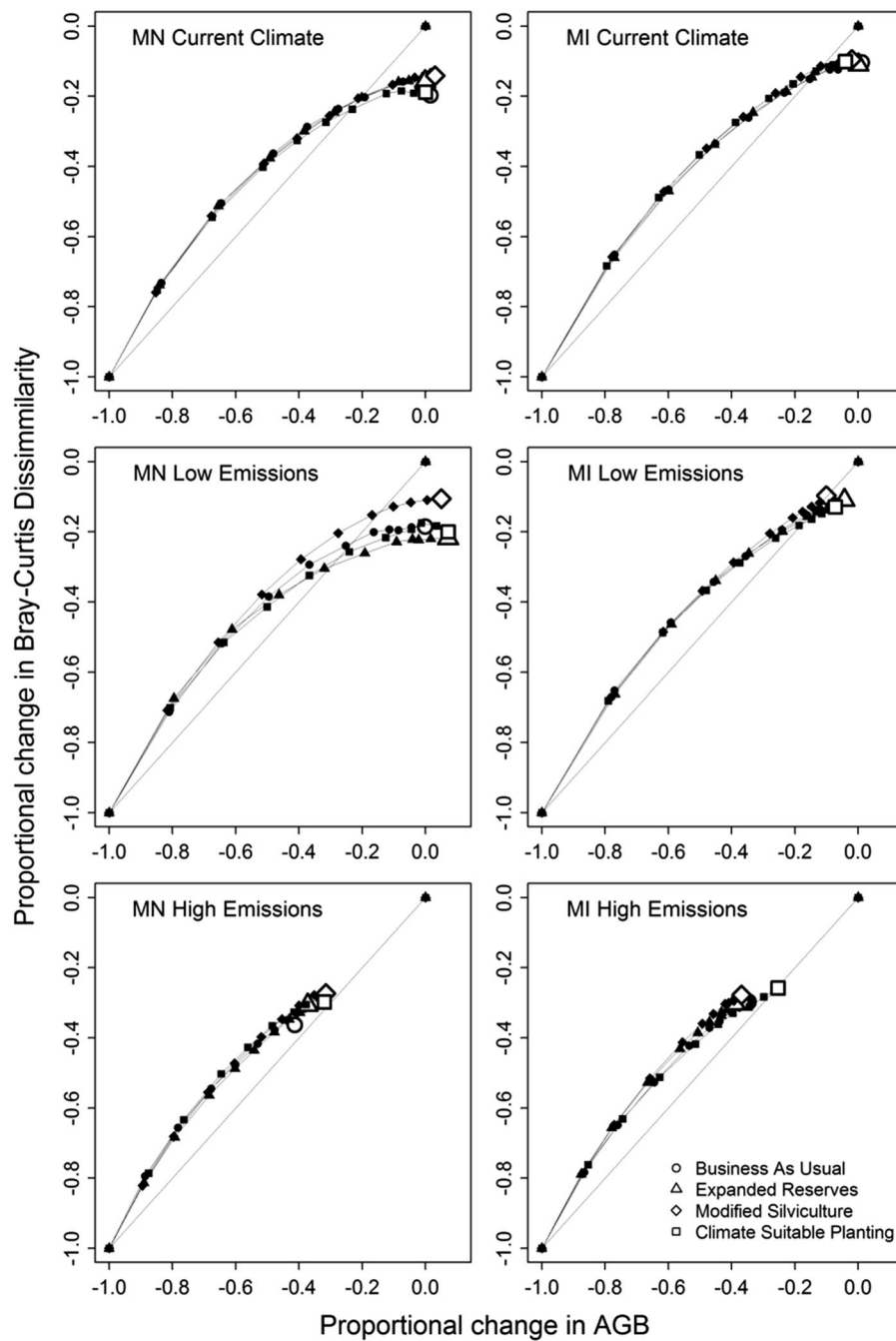
Fig. 8 Resilience of proportional change in forest AGB and species dissimilarity to the effect of simulated fires and climate change at year 2100 under alternative management regimes. Full description of graph is provided in Fig. 7 caption

Discussion

Effect of diversity on resistance

We hypothesized that diversity would increase future resistance as measured by dissimilarity. Our results were consistent with this hypothesis under low diversity although (and despite the fact that) our simulated landscapes had a relatively small range of variation in diversity. Nevertheless, resistance may not be affected by diversity above a threshold of relatively high diversity (e.g., the Michigan landscape), however below this threshold, resistance was positively correlated with diversity (i.e., *dissimilarity* was negatively correlated with diversity in the Minnesota landscape). This is consistent with conceptual frameworks discussed by Peterson et al. (1998) who described how functionally overlapping species will result in complementary effects. Above some threshold, however, higher species diversity may result in duplication within functional space. Thereby, the diversity-stability (i.e., diversity -resistance) relationship is positive at low diversity but reaches an asymptote at higher diversity as functional space is expended (Peterson et al. 1998; Potter and Woodall 2014).

Effect of climate change on resistance

We hypothesized that climate change would reduce the resistance (measured as community composition) over time. Our results were inconsistent with this hypothesis. Our Minnesota simulations suggest that the high emissions climate future will reduce the resistance of current communities to change compared to current and low emissions climate (Fig. 4). In the Michigan landscape, simulations suggest that the high emissions climate future will increase resistance of current communities compared to current and low emissions climate (Fig. 5). Large shifts in forest type and species composition are expected in the Michigan landscape under current climate and BAU management (Duveneck et al. 2014a). This suggests that climate change may slow the successional trajectory that would otherwise shift the species composition under current climate. Later successional species, for example, may be less likely to replace current species assemblages under climate change (Fisichelli et al. 2014).

The Minnesota landscape is closer to the boreal transition zone (Curtis 1959) where more dramatic changes are expected under climate change (Duveneck et al. 2014a). Boreal species (e.g., balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*)) are expected to decline in both landscapes under climate change but are presently more abundant in Minnesota (Duveneck et al. 2014a).

Effect of management on resistance

We hypothesized that management for climate change could increase resistance. Our results could not confirm this hypothesis. Specifically, our results showed limited ability to increase resistance as measured by dissimilarity (Figs. 4, 5). However, previous work in the region has indicated positive alternative management effects. Specifically, Duveneck et al. (2014b) found increased simulated diversity within expanded reserves under climate change in these landscapes. Compared to BAU management, Duveneck et al. (2014b) and Duveneck and Scheller (2015) found greater simulated AGB under modified silviculture, and CSP regimes with climate change. Nevertheless, the previous work did not measure resistance explicitly with dissimilarity. We expect that at some sites, strategies to increase resistance can be effective. However at a landscape scale, our scenarios were not affective at increasing resistance as measured by dissimilarity.

Effect of climate change on resilience

We hypothesized that following acute disturbance, climate change will reduce resilience. Our results were consistent with this hypothesis. Under the high emission climate future, simulated fires in year 2100 resulted in less resilience as measured by structure (AGB) and composition compared to the current and low emissions climate futures. The resilience of boreal-temperate transition forests to acute disturbance (e.g., fire) will be altered by climate change (Anderson-Teixeira et al. 2013) likely resulting in a decline (Dale et al. 2001; Moritz and Agudo 2013).

Systems with low frequency of disturbances may be the most poorly poised to naturally adapt (Puettmann

2011). Northern Great Lake forests may be more vulnerable to regime shifts than ecosystems with more frequent natural disturbance regimes. For example, Rocky Mountain forests may be more resilient to frequent natural disturbance regimes, including fire, drought, and insect outbreaks (Minckley et al. 2012; Yang et al. 2015). Although Minnesota includes a highser frequency of harvest disturbances (Duveneck et al. 2014a), both landscapes in our study recovered similarly to simulated fires (Fig. 7, 8). Although a longer time frame may be required to assess the effect of our disturbance regimes, the variation in disturbance frequency between our two landscapes suggests that climate effects on resilience outweigh disturbance effects.

Effect of management on resilience

We hypothesized that management could increase resilience under climate change. Our results were inconsistent with this hypothesis. Despite attempts to design alternative management regimes to make forests more resilient and resistant, our simulations suggest that the management regimes tested will have limited ability to increase resilience of species composition in the face of climate change. Compared to BAU management, some of the alternative management regimes did result in greater resilience. These management differences were minor compared to the effect of climate (Figs. 7, 8).

Although there is strong support to adapt existing management to climate change (e.g., Millar et al. 2007), others emphasize the risk to managing for resilience may inadvertently increase the vulnerability of a system (Côté and Darling 2010). Ultimately, management under a high emissions climate future will likely be outweighed by the effects of climate change. This is consistent with other modeling research that found a limited effect to resilience with management alternatives (including CSP) under a high emission climate future (Buma and Wessman 2013). Forest management under climate change may need to be far more innovative and aggressive than conventional management regimes. For example, in our CSP regime, we selected species adjacent to current landscapes. Although these species are currently present in warmer climates to the south of the landscapes, the high emission climate future may not have been optimized for these species (Duveneck and

Scheller in press; Iverson et al. 2008). Planting species found *farther* south may be more effective at increasing resilience of forests under climate change. Determining appropriate CSP species for desired functional traits is possible through climate envelope modeling (Iverson et al. 2008). The challenge will be to choose which emission future and time horizon to match climate suitability given the uncertainty and limits to social change (Adger et al. 2009).

Another management strategy may be to shorten rotation ages to make sites more adaptable to climate change. As trees have long generation times, genetic adaptation to climate is expected to be slow (St Clair and Howe 2007). In sites that are already degraded, shortening generation times by decreasing rotation ages will increase the number of generations over the coming century and will increase the likelihood for genetic adaptation. In addition, shortening rotation ages will create more opportunities to adapt management options (Puettmann 2011). Advance regeneration (i.e., planting climate adapted species below a canopy prior to harvest) can also result in more frequent turnover (Kuehne and Puettmann 2008) and provide protection for seedlings that are vulnerable to environmental conditions (Puettmann 2011; De Frenne et al. 2013). Experimental treatments should not be limited to degraded landscapes, however these sites may provide the most socially accepted sites to experiment with innovative approaches (Adger et al. 2009).

Uncertainty

There is a large amount of uncertainty with simulations of climate change on forests, and northern forests specifically (Xu et al. 2009). We present a high and low emission climate future to represent a range of uncertainty associated with climate change. Our current trajectory in carbon emissions however, has been observed at or above our high emission future (Jennings 2012). The uncertainty in future emissions may represent the largest amount of uncertainty in models of future forests. In addition to climate uncertainty, there is a large amount of uncertainty in future management. Our BAU management regimes are best guess estimates of what is currently practiced. We recognize that future forest management will be largely driven by an uncertain market demand for ecosystem services such as timber, housing development, and agriculture.

The challenge to any simulation modeling research is to balance realistic assumptions against pure theory (i.e., that might require completely artificial landscapes and millennia time scales). Although we tested reasonable parameters, we did not attempt to include every ecological process effecting northern forests. Therefore, our simulations are not predictions, rather plausible futures where we can explore the effects of alternative assumptions. Although we did not assess variation in local environmental conditions response to resilience, we recognize that variation in resilience will be effected by local conditions such as high soil moisture (Speed et al. 2010). In addition, we did not include the effect of carbon dioxide fertilization on tree growth. We recognize that carbon dioxide fertilization will affect growth however we don't know where a fertilization effect will be limited by other factors such as nitrogen (Luo et al. 2004; Reich and Hobbie 2012). Some of the factors that we did not include in our analysis along with additional alternative management strategies (e.g., planting more southern species) represent future opportunities for research. Finally, we recognize that our methods are complex because of the use of multiple models and parameters; such complexity adds additional uncertainty and potential error.

Conclusions

Given the large range of uncertainty in climate change and other factors, there will not be one clear forest management strategy effective for all circumstances. Rather, a broad range of tools must be explored (Millar et al. 2007). Innovative strategies must consider both resistance and resilience. Resistance strategies may provide remnant ecosystem services and functions such as preserving spruce-fir species in forest reserves (Duveneck et al. 2014b). Resilience strategies may increase the ability to recover some ecological identity following disturbances. Disturbances such as timber harvest, fire, wind, and insect outbreaks will immediately affect forests. Not only will climate change alter the frequency and direct effects of these disturbances, our results suggest that when disturbances occur, climate change may result in larger long-term effects. Increasing resilience further may require changing the measurement

of resilience. Rather than measure dissimilarity from current species composition to a future condition, a next step may be to measure dissimilarity from a future condition to a pre-defined climate suitable species composition. Nevertheless, our measure of resilience using multiple dimensions was valuable and this approach can be applied to other systems where resilience of structure and composition are both important.

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