



# Forest resilience, climate change, and opportunities for adaptation: A specific case of a general problem



B. Buma<sup>\*</sup>, C.A. Wessman

University of Colorado, Ecology and Evolutionary Biology & CIRES, 216 UCB, Boulder, CO 80309, United States

## ARTICLE INFO

### Article history:

Received 27 September 2012

Received in revised form 20 June 2013

Accepted 21 June 2013

### Keywords:

Resilience

Climate change

Adaptive management

Forest disturbance recovery

Carbon sequestration

Modeling

## ABSTRACT

Ecosystems and ecosystem services are subjected to both typical disturbances (e.g., fire) and shifting climatic baselines resulting from anthropogenic drivers. Recovery from these perturbations is of prime interest to researchers and land managers. We explore how differing regeneration of the coniferous forest to specific disturbances and a shifting climate are mediated through managerial responses, in terms of both species composition and an important ecosystem service, carbon sequestration in the southern Rocky Mountains, Colorado, USA. 112 sites across a variety of disturbance histories were surveyed for post-fire regeneration; carbon stock growth was then simulated in the US Forest Service Forest Vegetation Simulator under a variety of climate change scenarios for 100 years. Simultaneously, we simulated three managerial responses to the disturbance: no action, planting of local species (resilience-oriented management), and planting of the most climatically suitable species (adaptation-oriented management). These managerial responses simulate varying levels of intervention which attempt to maintain forest properties and associated carbon stocks. Carbon stocks, initially, were more resilient than the coniferous forest system; areas with little coniferous regeneration recovered carbon at a similar pace due to an influx of deciduous seedlings. However, future climate exerts a strong influence on carbon stocks. Both the no-action scenario and the resilience-oriented management scenario transitioned to non-forest by the end of the simulation period, due to climatic changes. Active, adaptation-oriented management, which included establishment of non-local species, maintained forest structure and carbon stocks under most future climate projections, albeit at lower densities. So while this preserves the presence of a forest, it does not preserve the presence of a specific forest. However, for ecosystem services associated with the mere existence of forest cover (e.g., carbon stocks and general forest habitat), this may be sufficient. In a sense, disturbances are opportunities for more climatically-adapted species/communities to establish, although the complexities of assisted migration and novel ecosystems remain.

© 2013 Elsevier B.V. All rights reserved.

## 1. Introduction

Ecosystems, and the services they provide, will experience two types of perturbations in the future: discrete disturbances such as fire and the slower change imposed by shifting climatic regimes. Disturbances are inevitable in the majority of forests around the world. Continuation of a forest in any given location through multiple cycles of disturbances is contingent upon ecosystem resilience: the recovery of the system to a similar state (Holling, 1973; Gunderson, 2000). This may be rapid, depending on initial post-disturbance establishment (Brown and Johnstone, 2012) or protracted through early and late successional stages. In the future, however, recovery will take place in an era of changing temperatures, precipitation, and disturbance regimes, and so any long-term projection of ecosystem recovery must take those factors into account.

Disturbances are expected to increase across a wide range of forest ecosystems (e.g., Dale et al., 2001; Flannigan et al., 2009) and may trigger shifts in species ranges (e.g., Johnstone and Chapin, 2003) or eliminate forests all together (Brown and Johnstone, 2012). Interactions between multiple disturbances may cause novel disturbance characteristics (Buma and Wessman, 2011), differential recovery (D'Amato et al., 2011; Brown and Johnstone, 2012), and/or regime shifts (Paine et al., 1998). Given the potential for disturbances to cause such large changes in ecosystem character, and the likely increasing rates of disturbance, it is important to investigate their impact on ecosystems and their properties going forward.

Carbon storage in ecosystems is related to local climate (Davidson and Janssens, 2006), topography, species composition and structure (Wessman et al., 2004), soil characteristics (Lal, 2005) and disturbance history (Brown and Johnstone, 2011), among other factors. Forest growth sequesters a large amount of carbon in biomass and soils (1086 Pg globally, Lal, 2005). They do not store that carbon in perpetuity, however; disturbances and mortality return a portion of that carbon to the atmosphere through either combustion (direct

<sup>\*</sup> Corresponding author. Tel.: +1 360 389 6350; fax: +1 303 492 1149.

E-mail address: [brian.buma@colorado.edu](mailto:brian.buma@colorado.edu) (B. Buma).

carbon emissions, usually as CO<sub>2</sub>) or through the resultant decomposition of the killed biomass. Yet if the forest recovers to a similar structure and density, the total carbon exchange will be neutral over the time period of recovery (Kashian et al., 2006). This recovery may be fairly rapid; regenerating vegetation may quickly take up enough carbon to offset decomposition. Investigation in Canadian lodgepole pine forests with heavy insect infestations found that even high mortality stands were a growing season carbon sink within a few years (Brown et al., 2010). This was attributed to the understory vegetation rapidly fixing carbon in response to the newly available resources freed up by the death of the overstory trees (Bowler et al., 2012). Given that the system recovers to a similar state, it is likely that carbon stocks will recover as well. Changing ecosystem states, however, may have large impacts on total carbon stocks due to fundamental changes in plant structure, density, and soil inputs. For example, woody plant encroachment may have a strong effect on the carbon balance of the landscape, mainly through the increase in plant biomass (Wessman et al., 2004), although the magnitude of change depends upon moisture and other factors. In other cases, regimes may change without a concurrent shift in carbon stocks.

Using a forest growth simulator supported by extensive field measurements in disturbed forest landscapes, carbon stock recovery was simulated in the context of a changing climate and various regeneration/management scenarios. The pre-disturbance ecosystem was mature spruce-fir forest; the post-disturbance recovery is highly heterogeneous – in some areas, dominated by coniferous regeneration, in others, deciduous or graminoid, as a result of the different disturbance histories in the area (Buma and Wessman, 2011). Here the resilience of the coniferous forest is defined as the relative amount of conifer regeneration one decade post-fire. This heterogeneity is followed through the coming century and total ecosystem carbon (non-mineral soil) was simulated to determine the relative influence of disturbance history/regeneration, management, and climate change on forest carbon stocks. We ask the following questions:

1. How does differing post-fire regeneration (both in species and amount) influence carbon stock growth under various climate scenarios?
2. How do differing management scenarios affect carbon stock growth under various climate scenarios?

## 2. Methods

### 2.1. Site and plot design

A combination of disturbances (blowdown, logging, fire) in the Routt National Forest in north central Colorado, USA, resulted in a spectrum of post-fire recovery rates and trajectories in a subalpine spruce-fir forest (Buma and Wessman 2011, 2012). The forest (approx. 2700–3300 m elevation) is comprised of spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and quaking aspen (*Populus tremuloides*). Precipitation averages approximately 1000 mm a year, mostly as snow (NRCS 2010). The blowdown (October 1997, approx. 10,000 ha, Baker et al., 2002) left a mosaic of severities, from zero to near 100% blowdown. Salvage logging, conducted post-blowdown (1998–2001), took place on approximately 900 ha. In the summer of 2002, the Mt. Zirkel fire complex burned approximately 12,500 ha of undisturbed, blown-down, and salvage logged forest. The blowdown altered fire severity (Kulakowski and Veblen, 2007), as well as postfire recovery (Buma and Wessman, 2012).

112 15 × 15 m plots were censused for post-fire regeneration of woody plant species and woody debris. All plots were located in areas identified as closed-canopy spruce-fir forests prior to the

disturbances (US Forest Service RIS (Resource Information System) data and personal observation, unpublished). These plots were grouped according to their disturbance history (Fig. 1): no/low blowdown and fire (0–20 downed trees/ha;  $n = 27$ ), medium blowdown/fire (20–55 downed trees/ha;  $n = 41$ ), areas of high blowdown/fire (55 + downed trees/ha;  $n = 33$ ), and logged blowdown/fire (55 + downed trees/ha and prior logging;  $n = 11$ ). Standing dead trees (snags) were measured on a subset of plots (no/low = 22 plots; medium = 8 plots; high = 10 plots; logged = 8 plots). This grouping scheme corresponds with decreasing conifer resilience (as defined by seedling densities, Fig. 1 middle); areas with little to no conifer regeneration were considered non-resilient, for example.

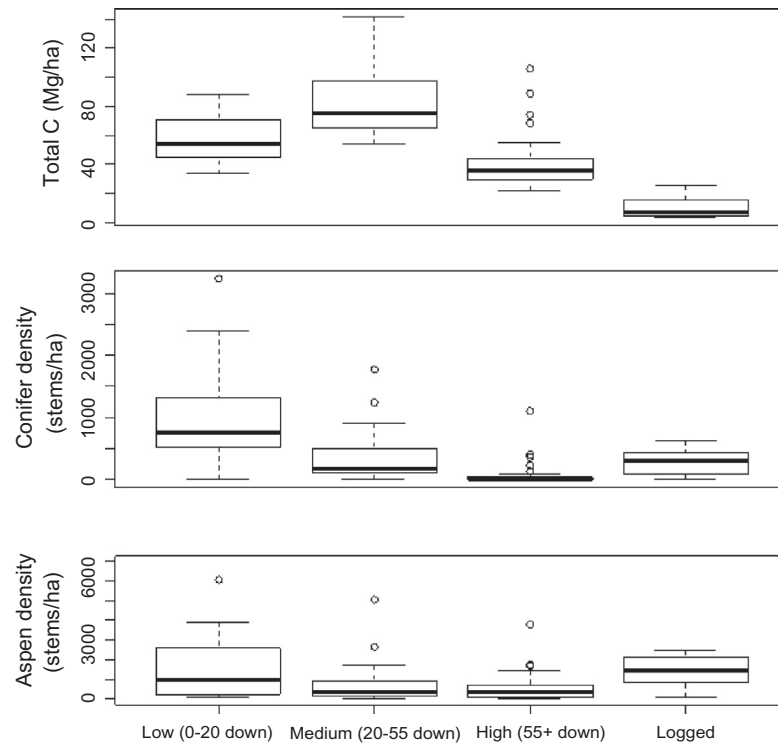
At each plot, seedlings were counted and measured for height. Coarse woody debris (CWD) totals were estimated via methods from Brown (1974). All standing dead trees were measured for their diameter at breast height (DBH) and height. To compare recovering carbon stocks to undisturbed forests and estimate belowground carbon stocks, 10 additional plots were established within undisturbed spruce-fir forests. The same measurements were conducted, with species, DBH and height recorded for all trees.

### 2.2. FVS

Carbon dynamics were simulated in the USDA Forest Vegetation Simulator (FVS) using the carbon sub-model contained in the Fires and Fuels extension (FVS-FFE, Rebain, 2010) and the climate extension module (Climate-FVS, Crookston et al., 2010), for 100 years (2010–2109). FVS is a well-known forest simulator often used for carbon and disturbance simulation (e.g., Hurteau and North, 2009) and is parameterized for different geographical regions; the Central Rockies variant was used here. Plant growth (calculated decadal) occurs based on species-specific relationships between local climate/topography and the local community (e.g., crown closure and tree density), and was calibrated according to DBH (diameter at breast height) and height allometric relationships (Jenkins et al., 2003). Mortality occurs via two processes, background mortality (species and size specific probabilities) and density dependent mortality, which is species specific and determined based on stand density and species shade tolerance. Regeneration is user specified, and so was implemented according to the management strategies described below. Each plot was grown independently. Elevation was obtained from the national elevation dataset (USGS 2009), with a resolution of 30 m. Aspect and slope were calculated from this dataset using ArcMap (ESRI, 2010).

Live seedlings were input into the simulator and their total C was calculated according to Jenkins et al. (2003). Field estimated CWD was used to initialize downed debris loads; FVS-FFE allometrics were used to calculate C in initial snags (based on field survey). Because species could not be determined for the burned snags, all snags were considered Engelmann spruce, the dominant species in unburned stands. Forest floor (e.g., duff) and shrub/herb layers were calculated using Smith and Heath (2002) via FVS-FFE and based on canopy cover percent, age, and dominant tree species.

The initial amount of dead coarse roots could not be determined for each plot because it was impossible to determine pre-fire tree sizes and densities with any certainty. In addition, logging removed the majority of the tree boles, and some stumps, so their coarse roots would be unaccounted for if stumps or snags were used to initialize belowground dead coarse roots. Instead, the mean belowground coarse root carbon totals (live and dead) from the undisturbed plots was used to initialize all the burned plots. This makes the assumption that the burned plots were compositionally similar to the control plots, and is a statistically conservative decision, reducing the variability between the treatments. The



**Fig. 1.** Groupings for the simulations, and their corresponding initial carbon totals (mineral soil excluded, top), conifer seedling densities (middle), and aspen seedling densities (bottom). Differences are in terms of pre-fire blowdown severity (downed trees/ha) and the presence or absence of salvage logging.

initial root carbon value was decayed for 8 years to match the initial time since fire, and the resulting value was used as the initial dead coarse root C for all disturbed plots. Root decay was set at the FVS Central Rockies variant default of 4.25%/year. Movement between pools and decay (e.g., standing dead trees to CWD) is calculated according to species specific rates found in [Rebain \(2010\)](#) and references therein. Mineral soil dynamics are not simulated in FVS. Carbon estimates are calculated every year for the simulation period and are the sum of living tree biomass (above and belowground), dead trees (standing and fallen), dead roots, the herbaceous layer and the organic soil.

### 2.3. Regeneration/management scenarios

Estimating future establishment is difficult, and so this study bracketed potential establishment by looking at the endpoints – no (further) future establishment, and two scenarios for future establishment – heavy establishment of local species (resilience-oriented) and heavy establishment of climatically suitable tree species, local or not (adaptation-oriented). These scenarios parallel the actions proposed by [Millar et al. \(2007\)](#) for forest management responses to climate change. The *no action* scenario explores the effect of differing resilience on long-term carbon stocks, without human intervention or further establishment. The plots are simulated using only seedling densities observed in the field.

The *resilience* scenario describes a high-conifer resilience situation, bolstering current seedling levels by establishing Engelmann spruce (990 trees/ha (400 trees/acre, standard planting density, USFS personal communication); 0.3 m average height) whenever the tree densities fell below 40% of optimal (full stocking, defined via FVS defaults, [Rebain, 2010](#)). Engelmann spruce can survive planting on the open, bare mineral soil found in the plots. The no action and resilience scenarios can also be considered as bracketing potential natural recovery, from no further establishment to prolific recovery of the local forest.

The *adaptation* scenario allowed establishment of any central Rockies tree species. The species in the adaptation scenario were chosen based on what would survive the best based on climatic conditions at the time (full listing of the species is in [Appendix A](#)). This option simulates management oriented towards maintenance of a *forest*, rather than maintenance of a *specific forest*. This should provide better continuity in forest-specific (as opposed to species-specific) ecosystem services, like snow interception and carbon stocks. The four most adapted species, as determined by the Climate-FVS model (Section 2.4), are established in each plot in the same fashion as spruce in the resilience scenario.

### 2.4. Growth and climate

Climate-FVS modifies growth in the context of three general circulation models (GCMs) and four emission scenarios, for a total of seven GCM/scenario combinations which cover a range of severities of projected climate changes ([Table 1](#)). First, species-specific climate suitability profiles were created from 35 climate variables such as mean annual temperature and frost free period length. Climate variables to build these profiles were calculated based on splined 1961–1990 climate normals and presence/absence data largely from USFS plots ( $n = 45,000$ ); each species does not necessarily use all 35 variables in determining its climatic suitability profile. Full details are available in [Crookston et al. \(2010\)](#) and based on methodology from [Rehfeldt et al. \(2009\)](#); climate/suitability maps can be found at <http://forest.moscowfl.wsu.edu/climate/> (retrieved August 2012). Climate-FVS then incorporates the simulated change in those climate variables derived from the GCMs and underlying climate (from 2010 to 2109) to alter tree growth, mortality, and site carrying capacity, with deviations from “suitable climate” for a given species resulting in altered growth and/or mortality rates ([Crookston et al., 2010](#)).

Each plot was run from 2010 to 2109 under each climate scenario. Because FVS is usually run as deterministic simulator,

**Table 1**  
GCM and emission scenarios used in the simulations.

Abbreviation	Group	SRES scenario	Description	Name
CGCM3	Canadian Center for Climate Modeling and Analysis	A2	Heterogeneous world, rapidly increasing population, production oriented	CGCM3 A2
CGCM3		A1B	Homogenizing world, rapid growth, balanced energy sources	CGCM3 A1B
CGCM3		B2	Heterogeneous world, slowly increasing population, more environmentally friendly	CGCM3 B2
GFDL A2	Geophysical Fluid Dynamics Laboratory	A2	Heterogeneous world, rapidly increasing population, production oriented	GFDL A2
GFDL B1		B1	Rapid growth, global problem solving, service and information economy emphasis	GFDL B1
HAD A2	Hadley Center for Climate Prediction and Research	A2	Heterogeneous world, rapidly increasing population, production oriented	HAD A2
HAD B2		B2	Heterogeneous world, slowly increasing population, more environmentally friendly	HAD B2

estimating uncertainty requires an extra step. To generate means and confidence distributions which better describe the variability in sampling, each group was bootstrapped 1000 times: At each time step, 1000 random subsamples ( $n$  = group size) with replacement was selected from the group, and the mean and 5/95% quantiles were calculated from that 1000 sample population.

Carbon budgets are sensitive to the model used (Melson et al., 2011), however the main purpose of this study is comparison between resilience levels and management choices, rather than absolute prediction, and the results should be viewed as such. For the most severe climate change scenario (“severe” in terms of its effect on the species present in the plots), GFDL A2, the total number of live trees/ha was followed to explore the consequences on forest persistence in addition to total C stocks.

### 3. Results

#### 3.1. Initial differences

Each group was significantly different in terms of initial non-soil C as a result of their disturbance history (Table 2). The groups also had different levels of conifer establishment, according to their disturbance history (Fig. 1, middle), with all pairwise comparisons significantly different except the medium and logged groups (Wilcoxon rank sum test,  $p < 0.05$ ). Aspen establishment was abundant in all groups and highly variable (Fig. 1, bottom; and Table 2).

#### 3.2. Near term (2010–2060)

Carbon stocks began to recover after a period of negative carbon balance (yearly loss) due to decomposition (Fig. 2) and the source-to-sink conversion predicted by Kashian et al. (2006) was produced. Despite the fact that conifer regeneration essentially failed as a result of the compound disturbance interaction in the high interaction group (averaging 88 seedlings/ha), aspen established prolifically. The logged site, which started with substantially lower C than the other groups as a result of CWD/snag removal, grew equal to the other groups within approximately 40 years (Fig. 2); logged plots also saw the highest aspen seedling densities, at 2570 seedlings/ha on average (Table 2). In the end, the differential conifer regeneration observed had little effect on C stocks.

#### 3.3. Long term (2060–2109)

In terms of management strategies, there was no long-term difference between no-action and resilience-oriented management. The adaptation oriented approach diverged from the other strategies around 2060, and large differences appear by the end for some climate scenarios (Table 3). Low emission projections (CGCM3 B1

**Table 2**

Initial values for the groupings presented in Fig. 1; mean and standard deviation (in parentheses). Significance groupings denoted by superscripts (pairwise Wilcoxon rank sum test, Holm correction). Groups were significantly different in terms of initial carbon and conifers (except for the medium and logged groups); aspen was more variable.

Group	Non-soil carbon (Mg/ha)	Conifer (seedlings/ha)	Aspen (seedlings/ha)
Low	68.6 (16.9) <sup>1</sup>	1052 (875) <sup>1</sup>	1484 (1702) <sup>1,2</sup>
Medium	94.7 (23.4) <sup>2</sup>	336 (390) <sup>2</sup>	709 (928) <sup>1,2</sup>
High	52.7 (18.6) <sup>3</sup>	88 (207) <sup>3</sup>	795 (1451) <sup>1</sup>
Logged	24.6 (8.3) <sup>4</sup>	283 (209) <sup>2</sup>	2570 (4226) <sup>2</sup>

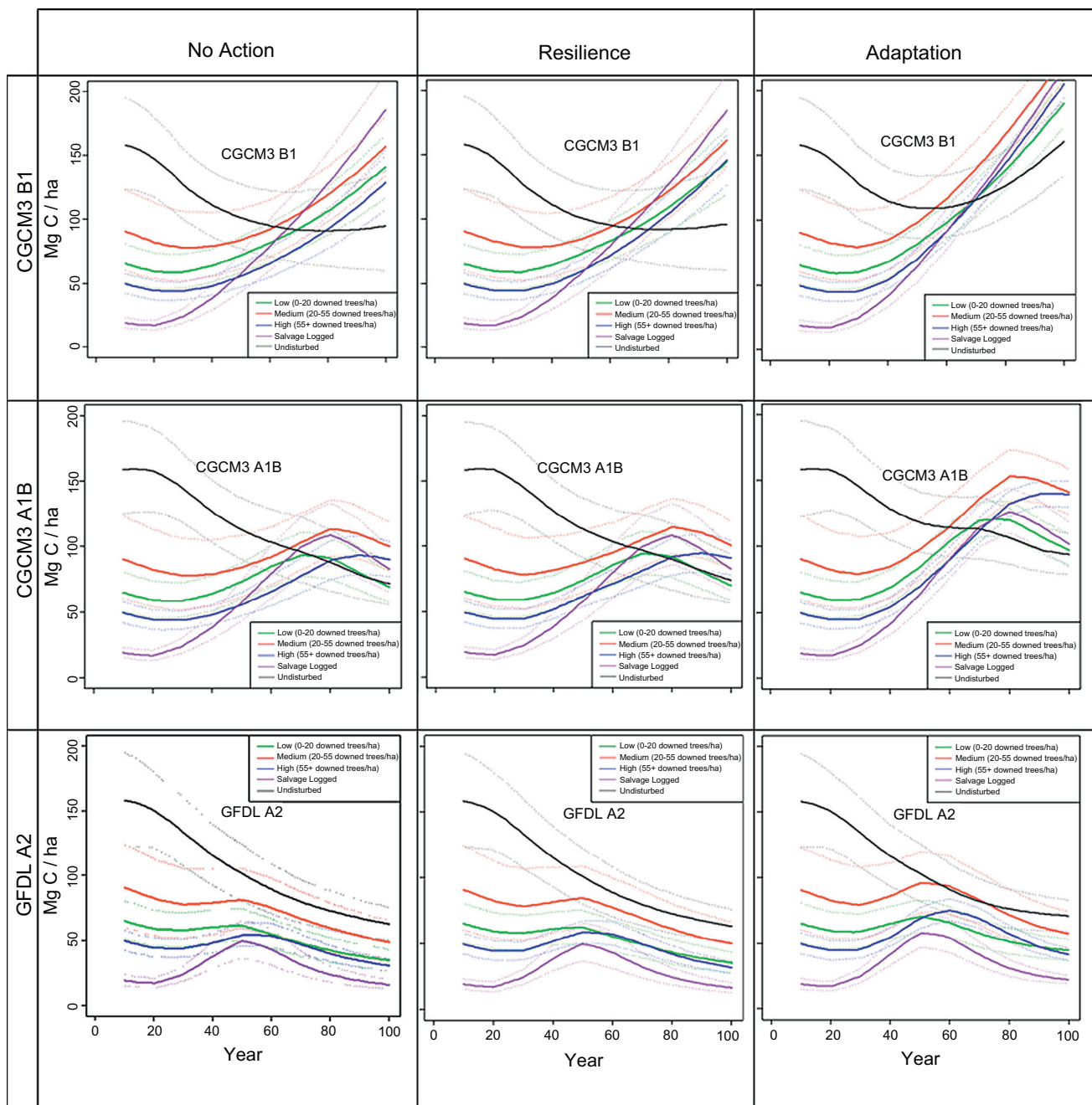
and GFDL B1) maintained climates mostly hospitable to current species, and carbon stocks continued to recover under the projected climate regime regardless of managerial strategy, although the adaptation approach did have higher C stocks (Fig. 2, top row; and Table 3). For the other climate scenarios, current species were unable to survive in the projected climate, and high rates of mortality reduced tree levels and carbon stocks. Differences between the no-action and resilience scenarios were slight, and by the end of the simulation were minimal; the adaptation plan had consistently higher C stocks, although the magnitude of the difference depended upon the climate scenario (Fig. 3; note that this combines the disturbance histories into single management scenarios, which makes the assumption that the plots are essentially interchangeable. Given their rapid convergence (e.g., Fig. 2) this seems valid, but the figure should be interpreted with this caveat in mind.) The forest type transitioned, however, from a spruce/fir/lodgepole/aspen community to oak/juniper/pine dominated woodland (Fig. 4).

#### 3.4. Tree densities

Disturbance history had no influence on final tree densities (Table 4), however they were much higher in the adaptation oriented scenario than in the no action and resilience oriented approaches, which both had zero live trees at the end of the simulation period (Fig. 5). Tree numbers were slightly declining in the adaptation scenario, likely due to natural thinning. This is also likely responsible for the leveling off and even slight reductions in carbon stocks as the forest moved into a more open woodland configuration (Fig. 2).

The complete simulation outputs can be found in Appendix A (species composition and relative contribution to total C in the adaptation scenarios, as in Fig. 4) and Appendix B (total C for all scenarios, as in Fig. 2).





**Fig. 2.** Carbon stocks for each group, undisturbed plots, and three model/emission scenarios (CGCM3 B1, CGCM3 A1B, and GFDL A2). Differences in categories (low, medium, high, and salvaged) reflect the different initial densities of the current species related to their fire resilience, their longevity under the different scenarios, and how much flexibility that afforded to the plantings. The effect of differing resilience levels is found in the spread of projections within each graph, the question of differences between management scenarios are addressed by comparison between columns, differing climate scenarios are on different rows. Lines show each resilience grouping bootstrapped 1000 $\times$ , dotted lines represent the 5/95% percentiles. Each line was smoothed with a 10 years moving average.

#### 4. Discussion

##### 4.1. The effects of regeneration and climate on carbon stocks

Differences in coniferous regeneration amongst the disturbance histories had minimal effect on carbon stocks (Fig. 2). In the near term, the establishment of aspen more than compensated for any loss of coniferous species, to the point where plots with zero coniferous seedlings were similar in terms of total carbon stocks to areas with ample coniferous regeneration. So while the aspen forest will be different in many other respects (e.g., forage, understory composition, phenology), carbon stocks should recover more or

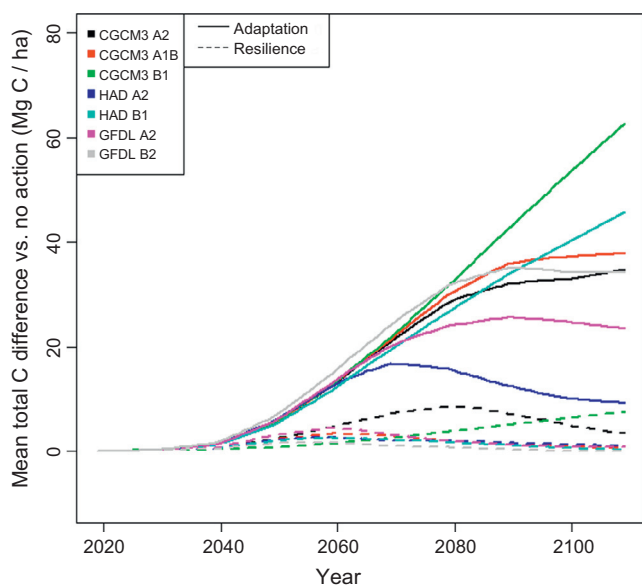
less similarly across the groups in the near to mid-term due to the aspen. This parallels the results of Kashian et al. (2006), who hypothesized that differences in post-fire recruitment rates would cause changes in carbon stocks initially but those levels would converge as forests developed (however that study did not simulate growth/mortality changes due to climate). The rapid growth of aspen (relative to the conifer species) appears to have accelerated this process, and further infilling and establishment may hasten recovery, at least in the near term.

In the long-term, C stocks were more responsive to the climate scenario than their initial conditions. The majority of the GCM/emission scenarios used here resulted in climatic conditions

**Table 3**

Simulated carbon outputs for each climate and management scenario for the midpoint (2060) and final year (2109) in the projections. Values represent the median plot level totals (non-soil pools), over all disturbance histories. 5% and 95% percentile values are from the bootstrapped distribution to give an estimate of variability. Totals are quite similar for 2060, but diverge for many of the projections by 2109.

Climate model	Management scenario	Projection year 2060 (Mg/ha C)			Projection year 2109 (Mg/ha C)		
		Median	5%	95%	Median	5%	95%
CGCM3 A1B	No plant	82.9	55.9	118.2	82.1	53.9	114.1
CGCM3 A2	No plant	82.4	55.9	118.9	69.6	46.6	99.0
CGCM3 B1	No plant	81.4	55.3	118.1	147.8	106.8	214.1
GFDL A2	No plant	57.1	34.0	101.9	31.3	11.7	61.8
GFDL B1	No plant	79.9	55.2	116.8	119.2	58.9	158.4
HAD A2	No plant	73.9	53.8	118.5	44.9	24.8	80.0
HAD B2	No plant	77.0	55.0	116.7	71.4	43.3	101.8
CGCM3 A1B	Plant spruce	83.3	60.1	121.0	82.6	55.5	115.3
CGCM3 A2	Plant spruce	83.3	60.8	124.8	71.2	48.5	100.9
CGCM3 B1	Plant spruce	82.4	60.5	119.4	152.5	119.5	210.0
GFDL A2	Plant spruce	59.8	34.4	103.8	32.3	12.4	64.1
GFDL B1	Plant spruce	80.1	58.7	120.8	118.6	59.4	158.3
HAD A2	Plant spruce	75.0	53.9	121.1	45.7	25.6	79.0
HAD B2	Plant spruce	77.3	58.6	119.0	71.4	43.2	102.4
CGCM3 A1B	Plant any	97.9	75.0	141.4	115.1	80.4	152.6
CGCM3 A2	Plant any	97.4	75.3	139.2	99.2	64.1	136.9
CGCM3 B1	Plant any	95.7	76.9	140.8	210.6	169.6	241.5
GFDL A2	Plant any	74.5	46.9	122.2	40.8	18.0	69.6
GFDL B1	Plant any	93.9	73.3	136.9	159.4	87.6	204.4
HAD A2	Plant any	91.2	69.6	138.0	68.1	36.0	102.2
HAD B2	Plant any	94.4	78.6	143.4	99.3	63.0	136.9



**Fig. 3.** Different management/regeneration scenarios compared to the no action/no further establishment scenario. The resilience strategy, simulating the establishment of ample spruce on each plot, did not provide any long term benefit under any climate scenario save the CGCM3 B1, which had a slight (~8 Mg/ha) increase in C. In contrast, the adaptation scenario saw larger increases in C stocks for all climate models, although the magnitude was highly variable. See the text for further interpretation.

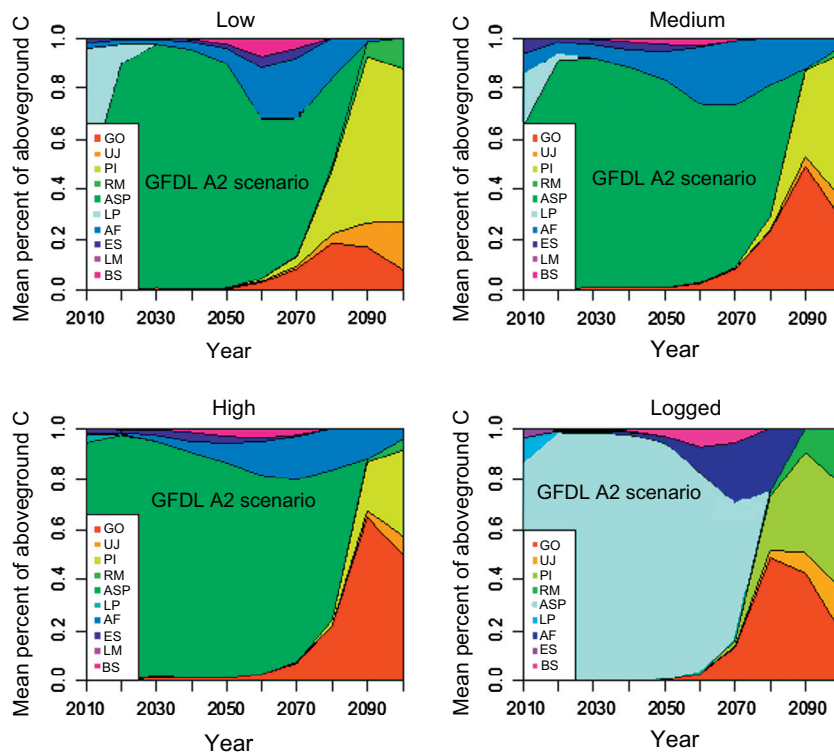
outside the range of the current suite of species, which overwhelmed any signal of the differential response to the disturbances. Planting of spruce increased carbon stocks in the mid-term (20–50 years) by filling in low density plots, but was not successful in the longer term (50+ years), as the simulated climate conditions moved outside the expected tolerance of spruce. Large-scale climate related mortality has been observed; for example, sudden aspen decline (SAD), the large scale dieoff of aspen stands in the southern Rockies, has been tied to climate drivers (moisture stress/hydraulic

failure, Worrall et al., 2010; Anderegg et al., 2011). To the extent that these drivers become more common, further dieoffs (as simulated here) may become more likely. In any case, rapid die-offs are certainly possible, and must be considered in any long-term planning.

Allowing for species shifts (Fig. 4) resulted in higher carbon stocks and maintained tree cover (Figs. 3 and 5). These species are different in many respects, but could provide many of the same ecosystem services going forward (i.e., snow capture, and soil temperature regulation). Even in the most severe change scenarios (e.g., GFDL A2), tree species were still viable, albeit at a low density, resulting in low standing carbon stocks (Fig. 2, bottom row).

The control plots further illustrate this point. The control plots were comprised primarily of spruce and fir, two species which were extirpated in many of the climate scenarios quickly. In many of the simulations, the control plots were very similar to the disturbed plots by the end of the period due to mortality of the spruce and fir. Interestingly, the control plots were often lower in the adaptation-oriented scenarios, lagging behind the disturbed plots in terms of carbon stocks (Fig. 2, Appendix B). This is likely due to the lack of opportunity for alternate species establishment, which required a minimum number of stems on the plots before planting could commence. This would likely reflect reality to a degree, in that competition from living trees may inhibit the establishment of non-local species. The disturbance facilitated their establishment by eliminating that competition.

This suggests the hypothesis that perhaps disturbances may facilitate the establishment of more climatically suitable species – species more tolerant of the hot and dry post-disturbance environments – facilitating natural adaptation towards warmer and dryer climates, in the near-term at least. In this study, the lower magnitude climate change scenarios showed higher C in the disturbed plots than the undisturbed plots (at the end of the simulated period; CGCM3 B1 and GFDL B1), as did the majority of the adaptation-oriented simulations. Simulation results in Scandinavia (Sykes and Prentice 1996) also demonstrated that more disturbances facilitated faster adaptation to changing climates, assuming no dispersal limitations. This exercise made a similar assumption by relying on managerial actions to get suitable species to the area. There are dispersal limitations in reality, however. Given the rapid-



**Fig. 4.** Species proportions for aboveground carbon stocks for one climate scenario (GFDL A2), the adaptation management scenario, and the four groups. These correspond to the bottom right graph in Fig. 2. Abbreviations: GO, gambel oak; UJ, utah juniper; PI, common pinyon; RM, Rocky Mountain juniper; ASP, quaking aspen; LP, lodgepole pine; AF, subalpine fir; ES, Engelmann spruce; LM, limber pine; BS, blue spruce; DF, douglas fir; OJ, oneseed juniper; PM, singleleaf pinyon. The remainder of the climate/management outputs are found in Appendix A.

**Table 4**

Numbers of live trees/hectare (GFDL A2 climate model) for the adaptation oriented management scenario for the final year. Each group was bootstrapped 1000×, the 5/95% percentiles are reported. Groups are not significantly different.

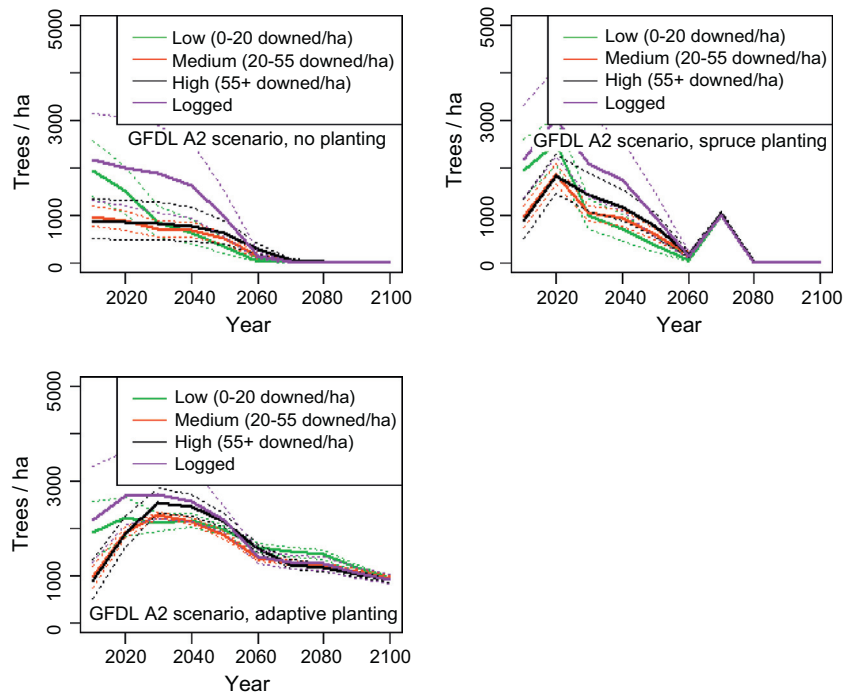
Treatment	Mean	5%	95%
Low	938	889	987
Medium	956	909	1004
High	917	872	966
Logged	925	816	1033

ity of expected temperature shifts, populations must migrate very quickly (for example, [Loarie et al., 2009](#) estimate a mean temperature movement of 0.42 km/year for the A1B scenario, meaning species ranges would need to shift at that rate to maintain equilibrium with temperature). Naturally migrating populations require not only the ability to move that distance, but also opportunity to establish and time to reach maturity prior to the next dispersal event. Spatially explicit models may be of use in simulating these dynamics (for example, LANDIS-II; see [Scheller and Mladenoff, 2007](#)). The extent to which disturbances may facilitate the transition to more climatically suitable species assemblages will be limited by the dispersal ability of the species themselves, and the community dynamics that emerge from the assemblage of establishing species.

Post-disturbance management, especially management oriented towards adaptation to future conditions, must deal with both high variation in climate/emission scenarios (which makes it difficult to select an objective) and the fact that species suitable in 50–100 years are not necessarily suitable now, which will make planting/establishment of species suitable for future conditions difficult. A hybrid approach to post-disturbance forest management is likely the most reasonable – planting currently viable species en masse (using more climate appropriate provenances where

possible, e.g., [Rehfeldt et al., 1999](#)), but also providing for “seed islands” of species which may be viable in the future and that cannot be expected to migrate naturally. These seed islands would provide critical information on how a changing forest would alter ecosystem components such as understory composition, biogeochemistry, and herbivores (e.g., [Chapin et al., 2007](#)), needed before any mass transplanting should commence, and potentially provide seed to replace the current species as the increasingly inhospitable climate and future disturbances remove them. There are valid concerns about this strategy, which essentially amounts to assisted migration, and they should be considered ([McLachlan et al., 2007](#)). The way bioclimatic tolerances are defined should be considered, as well as how uncertainty is considered when using bioclimatic models ([Mbogga et al., 2010](#)), as well as the potential for invasive species and other detrimental effects of relocating species. Local knowledge and skills will be needed to establish species in currently non-hospitable climates. However, the risks of inaction must also be considered, and they may be outweighed by the risks associated with assisted migration (e.g., [Gray et al., 2011](#)). In addition to planting individuals from more southerly provenances, nurseries are working with geneticists to develop more appropriate genotypes for future conditions ([Tepe and Meretsky, 2011](#)). In any case climatic adaptation, facilitated by humans or not, is inevitable. Whether that adaptation occurs naturally, subject to the dispersal limitations discussed earlier, or is facilitated via planting is a matter of policy, and should consider the extent to which specific ecosystems and ecosystem services are desirable or irreplaceable.

Resilience to future disturbances should also be considered ([Solomon and Freer-Smith, 2007](#)). This study looks at the effect of subalpine conifer resilience to a fire now (and did not simulate future disturbance events), but potential future fire events must be considered. Further work needs to explore some potentially contrasting effects of climate change on future fire behavior, and



**Fig. 5.** Mean live individuals per hectare under the three management scenarios for each group. Upper left: no action scenario. Upper right: resilience oriented scenario, the bumps represent simulated Engelmann spruce planting efforts. Lower left: adaptation oriented scenario. The no action scenario and the resilience oriented scenario both result in zero trees per hectare, despite planting in the resilience management strategy. The adaptation oriented scenario left a higher density of trees; while total was declining; this is likely due to self-thinning. Lines represent the bootstrapped means ( $1000\times$ ) and 5/95% percentiles (dotted lines).

from there, future fire resilience. Fire weather is almost universally expected to increase in western North America (Moritz et al., 2012). Severity (in terms of post-fire regeneration) is more difficult to forecast, but is likely dependent upon species composition and the relative proportion of fire adapted species. The increase in tree mortality expected to result from climate change (e.g., SAD) may result in less continuous fuel loading, which may alter fire behavior and severity as well. Combinations of vegetation simulation results, like those presented here, need to be further integrated with models of future fire likelihood, which are often statistical and do not consider feedbacks with vegetation (e.g., Westerling et al., 2006, 2011). This would extend the range of planning options to not only look at a single ecosystem service, but also the value of different management options to potential future events.

#### 4.2. Limitations

As in all studies which explore non-analog conditions (such as future climate), questions about FVS's ability to handle projections which are inherently extrapolations occur. Bioclimatic envelope based models are prime examples. Bioclimatic envelopes make several assumptions, including the lack of biotic interactions, the lack of local adaptation, and the exclusion of dispersal limitations in terms of the current range of species (Hampe, 2004). However, they are still useful for baseline estimates of general future change (Pearson and Dawson, 2004; Lawler et al., 2009).

It should also be noted that these GCM projections involve the mean monthly temperature, precipitation, etc., whereas in some cases distributions and survivorship may be better described by climatic variability, such as extreme cold weather events, which are relatively infrequent but may have a disproportionate influence of distributions, but are not currently considered in Climate-FVS. In addition, this simulation did not consider potential future disturbances. Subalpine forest ecosystems typically see infrequent, yet severe, disturbances on a multi-century timescale (Veblen, 2000) and so this omission is reasonable.

Another limitation regards the role of mortality in FVS. The mechanistic nature of climate-induced mortality is still under investigation, with several non-exclusive means by which the trees may be killed, such as hydraulic failure due to xylem cavitation/collapse, carbon starvation, biotic attack, and the interaction between these and other stressors (Hartmann, 2011; McDowell et al., 2011). This is an active area of research, and it is likely that the relative contribution of these mechanistic factors are species dependent, varying on several factors including stomatal behavior, rooting depth, and relative growth. One could argue that these mechanistic causes for mortality are built into bioclimatic envelopes, especially for ecosystems strongly structured by abiotic constraints. However, current distributions may not reflect the actual physiological bounds of a species in historical time, either. For example, Minckley et al. (2012) have recorded stable coniferous ecosystems despite variation in climate over a 6000 years period in lake cores approximately 100 km from the study area, indicating that lodgepole pine is resilient to somewhat variable disturbance and climate regimes over long time periods. FVS increases probabilistic mortality when the climate shifts out of that observed for a given species. The basic mortality methodology present in Climate-FVS was successful in mapping areas of sudden aspen decline (Rehfeldt et al., 2009), and the majority of research agrees that mortality will rise (McDowell et al., 2011); supporting the conclusion that active management will be required to maintain tree cover if natural dispersal of more climatically appropriate species proves insufficient.

Finally, future establishment is an unknown. The scenarios used here bracket the possibilities – either no future establishment or prolific establishment, both with local and more climatically suitable species. Results should be interpreted with this in mind.

#### 5. Conclusions

Disturbances can be seen as opportunities for adaptation. They allow for new species to establish, and (potentially) reset the



community to something that is more in tune with the current climate. For this system, the importance of differing levels of conifer regeneration (on ecosystem carbon accumulation) appears to be relatively minor due to the prolific establishment and rapid growth of aspen. In addition, the implications of climate change on tree viability are more predominant than the differing levels of regeneration in the long term.

Maintaining natural system dynamics (no action) may have an ecological appeal. However, an approach that preserves the structural system (e.g., a forest) may, in some cases, better sustain critical or desired ecosystem services even if it requires direct intervention. In the resilience parlance, this is an example of adaptive transformation; the social system transforms the ecological system to maintain resilience in the face of climatic change, using disturbances as windows of opportunity to move the system into a more adaptive state. There are drastic transformations at the community level (and so the concept of resilience at the species/community level may be of less value due to shifting baseline conditions from climate change), but at the ecosystem service level, resilience is maintained. The tools of restoration ecology, which have been long developed both professionally and academically, will certainly be of use in conjunction with silvicultural techniques to both plan and establish communities resilient to emerging conditions (e.g., Tepe and Meretsky, 2011; Seidl et al., 2011).

This is a place-based analysis, one specific example of a broader issue. It brings an important reference point to discussions on resilience and climate change – these simulations are based on actual plots, at an actual place, and simulated for that place. A look at climate projections shows that this degree of change is not unusual throughout the globe, so while this example is place-specific, the generalities it explores are not. Resilience of ecosystems is not guaranteed, nor is the background climate on which that resilience plays out. Timely action is needed and has already been explored in some parts of the globe (Seidl et al., 2011). Species ranges are moving, often faster than the species themselves can disperse (Loarie et al., 2009). Ecosystem resilience to disturbances may be less important than their tolerance to shifting temperature and precipitation regimes expected in the next century.

## Acknowledgements

Funding for this research came from the University of Colorado Department of Ecology and Evolutionary Biology, CIRES, and the National Science Foundation. Becky Poore provided excellent feedback on the initial manuscript. We would also like to thank Eva Adler, Danielle Clucky, Adam Markovits, and Austin Rempel for considerable field help. Two reviewers made comments that greatly improved the manuscript.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.06.044>.

## References

Anderegg, W.R.L., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D.L., Field, C.B., 2011. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *PNAS* 109, 233–237.

Baker, W., Flaherty, P., Lindemann, J.D., Veblen, T.T., Eisenhart, K.S., Kulakowski, D., 2002. Effect of vegetation on the impact of a severe blowdown in the southern Rocky Mountains, USA. *Forest Ecol. Manage.* 168 (1–3), 63–75.

Bowler, R., Fredeen, A.L., Brown, M., Black, T.A., 2012. Residual vegetation importance to net CO<sub>2</sub> uptake in pine-dominated stands following mountain pine beetle attack in British Columbia, Canada. *Forest Ecol. Manage.* 269, 82–91.

Brown, J.K., 1974. Handbook for inventorying downed woody material. In: USDA Forest Service Gen. Tech. Report INT-16, Ogden, UT 84401.

Brown, C.D., Johnstone, J.F., 2011. How does increased fire frequency affect carbon loss from fire? A case study in the northern boreal forest. *Int. J. Wildland Fire* 20 (7), 829–837.

Brown, C.D., Johnstone, J.F., 2012. Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecol. Manage.* 266, 34–41.

Brown, M., Black, T.A., Nesic, Z., Foord, V.N., Spittlehouse, D.L., Fredeen, A.L., Grant, N.J., Burton, P.J., Trofymow, J.A., 2010. Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia. *Agric. Forest Meteorol.* 150, 254–264.

Buma, B., Wessman, C.A., 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2, art64.

Buma, B., Wessman, C.A., 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. *Forest Ecol. Manage.* 266, 25–33.

Chapin III, F.S., Danell, K., Elmqvist, T., Folke, C., Fresco, N., 2007. Managing climate change impacts to enhance the resilience and sustainability of Fennoscandian forests. *Ambio* 36, 528–533.

Crookston, N.L., Rehfeldt, G.E., Dixon, G.E., Weiskittel, A.R., 2010. Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. *Forest Ecol. Manage.* 260, 1198–1211.

Dale, V.H., Joyce, L.A., McNulty, S., et al., 2001. Climate change and forest disturbances. *Bioscience* 51, 723–734.

D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B., Patty, L., 2011. Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *Forest Ecol. Manage.* 262, 2070–2078.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173.

ESRI, 2010. ArcMap 9.2. Environmental Systems Resource Institute, Redlands, California, USA.

Flannigan, M.D., Krawchuk, M.A., Groot, W.J.D., Wotton, B.M., Gowman, L., 2009. Implications of changing climate for global wildland fire. *Int. J. Wildland Fire* 18, 483–507.

Gray, L.K., Gylander, T., Mbogga, M.S., Chen, P.Y., Hamann, A., 2011. Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecol. Appl.* 21, 1591–1603.

Gunderson, L.H., 2000. Ecological resilience in theory and application. *Ann. Rev. Ecol. Syst.* 9, 439–473.

Hampe, A., 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecol. Biogeogr.* 13, 469–471.

Hartmann, H., 2011. Will a 385 million year struggle for light become a struggle for water and carbon? How trees may cope with more frequent climate change-type drought events. *Global Chem. Biol.* 17, 642–655.

Holling, C.S., 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4, 1–23.

Hurteau, M., North, M., 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. *Front. Ecol. Environ.* 7, 409–414.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National scale biomass estimators for United States tree species. *Forest Sci.* 49 (1), 12–35.

Johnstone, J.F., Chapin III, F.S., 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biol.* 9, 1401–1409.

Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., Ryan, M.G., 2006. Carbon storage on landscapes with stand-replacing fires. *Bioscience* 56, 598–606.

Kulakowski, D., Veblen, T.T., 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* 88, 759–769.

Lal, R., 2005. Forest soils and carbon sequestration. *Forest Ecol. Manage.* 220, 242–258.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R., Bartlein, P.J., 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90 (3), 588–597.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. *Nature* 462, 1052–1055.

Mbogga, M.S., Wang, X., Hamann, A., 2010. Bioclimate envelope model predictions for natural resource management: dealing with uncertainty. *J. Appl. Ecol.* 47, 731–740.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *TREE* 26 (11), 523–532.

McLachlan, J.S., Hellmann, J.J., Schwartz, M.W., 2007. A framework for debate of assisted migration in an era of climate change. *Cons. Biol.* 21, 297–302.

Melson, S.L., Harmon, M.E., Fried, J.S., Domingo, J.B., 2011. Estimates of live-tree carbon stores in the Pacific Northwest are sensitive to model selection. *Carbon Balance Manage.* 6, 1–16.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151.

Minkley, T.A., Shriver, R.K., Shuman, B., 2012. Resilience and regime change in a southern Rocky Mountain ecosystem during the past 17,000 years. *Ecol. Mono.* 82 (1), 49–68.

Moritz, M.A., Parisien, M.-A., Batllori, E., Krawchuk, M.A., Van Dorn, J., Ganz, D.J., Hayhoe, K., 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3 (6), art49.

- Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1 (6), 535–545.
- Pearson, R.G., Dawson, T.P., 2004. Bioclimate envelope models: what they detect and what they hide; response to Hampe. *Global Ecol. Biogeogr.* 13, 471–473.
- Rebain, S.A., 2010. The Fire and Fuels Extension to the Forest Vegetation Simulator: Updated Model Documentation. In: Internal Rep. Fort Collins, US Department of Agriculture, CO, p. 366. Forest Service, Forest Management Service Center, p. 406. <<http://www.fs.fed.us/fmfc/ftp/fvs/docs/gtr/FFEguide.pdf>>.
- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton, D.A., 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecol. Mono.* 69, 375–407.
- Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. *Forest Ecol. Manage.* 258, 2353–2364.
- Scheller, R.M., Mladenoff, D.J., 2007. An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. *Land. Ecol.* 22, 491–505.
- Seidl, R., Rammer, W., Lexer, M.J., 2011. Adaptation options to reduce climate change vulnerability of sustainable forest management in the Austrian Alps. *Can. J. Forest Res.* 706, 694–706.
- Smith, J.E., Heath, L.S., 2002. A model of forest floor carbon biomass for United States forest types. In: Res. Pap. NE-722, USDA, Forest Service, Northeastern Research Station, Newtown Square, PA, p. 37.
- Solomon, A.M., Freer-Smith, P.H., 2007. Forest responses to global change in North America: interacting forces define a research agenda. In: Freer-Smith, P.H., Broadmeadow, M.S.J., Lynch, J.M. (Eds.), *Forestry and Climate Change*. CAB International, pp. 151–159.
- Tepe, T.L., Meretsky, V.J., 2011. Forward-looking forest restoration under climate change—are US nurseries ready? *Rest. Ecol.* 19, 295–298.
- Veblen, T.T., 2000. Disturbance patterns in southern Rocky Mountain forests. In: Knight, R.L., Smith, F.W., Buskirk, S.W., Romme, W.H., Baker, W.L. (Eds.), *Forest Fragmentation in the Southern Rocky Mountains*. University Press of Colorado, Boulder, Colorado, USA, pp. 31–43.
- Wessman, C.A., Archer, S., Johnston, L.C., Asner, G.P., 2004. Woodland expansion in US grasslands. In: Gutman, G., Janetos, A.C., Justice, C.O., Moran, E.F., Mustard, J.F., Rindfuss, R.R., Skole, D., Turner, B.L., Cochrane, M.A. (Eds.), *Land Change Science*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943.
- Westerling, A.L., Turner, M.G., Smithwick, E.A.H., Romme, W.H., Ryan, M.G., 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *P. Natl. A.Sci.* 108, 13165–13170.
- Worrall, J.J., Marchetti, S.B., Egeland, L., Mask, R.A., Eager, T., Howell, B., 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *Forest Ecol. Manage.* 260, 638–648.