

Management trade-off between aboveground carbon storage and understory plant species richness in temperate forests

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Abstract. Because forest ecosystems have the capacity to store large quantities of carbon (C), there is interest in managing forests to mitigate elevated CO₂ concentrations and associated effects on the global climate. However, some mitigation techniques may contrast with management strategies for other goals, such as maintaining and restoring biodiversity. Forest thinning reduces C storage in the overstory and recruitment of detrital C. These C stores can affect environmental conditions and resource availability in the understory, driving patterns in the distribution of early and late-seral species. We examined the effects of replicated ($N = 7$) thinning experiments on aboveground C and understory vascular plant species richness, and we contrasted relationships between aboveground C and early- vs. late-seral species richness. Finally, we used structural equation modeling (SEM) to examine relationships among early- and late-seral species richness and live and detrital aboveground C stores.

Six years following thinning, aboveground C was greater in the high-density treatment and untreated control than in moderate- (MD) and variable-density (VD) treatments as a result of reductions in live overstory C. In contrast, all thinning treatments increased species richness relative to controls. Between the growing seasons of years 6 and 11 following treatments, the live overstory C increment tended to increase with residual density, while richness decreased in MD and VD treatments. The richness of early-seral species was negatively related to aboveground C in MD and VD, while late-seral species richness was positively (albeit weakly) related to aboveground C. Structural equation modeling analysis revealed strong negative effects of live overstory C on early-seral species richness balanced against weaker positive effects on late-seral species richness, as well as positive effects of detrital C stocks. A trade-off between carbon and plant species richness thus emerges as a net result of these relationships among species traits, thinning treatments, and live and detrital C storage. Integrating C storage with traditional conservation objectives may require managing this trade-off within stands and landscapes (e.g., maintain early-seral habitat and species within dense, C-rich forests and, conversely, live and detrital C stores in early-seral habitats) or separating these goals across scales and species groupings.

Key words: carbon mitigation; coarse woody debris; down wood; emergent properties; ground-layer plant communities; herbaceous layer; old growth; structural equation modeling.

INTRODUCTION

Management objectives on many forest ownerships, particularly on public lands, have broadened from a traditional focus on timber production to include a larger suite of ecosystem goods and services. Much of this shift in the United States and other regions of the world is due to an interest in conserving biodiversity (FEMAT 1993, Montréal Process Working Group 2009, Forest Europe 2011), often represented by the diversity of plant and animal species and habitat conditions (Lindenmayer et al. 2000, Chirici et al. 2012). Recent concerns about climate change have extended manage-

ment objectives further to include carbon (C) storage for the abatement of increases in atmospheric CO₂ (Pacala and Socolow 2004, McKinley et al. 2011). Such changes are particularly relevant in areas where easements and subsidies for C storage may provide an important economic incentive. C storage is closely related to timber production, and related practices may also apply to management for C (e.g., Tavoni et al. 2007). Although a few studies have provided data highlighting potential trade-offs or synergies associated with this broad suite of goals (Bradford and Kastendick 2010, D'Amato et al. 2011, Bradford and D'Amato 2012), it remains unclear how managing forests for C affects other important objectives, such as those related to biodiversity, adaptability, and resilience (Huston and Marland 2003, Puettmann et al. 2009). In particular, the majority of plant diversity in forests is found in the

Manuscript received 27 August 2012; revised 1 March 2013; accepted 12 March 2013. Corresponding editor: E. Cienciala.

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understory, yet few studies have drawn out the linkages among understory plant communities and forest C stores.

The relationship between C storage and plant diversity in forests is related to the broader longstanding discussion about diversity and productivity. Recent meta-analyses have shown that there is no single relationship between plant species richness and productivity, and that a combination of ecological and evolutionary factors may be influencing patterns (Gillman and Wright 2006, Pärtel et al. 2010). Little is known, particularly, about effects of forest management on the relationship between productivity and plant species richness (Leuschner et al. 2009, Reich et al. 2012). Experiments investigating the relationships between plant diversity and productivity (Hooper et al. 2005, Grace et al. 2007) and diversity and stability (Tilman and Downing 1994) have typically been restricted to a single vegetation layer, often herbaceous vegetation in grassland plant communities. However, recent meta-analyses suggest that these relationships differ between woody and herbaceous species, and between grasslands and forest communities (Laanisto et al. 2008). Although overstory vegetation in northern temperate forests can store upwards of 200 times more C than the understory (Smithwick et al. 2002, Ares et al. 2007), understory vegetation consisting of woody and herbaceous plant species contains about 2–10 times the number of plant species found in the overstory (Gilliam 2007). Resource availability, and productivity, in the understory is thus partly controlled by C storage in overstory (e.g., Gray et al. 2002, Reich et al. 2012). Therefore, the relationship between plant species richness and productivity in temperate forest ecosystems may be negative simply as a result of interactions between canopy layers, and among herbaceous and woody species.

Maintaining dense forests and extending rotations to manage forests for C storage (Thornley and Cannell 2000, Nunery and Keeton 2010) contrasts with the practice of forest thinning. Thinning is a common management activity that provides income for landowners and material for the wood manufacturing industry, while increasing vigor and growth rates of residual trees (Nyland 2002). Over the past two decades, forest scientists have made progress toward understanding how common management practices such as thinning can be applied to increase plant diversity and accelerate the development of late-successional habitat features (Thomas et al. 1999, Ares et al. 2009, Bauhus et al. 2009, O'Hara et al. 2010, Dodson et al. 2012). The focus on late-seral conditions resulted from large reductions in extent of old growth in temperate forests and concern for associated species (FEMAT 1993, Lorimer and White 2003, Nonaka and Spies 2005). For example, the low mobility of late-seral plant species, in conjunction with low growth rates (i.e., shade tolerance) and long pre-reproductive periods can lead to a limited spatial

distribution as a result of time lags between the recovery of forest structure and associated understory conditions and the recolonization (Givnish 1982, Miller et al. 2002, Whigham 2004, Wyatt and Silman 2010, Burton et al. 2011). Scientists have recently grown more concerned about the role of traditional forestry practices in reducing the abundance and structural complexity of early-successional habitats on the landscape and within late-seral stands (Swanson et al. 2011, Donato et al. 2012). In contrast to late-seral species, early-seral species are typically good colonizers of disturbed areas (i.e., they are ubiquitous along edges, roadsides, and corridors), are shade intolerant and tall in stature, with faster growth rates and short pre-reproductive periods (Givnish 1988, Halpern 1989).

Although thinning apparently can accelerate the development of old-growth structural characteristics and increase abundance and richness of early-seral species, early-seral species can overtop and reduce the abundance and richness of late-seral species (Givnish 1982, Reich et al. 2012). Furthermore, thinning reduces C storage by lowering standing wood volume, as well as the amount of live wood transferred to detrital pools and eventually the soil, and may increase rates of heterotrophic respiration (Gough et al. 2007, Harmon et al. 2009, Stoffel et al. 2010, Forrester et al. 2012). This C stored as down wood can also provide a substrate for the establishment of plants, and increases resource and environmental heterogeneity in the understory (Harmon et al. 1994, Harmon and Sexton 1995, Campbell and Gower 2000, Spears et al. 2003, Devine and Harrington 2007, Kluber et al. 2009, Weaver et al. 2009).

At a global scale, species diversity, down wood, and carbon are considered key indicators of sustainable forest management (Forest Europe 2011, Montréal Process Working Group 2009), yet managers may not be able to maintain diversity and maximize the capacity for forests to store carbon simultaneously. Our first objective was to document patterns of understory plant species richness and C storage after thinning operations. Then, we investigated the relationship between carbon storage and understory plant species richness in more detail, specifically to distinguish different components of C storage and richness (i.e., early- vs. late-seral understory plant species).

METHODS

Study area

This study utilized large areas (i.e., study sites from 94 to 131 ha, with controls on 16 to 24 ha and thinning treatments on 14 and 69 ha) to allow for operational application of density management thinning treatments, and thus, avoiding the need to scale-up experimental results. Seven sites were selected to represent conditions in the Coast Range and western Cascade Range of northern Oregon, USA (Fig. 1). Seasonal and annual climate normals (1961–1990 averages) were obtained for each site based on geographic coordinates and elevation

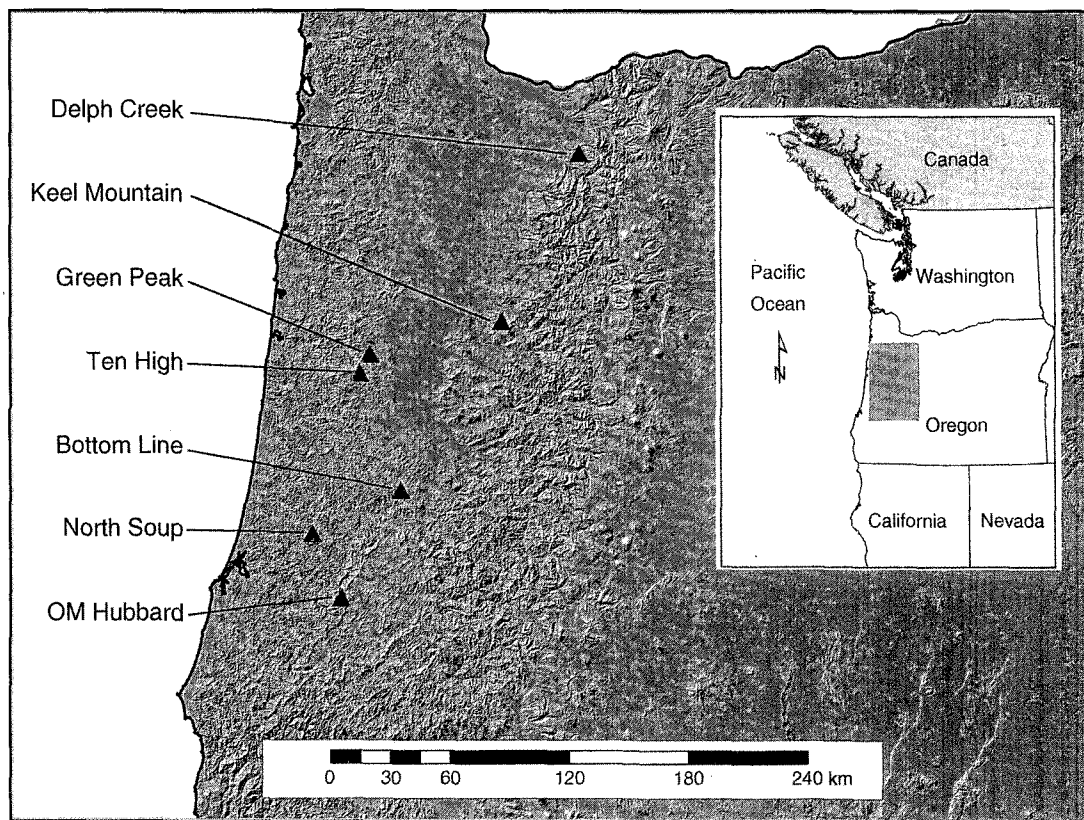


FIG. 1. Replicate experimental sites (triangles) in Oregon, USA. The main map layer highlights topography using 225° hill shading on a 10-m digital elevation model. The inset shows the location within the broader Pacific Northwest region (gray area).

from down-scaled spatial interpolations of monthly data, accounting for effects of local topography, rain shadows, coastal influence, and temperature inversions using ClimateWNA (Daly et al. 2002, Wang et al. 2012). Mean annual precipitation ranges from 1222 to 2559 mm, with little precipitation from June to August. Soils are moderately to very deep, poorly to well drained Ultisols and Inceptisols. Slopes range between 0% and 70%. Sites were occupied by 44- to 66-year-old conifer stands (at time of thinning; Cissel et al. 2006). At sites in the Coast Range ($n = 5$), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the dominant overstory species; at two sites in the western Cascade Range, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) prevails (i.e., Keel Mt. and Delph Creek) as a codominant with Douglas-fir.

Experimental design

The thinning treatments varied the residual tree densities and included a (1) high-density treatment with 300 trees/ha (HD); (2) moderate-density treatment with 200 trees/ha (MD); and (3) variable-density treatment with 300 trees/ha, 200 trees/ha and 100 trees/ha (VD). In HD and MD, 3–11% of the stand area was left unthinned in circular leave island reserves (i.e., patches of undisturbed forest trees). In MD, 3–10% of the area

was also cut in circular gap openings. In VD, 8.2–10.3% of the area was preserved in leave islands, and 8–17% of the area was left in circular gap openings. The sizes of gap openings and leave islands were 0.1, 0.2, and 0.4 ha. In addition to comparisons among the three thinning treatments, effects of thinning treatments were assessed by comparison with untreated control (CON) areas (387–972 trees/ha).

One complete set of the thinning treatments was applied in 1997 in three sites, 1998 in one site, and in 2000 in three sites. For all treatments, smaller trees were cut preferentially in a “low thinning” (Smith et al. 1997), and residual trees were approximately even spaced. Gaps and leave islands were spaced throughout the thinning treatments to accommodate harvesting operations without apparent bias in overstory and understory conditions. Unmerchantable tree tops and slash from delimbing were treated operationally and left on site; slash treatments included lop and scatter, and piling and burning, but varied among and within sites. When bole delimbing was not completely accomplished on site, remaining limbs were removed at landings. Also, defective log portions were sometimes cut at landings. Slash left on landings or patches was piled and some piles were burned at most sites. There was no slash treatment at one site.

Field sampling

Vegetation was sampled at 77 permanent 0.1-ha circular overstory plots at each site during year 6 and year 11 post-treatment. Fourteen plots were randomly installed in CON and 21 in each of the thinning treatments, with the stipulation of locating plots >15 m from another plot or from treatment boundaries. Within each overstory plot, four 0.002-ha circular understory vegetation subplots were installed at 9 m distances in each cardinal direction from plot centers.

In each overstory plot, all trees ≥ 5.1 cm in diameter at 1.37 m aboveground were numbered, identified by species, and measured for diameter at breast height (dbh) using a diameter tape. The height of 16 trees per plot (10 conifers and 6 hardwoods) was measured using a laser hypsometer (Laser Technology, Centennial, Colorado, USA). We visually estimated total cover of each vascular plant species <6 m tall in the understory subplots using cover classes: 1%, 5%, and then in 10% increments. We followed the USDA Plant Database (USDA Natural Resource Conservation Service [NRCS], available online)⁵ for taxonomic nomenclature. Taxa were classified as either early- or late-seral depending on whether they achieved peak abundance in disturbed or mature undisturbed forest, respectively (Halpern 1989, Halpern and Spies 1995; Appendix A). Species richness was calculated as the number of vascular plant species in the four understory subplots (a total area of 80 m²) for all species combined, early-seral species, and late-seral species. Results from our nonmetric multidimensional scaling ordination analysis show that these are powerful indicators of general patterns of compositional turnover within sites (Appendix B).

During year 6 post-treatment, the following four main detrital pools were sampled: snags, stumps, and large and small coarse down wood (CDW_{Lrg} and CDW_{Sm}, respectively). In the overstory plots, all standing dead trees (snags) ≥ 5.1 cm in dbh and ≥ 1.37 m in height and >45° angle above the ground were numbered and measured for dbh with diameter tapes. All stumps (≤ 1.37 m in height) within the northeast quarter section of the overstory plot were measured for diameter and height with tapes. We measured CDW_{Lrg} (≥ 25 cm in diameter and ≥ 0.3 m in length, $\leq 45^\circ$ angle above the ground) along four 12.9-m transects connecting the centers of the understory subplots (Harmon and Sexton 1996). CDW_{Sm} (≥ 7.6 cm and < 25.4 cm in diameter at the large piece end, and ≥ 0.3 m in length) was measured within the understory subplots. All pieces with their large ends inside the subplots were measured. Diameter at both ends and total length of each piece (including any part extending outside the subplot) were recorded. All diameter measurements of CDW_{Lrg} and CDW_{Sm} were taken with calipers. Decay condition of all CDW

types was assessed using a five-class scale from 1 (least decayed) to 5 (most decayed; Maser et al. 1979). CDW was not sampled in year 11 post-treatment.

Detailed descriptions of site conditions, treatments, and measurement protocols are provided by Cissel et al. (2006). General trends in overstory development and understory vegetation have been previously reported (Cissel et al. 2006, Fahey and Puettmann 2007, 2008, Ares et al. 2009, 2010, Dodson et al. 2012).

Calculations of C stores

Live overstory.—We estimated biomass of above-ground tree components (bole, bark, live and dead branches, and foliage) from dbh and height for Douglas-fir and western hemlock with BIOPAK (Means et al. 1994). Douglas fir comprised 72–98% of total above-ground biomass in the coastal range sites, and 51–56% in the Cascades sites. For the rest of the tree species in the plots, BIOPAK rendered estimates of total above-ground biomass from dbh only as reliable biomass equations using height data were not available.

Missing tree heights for Douglas-fir and western hemlock were imputed using multilevel mixed effects model (Robinson and Wykoff 2004). The model form was

$$H = 1.37 + [b_0 + b_1 \times D^{b_2} + \phi_T + \phi_S + \phi_P]$$

where H is total tree height (m), D is diameter at breast height (cm), b_i 's are parameters estimated from the data, and ϕ_T , ϕ_S , and ϕ_P are random effects for species, site, and plot, respectively. Residual analysis indicated that this model form was more effective than others. The model had a root mean square error of 2.8 m.

Snags.—To estimate snag C, branch C and foliar C was subtracted from live tree biomass calculated from BIOPAK.

Stumps.—Stump volume (S) was calculated as

$$S = 7.854 \times 10^{-5} \left(B + \frac{T}{2} \right)^2 \times \frac{H}{100}$$

where B and T are the stump basal and top diameters (in cm), respectively, and H is stump height (in cm).

Coarse downed wood.—CDW_{Lrg} volume (m³/m²) was calculated as

$$\text{CDW}_{\text{Lrg}} = 9.869 \times \sum \frac{D^2}{8L}$$

where D is the log diameter (in m) and L is the total transect length (in m) (modified from Harmon and Sexton [1996]). We estimated CDW_{Sm} volume (m³/m²) using Smalian's formula:

$$\text{CDW}_{\text{Sm}} = 3.927 \times 10^{-5} (S^2 + L^2) \times M$$

where S and L are small- and large-end diameters (in cm) and M is length in m.

The volume of snags, stumps, and CDW_{Lrg} and CDW_{Sm} were converted to biomass by decay class using

⁵ <http://plants.usda.gov>

the specific gravity values reported by Ares et al. (2007). The biomass of tree components as well as snags, stumps, and CDW was converted to carbon using conversion reported by Ares et al. (2007). A C content of 0.5 kg C/kg was used for tree species other than Douglas-fir and western hemlock.

Statistical analysis

Mixed-model analysis of variance (ANOVA) was used to examine thinning treatment effects on understory plant species richness and aboveground C stocks (i.e., total aboveground C, live overstory, total CDW, and CDW by size and decay classes, snags, and stumps). Additionally, we examined the differences in C storage in the live overstory (overstory C increment) and richness between year 6 and year 11 post-treatment. Plots within treatment units were averaged prior to analysis. Thinning treatment (i.e., HD, MD, VD, and CON) was a fixed effect, and site was modeled as a random effect to control for underlying differences among sites (Littell et al. 1996). We compared treatment means using pairwise comparisons (Tukey's honest significant difference was used to correct *P* values for multiple comparisons) and orthogonal contrasts.

To reflect the spatial scale of plant interactions, relationships among species richness (i.e., all species, early-seral species, and late-seral species), treatments (HD, MD, VD, and CON), and total aboveground C were analyzed at the plot scale (i.e., subsamples within treatment units) using mixed models of fixed effects (treatments, aboveground C, and the interactions thereof) and random effects to account for differences among sites and nesting of plots within treatment units. In case of significant interactions, we tested the null hypothesis of no relationship between understory plant species richness and aboveground C for each treatment (CON, HD, MD, and VD), and then compared treatment slopes to test the null hypothesis of equal slopes between treatments. We used the mixed procedure of SAS 9.2 (SAS Institute 2004) for all mixed-effects models. Larger scale treatment effects have been reported on previously in Ares et al. 2009, and 2010, and Dodson et al. 2012.

Structural equation modeling.—To examine the network of relationships among C stores and richness of early- and late-seral plant species driving the relationship between C and understory plant diversity, we used a structural equation modeling approach (SEM). First, we developed a "meta-model" to conceptually delineate ecological relationships among carbon pools and the richness of early- and late-seral species (Grace et al. 2010). Then, conceptual variables from the meta-model were replaced with measured indicator variables for the analysis. SEM analysis permits statistical tests for the overall structure of the model (i.e., lack of fit between the observed and predicted covariance matrices), as well as standardized quantification and comparison of direct, indirect (i.e., mediation), and total effects (i.e., the sum

of all direct and indirect effects). Standardized effects are path coefficients standardized by their standard deviation (Grace and Bollen 2005); however, statistical tests are performed on the unstandardized coefficients. Although model fit is more sensitive to a lack of significant paths than the inclusion of nonsignificant paths, paths that were not significant ($P > 0.05$), or did not improve model fit (i.e., AIC) were excluded from the final model.

In the meta-model (Fig. 2), we postulated negative effects of overstory C on early-seral species richness arise as a result of low resource levels in the understory. In contrast, we hypothesized effects of overstory C on late-seral species richness would be positive as a result of the ability of late-seral species to tolerate low-resource levels, low colonization rates, as well as suppression of competitive early-seral species (Fig. 2). For detrital pools, we hypothesized that early-seral species richness is positively related to CDW in early stages of decay (classes 1, 2, and 3) because CDW can ameliorate harsh environmental conditions following thinning and lead to a pulse in nutrient availability locally as a result of bark decomposition (Harmon et al. 1994, Devine and Harrington 2007, Kluber et al. 2009). However, because it can interfere with access to mineral soil and associated resources, we hypothesized that early-seral species richness was negatively affected by CDW in late stages of decay (classes 4 and 5). These relationships with CDW may switch for late-seral species. We hypothesized that late-seral species richness is negatively related to CDW in early stages of decay as a result of direct disturbance, and positively related to CDW in later stages of decay as a result the slow release of nutrients to established vegetation and increased water retention during the dry part of the growing season (Harmon et al. 1994, Harmon and Sexton 1995, Campbell and Gower 2000, Spears et al. 2003). Snag C and stump C were hypothesized to have neutral effects (i.e., neither positive nor negative) on both early- and late-seral species richness.

To account for site-to-site variability, and indirect effects of site factors vs. thinning treatments, we included climate variables and potential productivity in our SEM. At the regional scale, aboveground C stores and the richness of early- and late-seral understory plant species can co-vary with potential productivity (i.e., site quality) and climate (Roberts and Gilliam 1995). The species pool and number of species that may be present at a site are directly related to climate and potential productivity, respectively. These site factors affect rates of C storage and can be reflected in the quantity of overstory and detrital C (Seidl et al. 2012, Fig. 2). Additionally, site factors can indirectly affect richness through effects on C storage.

Potential productivity was represented using site index, the height of dominant and codominant trees in an even-aged stand at age 50 (Larson et al. 2008). Site index was estimated for Douglas-fir at each site

following King (1966). To examine the relative roles of climate C stores and richness, and to control for these potentially confounding influences on the covariance of richness and C, we created a statistical composite variable using a two-stage compositing process to represent the general effect of multiple climate indicators, without sacrificing theoretical generality or interpretability (Grace and Bollen 2008). First, composite variables were developed by relating richness of early- and late-seral species to mean annual temperature (MAT), mean annual precipitation (MAP), proportion of precipitation as snow (PAS), and annual climatic moisture deficit (CMD) estimated from ClimateWNA (Wang et al. 2012) using generalized linear models (the GLM procedure; Appendix C; SAS Institute 2004). CMD integrates precipitation and temperature and an estimate of potential evapotranspiration (Hargreaves and Samni 1982) to estimate the moisture required to avoid drought stress (Wang et al. 2012). Then, predicted values from these models (Appendix A) were used in the SEM to represent effects of climate on richness of early- and late-seral species (e.g., Harrison et al. 2006, Grace et al. 2010, Burton et al. 2011).

The structural equation modeling analysis was performed in Amos version 20 (Arbuckle 2006). Modification indices were used to assess and incorporate unanalyzed correlations among variables. Snag C, stump C, and CDW in early and late stages of decay were log-transformed using natural logarithms to meet the assumption of multivariate normality, which improves the accuracy of statistical tests of overall model fit as well as individual paths (Shipley 2000). These transformations resulted in a multivariate kurtosis of -1.2 , and were more effective at improving multivariate normality than transformations of richness.

RESULTS

Carbon stores

By the sixth growing season after thinning, MD and VD treatments stored 78.2 ± 13 Mg/ha less above-ground total C than CON and HD ($T = -6.01$, $df = 18$, $P < 0.001$; Fig. 3a). C stored in the live overstory was greater in CON by an average of 67.2 Mg/ha than in the thinning treatments ($T = 6.31$, $df = 18$, $P < 0.001$), which did not differ significantly from one another (Table 1). Between years 6 and 11 post-treatment, live overstory C increased in all treatments (Fig. 3c). Although live overstory C increment was lower in thinning treatments with lower residual tree densities, this trend was not statistically significant ($P > 0.05$).

The largest C stock in CDW was in the large size class with diameters ≥ 25 cm (CDW_{Lrg}) and in logs that were in later stages of decomposition (Table 2); highlighting that most of this C was most likely a legacy from previous stands. C stored in snags and stumps did not vary among treatments. However, C stocks differed among treatments when CDW data were separated by

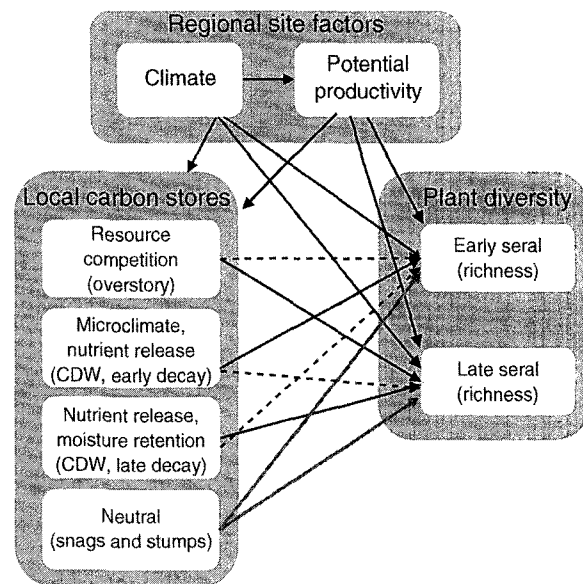


FIG. 2. Hypothesized meta-model guiding structural equation modeling analysis. Ecological relationships between carbon pools and diversity are represented in boxes; indicator variables used in the analysis are in parentheses. Straight, solid arrows denote positive effects, while dashed arrows show negative effects of variables. Hypothesized neutral relationships are marked with gray arrows. CDW stands for coarse down wood; "early decay" includes decay classes 1–3, and "late decay" includes decay classes 4 and 5.

decay class (Table 2). Specifically, C in CDW_{Lrg} in decay class 2 was greater in HD than in CON (difference = 3.8 Mg/ha, $T = -3.16$, $P = 0.03$), MD (difference = 3.5 Mg/ha, $T = -3.16$, $df = 18$, $P = 0.03$), and marginally greater in VD (difference = 3.4 Mg/ha, $T = -2.78$, $df = 18$, $P = 0.05$). Additionally, snag C in decay class 2 was greater in CON than in both HD (difference = 2.1 Mg/ha, $T = 3.09$, $df = 18$, $P = 0.03$) and VD (difference = 2.8 Mg/ha, $T = 4.24$, $df = 18$, $P = 0.003$), while MD was intermediate and did not differ from CON, HD, or VD (Table 2). Other detrital C stocks, such as stumps (note, that this included stumps from trees harvested prior to establishment of the current stand), and CDW_{Sm} did not differ among treatments.

Understory plant species richness

In contrast to patterns of aboveground C, understory plant species richness was higher in all thinning treatments than in CON (Fig. 3b). Species richness did not differ significantly among thinning treatments in year 6 post-treatment. Thinned treatments (HD, MD, and VD) contained 11.9 ± 1.4 species more than untreated controls on average ($T = 8.62$, $df = 18$, $P < 0.001$). Between years 6 and 11 post-treatment, richness declined by 4.4 ± 0.6 more species in MD and VD than in CON and HD ($T = -7.3$, $df = 18$, $P < 0.001$). Differences in species richness between year 6 and 11 did not differ from zero in CON and HD (Fig. 3d).

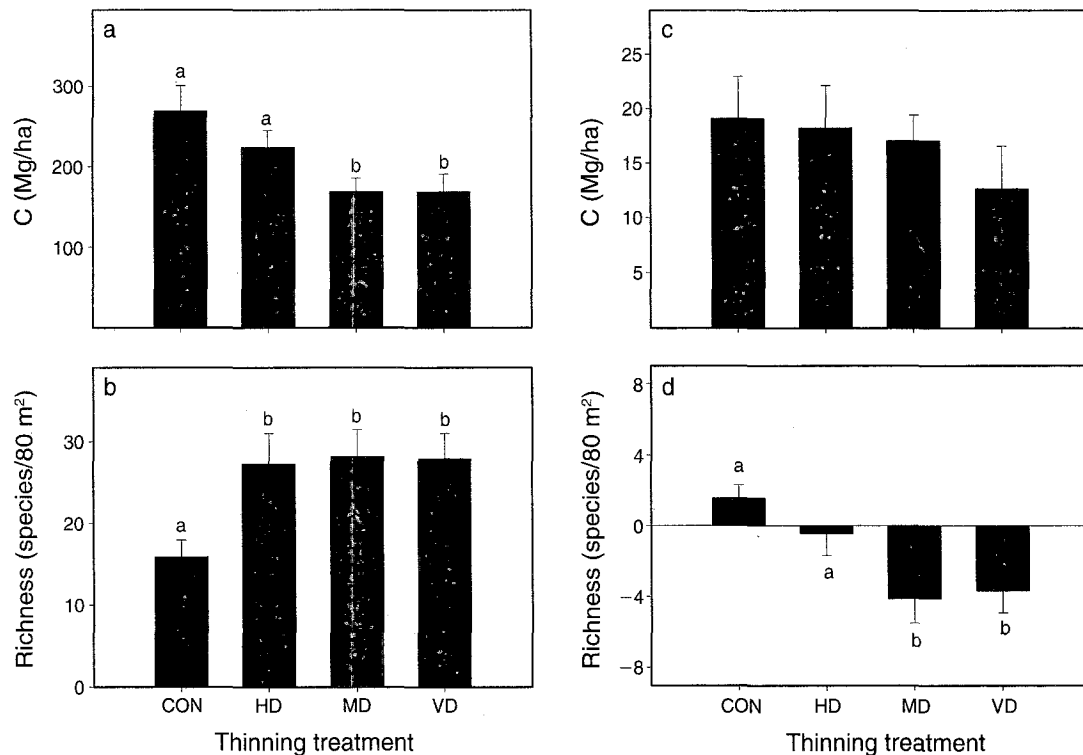


FIG. 3. (a) Total aboveground C and (b) understory plant species richness observed six years after thinning, and (c) differences in live overstory C and (d) understory plant species richness between years 6 and 11 post-thinning by treatment (CON, untreated control; HD, high-density treatment [300 trees/ha, includes leave islands]; MD, moderate-density treatment [200 trees/ha, includes leave islands and canopy gaps]; and VD, variable-density treatment [100, 200, and 300 trees/ha, includes leave islands and canopy gaps]; see *Methods: Experimental design* for details of leave island and gap inclusions). Shown are means $\pm$ SE. Lowercase letters indicate significant differences ($P \leq 0.05$).

Carbon–richness relationships

In year 6 post-treatment, species richness was related to aboveground C and thinning treatment. Evidence for an interaction between treatment and aboveground C was weak ($F = 2.42$, $df = 3$, 504, $P = 0.07$). The weak interaction resulted from the lack of a relationship between aboveground C and understory plant species richness in CON (slope estimate = -0.01 , $T = -1.1$, $df =$

504, $P = 0.27$) and HD treatments (slope estimate < -0.01 , $T = -0.01$, $df = 504$, $P = 0.99$). In contrast, in the MD (slope estimate = -0.02 ± 0.01 , $T = -2.5$, $df = 504$, $P = 0.01$) and VD (slope estimate = -0.03 ± 0.01 , $T = -3.3$, $df = 504$, $P < 0.01$) thinning treatments, the negative relationships between richness and C suggest a trade-off between richness and aboveground C.

The relationship between richness of early-seral species and C was similar to overall species richness

TABLE 1. Aboveground C stocks in live trees, snags, stumps, and large and small coarse downed wood (CDW) by treatment six years after thinning in western Oregon, USA.

Carbon stores	Aboveground C (Mg/ha), by treatment			
	CON	HD	MD	VD
Live trees	191.4 ^a $\pm$ 19.5	149.2 ^b $\pm$ 12.7	113.1 ^b $\pm$ 11.1	110.4 ^b $\pm$ 11.7
Snags	16.2 $\pm$ 2.0	19.0 $\pm$ 2.8	8.9 $\pm$ 1.5	10.4 $\pm$ 4.3
Stumps	7.5 $\pm$ 1.3	6.8 $\pm$ 1.1	7.8 $\pm$ 1.5	7.7 $\pm$ 1.6
CDW _{Lrg}	52.9 $\pm$ 13.3	47.1 $\pm$ 11.8	36.8 $\pm$ 8.7	38.7 $\pm$ 10.0
CDW _{Sm}	1.2 $\pm$ 0.2	1.6 $\pm$ 0.3	1.4 $\pm$ 0.3	1.3 $\pm$ 0.2
Total C	269.2 ^a $\pm$ 19.5	223.7 ^a $\pm$ 21.5	168.0 ^b $\pm$ 17.1	168.5 ^b $\pm$ 21.9

Notes: Abbreviations are: CON, untreated control; HD, high-density treatment (300 trees/ha, includes leave islands); MD, moderate-density treatment (200 trees/ha, includes leave islands and canopy gaps); and VD, variable-density treatment (100, 200, and 300 trees/ha, includes leave islands and canopy gaps; see *Methods: Experimental design* for details of leave island and gap inclusions). Values are means $\pm$ SE. Values followed by the same superscript letter in columns are not significantly different at $P \leq 0.05$. No significant differences were detected for treatment means not superscripted with letters.

TABLE 2. Carbon stores in snags, stumps, and large and small coarse downed wood (CDW) by decay class and treatment six years after thinning in western Oregon.

Carbon stores and treatment	Carbon stores (Mg/ha) by decay class				
	1	2	3	4	5
Snags					
CON	4.2 ± 0.9	3.8 ^a ± 0.7	3.6 ± 1.5	4.0 ± 1.2	0.5 ± 0.4
HD	5.3 ± 2.9	1.7 ^b ± 0.3	4.6 ± 1.4	5.9 ± 1.5	1.5 ± 1.1
MD	1.3 ± 0.4	2.5 ^{a,b} ± 0.6	2.9 ± 1.3	2.0 ± 1.2	0.3 ± 0.2
VD	1.3 ± 0.4	0.9 ^b ± 0.3	4.1 ± 2.4	3.9 ± 1.8	0.04 ± 0.02
Stumps					
CON	0.1 ^a ± 0.1	0.3 ± 0.1	2.8 ± 0.6	3.6 ± 0.8	0.8 ± 0.4
HD	1.0 ^b ± 0.2	0.4 ± 0.2	1.8 ± 0.5	3.2 ± 0.5	0.4 ± 0.4
MD	1.3 ^b ± 0.3	0.3 ± 0.1	1.8 ± 0.8	3.3 ± 0.8	1.0 ± 0.6
VD	1.1 ^b ± 0.3	0.6 ± 0.2	1.6 ± 0.5	2.8 ± 0.7	1.5 ± 0.7
CDW_{Lrg}					
CON	1.1 ± 0.3	1.2 ^a ± 0.6	22.1 ± 7.9	16.1 ± 4.4	12.4 ± 5.3
HD	1.4 ± 0.4	5.1 ^b ± 1.9	11.6 ± 2.5	19.0 ± 5.6	10.0 ± 4.1
MD	1.7 ± 0.4	1.6 ^a ± 0.6	10.8 ± 3.5	12.1 ± 3.0	10.7 ± 3.6
VD	0.9 ± 0.3	1.7 ^{a,b} ± 0.5	9.5 ± 2.5	13.9 ± 3.4	12.7 ± 5.8
CDW_{Sm}					
CON	0.15 ± 0.05	0.46 ± 0.13	0.37 ± 0.09	0.13 ± 0.04	0.10 ± 0.05
HD	0.33 ± 0.13	0.63 ± 0.15	0.39 ± 0.07	0.17 ± 0.03	0.05 ± 0.02
MD	0.26 ± 0.10	0.64 ± 0.16	0.36 ± 0.09	0.08 ± 0.02	0.03 ± 0.02
VD	0.25 ± 0.07	0.50 ± 0.11	0.36 ± 0.06	0.16 ± 0.04	0.05 ± 0.02

Notes: Key to treatment abbreviations: CON, untreated control; HD, high density (300 trees/ha, includes leave islands); MD, moderate density (200 trees/ha, includes leave islands and canopy gaps); VD, variable density (100, 200, and 300 trees/ha, includes leave islands and canopy gaps); see *Methods: Experimental design* for details of leave island and gap inclusions. Values are means ± SE. Values followed by the same letter in columns are not significantly different at $P \leq 0.05$. No significant differences were detected for treatment means not followed by letters.

(i.e., all species combined). However, evidence for an interaction between thinning treatment and C was stronger for early-seral species than for all species combined ($F = 2.84$, $df = 3$, 504, $P = 0.04$). As with overall species richness, relationships between richness of early-seral species and C were negative in MD (slope estimate = -0.02 ± 0.01 , $T = -3.8$, $df = 504$, $P < 0.001$) and VD (slope estimate = -0.02 ± 0.005 , $T = -4.56$, $df = 504$, $P < 0.001$) thinning treatments (Fig. 4) and not significantly different from zero in the HD ($T = -1.55$, $df = 504$, $P = 0.12$) treatment and CON ($T = -1.32$, $df = 504$, $P = 0.19$). The slope of the relationship between richness of early-seral species and C did not differ significantly between MD and VD ($T = 0.26$, $df = 504$, $P = 0.79$), or between HD and CON ($T = 0.10$, $df = 504$, $P = 0.92$).

In contrast to patterns for early-seral species, richness of late-seral species was positively related to above-ground C, increasing by one species for every increase in ~ 333 Mg C per hectare (slope = 0.003 ± 0.001 [mean ± SE]), $F = 5.95$, $df = 1$, 507, $P = 0.01$; Fig. 5). The richness of late-seral species was not related to treatment ($F = 0.88$, $df = 3$, 18, $P = 0.47$) or an interaction between treatment and C ($F = 2.20$, $df = 3$, 504, $P = 0.09$), so treatment was excluded the fixed effects of the final model. Our ordination analysis confirmed that patterns of richness were meaningful indicators of patterns of compositional turnover (Appendices A–C).

Structural equation modeling

The final structural equation model accounting for the hypothesized structure of the meta-model (Fig. 6) and unanalyzed correlations among variables showed no lack of fit ($\chi^2 = 14.4$, $df = 12$, $P = 0.28$). Together with site productivity and climate, C stores explained 45% of the variation in early-seral plant species richness and 23% of the variation in late-seral species richness. Overstory C was negatively related to early-seral species richness (standardized direct effect = -0.26), and positively related to late-seral species richness (standardized [std.] direct effect = 0.09). CDW C in early stages of decay (classes 1–3) was positively related to richness of early- and late-seral species (std. direct effect = 0.23 and 0.15 , respectively). CDW C in late stages of decay (classes 4 and 5) was negatively related to early-seral species (std. direct effect = -0.09) and positively related to late-seral species (std. direct effect = 0.08). Snag C was negatively related to early-seral species (std. direct effect = -0.09).

The influences of site productivity and climate were mainly related to direct effects of climate on early- and late-seral species richness; standardized total effects for climate were 0.53 and 0.43 for early- and late-seral species richness, respectively, with indirect effects on C stores accounting for only a small proportion of total effects (i.e., 0.06 and -0.02 , respectively). Standardized total effects for site index were comparably small (-0.08

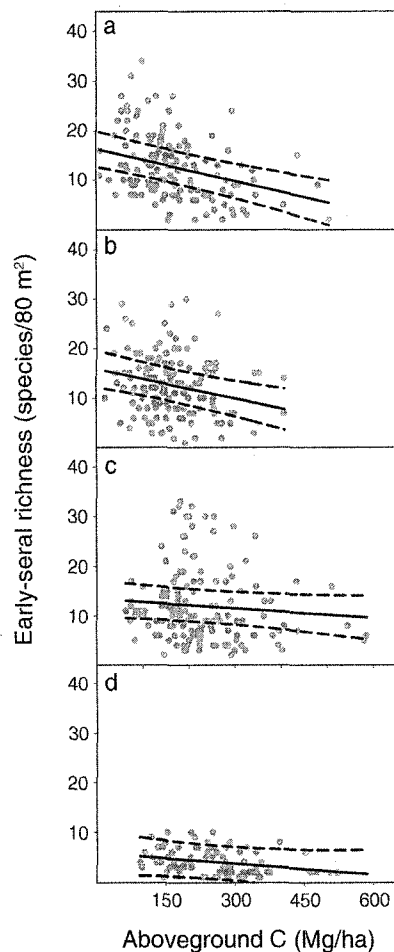


FIG. 4. Relationships between understory plant species richness (early-seral species) and aboveground carbon (C) in (a) VD, (b) MD, (c) HD, and (d) CON treatments (see Fig. 3 for clarification of the treatments). Solid lines are model estimates, and dashed lines show 95% confidence intervals. Points show observations from all sites. The random effect (site) is not shown.

and 0.02 for early- and late-seral species, respectively), and primarily a result of direct effects for early-seral species (standardized direct effects = -0.07) and indirect effects of site index on C stores for late-seral species (e.g., std. direct effect = 0.0). With the exception of the path coefficient from CDW C in late stages of decay ($P = 0.052$) and the unanalyzed correlation between snag C and CDW C in early stages of decay ($P = 0.073$) all unstandardized path coefficients were statistically significant ($P < 0.05$). Model fit is generally more sensitive to a lack of significant paths in the model than the inclusion of a nonsignificant path (e.g., Grace 2006).

DISCUSSION

Our results confirm that thinning results in a trade-off between maximizing C storage and promoting understory plant species richness, particularly the richness of early-seral species. However, late-seral species, which tend to be more tolerant of low-resource conditions in

the understory, seem to benefit from greater C storage levels associated with greater densities of live overstory trees. In conjunction with the structural equation modeling, these results suggest that the observed trade-off between understory plant richness and C storage can emerge after thinning as a result of complex positive and negative interactions among ground disturbance, overstory removal, C stocks, and the characteristics of understory plant species (e.g., shade tolerance, dispersal mechanism, and stature).

Effects of thinning on C storage

Consistent with other studies from this region, the live overstory comprised the largest stock of C aboveground (Smithwick et al. 2002); however, nearly one-third of the aboveground C was stored as CDW. These proportions likely represented a carryover from previous stands (Duvall and Grigal 1999), as the majority of CDW is in large size classes (≥ 25 cm diameter) and later stages of decay. The removal of live overstory C reduces rates of C recruitment into CDW in the short term, while potentially reducing belowground stocks in the forest floor and soil in the long term (Powers et al. 2012). Furthermore, as legacy wood continues to decompose over time, natural mortality patterns following thinning do not appear to be sufficient to maintain current sizes of CDW C pools (Dodson et al. 2012).

However, large differences in CDW C storage among treatments are not yet apparent, and our results show an initial increase in some thinning treatments. Greater CDW C storage in decay class 2 in the HD and VD treatments relative to the untreated control (CON) was not expected, but may be caused by greater levels of damage to residual trees (e.g., snags or low-vigor tree) in areas where high densities of trees are retained during harvesting operations. Significantly lower levels of snag C in decay class 2 in the HD and VD treatments relative to CON corroborate the observed increases in CDW C.

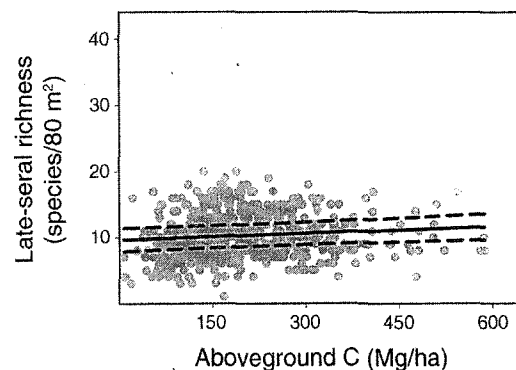


FIG. 5. Relationships between richness of late-seral plant species and aboveground carbon (C). Slopes and intercepts did not differ among thinning treatments; therefore, we did not plot treatments (CON, HD, MD, and VD) separately. Solid lines are model estimates, and dashed lines show 95% confidence intervals. Points show observations from all sites. The random effect (site) is not shown.

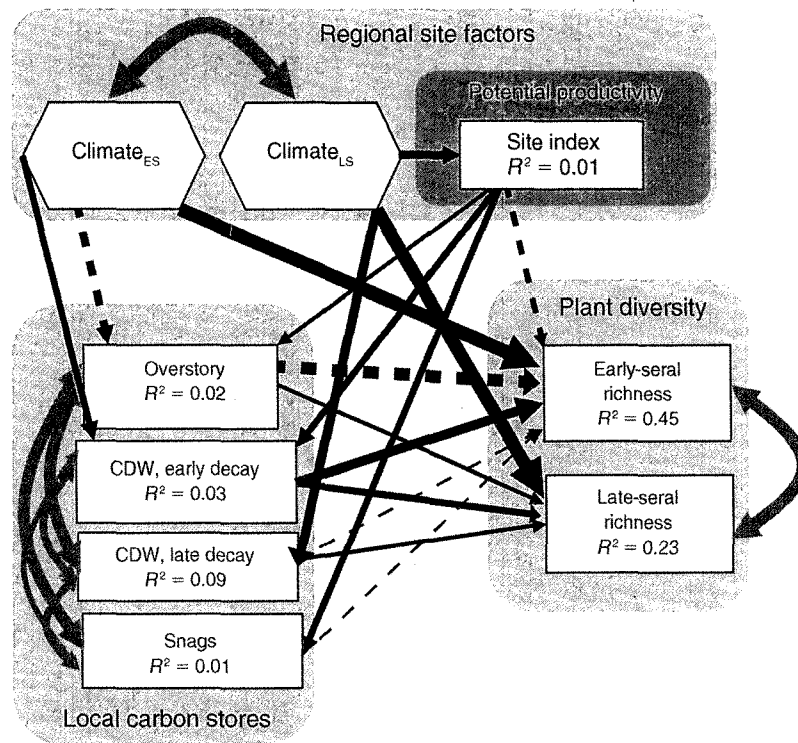


FIG. 6. Results of structural equation modeling analysis. Indicator variables are given in rectangles; composite variables are represented with hexagons. Dark solid lines indicate positive relationships between variables, and dark dashed lines indicate negative relationships. Line weight indicates the strength of the path relative to other paths in the model (i.e., standardized path coefficient). Unanalyzed correlations are shown as gray curved double-headed arrows. For endogenous variables, the proportion of variation explained is indicated (R^2). The final model fit well ($\chi^2 = 14.36$, $df = 12$, $P = 0.28$). CDW stands for coarse down wood; ES is early-seral species richness; LS is late-seral species richness; “early decay” represents decay classes 1–3, and “late decay” represents decay classes 4 and 5.

Furthermore, this pattern persisted following the removal of influential observations and transformations to improve residual patterns, suggesting that it is not merely related to initial differences among sites or treatment units.

Including forest floor and mineral soil C stores would likely lead to higher values of thinning related reductions of C storage in forests (Law and Harmon 2011). Initial losses may be related to increased rates of decomposition and litter inputs to soil (e.g., Covington 1981, Peltoniemi et al. 2004, Stoffel et al. 2010, Forrester et al. 2012, but see Yanai et al. 2003). Although, belowground C pools may recover over time (Cromack et al. 1999, McLaughlin and Phillips 2006, Powers et al. 2012), all treatments (thinned and unthinned) have most likely incurred a carbon debt as a result of clearcutting ~60–80 years ago (Rhemtulla et al. 2009). Thus, carbon pools in fully stocked untreated controls likely remain below the upper bound of on-site carbon storage for these sites (Smithwick et al. 2002, Peltoniemi et al. 2004).

C-diversity trade-off

A variety of mechanisms may contribute to negative relationships between aboveground C and plant species richness. First, thinning creates gaps in the overstory, altering the local microclimate and increasing resource

availability above- and belowground (Gray et al. 2002). Such changes in local abiotic environments interact with traits of individual plant species to drive changes in composition and structure of understory plant communities (Roberts and Gilliam 1995). Increases in resource availability associated with decreases in overstory C, and physical disturbance of the forest floor that provides safe sites for establishment, may explain the increased number of early-seral plant species (Fahey and Puettmann 2007, Ares et al. 2009, 2010).

However, decreased species richness over time (i.e., between years 6 and 11 post-treatment), suggests that increases in species richness following thinning are transient. Declines may be associated with competitive exclusion of late-seral species by early-seral species in the short term, while over the long term, late-seral species richness may increase (and early-seral species richness decreases) with canopy closure. Our previous work showed that declines in richness between years 6 and 11 were indeed associated with decreases in late-seral species, rather than in early-seral species (Ares et al. 2010). Thus, positive relationships between overstory C and late-seral species richness may be related to the role of canopy closure in reducing the abundance of competitive, early-seral species (Grime 1979, Reich et al. 2012). The relationship between overstory C and late-

seral species richness may be relatively weak due to dispersal limitation and pre-existing colonization deficits within second-growth stands (e.g., Vellend et al. 2007, Burton et al. 2011).

Most relationships between detrital C and richness corresponded to our original meta-model predictions (Fig. 2). Positive effects of CDW C on richness may be related to effects of CDW on environmental heterogeneity. For instance, recruitment of fresh down wood after thinning can reduce temperatures locally (Devine and Harrington 2007, Kluber et al. 2009), favoring a greater diversity of early-seral plant species. Initially and over time, as wood decays, CDW C may mediate nitrogen and water availability and provide germination sites for selected species (Harmon et al. 1994, Harmon and Sexton 1995, Campbell and Gower 2000, Spears et al. 2003, Weaver et al. 2009). The observed negative effect of snag C and early-seral species richness was not predicted, and it is not clear what process is responsible for this pattern. It may be related to safety considerations of loggers while harvesting, resulting in a lack of physical disturbance to the forest floor in the near vicinity.

Increases in the potential productivity associated with soil fertility (e.g., on mesic relative to xeric soils) and environmental conditions (e.g., lower climatic moisture deficit) can lead to both a greater diversity of plant species (e.g., Roberts and Gilliam 1995, Reich et al. 2001, Burton et al. 2011), as well as greater rates of productivity and carbon storage (e.g., Seidl et al. 2012). Thus, it is possible that positive relationships between species richness and C stores, such as CDW C, can arise as an artifact of common positive responses to potential productivity. Our results suggest that climate and potential productivity had direct effects on richness of early- and late-seral species as well as C stores; however, significant relationships between C stocks and richness existed that were independent of these regional site factors. This suggests differences in aboveground C stores and richness among treatments, and associated relationships among aboveground C and understory plant species richness were indeed driven primarily by thinning treatments.

In other ecosystems, such as grasslands, a trade-off between plant species richness and C may be alleviated to some extent by positive effects of plant species richness on productivity and stability (and hence C sequestration) due to sampling effects and niche complementarity (Tilman and Downing 1994, Hooper et al. 2005, Grace et al. 2007). In multilayered forest systems, however, any change in understory diversity will not likely have substantial short-term effects on productivity or C sequestration. The overstory layer influences understory plant species richness and is responsible for the majority of aboveground productivity and C storage. Yet, understory conditions likely have very little direct impact on overstory productivity in the short term. Over the long term, however, understory

vegetation can indirectly affect forest productivity through selectively filtering tree seedlings and thus changing overstory species composition (George and Bazzaz 1999a,b, Montgomery et al. 2010). Such feedbacks would be expected to be most important following disturbance, but may not manifest themselves as increased or reduced productivity and C storage until much later in the lives of those regenerating trees.

Conclusions

In summary, our results suggest linkages between C and plant diversity arise from positive and negative interactions among early- and late-seral plant species and different carbon pools as they mediate resources and environmental conditions in the understory. The net effect, or emergent property, of these interactions is a trade-off between vascular-plant species richness and C storage. Thinning and partial harvests can restore early-seral habitat and associated diversity within mature second-growth stands, whereas traditional forest management aimed at maximizing production tends to constrain these community or ecosystem properties (Ares et al. 2009, Swanson et al. 2011, Donato et al. 2012). Thinning can also accelerate development of old-growth characteristics within younger second-growth stands (Bauhus et al. 2009, O'Hara et al. 2010, Dodson et al. 2012). However, reductions in on-site C storage and late-seral species richness are also associated with thinning. Future work may confirm the generality these relationships, and elucidate the various mechanisms by which live and detrital C affects understory plant species using additional indicators (e.g., competition, resources, and micro-environment). Additionally, results may differ importantly among taxa. For instance, fungi and other saproxylic species would be expected to exhibit a greater dependence on CDW stocks (e.g., Siitonen 2001).

Integrating C storage goals into a larger suite of objectives (i.e., those articulated in FEMAT [1993], the Montréal Process Working Group [2009], and Forest Europe [2011]) requires an understanding of the linkages among species traits and different carbon stocks. In the case of negative relationships (i.e., trade-offs), plans that manage trade-offs, or that separate competing goals across temporal or spatial scales, may be required. For example, managers can reduce the trade-off between plant species richness and C storage by maintaining early-seral habitat and species within dense, C-rich forests or, conversely, by retaining live and detrital C stores in early-seral habitats. The latter likely also involves carefully preserving patches of undisturbed forest floor during logging operations. Alternatively, accepting trade-offs (i.e., tolerating some losses in realizing one management objective for the sake of gains in another) may require separation of goals across spatial and/or temporal scales and species groupings. Modeling tools may be required to delineate relation-

ships among harvesting (e.g., frequency and severity), carbon storage, and diversity.

ACKNOWLEDGMENTS

Funding was provided by the U.S. Department of Interior Bureau of Land Management (BLM) and the U.S. Department of Agriculture Forest Service. For their contributions to the study, we express our gratitude to Sara Mulford, Kathryn Ronnenberg, Andrew Neill, Aaron Weiskittel, and numerous dedicated field personnel, in addition to all participating BLM site coordinators. For discussions and helpful feedback, we also thank Paul Anderson, Rob Pabst, Maureen Puettmann, and Steve Voelker. The comments provided by two anonymous reviewers led to substantial improvements.

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SUPPLEMENTAL MATERIAL

Appendix A

List of understory vascular plant species by seral status (*Ecological Archives* A023-068-A1).

Appendix B

Detailed description of nonmetric multidimensional scaling analysis: methods and results (*Ecological Archives* A023-068-A2).

Appendix C

Figure depicting the relationships of climate variables to statistical composites used in structural equation models (*Ecological Archives* A023-068-A3).