Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments

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ABSTRACT

Developing management strategies for addressing global climate change has become an increasingly important issue influencing forest management around the globe. Currently, management approaches are being proposed that intend to (1) mitigate climate change by enhancing forest carbon stores and (2) foster adaptation by maintaining compositionally and structurally complex forests. However, little is known about the compatibility of these two objectives or the long-term efficacy of a given management regime at simultaneously achieving adaptation and mitigation. To address this need, we examined stand-level carbon and complexity responses using five long-term (>50 yrs) silviculture experiments within the upper Great Lakes region, USA. In particular, live tree carbon stores and sequestration rates, and compositional and structural complexity were analyzed from three thinning experiments in *Pinus resinosa* and two selection method experiments in northern hardwood systems to elucidate the long-term effects of management on these ecosystem attributes and the general compatibility of mitigation and adaptation objectives.

As expected, we observed a general increase in large tree densities with stand age and positive relationships between stand stocking level and live tree carbon stores. More importantly, our results clearly identify tradeoffs between the achievement of mitigation and adaptation objectives across each study. For example, maintaining higher stocking levels (i.e., enhanced mitigation by increasing carbon stores) resulted in decreases in stand-level structural and compositional complexity (i.e., reduced adaptation potential). In addition, rates of live tree carbon increment were also the lowest within the highest stocking levels; despite the benefits of these stand conditions to maximizing carbon stores. Collectively, these findings underscore the importance of avoiding rigid adherence to a single objective, such as maximum on-site carbon stores, without recognizing potential consequences to other ecosystem components crucial to ensuring long-term ecosystem functioning within the context of environmental change. One potential stand-level strategy for balancing these goals may be to employ multi-aged management systems, such as irregular shelterwood and selection systems, that maintain a large proportion of carbon stores in retained mature trees while using thinning to create spatial heterogeneity that promotes higher sequestration rates in smaller, younger trees and simultaneously enhances structural and compositional complexity.

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1. Introduction

The role of forest management within the context of global climate change is rapidly evolving. In particular, management approaches are being proposed that intend to (1) mitigate climate change by enhancing carbon stores and (2) foster adaptation by maintaining compositionally and structurally complex forests (Krankina et al., 1997; Birdsey et al., 2005; Ruddell et al., 2007; Malmsheimer et al., 2008). Despite widespread political and scientific acceptance of these approaches (Millar et al., 2007; Malmsheimer et al., 2008; Lawler, 2009), the potential incompatibility between mitigation and adaptation measures has received little attention.

Because forests are a critical component of the global carbon cycle, storing over 80% of global terrestrial aboveground carbon (Dixon et al., 1994), much attention has turned to forest management as a means of mitigating climate change. As such, efforts have focused on quantifying how forest management influences carbon stores (the mass of carbon present on a site) and/or sequestration (the rate at which carbon accumulates) (e.g., Dixon, 1997; Hoover and Stout, 2007; Harmon et al., 2009). Previous studies have

demonstrated that repeated thinnings over the course of a forest rotation increase carbon stores relative to stands that are clear-cut on short rotations (Thornley and Cannell, 2000; Harmon et al., 2009) and that the carbon benefits differ according to thinning method (e.g., thinning from above versus below; Hoover and Stout, 2007; Profft et al., 2009). In contrast, several short-term studies have shown that thinning reduces aboveground carbon stores relative to unthinned stands (Chiang et al., 2008; Finkral and Evans, 2008; Campbell et al., 2009). Despite these insights, long-term empirical evaluations of repeated thinning treatments are lacking. Likewise, age-related declines in aboveground carbon sequestration are widely documented for unmanaged systems (e.g., Pregitzer and Euskirchen, 2004; Bradford and Kastendick, 2010); however, the influence of repeated thinnings and different thinning methods on stand growth and hence long-term patterns of sequestration has not been fully explored (Hoover and Stout, 2007; Ryan et al., 2010).

Numerous management strategies have been proposed to create and maintain forest ecosystems able to adapt to future climatic conditions and disturbance regimes (Millar et al., 2007; Puettmann et al., 2009). Due to the uncertainties in predicting future climate conditions, most stand-level recommendations for adaptation have taken the precautionary approach of maintaining high levels of compositional, functional, and/or structural complexity to enhance the ability of an ecosystem to respond or adapt to new or changing conditions (Malmsheimer et al., 2008; Evans and Perschel, 2009; Puettmann et al., 2009). These approaches are largely based on principles of ecological resilience (Holling, 1973), which refers to the amount of disturbance or stress an ecosystem can withstand before experiencing dramatic shifts in structure and/or function. Adaptation potential stems from the greater variation of life-history strategies present in diverse systems and the resultant higher probability that some species, functional groups, or age classes will be able to respond favorably to new climactic conditions or disturbance regimes, thus allowing the overall system to maintain core ecosystem functions in light of these changes (Gunderson, 2000; Carpenter et al., 2001; Elmqvist et al., 2003; Walker et al., 2004). Relatedly, other strategies call for increasing the resistance of forests (i.e., the capacity of a system to absorb disturbance or stress and remain relatively unchanged; Holling, 1973) using various forest protection approaches and density management regimes (Millar et al., 2007).

Despite the recent evaluations of forest management practices as mitigation or adaption strategies, key uncertainties exist regarding possible conflicts between the two. For example, because traditional thinning approaches are directed at creating structurally and compositionally uniform stands (Nyland, 2007), it is quite possible that they unintentionally reduce a stand's adaptive capacity. Moreover, most studies examining the long-term impacts of forest management on carbon have relied on simulation models primarily addressing biomass production (e.g., Thornley and Cannell, 2000; Harmon et al., 2009; Nunery and Keeton, 2010). As a result, simultaneous evaluations of the impacts of mitigation strategies on structural and compositional complexity have not been undertaken. Yet, an evaluation of these ecosystem attributes is critical for ensuring that approaches aimed at maximizing carbon benefits are also maintaining systems well-poised to adapt to future climactic conditions and disturbance regimes (Ryan et al., 2010). Thus, understanding the tradeoffs between mitigation and adaptation is crucial to identifying management strategies that can simultaneously meet these potentially conflicting objectives.

Although the focus of forest management on mitigation and adaptation is relatively new, many of the suggested approaches for promoting high levels of carbon stores and stand complexity, such as thinning and mixed-species management (e.g., Larsen, 1995; Linder, 2000; Spiecker, 2003; Malmsheimer et al., 2008),

have been applied for centuries (Schutz, 1999). As such, data from long-term experiments originally designed to evaluate the consequences of forest management on growth and yield can provide valuable insights regarding mitigation and adaptation potential. Correspondingly, we examined the stand-level carbon and complexity responses within five long-term manipulative experiments including two common forest types, northern hardwoods and red pine (*Pinus resinosa*), within the upper Great Lakes region, USA. These experiments span more than 50 years of largely continuous silvicultural treatment, creating an ideal opportunity to retrospectively assess how alternative management strategies impact mitigation and adaptation objectives. Each long-term experiment includes management approaches proposed to influence carbon stores or sequestration, such as maintaining high levels of stocking, extending rotation periods, and applying thinning treatments. Moreover, the long-term nature of these field experiments allows for an empirical evaluation of trends in carbon dynamics and forest complexity not afforded by simulation modeling. Our specific objectives were to (1) quantify the influence of stocking level, rotation period, and thinning method on long-term patterns in carbon stores, live carbon increment (a measure of carbon sequestration), and stand structural and compositional complexity, and (2) determine under what conditions enhancing forest carbon stores and/or sequestration is compatible with maintaining compositional and structural complexity.

2. Methods

2.1. Study sites

This study takes advantage of data from five long-term manipulative experiments within the upper Great Lakes region, USA, established by the US Forest Service between 1949 and 1957 (Table 1). All sites, with the exception of the Dukes experiment, have temperate continental climates with average annual temperatures of 3.2–5.0 °C and average annual precipitation of 716–813 mm (Adams et al., 2004). Due to its proximity to Lake Superior, the Dukes site has a lacustrine climate with average temperatures of 5.0 °C and average annual precipitation of 860 mm (Adams et al., 2004).

2.1.1. Red Pine Stocking Levels

The Red Pine Growing-Stock-Levels experiment (RPGS) was established between 1949 and 1951 within natural fire-origin red pine stands on the Cutfoot Experimental Forest in north-central Minnesota, USA (47°40′N, 94°5′W; D'Amato et al., 2010). Stands were 85 years old at the time of treatment establishment in 1949, and the study consists of a replicated growing-stock-level experiment with five levels of basal area (13.8, 18.4, 23.0, 27.5, and 32.1 $m^2 ha^{-1}$ basal area). Each treatment was assigned to experimental units ranging in size from 1 to 2.0 ha and replicated three times. Thinning treatments were initially applied every 5 years to maintain growing stock levels; however, the length between thinning entries was extended to 10 years in 1964 due to the small growth increment on some of the treatments. Thinnings occurred at 10-year intervals thereafter until 2004 for all stands with the exception of the 13.8 and 18.4 $m^2 ha^{-1}$ treatments, which did not receive thinning treatments from 1975 to 2003. Although the onset of thinning treatments was later in these stands than is typical for red pine within the upper Great Lakes region, this forest type is typically managed on many public ownerships with repeated thinnings on rotations from 120 to 200 years (e.g., WDNR, 2006). As such, the stand ages and responses we examined are applicable to the public ownerships in the region where such rotations are being employed. Three 0.08-ha permanent measurement plots

Table 1
Locations, site characteristics, and treatment histories for long-term forest management experiments used in this study.

Experiment	Location	Site index (m)[a]	Forest type	Soils	Treatments[b]	Frequency (years)	Age at treatment (years)
(a) Red Pine Growing Stock Levels (RPGS)	Cutfoot Exp. Forest, MN	15.2	*Pinus resinosa*	Sand	A, BA	5–10	85
(b) Red Pine Cutting Methods (RPCM)	Cutfoot Exp. Forest, MN	15.2	*Pinus resinosa*	Sand	A, T	10–15	85
(c) Birch Lake plantation (Birch Lake)	Superior National Forest, MN	18.3	*Pinus resinosa*	Sandy loam	A, T, BA	10	45
(d) Northern hardwood stocking levels (Dukes)	Dukes Exp. Forest, MI	19.5	*Acer saccharum*-dominated	Sandy loam	A, BA	5–15	Old growth (~300 yrs)
(e) Northern hardwood cutting methods (Argonne)	Argonne Exp. Forest, WI	20.3	*Acer saccharum*-dominated	Silt loam	A, BA	10	45

[a] Correspond to dominant species at each site at base age of 50 years.
[b] A = stand age, S = stocking level, and T = thinning method.

were established in each treatment unit and were measured at roughly 5-year intervals beginning in 1949. Within each plot, species and diameter were measured on all trees greater than 8.9 cm DBH (diameter at breast height). As with all experiments described here, measurements were made prior to the treatment application within a given year.

2.1.2. Red Pine Cutting Methods

The Red Pine Cutting Methods (RPCM) experiment was established in 1950 within the red pine stands on the Cutfoot Experimental Forest mentioned above (Bradford and Palik, 2009). A single stocking level was established (25 m² ha⁻¹ basal area) and maintained using three thinning methods: *thinning from above*, the removal of trees primarily in codominant crown classes, but also occasional dominant and intermediate individuals to favor the best trees in the codominant and dominant crown classes (Smith et al., 1997); *thinning from below*, the removal of trees from the lower crown classes (overtopped and intermediate) to favor trees in the upper crown classes (Smith et al., 1997); and thinning with a combination of above and below (hereafter referred to as "*proportional thinning*"). Each treatment (i.e., thinning method) was randomly assigned to 4-ha treatment units and replicated three times. Treatments were applied at 10-year intervals from 1950 to 1970, and then again in 1985. Ten 0.08 ha plots were randomly located within each treatment unit, and species and diameter were recorded for all trees greater than 8.9 cm DBH. Measurements were made on roughly 5-year intervals.

2.1.3. Birch Lake Cutting Methods

The Birch Lake Cutting Method (Birch Lake) experiment was established in 1957 within a direct seed-origin red pine plantation within the Superior National Forest in north-eastern Minnesota, USA (47°42′N, 91°56′W; Bradford and Palik, 2009). Stands were 45 years old at the time of treatment establishment, and the experiment consists of a replicated growing-stock-level experiment with five levels of residual red pine growing stock (7, 14, 21, 28, and 34 m² ha⁻¹ basal area) crossed with three methods of thinning (thinning from above, thinning from below, and proportional, as above). Each treatment combination was randomly assigned to 0.8-ha treatment units and replicated three times. Treatments were applied at a 5-year interval between 1957 and 1962 and at 10-year intervals for the remainder of the experiment (i.e., 1962–1992). One 0.08 ha plot was randomly located within each treatment unit, and species and diameters were recorded for all trees greater than 8.9 cm DBH on roughly 5-year intervals.

2.1.4. Northern Hardwoods Cutting Methods

The Northern Hardwoods Cutting Methods (Argonne) experiment was established in 1951 within 45-year-old, even-aged northern hardwood forests on the Argonne Experimental Forest in northeastern Wisconsin, USA (45°45′N, 89°0′W; Niese and Strong, 1992). This study examines the light, medium, and heavy selection treatments, which maintained a basal area of 13.8, 17.3, and 20.7 m² ha⁻¹, respectively. Each treatment was randomly assigned to 1.0-ha treatment units and replicated three times, with treatments applied at 10-year intervals from 1952 to 1992. Five 0.04-ha plots were randomly located within each treatment unit, and species and diameter were recorded for all trees greater than 11.7 cm DBH on a 5-year interval.

2.1.5. Northern Hardwoods Cutting Cycles and Stocking Levels

The Cutting Cycles and Stocking Levels (Dukes) experiment was established in 1952 within old-growth northern hardwood forests on the Dukes Experimental Forest in the Upper Peninsula of Michigan, USA (46°21′N, 87°10′W; Gronewold et al., 2010). Three replicates of ten treatments were established in a completely randomized block design to compare single-tree selection under various residual stocking levels and cutting cycles. The treatment combinations cross three levels of cutting cycle (5, 10, and 15 years) with three levels of residual stocking levels (11.5, 16.1, and 20.7 m² ha⁻¹ basal area). One additional treatment of a 20-year cutting cycle at 6.9 m² ha⁻¹ residual basal area (in trees >24 cm) was also established in each replicate. Previous analyses of growth and structure data from this study indicated no cutting-cycle effect (Gronewold et al., 2010), thus we focus exclusively on different stocking levels. Each treatment was 4–6 ha and contained 6–17 0.08-ha permanent circular plots. All trees on the plots greater than 11 cm DBH were inventoried for diameter and species prior to treatments and every 5 years thereafter until the 1974 when the study was closed. The plots were remeasured in 2002–2004 due to renewed interest. In contrast to the other studies, the Dukes experiment was established within an uneven-aged stand for which the assignment of a stand age has little relevance. Nonetheless, for the evaluation of temporal trends within this experiment, we assigned a stand age of 300 years for the onset of the study based on stand age assessments from Woods (2004).

2.2. Analysis

2.2.1. Carbon dynamics

To evaluate the effect of manipulative treatments on carbon, we used the total aboveground carbon stored in living trees as an indicator of carbon stores (C_{stores}). Specifically, aboveground biomass estimates were estimated from diameter measurements using species-specific allometric equations for aboveground bole and carbon biomass, branch biomass and foliage biomass compiled by Jenkins et al. (2003). Total aboveground biomass was converted

to aboveground carbon stores assuming that carbon represents 50% of a given tree's dry mass. We used the change in total aboveground live-tree carbon stores between measurements (hereafter aboveground live carbon increment; ALCI), which includes ingrowth, as an indicator of carbon sequestration. Although aboveground live carbon is certainly not the only carbon pool, it is typically both the largest and most dynamic carbon pool in forest ecosystems and the pool most directly influenced by forest management (Fahey et al., 2010). Note that these estimates of carbon dynamics represent mitigation potential via onsite, aboveground carbon stores and do not account for other life cycle components, such as off-site storage in long-lived wood products, conversion to biofuels, and wood substitution for other construction materials that also affect mitigation potential for a given management regime (e.g., Eriksson et al., 2007).

2.2.2. Complexity

We chose to focus on simple, readily available measures of structural and compositional complexity to assess how treatment and stand age (at the time of treatment) affect patterns in tree size and species diversity. Although other aspects of stand structure and composition, including coarse woody debris and many non-tree components of diversity, are also important components of ecosystem complexity, the lack of measurements for these attributes in this retrospective work limited our focus to living trees. Nonetheless, due to the "foundational" role overstory trees play in regulating ecosystem processes, including nutrient cycling rates, patterns of resource availability, and understory plant community dynamics (Ellison et al., 2005), the long-term trends in overstory trees represents one critical measure of the adaptive capacity of these systems over time (i.e., the ability of the tree community to react to changes in environmental conditions in a manner that maintains forest cover).

Structural complexity, for the purposes of this study, refers to the degree of heterogeneity in the vertical and horizontal distribution of biomass within a forest system, particularly among different tree sizes. We focused on tree sizes, and structural complexity within each plot was based on the diversity of tree diameters within a given plot, as well as the density of large trees. Tree size complexity was quantified using the Gini coefficient and Shannon's index. The Gini coefficient ($Gini_{DBH}$) was calculated from the tree list ordered by ascending DBH as:

$$Gini_{DBH} = \frac{\sum_{1}^{n}(2i - n - 1)x}{n^2 \mu}$$

where n is the number of trees in the plot, x is the diameter of tree i, and μ is the mean tree diameter. Values for this coefficient range from 0 to 1, with 0 values corresponding to stands with perfect size equality and values of 1 representing maximum size inequality (Weiner and Solbrig, 1984). Another useful measure for characterizing size complexity is Shannon's diversity index (H; Staudhammer and LeMay, 2001), which was applied to tree diameters and calculated with 5 cm DBH classes as:

$$H_{DBH} = -\sum_{1}^{S} \frac{n_i}{N} \ln\left(\frac{n_i}{N}\right)$$

where S is the total number of size classes in the plot, N is the total number of trees on the plot, and n_i is the number of trees in size class i, with values generally increasing with greater numbers of size classes in a stand. In addition to these indices, the density of trees $\geqslant 40$ cm DBH ($Dens_{>40}$) was calculated for each plot due to the association of this structural characteristic with later stages of stand development for red pine and northern hardwood forests (Whitman and Hagan, 2007; Zenner and Peck, 2009).

Compositional complexity refers to the relative abundance and diversity of tree species and functional groups within a given forest system. For each plot at each measurement, the Shannon diversity index was used to estimate species diversity in terms of basal area. Species diversity (H_{spp}) was calculated as:

$$H_{spp} = -\sum_{1}^{S} \frac{b_i}{B} \ln\left(\frac{b_i}{B}\right)$$

where S is the total number of species in the plot, B is the total basal area on the plot, and b_i is the basal area of species i. In addition, species richness ($\#_{spp}$) was calculated for each plot and measurement period based on the total number of tree species present.

2.3. Statistical analysis

The influence of stocking level and stand age on carbon stores, live carbon increment, and compositional and structural complexity for the RPGS, Dukes, and Argonne experiments was examined using mixed-model repeated-measures analysis of variance (ANOVA) in which block was treated as a random effect and stocking level and age as fixed effects, following the SAS MIXED Procedure (SAS Institute, 2008). In cases where significant interactions were present between fixed effects (i.e., age and stocking level), the statistical significance of a given factor at different levels of the other factor was obtained using the least square means SLICE option in PROC MIXED (SAS Institute, 2008). Similarly, the influence of thinning method and stand age on the abovementioned parameters at the RPCM experiment was examined using mixed-model repeated-measures ANOVA in which block was treated as a random effect and thinning method and age were treated as fixed effects. For the Birch Lake experiment, a three-way, repeated-measures mixed-model ANOVA was performed with measurement period, stocking level, thinning method, and the interaction terms included in the model. A SP(POW) covariance structure, which is a generalized autoregressive covariance structure appropriate for the unequal spacing between measurement periods across studies, was used for all models (Littell et al., 2006). For all analyses, residuals were checked for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Levene test) and data transformed as necessary. In cases in which transformation could not achieve normality, non-parametric repeated measures, mixed-model ANOVA was used (SAS-macro npar, http://www.ams.med.uni-goettingen.de/Projekte/makros/run_npar.html). A p-value of 0.05 or less was defined as statistically significant.

3. Results

3.1. Aboveground carbon stores and sequestration

Live carbon increment patterns within the three stocking level experiments (i.e., RPGS, Argonne, and Dukes) were primarily related to stand age, with sequestration rates generally declining over time (Table 2 and Fig. 1a, c and e). The greatest levels of live carbon increment occurred within the earliest measurement periods at the Argonne and RPGS experiments (Fig. 1a and c), whereas the highest level observed at the Dukes occurred 15 years after treatment initiation (Fig. 1e). Variation in carbon stores was primarily related to stocking level, stand age, and their interaction within all stocking level experiments (Table 2). Overall, carbon stores increased with residual stocking level and fluctuated over time in response to thinning treatments (Fig. 1b, d and f).

Thinning method and stand age both influenced live carbon increment within the RPCM experiment (Table 2). In particular, live carbon increment generally declined over time and was

Table 2
Summary of type three tests of fixed effects for mixed model, repeated measures ANOVAs evaluating variation in aboveground live carbon increment (ALCI), live tree carbon stores, and measures of compositional and structural complexity with respect to stand age (A), stocking level (BA), and thinning method (M).

Study	Source	df	ALCI F	C_{stores} F	$Gini_{DBH}$ F	H_{DBH} F	$Dens_{>40}$ F	H_{spp} F	$\#_{spp}$ F
(a) RPGS	A	9	**60.27*****	**181.93*****	**38.44*****	**74.93*****	**140.10*****	**6.53*****	**15.22*****
	BA	4	2.40	**159.55*****	3.05	1.33	1.37	**5.30****	**6.17****
	A × BA	36	1.11	**17.36*****	**5.65*****	**3.84*****	**3.91*****	**1.76***	**3.35*****
(b) Argonne	A	9	**26.46*****	**33.26*****	**4.29****	**7.02*****	**26.21*****	**28.92*****	**39.06*****
	BA	2	0.23	**193.20*****	0.08	3.96	2.49	0.20	0.45
	A × BA	18	1.01	**2.13***	0.22	0.42	0.84	**2.05***	**3.45****
(c) Dukes	A	4	**68.27*****	**158.51*****	**31.70*****	**73.15*****	**77.43*****	**3.26***	**7.59****
	BA	3	3.42	**63.71*****	**21.05*****	**12.95****	**55.31*****	0.62	0.24
	A × BA	12	**5.48*****	**3.88****	0.42	**6.15*****	**14.60*****	0.32	1.01
(d) RPCM	A	2	**119.92*****	**56.28*****	**26.35*****	**29.06*****	**263.98*****	**50.50*****	**30.31****
	M	9	**33.80****	**8.72****	**32.07****	**12.41****	**9.18***	1.49	1.18
	A × M	18	0.98	0.59	**4.75*****	**8.75*****	**4.60*****	1.28	0.76
(e) Birch Lake	A	7	**94.11*****	**695.18*****	**19.01*****	**24.46*****	**83.22****	**5.13*****	**14.69*****
	BA	4	**25.38*****	**148.46*****	**12.54****	0.96	**6.72****	0.61	0.38
	M	2	**8.77****	**16.23*****	**157.40*****	**325.22*****	**27.64*****	1.60	**11.24****
	A × BA	14	**29.25*****	**102.25*****	**19.98*****	**3.38****	**11.55*****	**3.19****	**4.19*****
	A × M	14	1.71	1.49	**2.98****	1.26	**5.73*****	0.13	0.50
	M × BA	8	2.20	**4.76****	**24.55*****	**8.66*****	**7.41*****	**7.06****	**2.80***
	A × BA × M	56	0.70	0.59	**5.56*****	1.10	1.38	0.33	0.51

Bold values are significant at P-values of 0.05 or lower.

 * $P < 0.05$.
 ** $P < 0.001$.
 *** $P < 0.0001$.

greater in stands thinned from above relative to those thinned from below or proportionally (Fig. 1g). Similarly, variation in carbon stores was related to thinning method and stand age. Stores increased with stand age and were lower in stands thinned from above compared with stands thinned from below or proportionally (Fig. 1h). Both live carbon increment and carbon stores at Birch Lake were influenced by thinning method, stocking level, stand age, and the interaction of stocking level with stand age (Table 2). In addition, carbon stores were also influenced by the interaction between stocking level and thinning method (Table 2). Live carbon increment generally declined with age (Fig. 1i), and the primary differences in live carbon increment between stocking levels within a given thinning method were due to lower live carbon increment in the 6.9 m^2 ha^{-1} treatments (Fig. 2). Stands thinned from below had lower live carbon increments than stands thinned from above or proportionally, whereas there was no difference between stands thinned from above and those thinned proportionally (Fig. 1i). Carbon stores increased with age as well as with stocking level within a given thinning method (Figs. 1j and 2). Thinning methods influenced carbon stores only at the lowest stocking level, in which stands thinned from above and stands thinned from below had lower stores compared to stands thinned proportionally (Appendix A – available only online).

3.2. Forest structural complexity

Within the RPGS experiment, variation in size inequality and size-class diversity, as measured with the Gini coefficient (Gini$_{DBH}$) and Shannon's index (H_{DBH}), respectively, were affected by stand age and the interaction between stand age and stocking level (Table 2). In particular, both size inequality and size-class diversity increased markedly during prolonged intervals in which understory trees were not removed in thinnings (stand ages 100–110 and post 130 years), particularly within the lowest growing stock levels (Fig. 3a and b). The density of large trees (DBH ⩾40 cm) generally increased with stand age (Fig. 4a) and was also affected by the interaction between stand age and stocking level (Table 2).

Within the Argonne experiment, variation in size inequality and size-class diversity was related solely to stand age, with the highest degrees of inequality and diversity occurring between ages 70 and 80 (Fig. 3d and e). Overall, the density of large trees increased over time (Table 2 and Fig. 4b). Within the Dukes experiment, size inequality and size-class diversity was related to stocking level and stand age (Table 2) with older stands and higher stocking levels (i.e., 16.1 and 20.7 m^2 ha^{-1}) containing greater levels of inequality than younger ages and lower stocking levels, respectively (Fig. 3g). Large tree density followed a similar trend (Table 2 and Fig. 4c).

Within the RPCM experiment, thinning method, stand age, and their interaction affected patterns of size inequality, size-class diversity, and large tree densities (Table 2). In particular, stands thinned from above had little variation in size inequality and diversity over time, whereas Gini coefficients and Shannon's indices for stands thinned from below and proportionally followed U-shaped trends over time (Fig. 3j and k). The density of large trees increased in all treatments over time, with stands thinned from below having greater densities of large trees than stands thinned from above, regardless of stand age (Fig. 4d). In addition, stands thinned proportionally had greater densities of large trees than stands thinned from above at stand ages 115–140 (Fig. 4d). At Birch Lake, size inequality was affected by stand age, stocking level, thinning method, the interactions between stand age and stocking level, between stocking level and thinning method, and a three-way interaction between stand age, stocking level, and thinning method (Table 2). The highest levels of size inequality occurred in stands thinned from above, with the exception of the lowest stocking level treatment (6.9 m^2 ha^{-1}; Appendix B – available only online). Size-class diversity at Birch Lake was related to stand age, thinning method and the interactions between stand age and stocking level and between thinning method and stocking level (Table 2). Size-class diversity increased with stand age and was greater in stands thinned from above relative to stands thinned from below and proportionally (Fig. 3n and Appendix A). Thinning method influenced size class diversity only in the highest stocking level
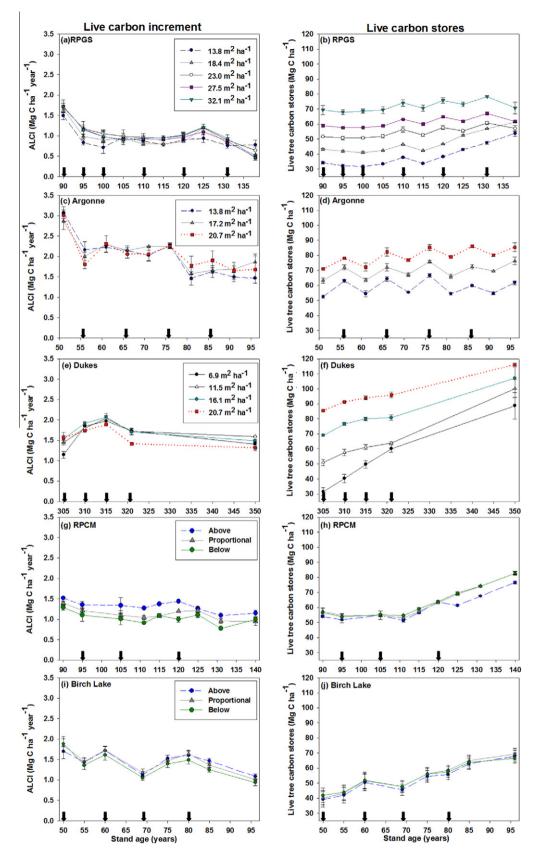
Fig. 1. Long-term patterns in aboveground live carbon increment (ALCI) and aboveground live tree carbon stores at the (a and b) Red Pine Growing Stock Levels (RPGS), (c and d) Argonne, (e and f) Dukes, (g and h) Red Pine Cutting Methods (RPCM), and (i and j) Birch Lake experiments. Error bars represent one standard error. Arrows along the *x*-axis indicate timing of treatment application within a given experiment. Measurements were made prior to treatment application within a given year.
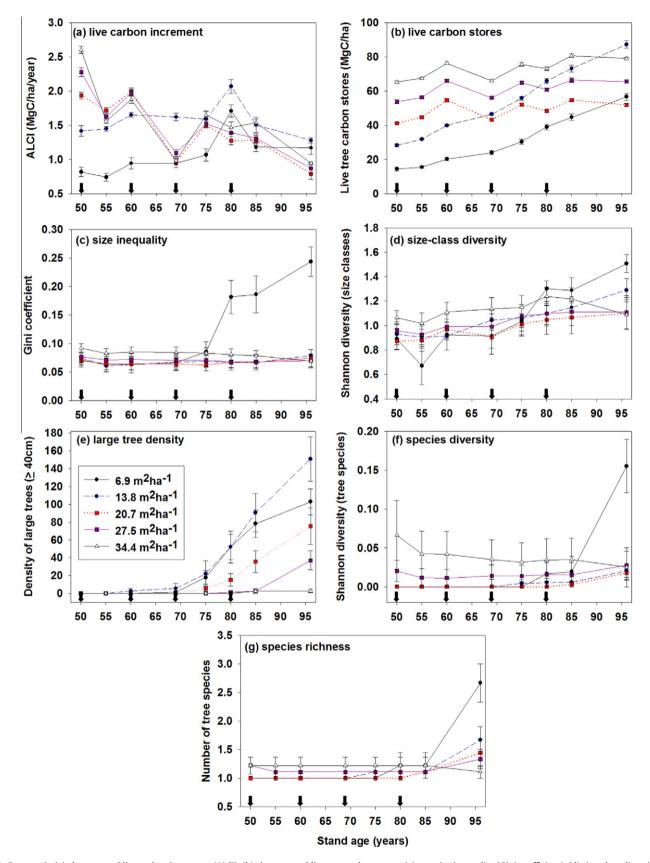
Fig. 2. Patterns in (a) aboveground live carbon increment (ALCI), (b) aboveground live tree carbon stores, (c) tree size inequality (Gini coefficient), (d) size-class diversity, (e) large tree density, (f) tree species diversity, and (g) tree species richness as a function of stand age for multiple stocking level treatments at the Birch Lake experiment. Error bars represent one standard error. Arrows along the x-axis indicate timing of treatment application within a given experiment. Measurements were made prior to treatment application within a given year.
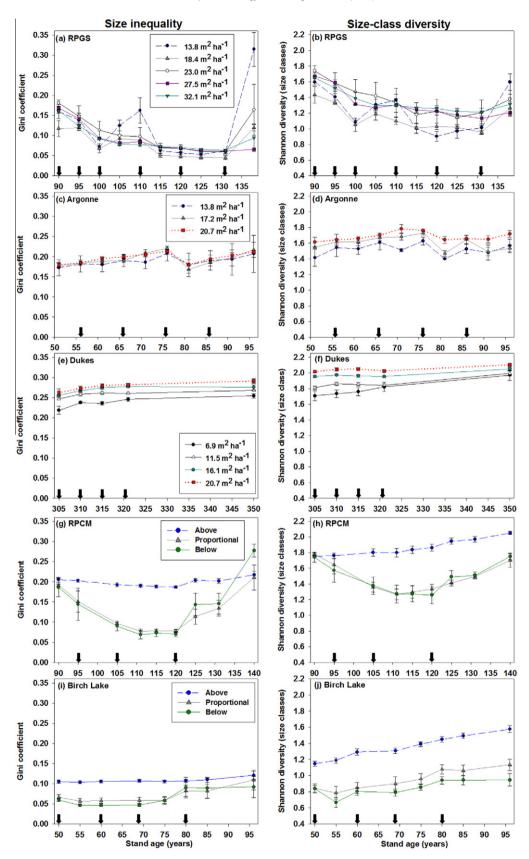
Fig. 3. Long-term patterns in Gini coefficient of tree diameters (tree size inequality) and size-class diversity, at the (a and b) Red Pine Growing Stock Levels (RPGS), (c and d) Argonne, (e and f) Dukes, (g and h) Red Pine Cutting Methods (RPCM), and (i and j) Birch Lake experiments. Error bars represent one standard error. Arrows along *x*-axis indicate timing of treatment application. Measurements were made prior to treatment application within a given year.

Fig. 4. Long-term patterns in large tree density (diameter at breast height ⩾40 cm) at the (a) Red Pine Growing Stock Levels (RPGS), (b) Argonne, (c) Dukes, (d) Red Pine Cutting Methods (RPCM), and (e) Birch Lake experiments. Error bars represent one standard error. Arrows along x-axis indicate timing of treatment application. Measurements were made prior to treatment application within a given year.
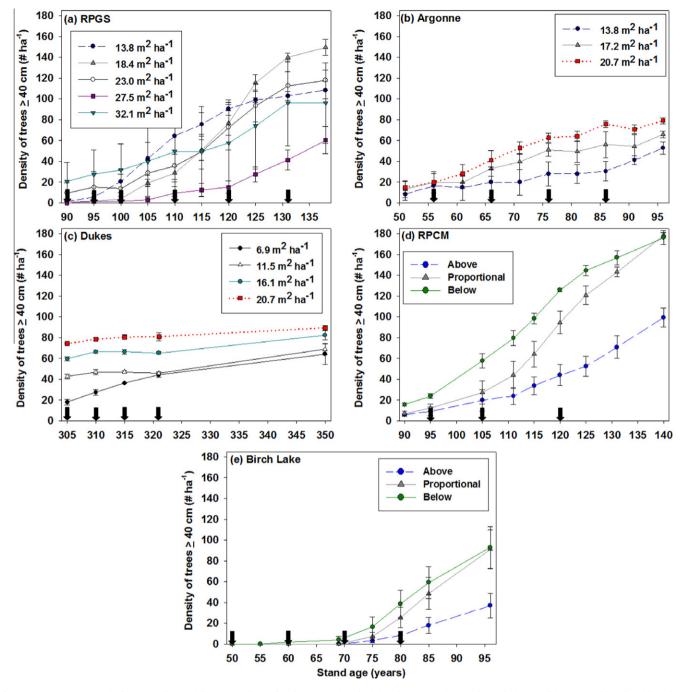
treatments (27.5 and 34.4 m² ha⁻¹; Appendix A). Large tree densities were influenced by stand age, stocking level, thinning method, and the interactions between age and stocking level, between age and thinning method, and between thinning method and stocking level (Table 2).

3.3. Forest compositional complexity

Within the RPGS experiment, stocking level, stand age, and their interaction affected tree species diversity and richness, with compositional complexity generally increasing over time and decreasing with stocking levels (Fig. 5a and b). Other species beyond red pine occurring within these stands at the final measurement peri-

od included *Abies balsamea*, *Acer rubrum*, *Quercus rubra*, and *Betula papyrifera*.

Patterns in compositional complexity within the northern hardwood systems (Argonne and Dukes) declined with age (Table 2 and Fig. 5c–f) and were related to the interaction between stocking level and stand age (Table 2). Species present within the Argonne experiment at the final measurement period included *Acer saccharum*, *Tilia americana*, *Fraxinus americana*, and *Betula alleghaniensis*, whereas *A. saccharum*, *B. alleghaniensis*, *A. rubrum*, and *Fagus grandifolia* were the primary species at the Dukes experiment.

Thinning method had no effect on compositional complexity within the RPCM experiment, as patterns in tree species diversity
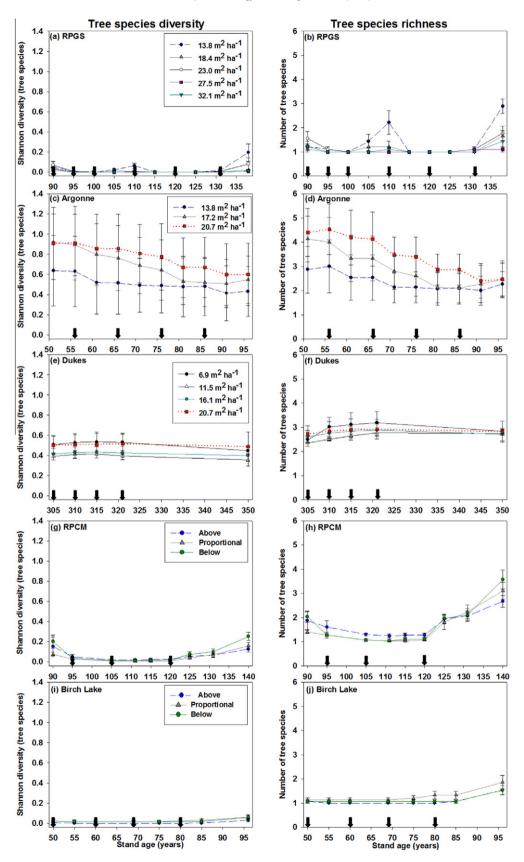
Fig. 5. Long-term patterns in tree species diversity and richness at the (a and b) Red Pine Growing Stock Levels (RPGS), (c and d) Argonne, (e and f) Dukes, (g and h) Red Pine Cutting Methods (RPCM), and (i and j) Birch Lake experiments. Error bars represent one standard error. Arrows along the x-axis indicate timing of treatment application within a given experiment. Measurements were made prior to treatment application within a given year.

and richness were related solely to stand age (Table 2). Patterns in diversity generally followed a U-shaped trend with age, whereas richness generally increased over time (Fig. 3g and h). Within the Birch Lake experiment, both diversity and richness were affected by stand age and the interactions between stand age and stocking level and between thinning method and stocking (Table 2). Tree species diversity was also affected by thinning method (Table 2). Both tree species diversity and richness generally increased over time (Fig. 5i and j), particularly at the lowest stocking level (Fig. 2). In addition, tree species richness was significantly higher within stands thinned from above and below relative to the other thinning methods at the 27.5 m^2 ha^{-1} stocking level (Fig. 5j and Appendix A). Composition at the RPCM and Birch Lake experiments at the final measurement period was strongly dominated by *P. resinosa*; however, other species included *Populus tremuloides*, *A. balsamea*, and *P. strobus* at the Birch Lake experiment, and *A. balsamea* and *P. strobus* at the RPCM experiment.

4. Discussion

Forest management is increasingly being viewed as a central component to regional and global strategies for climate-change mitigation and adaptation in the face of changing global conditions (Malmsheimer et al., 2008; Puettmann et al., 2009). Although many of the approaches being recommended for achieving these diverse objectives have been in existence for centuries (Schutz, 1999), there has been, to our knowledge, no formal empirical evaluation of the long-term effectiveness of a given management regime or silvicultural system at simultaneously meeting climate change mitigation and adaptation goals. These experimental treatments represent widely employed forest management approaches, and provide an invaluable long-term record of how forest management can simultaneously influence both carbon dynamics (mitigation) and complexity (adaptation).

4.1. Carbon

Given the importance of forest ecosystems to the terrestrial carbon cycle, numerous studies have examined the influence of forest management practices on ecosystem carbon stores and sequestration (Birdsey et al., 2006; Harmon et al., 2009; Ryan et al., 2010). A general conclusion of simulation and field studies is that regeneration methods and thinning treatments that maintain a large proportion of mature trees are superior, in terms of maintaining carbon stores, to those associated with more intensive removals (Taylor et al., 2008; Harmon et al., 2009; Keyser, 2010; Nunery and Keeton, 2010), even in cases when off-site storage is considered (Harmon et al., 2009). The long-term trends across the five studies we examined support this conclusion, as higher stocking-level treatments generally had the highest carbon stores. Moreover, the rapid increases in carbon stores observed during periods of treatment cessation (e.g., ages 110–135 for the 13.8 and 18.4 m^2 ha^{-1} stocking levels at the RPGS experiment and ages 322–350 at Dukes; Fig. 1), are consistent with studies that have highlighted the impact of partial disturbances, such as thinning treatments, on aboveground carbon stores (Law et al., 2003; Chiang et al., 2008; Harmon et al., 2009). Nonetheless, it is important to recognize that these treatments often provide the opportunity for long-term off-site storage in forest products (Eriksson et al., 2007); however, examining this carbon pool was beyond the scope of this study.

The use of extended rotations, in which forest stands are harvested at ages beyond those recommended by economic or biological production criteria, has been suggested as a means to increase carbon stores (Harmon and Marks, 2002). These recommendations are supported by widely documented positive relationships between aboveground carbon stores and stand age (Law et al., 2003; Pregitzer and Euskirchen, 2004; Taylor et al., 2007; Bradford and Kastendick, 2010). Our results support this notion, as aboveground carbon stores increased with stand age across all sites, independent of silvicultural treatment or forest type. In fact, some of these treatments had aboveground live-tree carbon stores approaching those documented for old-growth forest systems in the region (Rhemtulla et al., 2009).

Forest thinning has been suggested as a means to maintain relatively rapid carbon sequestration by minimizing resource competition between trees so as to promote rapid growth of retained trees (Dwyer et al., 2010). Regardless of thinning method or stocking level, we observed a general decline in live carbon increment with increasing stand age across all studies (Fig. 1). These trends are consistent with the body of literature that has demonstrated a decline in aboveground primary production with stand age due to several postulated factors, including age-related physiological limitations to growth (Ryan et al., 1997) and shifts in stand structure over the course of stand development (Smith and Long, 2001).

In the experiments that explicitly compared thinning methods (i.e., RPCM and Birch Lake), we found that stands thinned from below and proportionally had higher carbon stores relative to stands thinned from above, particularly at advanced stand ages within the RPCM experiment (Fig. 1). These findings are consistent with work in mixed hardwood forests (Hoover and Stout, 2007) and are likely due to the higher number of large trees retained within stands thinned from below and proportionally, compared to stands thinned from above (Fig. 3c). In contrast, stands thinned from above and proportionally tended to have higher live carbon increment than stands thinned from below, particularly at the Birch Lake site (Fig. 1 and Appendix A). These higher rates are likely due to the residual stand structures created by these thinning methods. In particular, stands thinned from above or thinned proportionally generally result in more growing space for the remaining crop trees. As such, these stands were able to maintain faster growth than stands thinned from below in which trees are removed primarily from the lower crown classes.

4.2. Complexity

Increasing and maintaining structural and compositional complexity in forest stands has become a recent focus of forest management paradigms related to climate change adaptation (Puettmann et al., 2009). In particular, differences in resource requirements and functional traits among tree sizes, ages, and species may confer greater adaptive capacity and resilience in response to fluctuating climactic or disturbance regimes (Dale et al., 2001; Elmqvist et al., 2003; Evans and Perschel, 2009; Puettmann et al., 2009). Although aspects of structural and compositional complexity span components and taxa well beyond those available here, the temporal- and treatment-related trends within and among our studies highlight important commonalities linking forest management to these ecosystem attributes.

The temporal patterns in compositional complexity observed across experiments were largely attributable to the interaction between stand dynamics and treatment frequency and intensity. Within the *P. resinosa*-dominated experiments, compositional complexity generally increased with stand age largely due to the extended periods (>10 years) without treatment application toward the end of each experiment. Increased compositional complexity was related to the recruitment of shade-tolerant and midtolerant species, including *A. balsamea*, *A. rubrum*, *Q. rubra*,

and *P. strobus*, and is a trend documented elsewhere in red pine systems lacking frequent surface-fire disturbance (Day and Carter, 1990; Zenner and Peck, 2009). The most pronounced increases in compositional complexity were within the lowest stocking-level treatments at the RPGS and Birch Lake studies and likely reflect greater resource availability for understory trees due to the lower density of overstory trees (Bailey and Tappeiner, 1998).

In contrast to the red pine experiments, the northern hardwood experiments generally displayed declining compositional complexity over time. These declines were largely due to an increasing component of shade-tolerant species, particularly *A. saccharum*, coupled with a decline and loss of midtolerant species such as *B. alleghaniensis* (cf. Gronewold et al., 2010). These trends likely reflect the removal of midtolerant species from the canopy and the creation of harvest gaps too small for their subsequent recruitment (Webster and Lorimer, 2005) and are consistent with the findings of other long-term studies of single-tree selection (Sendak et al., 2003; Schuler, 2004; Yoshida et al., 2006; Webster and Jensen, 2007).

A key component of complexity is the degree of response diversity (sensu Elmqvist et al., 2003). In particular, response diversity is a vital contributor to ecosystem resilience and is related to the varied abilities to respond to environmental change among species that contribute to the same ecosystem function (e.g., primary productivity; Elmqvist et al., 2003). Systems with low levels of response diversity may be more vulnerable to potential changes in climate and disturbance regimes, with these changes generating adverse effects on ecosystem attributes and services, including native biodiversity, timber production capacity, and carbon stocks (Seidl et al., 2011). Based on the temporal- and treatment-related trends in composition described above, the levels of response diversity have increased within the red pine dominated systems, particularly the stands maintained at lower stocking levels, whereas response diversity has declined over time in the single-tree selection experiments within northern hardwoods.

Beyond species-specific differences in functional traits, there are often ontogenetic shifts in the functional response of a given tree species to environmental stressors as they grow in size and increase in age (Cavender-Bares and Bazzaz, 2000; Thomas and Winner, 2002). Patterns of size inequality and diversity within the red pine dominated experiments were largely related to the stand dynamics described above, as structural complexity increased over time in response to the recruitment of a second cohort (cf. O'Hara et al., 2007), particularly within the lowest stocking levels. Structural complexity also generally increased over time within the northern hardwood dominated experiments, with the highest stocking-levels tending to have the greatest size inequality and size-class diversity (Fig. 2). These patterns likely reflect the wider range of tree sizes maintained in the higher stocking-level treatments through the retention of larger trees (Fig. 2; McRoberts et al., 2008) and periodic recruitment of *A. saccharum* and other shade-tolerant species into smaller diameter classes (Niese and Strong, 1992; Gronewold et al., 2010). A similar dynamic was observed in the experiments comparing thinning methods, in which thinning from above resulted in the highest levels of size-class diversity and inequality (Fig. 3).

Although large diameter trees represent only one component of size-related response diversity, their abundance is widely regarded as an important component in the maintenance of forest biodiversity within managed systems (e.g., Berg et al., 1995). As would be expected, the density of large trees increased with stand age, reflecting natural stand developmental processes (cf. Whitman and Hagan, 2007). In addition, stocking level also affected the density of large trees within the Birch Lake and Dukes experiments; however, the nature of these effects differed between the two studies. The density of large trees at Birch Lake was greatest within the

lower stocking-level treatments, a finding consistent with the widely documented inverse relationship between tree diameter and overall stocking in forest systems (Drew and Flewelling, 1979). In contrast, stocking level positively affected the density of large trees in the Dukes experiment likely reflecting the old-growth condition of these forests at the onset of the experiment. In particular, these stands contained a high density of large trees at the beginning of the experiment (Gronewold et al., 2010), and therefore stands with higher levels of residual stocking maintained a great proportion of these original large trees, while also recruiting other large-diameter individuals over time. Similarly, both thinning method experiments demonstrated that thinning from below or thinning proportionally are more effective at increasing the density of large trees relative to thinning from above, even though the latter typically favors growth of co-dominant and dominant trees (Bradford et al., 2010).

4.3. Tradeoffs between mitigation and adaptation

Although the results of these five long-term silviculture experiments identify several consistent patterns within and across experiments, notably the positive effect of rotation age on the development of large trees and the positive relationships between stocking level and aboveground live tree carbon stores, the most significant finding is that managing to maximize one objective (either mitigation of adaptation) may inadvertently compromise the other. For example, our results illustrate that maintaining higher stocking levels (i.e., enhancing mitigation by increasing carbon stores) decreases stand-level structural and compositional complexity (i.e., reduces possible adaptation potential), suggesting that such tradeoffs require close attention when managing forests for climate change. These tradeoffs also underscore the importance of avoiding rigid adherence to a single objective, such as maximum on-site carbon stores, without recognizing potential consequences to other ecosystem components crucial to ensuring long-term ecosystem functioning within the context of environmental change (cf. Ryan et al., 2010). For example, maximizing on-site carbon stores by maintaining high stocking levels in fire-prone regions or where insect outbreaks are exacerbated by such conditions may increase ecosystem vulnerability to disturbance and thus presents a tradeoff between increasing mitigation and minimizing the impacts of these events.

The results of this and other studies have highlighted that minimizing harvesting is critical to maximizing aboveground carbon stores (Harmon et al., 2009; Nunery and Keeton, 2010). Nonetheless, this approach can also lead to a simplification of forest composition, particularly in systems dominated by shade-tolerant species, in which low levels of canopy disturbance tend to favor shade-tolerant species at the expense of others (Leak and Filip, 1977). This was demonstrated within our northern hardwood experiments, as response diversity in these stands declined over time due to an increasing component of shade-tolerant tree species. Consequently, tradeoffs may exist in terms of satisfying objectives for carbon storage in these stands, relative to maintaining an adequate level of response diversity to ensure long-term ecosystem functioning and resilience. Two-aged or uneven-aged silvicultural approaches, such as irregular shelterwood or group and patch selection methods, which allocate adequate growing space for mid-tolerant species recruitment while also maintaining a large proportion of a given stand in mature forest conditions (O'Hara and Gersonde, 2004; Hanson and Lorimer, 2007; Raymond et al., 2009), may represent a potential stand-level compromise for maintaining these critical elements of complexity and carbon in managed systems.

In addition, our results indicate that managing for aboveground carbon stores and sequestration represents another level of

tradeoffs, as maximizing one objective (either stores or live carbon increment) may inadvertently compromise the other. For example, the results of this study would argue for extended rotations with high stocking levels to maximize on-site stores; however, these conditions also resulted in the lowest levels of live carbon increment. As a result, balancing carbon stores versus sequestration requires a compromise that maintains adequate stocking of large trees, while also allocating growing space to younger age classes to maintain higher rates of stand-level aboveground net primary productivity (cf. McGuire et al., 2010). The two-aged and uneven-aged approaches mentioned above for balancing carbon stores and response diversity might also provide conditions for balancing objectives related to stores and sequestration.

In sum, our results clearly identify tradeoffs between stand-level strategies aimed at climate-change mitigation and those aimed at adaptation. These tradeoffs suggest the need for simultaneous evaluation of both strategies in order to arrive at an optimal set of management prescriptions that maintain vital ecosystem functions in an uncertain future. Our findings, based on two forest types in one region, also suggest the need for much additional research on this topic, especially considering the worldwide impetus to manage forests with regard to climate change as well as the potential risks of selecting a strategy that is ultimately counterproductive.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.05.014.

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