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Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests

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Abstract

Forest carbon stocks and fluxes vary with forest age, and relationships with forest age are often used to estimate fluxes for regional or national carbon inventories. Two methods are commonly used to estimate forest age: observed tree age or time since a known disturbance. To clarify the relationships between tree age, time since disturbance and forest carbon storage and cycling, we examined stands of known disturbance history in three landscapes of the southern Rocky Mountains. Our objectives were to assess the similarity between carbon stocks and fluxes for these three landscapes that differed in climate and disturbance history, characterize the relationship between observed tree age and time since disturbance and quantify the predictive capability of tree age or time since disturbance on carbon stocks and fluxes. Carbon pools and fluxes were remarkably similar across the three landscapes, despite differences in elevation, climate, species composition, disturbance history, and forest age. Observed tree age was a poor predictor of time since disturbance. Maximum tree age overestimated time since disturbance for young forests and underestimated it for older forests. Carbon pools and fluxes were related to both tree age and disturbance history, but the relationships differed between these two predictors and were generally less variable for pools than for fluxes. Using tree age in a relationship developed with time since disturbance or *vice versa* increases errors in estimates of carbon stocks or fluxes. Little change in most carbon stocks and fluxes occurs after the first 100 years following stand-replacing disturbance, simplifying landscape scale estimates. We conclude that subalpine forests in the Central Rocky Mountains can be treated as a single forest type for the purpose of assessment and modeling of carbon, and that the critical period for change in carbon is <100 years.

Keywords: carbon dynamics, disturbance, forest age, scaling

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Introduction

Terrestrial vegetation is an important component of the global carbon cycle, storing over 600 Gt of carbon and annually exchanging approximately 10% of that carbon with the atmosphere via photosynthesis and respiration (Schimel, 1995). Covering over 4.1 billion hectares, forests contain over 80% of aboveground terrestrial carbon, and relatively minor alterations to carbon storage or cycling in forest ecosystems may have substantial impact on atmospheric carbon dioxide concentrations (Dixon *et al.*, 1994; Pacala *et al.*, 2001). Consequently, developing techniques to accurately assess forest carbon over large areas has increasing global relevance.

Methods to estimate terrestrial carbon storage and flux for large areas typically include some combination of simulation modeling, remote sensing, or analysis of inventory data (e.g. Potter *et al.*, 1993; Goodale *et al.*, 2002; Ollinger *et al.*, 2002; Turner *et al.*, 2004). Remote sensing can provide robust estimates of aboveground live biomass (Popescu *et al.*, 2004; Schlerf *et al.*, 2005), net primary productivity (NPP) (e.g. Turner *et al.*, 2005)

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and leaf area index (LAI) (Goodenough *et al*., 2003; Hall *et al*., 2005). However, many components of the carbon cycle cannot be accurately estimated by remote sensing, and must be approximated using other approaches. Notably, efforts to quantify detrital biomass and decomposition with remote sensing have only achieved marginal success (Brown, 2002).

Forest age is generally accepted as a primary driver of forest structure and function, and many components of the forest carbon cycle are related to forest age. Age-driven successional patterns of forest structure and live biomass are one of the basic principles of forest ecology (Chapin *et al*., 2002). Many other forest carbon stocks and fluxes have also been related to forest age: coarse woody debris biomass (CWD) (Fahey, 1983; Bond-Lamberty *et al*., 2002), soil organic layer or forest floor biomass (Little *et al*., 2002; Pregitzer & Euskirchen, 2004), mineral soil carbon (Sun *et al*., 2004), biomass accumulation (Johnson *et al*., 2000), NPP (Gower *et al*., 1996; Ryan *et al*., 1997; Chen *et al*., 2002) and carbon balance (Euskirchen *et al*., 2006). Because of these relationships, most attempts to quantify carbon storage and cycling rely on models based on forest age or disturbance history.

Generating accurate predictions based on age still contains challenges. Relationships of carbon cycle components with tree age have typically been developed in single-species, even-aged forests (Pearson *et al*., 1987) – conditions rarely found outside of plantation forests. In addition, relationships developed for simple forest systems may not apply in areas with greater structural or compositional complexity. Characterizing the specific relationship with forest age is also complicated because forest age is used in simulation models as either time since the last disturbance (Radeloff *et al*., 2006; Desai *et al*., 2007) or the observed age of trees within the stand (Kurz & Apps, 1999; Goodale *et al*., 2002), and these alternative definitions of forest age are often used interchangeably (Wang *et al*., 2003; Law *et al*., 2004; Forrester *et al*., 2005; Masek & Collatz, 2006). As a consequence, the relationship between observed age, disturbance history and forest structure and function remains unclear, especially in the unmanaged, mixed forests that make up over 90% of global forest area (Dixon *et al*., 1994).

Two factors could limit the connection between observed tree age and time since disturbance. Disturbances such as fire, insect outbreak, or logging often leave patches of surviving mature and understory trees that will be older than the time since disturbance, even if the disturbance is 'stand replacing.' Inventories in the future will assign a forest age much older than the time since disturbance if sampled in these patches. For old forests, if tree life span is less than the return interval of the disturbance or if a more recent but unrecognized disturbance occurred, tree age will underestimate time since disturbance. Even in forests where stand replacing fire and mass reproduction are common, substantial recruitment can occur, also making average tree age a poor estimate of time since disturbance (Kashian *et al*., 2005). Discrepancies in the relationship between tree age and time since disturbance may promote poor estimates of carbon stocks and fluxes, particularly when one metric is used in a relationship developed with the other.

To estimate carbon stocks and fluxes for landscapes, we need answers to the following questions. How much do forest structure, stocks and fluxes vary among and within sites? What is the relationship between time since disturbance and observed tree age? How closely are stand structure and carbon cycling related to observed age or time since disturbance, and how accurate are predictions based on these relationships? What is the consequence of confounding tree age and time since disturbance in generating landscape-scale estimates of the carbon cycle?

Our goal was to determine how disturbance history and tree age influence forest structure and carbon stocks and fluxes for subalpine forests in the Central Rocky Mountains. Our objectives were to determine if:

(1) Forest structure and carbon pools and fluxes differ at the site level among three subalpine forested landscapes with different elevation and disturbance history.
(2) Time since disturbance can be estimated using measured tree age.
(3) Stand structure and carbon pools and fluxes are related to time since disturbance or tree age and, if so, to quantify the predictive capability of these relationships. Also, to quantify the error incurred by confounding tree age and time since disturbance in landscape-scale carbon assessments.

Materials and methods

Site description

We collected field data at seven stands located at three sites in the subalpine central Rocky Mountains: the Fraser Experimental Forest (Fraser), located near Fraser Colorado, the Glacier Lakes Ecosystem Experiments Site (GLEES), located near Centennial Wyoming, and the Niwot Ridge AmeriFlux study site (Niwot) located near Nederland, Colorado. Climatic conditions at all sites are characterized by cold and relatively long winters (Table 1). GLEES has the highest elevation and precipitation, lowest temperatures and largest

Table 1 Sites, location climatic conditions, elevation, and the number of plots installed at each of seven stands examined

Site	Stand	Plots	Lat Long	Mean annual temperature (°C)	Mean annual precipitation (mm)	Elevation (m)
Fraser	F-320	27	39°4′N, 105°52′W	0	737	2900–3100
	F-50	13				
	F-20	8				
GLEES	G-OLD	35	41°22′N, 106°15′W	−2	1000	3000–3100
	G-20	8				
Niwot	N-Aspen	8	40°2′N, 105°33′W	4	800	2850–3050
	N-CON	40				

See text for additional details about the stands.

average snowpack whereas Niwot is the lowest, warmest, and driest of the three sites. Disturbance regimes in subalpine forests of the southern Rocky Mountains are typically characterized by infrequent, extensive stand-replacing fires (Sibold *et al*., 2006), episodic insect outbreaks (Bebi *et al*., 2003), and occasional wind damage (Veblen *et al*., 1989). While only minor scattered logging occurred at GLEES over 100 years ago, Niwot was clearcut between 1900 and 1910, and selected patches were clearcut at Fraser in the 1950s. Fraser is the only site with a documented fire history and experienced a widespread stand-replacing fire in approximately 1685 (P. Brown, personal communication). The fire history for Niwot for the stand logged in 1900–1910 is unknown, but the stumps remaining from the logging and the logging itself suggest it was a mature forest, perhaps at least 200 years old at the time of logging. GLEES has many trees older than 400 years, but many younger than that. The age distribution at GLEES suggests either a stand-replacing disturbance about 400 years ago with very slow recovery, or smaller, patchier disturbances over the last several centuries.

To address objective 1, we used data from 1 km^2 landscapes at each site. Each km^2 contained 36 plots oriented on a grid to minimize bias. Data from these 108 plots from the three sites were used to assess variability within and among sites. To address objectives 2 and 3, we used the 108 plots from the km^2 landscapes, as well as 36 additional plots selected to ensure a range of stand ages. At Fraser, plots for the km^2 were established in forest originating from a major wildfire in 1685 and a forest that was clearcut in the mid 1950s. Twelve additional plots were established, eight in a nearby stand clearcut in the late 1980s, and four in the forest originating in 1685. At GLEES the km^2 was located in the upwind footprint of the AmeriFlux tower and encompassed an old growth forest with no recorded harvesting mixed with dry and wet meadows. Five of the 36 plots that were solely meadow were not used for objectives 2 and 3. Eight additional plots were established in a nearby stand clearcut in the mid 1980s and four additional plots were established in nearby mature forest. At Niwot, the km^2 sample surrounded the AmeriFlux tower, where the forest was mixed conifer with aspen in the southeast corner. Twelve additional plots were established outside of the km^2, four in aspen, and 8 in mixed conifer. The number of plots in each age or forest type varied depending on the prevalence of each class within our study areas (Table 1). Plots were designed to closely match USDA forest inventory and analysis plots (Bechtold & Patterson, 2005), although we measured more variables. Like FIA plots, our plots were clustered in groups of 4: a center plot and three satellite plots located 35 m away at 0, 120, and 240°. An analysis of variance showed that these plots, while clustered, contain substantial variability within clusters, and could be analyzed as being statistically independent (Bradford *et al*., in review). In addition, the $\sim 200\,m^2$ covered by each plot contained an average of >50 stems, providing a reasonably large sample of stand age and supporting our use of individual plots for identifying age-related trends.

Field measurements

At each plot, we recorded species, location, and diameter at breast height (DBH: diameter at 1.37 m) for all trees within 8 m of plot centers. Height was measured on 10 trees, selected to include the largest three trees. Sapling and seedlings were measured in a 3 m radius microplot located within the plot. We cored 10 randomly selected trees in each plot at 1.37 m and measured radial growth to the nearest 0.1 mm for each of the past 10 years. To estimate stand age (maximum or mean), the five largest trees were cored to the pith for aging, consistent with other studies of forest age effects (Bergeron *et al*., 2004; Lecomte & Bergeron, 2005), and exceeding USDA FIA protocol, which calls for only 'two or three dominant or co-dominant trees from the overstory' for each four-subplot plot. Maximum age was the maximum of those largest trees, while mean age was the mean of those largest trees. Litterfall was estimated by collecting litter twice a year in five $0.15\,m^2$ traps plot^{-1}. Aboveground herbaceous biomass of understory grasses, forbs and shrubs, as well as shrub woody biomass, was collected at peak biomass (late summer) from three $0.25\,m^2$ quadrats plot^{-1}.

Volume of CWD (diameter >7.5 cm) and fine CWD (diameter <7.5 cm) was quantified using Brown (1971), with eight 15 m transects at each plot. Fine CWD was quantified only on the first 4 m of each transect. We recorded diameter and decay classes I–V (Arthur & Fahey, 1990; Busse, 1994) for all CWD.

Soil organic layer or 'forest floor' biomass was measured by harvesting all organic material (other than live biomass and CWD) above mineral soil within three 30 cm $\times$ 30 cm quadrats located 7 m from plot center. Fine roots (diameter <2 mm) were included in the forest floor samples. To estimate the proportion of forest floor biomass in recent needles vs. humus, we collected three 10.2 cm diameter samples of forest floor and divided them into recent needles and humus. Mineral soil (0–15 cm below the forest floor) was sampled with two 5 cm diameter cores within the quadrats sampled for forest floor, so that any organic material went to one of the two samples.

Analysis

Stand structure. We calculated stand age from both maximum age and mean age for each plot from the measured tree ages. We used nonlinear regression to estimate height from DBH for the trees not measured for height. Equations were specific to a species within a cluster of four plots where possible, or to the site where not. LAI was estimated for each tree from allometric equations (Appendix S1) and summed for each plot. Basal area was estimated using tree and saplings, and divided into species.

Carbon pools. Allometric equations were used to estimate biomass in foliage, branches, stems and roots for trees, saplings, and seedlings (Appendix S1). Biomass was assumed to be 50% carbon (Schlesinger, 1997). For understory vegetation, only perennial woody shrub material was considered as a stable carbon pool (leaves are addressed in carbon fluxes). Samples of understory stems, forest floor, and rock free mineral soil were dried to constant mass at 65 °C, weighed and analyzed for carbon and nitrogen content. We estimated values for these carbon stocks for each plot by multiplying total sample biomass by carbon concentration and dividing by sample area. For carbon in CWD, we converted measured diameters into area by assuming that class I–III logs are circular while class IV and V logs are oval shaped with an axis ratio of 1.45 (D. B. Tinker & D. H. Knight, unpublished data). Volume was estimated from area following Van Wagner (1968) and Brown (1971) and undecomposed biomass using a specific gravity of $0.35\,g\,cm^{-3}$ (Jenkins *et al*., 2003). Since wood density declines with decomposition, carbon storage was estimated by multiplying undecomposed biomass by 0.96, 0.83, 0.72, 0.54, and 0.33 for class I–V, respectively (Kueppers *et al*., 2004) and assuming 50% carbon. We also summed individual components to estimate aboveground and belowground carbon, carbon in live biomass, and carbon in detrital biomass (sum of CWD, standing dead trees, and aboveground stumps).

Carbon fluxes – NPP. We used linear regression to estimate basal area increment from DBH for the trees and saplings not cored. Equations were developed for each year, and were specific to a species within a plot where $n \geq 5$, or to the site if not. Basal area increment was converted into DBH for previous years, which were used with allometric equations (Appendix S1) to estimate standing biomass at each year. Live biomass increment (B_{inc}) was calculated as the differences in biomass between subsequent years, and was calculated on an individual tree basis and summed to the plot. Litterfall collections were dried, weighed, and analyzed for carbon content. Understory production was estimated from leaf samples, which were dried, weighed, and analyzed for carbon content, as well as shrub woody production, which was estimated as 10% of the standing woody shrub biomass. NPP was calculated as the sum of biomass increment from trees and saplings, litterfall, and understory production.

Carbon fluxes – decomposition. We calculated carbon flux from CWD by multiplying total CWD carbon by the long-term decomposition rate of $0.0057\,g\,C\,g\,C^{-1}\,yr^{-1}$ that was previously identified for downed trees at one of our sites (Brown *et al*., 1998). To calculate carbon flux from forest floor, we divided the samples into two components, recent needles and humic material (Prescott *et al*., 2000), and applied decomposition rates of $0.04\,g\,C\,g\,C^{-1}\,yr^{-1}$ (Smith & Resh, 1999) and $0.004\,g\,C\,g\,C^{-1}\,yr^{-1}$ (Aber, 1991), respectively, to these pools. Mineral soil carbon was assumed to consist entirely of humic material, so decay was calculated using the value of $0.004\,g\,C\,g\,C^{-1}\,yr^{-1}$ from Aber (1991). Total decomposition was estimated as the sum of decomposition from woody material, forest floor and mineral soil.

Carbon fluxes – NECB. Net ecosystem carbon balance (NECB) was estimated as the difference between total NPP and total decomposition. Our NPP estimates incorporate live biomass increment based on published allometric equations. In addition, our decomposition estimates are from general published rates. Consequently, these estimates miss some fluxes (fine root turnover) and incorporate uncertainty about decomposition rates for humus and needles. To assess the importance of this uncertainty, we also calculated three alternative estimates of NECB assuming that forest floor is at steady state, that mineral soil is at steady state, and that both are at steady state (Appendix S2). Estimates of NECB are highly correlated (minimum correlation coefficient between estimates is 0.86) and selection between them did not influence the results of variability within and among landscapes (objective 1) or relationships with age or time since disturbance (objective 3). However, the method for calculating NECB does affect its magnitude, and the coefficient of the equations developed for objective 3.

Statistical analysis. For objective 1, we used analysis of variance with site as the class and the km^2 plots to quantify variability within and among landscapes. Because the sites were very similar, we used all forested plots ($n = 139$) for objectives 2 and 3. We used linear regression of maximum and mean tree age (plot level) on time since disturbance to meet objective 2. We used regression analysis to characterize how stand age or time since disturbance influenced carbon stocks and fluxes (objective 3). Although we recognize that stand age can depend on which trees are included in calculation of age, we used only maximum age to relate to stand structure, carbon pools and carbon fluxes because maximum and mean age were highly related ($r^2 = 0.87$). We explored linear, power function, exponential function, and a combination of exponential and power functions to allow the response to be nonlinear or negative through time and to have intermediate maxima or minima. We used Akaike's information criteria (Burnham & Anderson, 2001) to identify the statistical model form (relating the response variable to either stand age or time since disturbance) that is most supported by the data. To determine the consequences of confounding these relationships (e.g. using stand age in a relationship derived from observations of time since disturbance or vice versa), we calculated the root mean squared error (RMSE) of the stand age or time since disturbance regression models when applied to the alternative observations and compared these new RMSE values to the RMSE values from the original best models. Analyses were performed using SAS (SAS, 2001; System for Windows, Version 8.02 of the SAS System for Windows, Copyright © 1999–2001, SAS Institute Inc., Cary, NC, USA).

Results

Objective 1 – landscape variability using the km^2 samples

Despite spanning the range in elevation for subalpine forests in the southern Rocky Mountains and differences in disturbance history and forest age, the 3 km^2 sites had similar carbon stocks and fluxes. Ecosystem carbon stocks (to 15 cm in mineral soil) averaged 287 Mg C ha^{-1} in the km^2 samples and ranged from roughly 260 Mg C ha^{-1} at both Fraser and Niwot to over 330 Mg C ha^{-1} at GLEES (Fig. 1a; Appendix S3). Carbon stored in live biomass, also higher at GLEES, averaged 116 Mg C ha^{-1} across sites. At all sites, between 80% and 90% of live carbon was comprised of live trees, with only minor components of saplings, seedlings, or understory vegetation (Appendix S4). Carbon stored in detrital biomass averaged 171 Mg C ha^{-1}, with slightly higher values at GLEES and lower values at Fraser and Niwot. Detrital carbon was stored primarily in mineral soil and forest floor; both averaged between roughly 50 and 80 Mg C ha^{-1} (Fig. 1). Forest floor carbon did not differ among sites, whereas mineral soil carbon and carbon in dead woody material was highest at GLEES.

Fluxes differed little across the three sites. Total NPP (not including fine root production) averaged 2.8 Mg C ha^{-1} yr^{-1}, and was slightly lower at Fraser than GLEES and Niwot, (Fig. 1b, Appendix S5). Live tree biomass increment, litterfall, and understory productivity accounted for 36%, 33%, and 16% of NPP, respectively, and were all lowest at Fraser (Appendix S6). Sapling biomass increment represented only 14% of total carbon gain and was lowest at GLEES. Our estimates of total decomposition averaged 1.42 Mg C ha^{-1} yr^{-1}, about half of NPP, and did not differ among sites (Fig. 1b). Total decomposition consisted of 62% forest floor decay, which did not differ among sites. Mineral soil decomposition and woody decay represented 25% and 12% of total decomposition, respectively, and were both higher at GLEES. NECB was consistently positive in all sites, and under all alternative assumptions about forest floor and mineral soil dynamics (Fig. 1c). The general lack of significant differences in carbon pools and fluxes among sites supported our approach to consolidate results from all three sites into a single chronosequence for examining age-related patterns in carbon dynamics.

The sites differed more in species, age, and structure than in carbon stocks and fluxes. These stands consist of

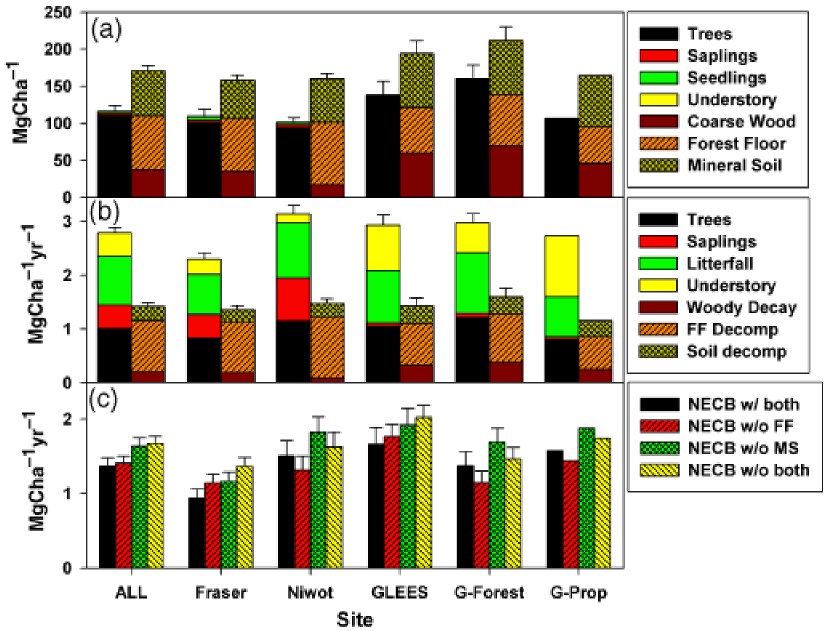

Fig. 1 Biome and landscape-scale estimates of carbon stocks (a), fluxes (b), and net ecosystem carbon balance calculated four ways (c) for subalpine forests of the central Rocky Mountains using only plots in the km^2 landscape. Shaded bars are live biomass (a) and carbon gain fluxes (b) whereas clear bars are detrital carbon (a) and carbon loss fluxes (b). Landscapes are Fraser, Niwot, and GLEES. GLEES is a matrix of forest and meadows, so values for only the forest are also presented (G-Forest) as well as a landscape estimate based on mean values of forest and meadow combined with proportions of each cover type derived from classification (G-Prop). Error bars are standard errors of total live or detrital carbon (a), total carbon gain or loss (b), or NECB estimate (c) and are not applicable to the G-Prop estimates. Approaches to calculating NECB (c) include incorporating estimates of decay from forest floor and mineral soil (NECB w/both), assuming forest floor is at steady state (NECB w/o FF), assuming that mineral soil is at steady state (NECB w/o MS), and assuming that both forest floor and mineral soil are at steady state (NECB w/o both). For significant ANOVA difference between total pools and fluxes or components see Appendix S2.

mixed species and mixed ages, with the dominant species having 70–88% of the plot basal area (Table 2). Across all three sites, the average stand age (based on maximum age) at each plot was 199 years and was significantly lower at Niwot (Table 2). Canopy height and basal area were consistent across sites whereas LAI was highest at GLEES and stem density was highest at Niwot and lowest at GLEES (Table 2).

Objective 2: time since disturbance vs. stand age using all forested plots

Stand age was a poor predictor of time since disturbance. Linear regression showed large biases for forests of all ages compared with a 1 : 1 line (Fig. 2). Stand age, as estimated from either maximum tree age or mean tree age, overestimated time since disturbance for young forests and underestimated it for older forests. The modern clearcuts (1980s) were the exception, and stand ages were consistently younger than time since disturbance. Unlike the modern clearcuts, harvests in the 1950s (F-50 = Fraser, clearcut 50 years ago) and the early 1900s (N-CON = Niwot, clearcut 100 years ago) did not remove or cut all trees, and almost all plots on these sites had trees older than the time since disturbance. Stand age in our oldest stands was substantially less than the time since disturbance. Maximum age in F-320 (Fraser, established after a wildfire 320 years ago) averaged 276 years (range 207–334). Maximum age at G-OLD (GLEES, no known disturbance) averaged 242 years, with a range of observed stand ages between 73 and 568 years.

Objective 3: effect of tree age and time since disturbance using all forested plots

Stand structure varied with both stand age (maximum tree age) and time since disturbance ($P < 0.0001$), and the shape of the response was similar for both metrics (Fig. 3). Height, leaf area, and basal area all increased with stand age, while stem density decreased with stand age. At the plot level, stand age explained more of the variance in these structural variables than did time since disturbance (Fig. 3, Table 3). Stem density

Table 2 Biome and site-level means and standard errors of age, stand structure and species composition for three small subalpine forested landscapes in the southern Rocky Mountains

	Site			
	ALL	Fraser	NIWOT	GLEES
Maximum Age (year)	199 (16)	246 (11)	*137* (15)	213 (23)
Canopy height (m)	11.9 (0.5)	12.9 (0.4)	10.8 (0.2)	12.1 (0.9)
Projected leaf area ($m^2\,m^{-2}$)	5.6 (0.6)	4.9 (0.5)	4.1 (0.4)	*7.7* (0.9)
Stem density (trees ha^{-1})	2416 263	2218 185	*3697* 372	*1331* 231
Basal area ($m^2\,ha^{-1}$)	47.0 (4.2)	41.4 (3.1)	47.9 (3.2)	51.8 (6.3)
% Lodgepole pine	30% (3%)	30% (6%)	61% (5%)	0%
% Subalpine Fir	19% (2%)	24% (4%)	18% (3%)	15% (4%)
% Engleman Spruce	51% (3%)	46% (5%)	17% (3%)	85% (6%)
% Trembling Aspen	0% (1%)	0%	1% (3%)	0%
% Limber Pine	1% (0.2%)	0%	2% (1%)	0%

Italics indicate significant ($P<0.05$) differences between sites.

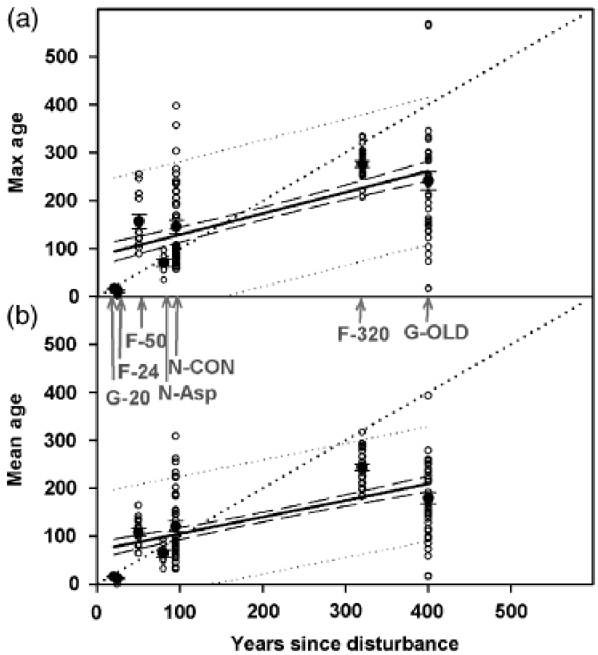

Fig. 2 Stand age as a function of time since disturbance for all forested plots at Fraser, GLEES and Niwot in subalpine Rocky Mountain forests. Stand age is expressed as either the maximum observed age (a: $\text{MaxAge} = 0.441 \times \text{DTime} + 85$, $r^2 = 0.35$) or the mean age of the 3–5 largest trees (b: $\text{MeanAge} = 0.345 \times \text{DTime} + 71$, $r^2 = 0.35$). Open symbols are individual plots, black symbols with error bars are means and standard errors of each forest stand, labeled arrows identify the stands (see Table 1 for abbreviations) and dotted line is 1 : 1. This figure illustrates how measurements of tree age often overestimate time since disturbance for young forests and underestimate time since disturbance for old forests.

was poorly related to both stand age ($r^2 = 0.11$) and time since disturbance ($r^2 = 0.16$).

Ecosystem carbon stocks all increased with stand age and time since disturbance ($P<0.0001$, Fig. 4). Total carbon, live carbon and aboveground carbon had the strongest relationships with stand age and the largest increases. Detrital and belowground carbon increased less and had weaker relationships with stand age.

NPP, live biomass increment, litterfall, and total decomposition all increased with both stand age and time since disturbance whereas NECB decreased ($P<0.0001$, Fig. 5). However, none of these relationships accounted for more than 25% of the variability among plots. Most of the change in carbon flux with time occurred in the first 100 years after disturbance, with little to no change after that (Fig. 5).

Stand age explained more of the plot-level variability in carbon stocks and fluxes than did time since disturbance, yet had higher average errors than predictions based on time since disturbance (Table 3). Of the 15 carbon stock and flux variables with >10% of their variation explained by stand age, regression on time since disturbance yielded lower RMSE and lower r^2-values for every variable except litterfall. Applying stand age data to a disturbance relationship or vice-verse increased RMSE of the predictions from between 23% and 950% (Table 3).

Discussion

Variability among sites using the km^2 samples

Carbon pools and especially carbon fluxes were remarkably consistent across these three sites. Despite differences in elevation, climate, disturbance type, management history, and tree species composition, all three sites displayed similar patterns of the size of carbon pools, the magnitude of carbon fluxes and the partitioning of pools and fluxes into component parts (Fig. 1, Appendix S2). These similarities suggest that it would be reasonable to treat subalpine forests in the

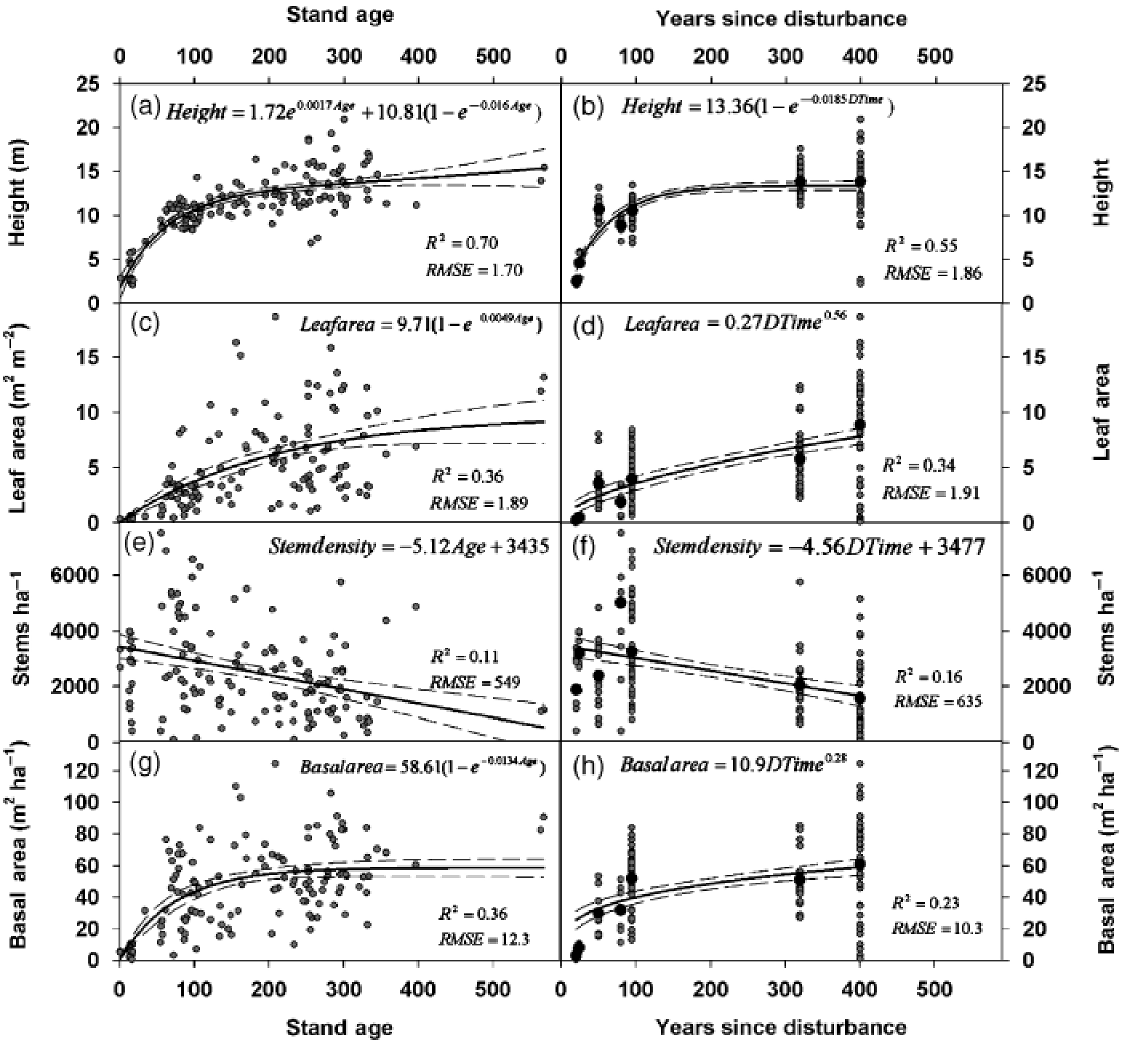

Fig. 3 Stand structural variables as a function of either stand age (Age) or time since disturbance (DTime) for all forested plots at Fraser, GLEES and Niwot. Stand age is maximum observed tree age. Response variables include tree height (a and b), projected leaf area (c and d), stem density (e and f), and basal area (g and h). Solid line is best-fit regression on either plot age or time since disturbance, dashed line is 90% confidence interval of the regression. Gray symbols are individual plots and black symbols in regressions on time since disturbance are stand means.

central Rocky Mountains as a single entity in large-scale assessments, particularly if they have not been disturbed in the past 100 years. All km^2 samples contained plots with a wide range of stand ages, and any large sample would likely include a similar range of conditions, suggesting that these estimates of carbon stocks and fluxes might apply even to landscapes where a portion had been recently disturbed. Furthermore, our estimates of stand structure, carbon pools and carbon fluxes are consistent with other studies in subalpine rocky mountain forests (Table 4).

Our results suggest some patterns that may be important for large-scale carbon assessments. Not surprisingly, trees consistently comprise $>80\%$ of the live biomass, and tree primary production (live biomass increment and litterfall) represents almost 70% of total production (Fig. 1, Appendix S2). Carbon stored in understory vegetation is small, and accounts for only 6% of total carbon. Production of understory vegetation can represent a more substantial fraction of primary production in young forests or sites like GLEES, which is a mosaic of forest and meadow. These forests consistently store over 25% of total ecosystem carbon in the forest floor, implying that understanding the input and decomposition for this pool may be necessary for accurate carbon accounting. Some of the minor variation among sites can be attributed to disturbance history. For example, carbon stored in woody detritus was highest at GLEES, probably because of the lack of logging. In contrast, woody detritus was much lower at

Table 3 Regression results for stand structure, carbon pools, and carbon fluxes as a function of measured tree age or time since disturbance in subalpine rocky mountain forests

Dependent variable	Age regression		Disturbance regression		Age using disturbance relationship		Disturbance using age relationship	
	r^2	RMSE	r^2	RMSE	RMSE	RMSE increase (%)	RMSE	RMSE increase (%)
Tree height (m)	0.70	1.705	0.55	1.859	2.10	23	2.60	40
Leaf area ($m^2 m^{-2}$)	0.36	1.892	0.34	1.91	3.30	74	3.19	67
Stem density (ha^{-1})	0.11	549	0.16	635.8	1648	200	1625	156
Basal area ($m^2 m^{-2}$)	0.36	12.31	0.23	10.3	21.89	78	21.27	107
Total carbon	0.40	60.94	0.30	55.93	99.04	63	109.2	95
Aboveground carbon	0.42	41.53	0.34	39.63	66.25	60	70.31	77
Belowground carbon	0.21	20.12	0.12	15.03	43.49	116	44.89	199
Live carbon	0.42	36.1	0.31	32.86	58.92	63	62.17	89
Tree and sapling carbon	0.40	35.84	0.30	32.63	59.44	66	62.45	91
Understory carbon	0.06	0.677	0.03	0.447	2.76	308	2.85	537
Detrital carbon	0.22	29.17	0.14	23.9	62.86	115	65.80	175
Woody detrital carbon	0.20	18.81	0.17	17.54	41.23	119	42.33	141
Forest floor carbon	0.15	12.78	0.04	6.984	34.14	167	35.78	412
Mineral soil carbon	0.01	1.871	0.02	3.057	19.72	954	19.53	539
Net primary production	0.10	0.246	0.07	0.238	0.99	303	0.97	307
Tree and sapling biomass increment	0.10	0.138	0.05	0.127	0.75	440	0.72	469
Litterfall	0.19	0.19	0.22	0.215	0.48	154	0.46	113
Decomposition	0.15	0.234	0.06	0.158	0.61	160	0.66	318
Net ecosystem production	0.04	0.215	0.01	0.133	1.08	405	1.12	742

Coefficient of determination and root mean squared error (RMSE) for regressions based on age and time since disturbance characterize the strength of those predictive relationships. RMSE, increase in RMSE and landscape error for predictions from age of disturbance using the alternative predictor illustrate how confounding these variables substantially increases the average error and consistently influences overall landscape-scale errors. Carbon pool units are $Mg\,C\,ha^{-1}$; carbon flux units are $Mg\,C\,ha^{-1}\,yr^{-1}$.

Niwot and Fraser, where harvesting occurred 50–100 years ago and removed woody biomass. The consistent positive estimates for NECB (Fig. 1c) suggest that these forests are likely acting as carbon sinks, and implies that episodic events (i.e. fires, insect outbreaks, and harvesting) may release the carbon stocks that accumulate between events (Kurz & Apps, 1999; Fahey *et al*., 2005).

Stand age vs. disturbance history using all forested plots

Stand age, by any definition, was poorly related to time since disturbance in both young and old forests. Older trees present in the recently disturbed plots imply survival during the disturbances. Leaving smaller advanced regeneration and unmerchantable trees was a common management practice earlier in the 20th century, but more recent harvests involved clearcuts where all trees are removed. In older plots stand age was often substantially less than the time since disturbance suggesting that a substantial time lag occurred between disturbance and tree establishment, or that mortality and tree establishment was a continuous process since the last known disturbance. Despite the poor relationship between stand age and time since disturbance, the general shape of the relationships were similar between these two metrics and stand structure and carbon stocks and fluxes (e.g. compare right and left columns of Figs 3–5).

Patterns with age and disturbance history using all forested plots

Our predictive equations for stand structure variables were generally strong and consistent with previous studies. As stand age and time since disturbance increase, the patterns in height, leaf area basal area, stem density were similar to those observed in for forests in general (Horn, 1975; Oliver, 1981; Barbour *et al*., 1987) and in the Rocky Mountains in particular (Pearson *et al*., 1987; Peet, 2000).

Carbon pools increased with both stand age and time since disturbance, but some of the detrital pools had poor relationships. Although many studies have documented increases in total carbon and live carbon with age (Harmon *et al*., 1990; Janisch & Harmon, 2002; Wang *et al*., 2003; Peichl & Arain, 2006), patterns of

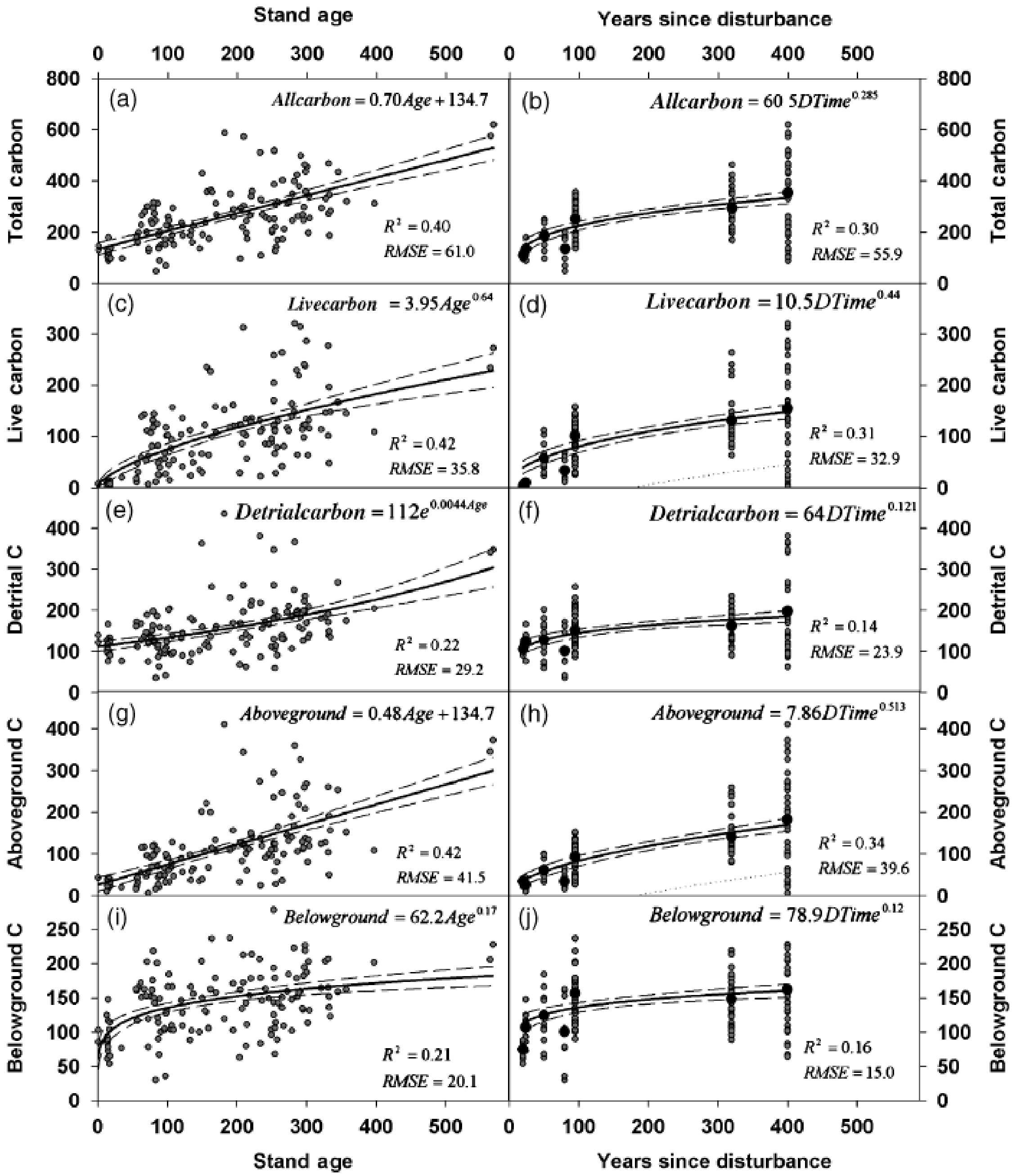

Fig. 4 Carbon pools as a function of either stand age (Age) or time since disturbance (DTime) for all forested plots at Fraser, GLEES and Niwot. Stand age is maximum observed tree age. All units are Mg C ha^{-1} and response variables include total carbon (a and b), live carbon (c and d), detrital carbon (e and f), aboveground carbon (g and h) and belowground carbon (i and j). Solid line is best fit regression on either plot age or time since disturbance and dashed line is 90% confidence interval of the regression. Gray symbols are individual plots and black symbols in regressions on time since disturbance are stand means.

detrital carbon are more variable, often displaying more complicated and inconsistent patterns with age, depending on the type and severity of disturbance (Clark *et al*., 1998; Janisch & Harmon, 2002; Yanai *et al*., 2003; Pregitzer & Euskirchen, 2004; Hall *et al*., 2006).

Carbon stored in forest floor is a challenging pool to model. The high amount of forest floor carbon at Fraser and Niwot, regardless of stand age, suggests that the logging 50–100 years ago left much of the forest floor. At Fraser, a basin-wide stand replacing fire in 1685 would have likely removed the forest floor, but the forest floor would have had a high biomass and been accumulating very slowly at the time of logging (Smith & Resh, 1999). At Niwot, the high stumps suggest that the logging

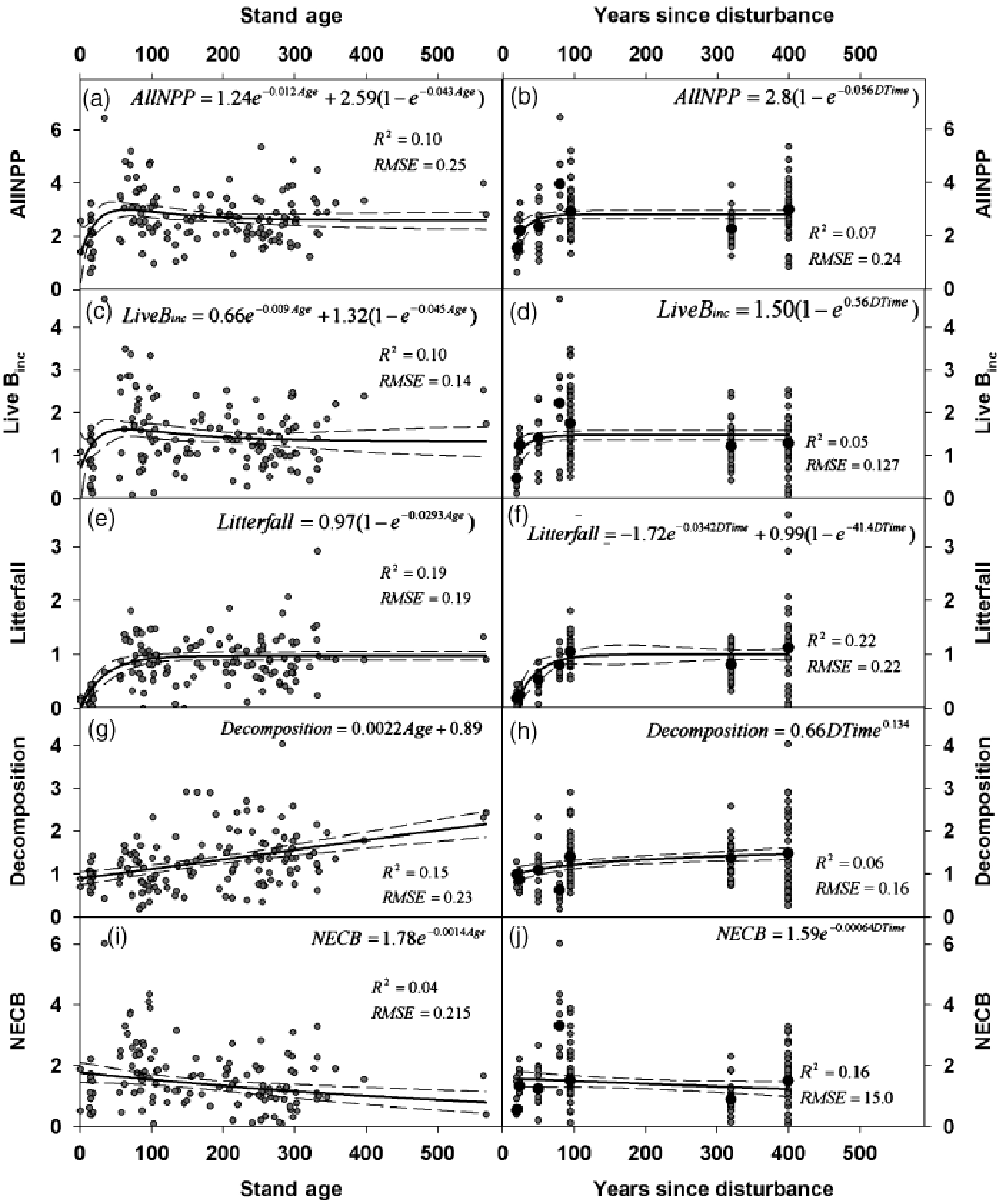

Fig. 5 Carbon fluxes as a function of either stand age (Age) or time since disturbance (DTime) for all forested plots at Fraser, GLEES and Niwot. Stand age is maximum observed tree age. All units are Mg C ha^{-1} yr^{-1} and response variables include total NPP (a and b), live biomass increment (LiveB$_{inc}$: c and d), litterfall (e and f), decomposition (g and h), and net ecosystem carbon balance (NECB: i and j). Solid line is best fit regression on either plot age or time since disturbance and dashed line is 90% confidence interval of the regression. Grey symbols are individual plots and black symbols in regressions on time since disturbance are stand means.

occurred in winter, where the snow would have protected and maintained the forest floor existing at the time of logging. These results suggest that knowing the type of disturbance may be necessary to understand forest floor dynamics, a conclusion that complicates efforts to characterize forest floor dynamics. Mineral soil carbon is fairly constant across stand age or time since disturbance compared with aboveground carbon, consistent with previous studies (Peichl & Arain, 2006).

Table 4 Mean (and range) of observations of stand structure, carbon pools, and carbon fluxes in subalpine rocky mountain forests

Location Species	Colorado and Wyoming* Pinus and Picea-Abies	Northcentral Colorado† Picea-Abies	Northcentral Colorado‡ Picea-Abies	Central Colorado§ Pinus and Picea-Abies	Southwestern Alberta¶ Pinus and Abies	Southeast Wyoming‖ Pinus
Age	158 (111–210)	325 (200–450)	250–500		90–350	75–240
Basal area	50 (45–53)	63 (36–104)	40 (16.4–72.9)	22–54	30–40	26–64
Leaf area index	5.6 (4.1–7.7)	9.2 (5.8–14.9)		4.4–24		4.5–9.9
Tree height	12 (10.8–12.9)		15–25			
Stem density	1224 (840–1820)	1140 (575–1700)			750–1700	420–14 000
Total carbon	287 (261–332)		210	160 (98–200)		
Aboveground tree carbon	91 (76–113)	127 (65–244)	62 (12–74)	85 (45–116)	76	62 (45–72)
Belowground tree carbon	20 (18–22)		8.5 (4–15)	9.3 (4.3–20)		21 (13–28)
Understory carbon	0.6 (0.1–1)			0.2 (0.02–5.2)		
Forest floor carbon	72 (62–84)		34 (12–74)	15 (8–25)		
Dead woody carbon	37 (17–60)		35 (2–78)	11 (2.5–28)		
Mineral soil carbon	61 (51–73)		63	27 (17–40)		
Net primary production	2.8 (2.3–3.1)		2.6 (1.5–3.8)		2.2–2.6	
Tree biomass increment	1.4 (1.1–2.0)	1.8 (1.3–2.6)	0.4 (0.2–7.5)	0.3 (0–0.7)		
Litterfall	0.9 (0.7–1.0)		0.9 (0.5–1.4)	0.74 (0.34–1.1)		

Studies are:
*This study.
†Binkley *et al*. (2003).
‡Arthur & Fahey (1992).
§Kueppers & Harte (2005).
¶Prescott *et al*. (1989).
‖Pearson *et al*. (1984).

Stand age or time since disturbance were only marginally related to carbon fluxes. In contrast to previous studies (Pearson *et al*., 1987; Gower *et al*., 1996; Ryan *et al*., 1997; Chen *et al*., 2002; Wang *et al*., 2003; Bond-Lamberty *et al*., 2004), neither tree biomass increment nor NPP declined in older stands. In these subalpine forest stands, tree biomass increment and litterfall rapidly increased with stand age until age 100, then was constant for older plots. While we do not know the age distribution for all trees on the plot, the variability in age for the largest trees we sampled suggests that most plots contain trees with diverse ages. These multiple-age plots may not show the typical pattern of declining NPP of even-aged stands (Gower *et al*., 1996; Ryan *et al*., 1997), because the more rapid growth of the younger trees may offset the slower growth of the older trees.

NECB declined over time and was only weakly related to stand age or time since disturbance. This finding contrasts with previous biome-wide studies that show that forests have an inverted U-shaped pattern of NECB with time since disturbance – NECB is initially negative in young stands as the trees killed in the disturbance decompose, is highest in early middle-aged forests and declines to near zero for very old forests (Bond-Lamberty *et al*., 2004; Euskirchen *et al*., 2006). The inconsistency with prior studies and the weak trends in NECB over time in our study is likely related to the type of disturbance and the mixed ages in many of the stands we examined. The youngest stands in our study were all harvested, with much of the woody biomass taken off site. If the trees were killed and left to decompose, NECB would likely have been negative for the youngest stands. Because aboveground NPP is a large component of NECB, the multiple tree ages in our plots would also minimize the decline in NECB with forest age. These mixed-age stands and prior logging are typical of many forests, suggesting predicting NECB from forest age for large-scale surveys may be difficult. Most of the important carbon fluxes, including NPP, B_{inc} and litterfall were consistent after stand age or time since disturbance reached 100 years. This consistency of carbon fluxes in mature forests provides an opportunity to simplify how older forests are represented in modeling and carbon accounting efforts.

Our results suggest that some stocks and fluxes are important yet not well captured by age-dependent relationships. For example, the proportion of production accounted for by understory vegetation was surprisingly high, averaging almost 20% and ranging from 11% to 37% of NPP (Appendix S6), yet neither tree age nor time since disturbance predicted even 10% of the variation in understory production (Appendix S7 and 8). Likewise, forest floor and woody detritus account for 25% and 11% of total ecosystem carbon, yet were not well predicted by age or time since disturbance, suggesting that these detrital pools may be influenced as much by the type of disturbance as the time of disturbance. Considering that remote sensing has not yet effectively quantified detrital carbon pools or fluxes of carbon from these pools, accurately relating these variables to stand age and/or disturbance would be extremely useful. However, much of the variation in ecosystem carbon is in live carbon and detrital pools are more consistent across ages and sites, suggesting that detrital pools can be effectively represented by more general models.

The consequences of confounding age and disturbance history

Confounding stand age and time since disturbance will result in dramatically increased errors for individual plot predictions, reflected in large RMSE increases (Table 3). Compared with predictions based on stand age, predictions based on time since disturbance have higher accuracy (lower RMSE), yet explain a smaller proportion of variance in the response variable (lower r^2). These results indicate that stand age provides the best insight into individual plot conditions while time since disturbance represents a more integrated stand-level measure of disturbance history and successional status.

Conclusions

These results have several implications for efforts to apply age-dependent relationships to understand forest carbon cycling and storage. First, the surprising consistency that we observed among sites supports modeling these diverse areas as a single forest type. Second, all carbon pools and fluxes were related to both stand age and time since disturbance, implying that measures of forest age can be useful for understanding and assessing carbon stocks and fluxes in these forests. Third, carbon stocks and fluxes change little after the first 100 years following stand replacing disturbance, suggesting that a focus on recent disturbance is key, and that knowing the age or disturbance history of older forests is less important. Fourth, observed stand age is poorly related to time since disturbance, that discrepancies between the two occur in young and old forests, and that confounding these variables consistently increases errors. This suggests that relationships based on stand age or disturbance history are not interchangeable.

Despite several studies that illustrate age-related patterns in forest carbon storage and cycling, few studies characterized the associated error estimates that can be easily used by simulation models. Our presentation of the uncertainty in both model selection and parameter estimation within individual models (Appendix S7) should provide valuable insight about the relative strength of age-dependent relationships and assist in the error assessment of modeling efforts that use age or disturbance history as a driving variable.

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Supporting Information

The following Supporting Information for this article is available online:

Appendix S1. References for allometric equations used to estimate leaf area index and carbon stocks from DBH and height measurements for the four dominant species in subalpine Rocky Mountain forests.

Appendix S2. Stand structure means and standard errors for all plots, each site and each stand.

Appendix S3. Carbon pool means and standard errors for all plots, each site and each stand.

Appendix S4. Carbon pool Partitioning means and standard errors for all plots, each site and each stand.

Appendix S5. Carbon flux means and standard errors for all plots, each site and each stand.

Appendix S6. Carbon flux partitioning means and standard errors for all plots, each site and each stand.

Appendix S7. Model selection results for stand structure, carbon pools and carbon fluxes as a function of time since disturbance.

Appendix S8. Model selection results for stand structure, carbon pools and carbon fluxes as a function of maximum tree age.

Additional Supporting Information may be found in the online version of this article.

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