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ARTICLE
Vegetation Ecology

Pre-fire structure drives variability in post-fire aboveground carbon and fuel profiles in wet temperate forests

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Abstract

Biological legacies (i.e., materials that persist following disturbance; "legacies") shape ecosystem functioning and feedbacks to future disturbances, yet how legacies are driven by pre-disturbance ecosystem state and disturbance severity is poorly understood—especially in ecosystems influenced by infrequent and severe disturbances. Focusing on wet temperate forests as an archetype of these ecosystems, we characterized live and dead aboveground biomass 2–5 years post-fire in western Washington and northwestern Oregon, USA, to ask: How do pre-fire stand age (i.e., pre-disturbance ecosystem state) and burn severity drive variability in initial post-fire legacies, specifically (1) aboveground biomass carbon and (2) fuel profiles? Dominant drivers of post-fire legacies varied by response variable, with pre-disturbance ecosystem state driving total legacy amounts and disturbance severity moderating legacy condition. Total post-fire carbon was ~3–4 times greater in mid- and late-seral stands compared to young stands. In unburned and low-severity fire stands, >70% of post-fire total carbon was live, and canopy fuel profiles were largely indistinguishable, suggesting greater continuity of structure and function following low-severity fire. Conversely, in high-severity stands, >95% of post-fire total carbon was dead and sparse canopy fuel remained. Regardless of burn severity, most biomass present pre-fire persisted following fire, suggesting high-carbon pre-fire stands lead to high-carbon post-fire stands (and vice versa). Persistence of legacy biomass in high-severity stands, even as it decays, will therefore buffer total ecosystem carbon storage as live carbon recovers over time. Further, all burned stands had considerable production of black carbon in charred wood biomass which can support ecosystem functioning and promote long-term carbon storage. Initial post-fire fuel profiles are likely sufficient to support fire in all stands, but reburn potential may be greater in high-severity stands due to rapid regeneration of flammable live surface vegetation and more exposed microclimatic conditions. Effects of fuel reduction from fire on mediating the occurrence and potential behavior of subsequent fires in high-productivity systems therefore appear short-lived. Our findings demonstrate the importance of pre-disturbance ecosystem state in dictating many aspects of initial post-disturbance structure and function, with important implications for managing post-fire recovery trajectories in some of Earth's most productive and high-biomass forests.

KEYWORDS
biomass, carbon storage, Cascade Mountains, disturbance, Douglas-fir, fire effects, forest structure, low-severity fire, old-growth forest, Pacific Northwest, stand-replacing fire, western hemlock

INTRODUCTION

As climate warms and disturbance activity increases (Seidl et al., 2017), understanding drivers of post-disturbance structure and function is essential for forecasting ecosystem futures. Biological legacies (i.e., individuals, materials, and adaptations that persist following disturbance; Franklin et al., 2000) are major structural components of post-disturbance ecosystems that can shape recovery trajectories for decades to centuries (Seidl & Turner, 2022). Two key drivers of legacies include the pre-disturbance ecosystem state and disturbance severity (i.e., degree of effect on ecosystem properties; Pickett & White, 1985) (Johnstone et al., 2016; Peters et al., 2011). The pre-disturbance ecosystem state sets the template for material available to persist as legacies. Intervals between disturbances typically dictate the range in biotic structure and composition of the pre-disturbance ecosystem state. For example, older temperate forest stands typically have greater amounts and more heterogeneous arrangements of large live trees, snags, and logs than younger stands (Burrascano et al., 2013; Franklin et al., 2002). Disturbance severity then interacts with the ecosystem state to influence the amount, composition, and arrangement of available material that is either killed, removed, or minimally altered. For example, greater burn severity (i.e., amount of vegetation killed by fire; Keeley, 2009) results in greater total loss and conversion from live to dead biomass (Meigs et al., 2011). While individual drivers of legacies have received attention, the relative and combined importance of multiple drivers are less well understood.

Legacies can strongly shape post-disturbance ecosystem functioning and feedbacks to future disturbances and are of particular importance in ecosystems influenced by infrequent and severe disturbances. For example, stand-replacing fires can shift ecosystems from carbon sinks to sources via mortality and subsequent decomposition of biomass (Kashian et al., 2006). However, live biomass can recover carbon quickly in high-productivity systems and legacy carbon can persist for centuries in large dead and charred material (Hudiburg et al., 2023). Legacies can also alter the likelihood, extent, or severity of a future disturbance via feedbacks (i.e., linked interactions; Simard et al., 2011). For example, fires can temporarily reduce the probability, spread, and severity of subsequent fires due to fuel consumption and changes in vegetation composition, though the strength of these effects diminishes over time as fuels recover (Buma et al., 2020). In highly productive ecosystems, rapid accumulation of fuels after fire may promote the likelihood of short-interval reburns (Gray & Franklin, 1997; Reilly et al., 2022) with implications for structure (e.g., Hoecker & Turner, 2022) and rates of recovery (e.g., Braziunas et al., 2023). Given the critical post-disturbance reorganization window (Seidl & Turner, 2022), characterizing legacies soon after disturbances is important for ecological forecasting and understanding management options (Lindenmayer et al., 2010). Yet, there are inherently few opportunities to study post-disturbance structure and function in ecosystems with relatively long disturbance-free intervals.

We tested the relative influence of pre-disturbance ecosystem state and disturbance severity on key legacies in forests influenced by long-interval stand-replacing fires. We focused on wet temperate forests of the Pacific Northwest, USA—an archetype of infrequent stand-replacing fire regimes shared by other forests at temperate latitudes in coastal margins worldwide (e.g., southwestern South America, southeastern Australia). Forests west of the Cascade Range crest in Washington and northern Oregon (hereafter "northwestern Cascadia") are shaped by a fire regime that includes stand-replacing fires with multi-century return intervals and extensive area burned (>50%) at high severity (Agee, 1993). Among the range of intermediate fires that can occur between these long-interval events, historical records suggest a strong tendency of these forests to reburn in the initial decades following a stand-replacing fire (i.e., fire begets fire; Gray & Franklin, 1997; Reilly et al., 2022), though mechanisms are not well understood. Northwestern Cascadia forests are among the most productive and carbon dense in the world, representing a vital carbon sink and economic resource (Case et al., 2021). Accordingly, the region is continually at the forefront of global forest and climate change policy and displays a wide variety of past disturbance and management histories (Spies et al., 2018). Recent fires have burned more than 200,000 ha across the region (Reilly et al., 2022), creating an opportunity to examine post-fire structure, function, and implications for future disturbances and management. Using field data from five recent fires in northwestern Cascadia, we asked: how do pre-fire stand age and burn severity drive variability in post-fire legacies—specifically initial post-fire (1) aboveground biomass carbon and (2) fuel profiles?

METHODS

Study area

Northwestern Cascadia comprises 6.1 Mha of wet temperate forests. Current structural conditions, which bear the marks of more than a century of timber harvest activity, are dominated by dense young plantations and mid-seral forests among unharvested old-growth stands (Donato et al., 2020; Spies et al., 2018). Forests are dominated by obligate-seeding gymnosperm species, with composition varying by elevation. At lower elevations (<1000 m), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*) are dominant, with noble fir (*Abies procera*) and Pacific silver fir (*Abies amabilis*) prevalent at relatively cooler and wetter middle elevations (1000–1600 m). Angiosperm tree species are less common, but can resprout and exist at high densities in mesic and recently disturbed areas (Franklin & Dyrness, 1973). Understory composition is dominated by abundant cover of shrub, fern, and forb species (Spies, 1991). Climate is Mediterranean with mild seasonal temperatures, wet winters, and dry summers (Franklin & Dyrness, 1973). Across our sampled area, 30-year normals (1991–2020) of annual mean temperature and total precipitation range from 4.0 to 10.7°C and 1435 to 3273 mm, with 76% of precipitation occurring November through April (PRISM Climate Group, 2024). Soils are primarily loamy, well-drained Inceptisols derived from pyroclastic and igneous parent materials (Franklin & Dyrness, 1973).

The long-interval (200–600 years) stand-replacing fire regime of northwestern Cascadia is limited primarily by climatic controls on region-scale weather events and fuel moisture (Agee, 1993). More frequent small fires may occur in the interim periods, commonly associated with the use of fire as a management tool by Indigenous peoples (Boyd, 1999; Johnston et al., 2023). Most large and severe fires occur toward the end of summer following prolonged periods of high temperature and low humidity that allow for sufficient drying of fine fuels to ignite and carry fire (Reilly et al., 2021). Such fires typically produce large patches (>10,000 ha) of area burned at high severity (Agee, 1998; Reilly et al., 2022) due to intense burning conditions and lack of fire-resistant traits for most tree species (Minore, 1979; Stevens et al., 2020), but also tend to include substantial portions burned at lower severity arising from periods of mild fire weather (Reilly et al., 2022). The largest fires (>50,000 ha) are driven by extreme weather events such as synoptic dry east winds that drive rapid fire spread (Reilly et al., 2021).

Sampling design

We established long-term monitoring plots ($n = 95$) in forest stands within five recent (2017–2020) fires across northwestern Cascadia (Figure 1, Table 1). Plots were established 2–5 years post-fire and systematically stratified by field-determined pre-fire stand age and burn severity (Figure 2). We positioned plot centers at least 100 m from roads and trails and excluded confounding features from the plot area (e.g., decommissioned roads, streams, riparian zones, and rock outcroppings). Within a sampled fire, plot centers were located at least 100 m apart for stands of different strata, and at least 400 m apart for stands of the same strata, though not all strata were represented in each fire (Appendix S1: Table S1).

We defined pre-fire stand age (i.e., age prior to the recent focal fires in our study) by development stage as a function of community structure attributes including morphology, canopy position(s), and spatial arrangement of the major tree species (Van Pelt, 2007). These stages are distinguished mainly by tree population demography and development rather than biomass specifically (Franklin et al., 2002). We then assigned each development stage a categorical age, classified as young, mid-seral, or late-seral (Appendix S1: Table S2). In general, young stands (~30–50 years) established after clearcut harvest in the late 1900s and had high densities of small-diameter shade-intolerant conifer trees starting to develop overlapping canopies. Mid-seral stands (~70–150 years) originated from fire or clearcut harvest after Euro-American settlement and were dominated by scant understory and near-total canopy cover of rapidly growing trees. Late-seral stands

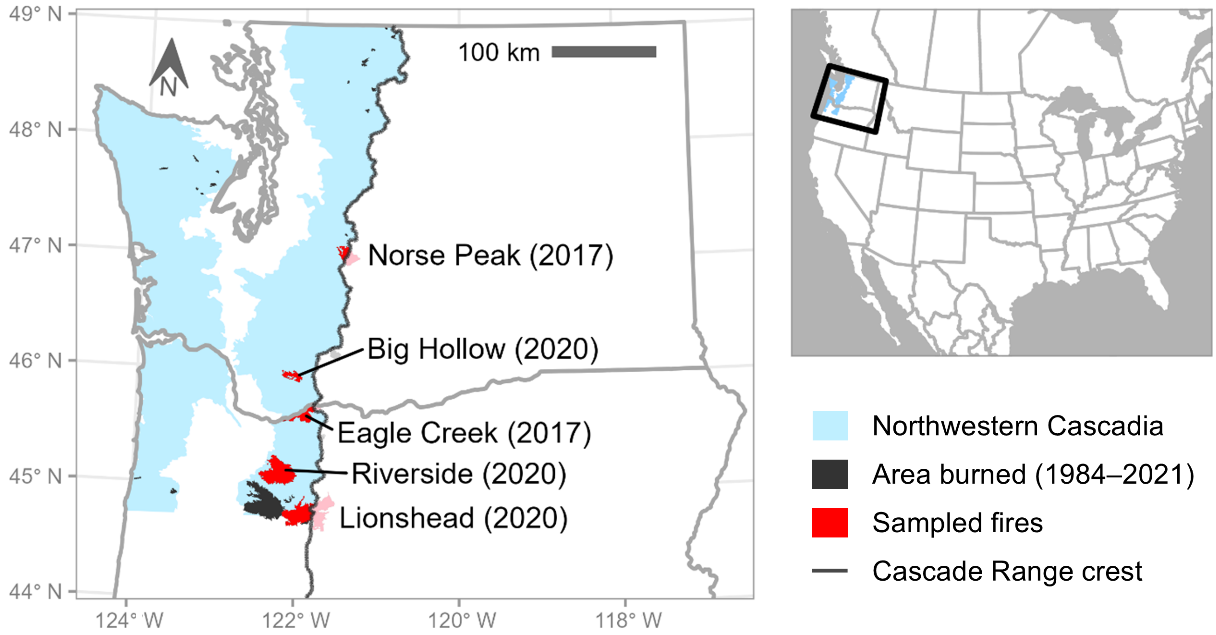

FIGURE 1 Study area in northwestern Cascadia, USA, including sampled fire perimeters, and recent area burned (1984–2021).

TABLE 1 Description of plots ($n = 95$) established across sampled fires within the study area.

Fire	Fire year	Fire size (ha)	Location	Sampling time since fire (year)	Plots (n)
Big Hollow	2020	9811	Gifford Pinchot National Forest	2	26
Eagle Creek	2017	17,666	Columbia River Gorge National Scenic Area and Mount Hood National Forest	4–5	3
Lionshead	2020	42,220	Willamette National Forest	3	4
Norse Peak	2017	8922	Mount Baker-Snoqualmie National Forest	2–4	55
Riverside	2020	55,920	Mount Hood National Forest	2–3	7

Note: Fire size only includes area burned on the west side of the Cascade Range crest (source: Monitoring Trends in Burn Severity, https://www.mtbs.gov/). See Appendix S1: Table S1 for stratification of plots by pre-fire stand age × burn severity classes.

(~160–500+ years) originated from fire generally prior to Euro-American settlement and were characterized by spatial heterogeneity in live and dead vegetation structures including multilayered tree canopies, abundant tree regeneration and down wood, and large diameter trees (Franklin et al., 2002).

We classified burn severity by percent of fire-killed tree basal area as unburned (0%, no evidence of recent fire), low (<30% mortality), or high (i.e., stand replacing, ≥90% mortality). We were unable to find patches of intermediate severity (30%–90% mortality) that were large enough to sample; these conditions existed mostly as narrow edges of transition from unburned or low severity patches to stand-replacing patches. Unburned stands with otherwise similar character were established both within and adjacent to sampled fire perimeters. In low-severity stands, evidence of fire was present across at least 50% of the plot area, though the spatial pattern of burned area was rarely uniform. We could not locate young stands of sufficient sampling size that burned at low severity, so this condition is not represented in this analysis.

Field data collection

We characterized post-fire aboveground biomass in each plot using standard methods. Total area sampled differed by pre-fire stand age, with lengths of cardinal transects, tree subplot radii, and down woody debris transects in young stands reduced by approximately half to account for scaling dynamics and improve sampling efficiency given the much higher tree densities characteristic of earlier successional stages. Lengths of sapling subplot radii, subcardinal plot transects and subplot radii, and fuel depth locations were consistent across all stands. Total

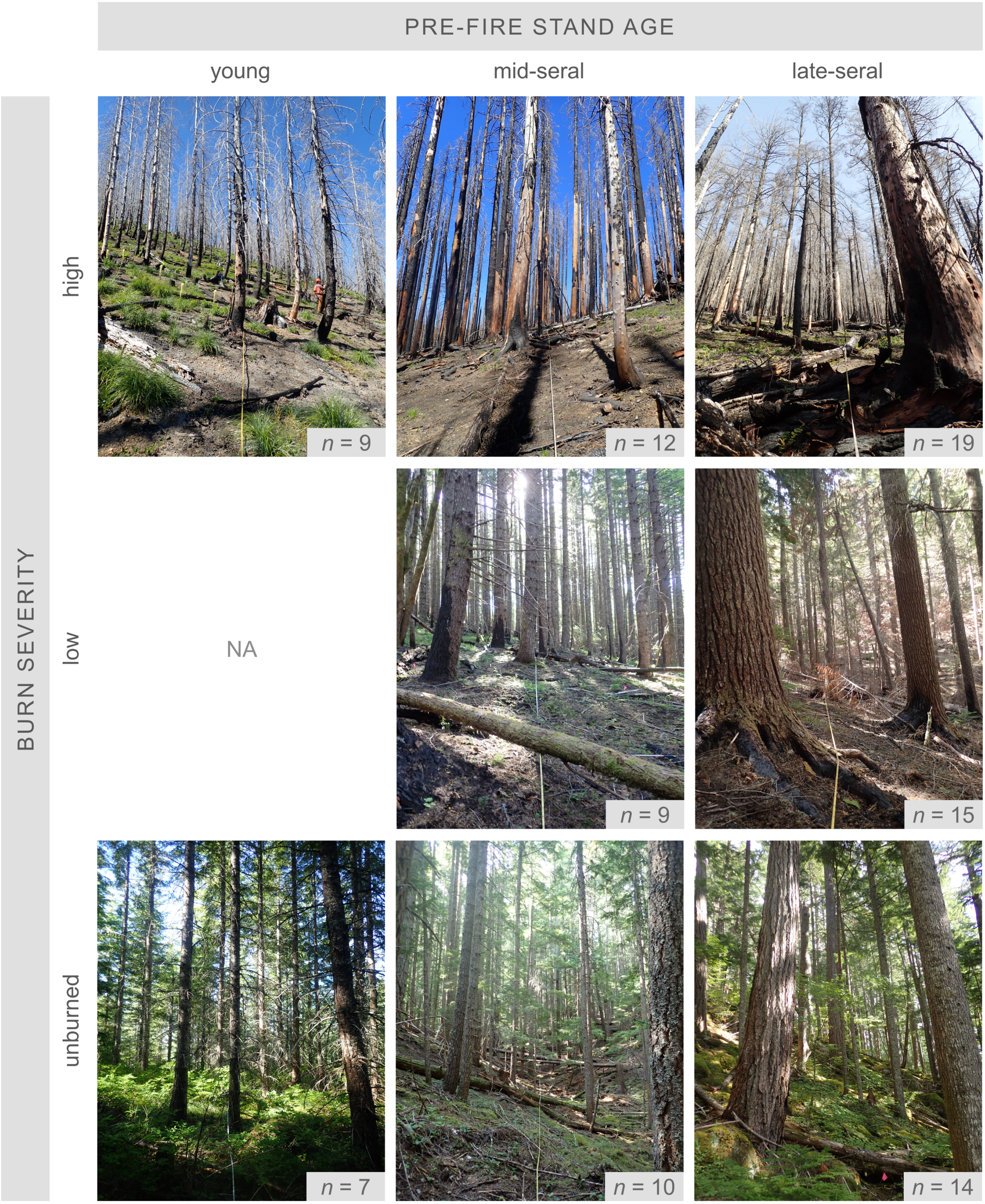

FIGURE 2 Representative photos taken two years post-fire within sampled stands illustrating the range in initial fire effects across pre-fire stand age × burn severity strata. Note differences in the abundance, size, and arrangement of live and dead biomass between strata. Insets denote the number of sampled plots (n) within each stratum. Young stands burned at low severity were not represented due to rare occurrence across the study area. Photo credit: UW Harvey Lab.

plot area was 1 ha in mid- and late-seral stands and 0.25 ha in young stands. See Appendix S1: Figure S1 for plot layout, Appendix S1: Table S3 for field measures, and Appendix S1: Table S4 for post-fire stand structure.

Trees

Live and dead trees were measured in four variable-radius subplots according to size class based on dbh (1.37 m). We selected subplot radii to ensure at least ~60 trees were measured within each plot. Radii were kept a consistent length for all subplots within a plot. In mid- and late-seral stands, subplots were located 30 m from plot center along each 56.5-m-long cardinal plot transect. Subplot radii for trees (dbh ≥ 10 cm) ranged from 8 to 16 m, with a default of 12 m (804–3217-m^2 total area). In young stands, subplots were located 15 m from plot center along each cardinal plot transect. Subplot radii for trees (dbh ≥ 10 cm) ranged from 3 to 9 m, with a default of 6 m (113–1018-m^2 total area). Regardless of pre-fire stand age, subplot radii for saplings (height ≥ 0.3 m, dbh < 10 cm) ranged from 2 to 5 m (50–314-m^2 total area), and large trees (dbh ≥ 100 cm) were measured across the entire plot.

For each tree, we recorded species, status (live or dead), total height, and presence of broken top. For trees taller than 1.37 m, we also recorded dbh, height to the base of live and dead crown, decay class (1–5; Lutes et al., 2006), percent bark present at dbh, and percent stem remaining. For stumps (i.e., trees with broken top and height <1.37 m), we recorded diameter at base instead of dbh. For trees in burned stands, we also recorded percentages of crown volume with needle scorch and stem wood surface area with char.

Live understory vegetation

Live tree seedlings (height < 0.3 m), woody shrubs, and herbaceous vegetation were measured in 12 fixed-radius subplots positioned at the 7-, 14-, and 21-m marks along each 24.5-m-long subcardinal plot transect. Subplot radii were 3.5 m for established seedlings (height ≥ 0.1 m; 462-m^2 total area), 0.5 m for small seedlings (height < 0.1 m; 9-m^2 total area), and 2 m for woody shrubs and herbaceous vegetation (150-m^2 total area). For tree seedlings, we tallied individuals by species and recorded height for those taller than 0.1 m. For woody shrubs, we recorded species, height, and basal diameter of all live stems. For herbaceous vegetation, we measured percent cover by species (non-vascular and graminoid species were grouped by functional type).

Dead surface fuel

Fine and coarse down woody debris (height < 2 m) and forest floor fuel (litter, duff) were measured along planar intercept transects (Brown, 1974; Lutes et al., 2006). Fuel transect lengths differed by size class (fine vs. coarse woody debris) and pre-fire stand age. Fine woody debris (1-, 10-, and 100-h fuels; diameter < 7.6 cm) was tallied by size class along eight fuel transects. Fuel transects were arranged in pairs located along each subcardinal plot transect, with the end of each fuel transect crossing the center of the 21-m subplot. Fine woody debris fuel transect pairs were oriented perpendicularly in the cardinal directions bisected by the subcardinal plot transects. Fuel transect lengths were 12 m in mid- and late-seral stands (96-m total sampled length) and reduced to 6 m in young stands (48-m total sampled length). For mid- and late-seral stands, we tallied 1-h fuels (diameter < 0.6 cm) along the first 3 m, 10-h fuels (diameter 0.6–2.5 cm) along the first 7 m, and 100-h fuels (diameter 2.5–7.6 cm) along the entire 12 m. For young stands, we tallied 1-h fuels along the first 1.5 m, 10-h fuels along the first 3.5 m, and 100-h fuels along the entire 6 m. Litter, duff, and dead fuel depths were measured along each fine woody debris fuel transect at consistent locations across all stands. Litter and duff depths were taken at 0.5 and 1.5 m, and dead fuel depths were taken at three intervals between 0.0–0.5, 0.5–1.0, and 1.0–1.5 m.

Coarse woody debris (1000-h fuels; diameter ≥ 7.6 cm) was sampled along four fuel transects originating at plot center and extending in cardinal directions. We measured the overall plot slope and the slope of each coarse woody debris fuel transect from plot center using a laser rangefinder. Fuel transect lengths were 56.5 m in mid- and late-seral stands (226-m total sampled length) and were reduced to 28 m in young stands (112-m total sampled length). For each 1000-h piece, we recorded species, diameter, decay class (1–5; Lutes et al., 2006), and the presence of char.

Biomass and fuels calculations

We derived aboveground biomass carbon and surface and canopy fuel profiles for each plot using component-, species-, and region-specific allometric equations. Equations were sourced primarily from the BIOPAK and TRY databases (Kattge et al., 2020; Means et al., 1994). When multiple suitable equations were available for a species (i.e., 2+

equations developed in the western Cascades from trees with size ranges overlapping our field measurements), we took the mean estimate across all sources to account for latitudinal differences in moisture and productivity, as well as derivation methods (e.g., sample size, function shape). When equations specific to the western Cascades were not available, we used equations developed in other regions. When no equations were available for a species, we substituted equations from analogous species based on shared structural and functional attributes. All measures were scaled to per-ha values.

Aboveground biomass carbon

Aboveground biomass carbon (i.e., carbon stored in plant matter) included wood, bark, branch, and foliage biomass for all measured vegetation. We estimated the aboveground biomass of all measured vegetation using allometric equations specific to each component (Appendix S1: Table S6). We then determined aboveground biomass carbon by multiplying the biomass of each component by its corresponding carbon content, based on species-, component-, position- (i.e., standing vs. down), and decay class-specific values presented in the literature (range 39.4%–58.3%; Appendix S1: Table S7).

We calculated total aboveground biomass of standing trees and large saplings (height ≥ 1.37 m) by summing individual estimates for crown (foliage, branches) and stem (wood, bark) components based on height and/or diameter. We corrected crown and stem biomass for mass loss due to foliage scorch, broken top, bark loss, decay class, and wood charring (Appendix S1). We derived total aboveground biomass of live understory vegetation—including tree seedlings and small saplings (height < 1.37 m), woody shrubs, and herbaceous vegetation (i.e., forbs, ferns, and graminoids)—based on height, percent cover, and/or basal diameter.

We derived biomass of down woody debris using standard methods (Brown, 1974). We corrected for the slope of each transect using our field-measured slopes and the slope correction factor equation from Brown (1974). For calculating biomass of fine woody debris (1-, 10-, 100-h particles), we used non-slash composite values from Brown (1974) for squared average diameters, specific gravities, and non-horizontal angle correction factors. For calculating biomass of coarse woody debris (1000-h particles), we used species- and decay class-specific wood densities (Harmon et al., 2008), adjusting for mass loss from wood charring (Appendix S1).

Charred wood

We characterized charred wood (i.e., solid organic material that remains after incomplete combustion of woody biomass) in order to correct for loss of mass due to combustion and to explicitly quantify the biomass of black carbon (i.e., carbon fraction of char) due to its role in long-term carbon storage and nutrient cycling (Bird et al., 2015). Carbon in charred stem wood on standing trees and coarse woody debris was quantified using methods from Donato, Campbell, et al. (2009), assuming a carbon content of 75% (Branca & Di Blasi, 2003). In general, we subtracted the mass of the uncharred inner portion of each stem or 1000-h particle from the total mass. The mass of the uncharred inner portion was calculated by adjusting measured diameter inputs for the allometric equations for both stem wood mass and coarse woody debris load to account for the depth of char (8.2 mm; Donato, Campbell, et al., 2009) and associated mass loss (70%; Dietenberger, 2002). See Appendix S1 for more details.

Fuel profiles

Fuel profiles were determined by separating biomass into surface and canopy fuel components. Surface fuels included down woody debris (height < 2 m), live tree seedlings and small saplings (height < 1.37 m), and live understory vegetation (woody shrubs, herbaceous vegetation). We separated down woody debris biomass by standard fuel size class and level of decay (sound, class 1–3 vs. rotten, class 3–4), and live surface fuel biomass into woody (tree seedlings and small saplings, shrubs) and herbaceous (forbs, graminoids) components.

Canopy fuels included foliage and branch biomass, available canopy fuel load, canopy bulk density, and canopy base height for live and dead standing trees and large saplings (height ≥ 1.37 m). We separated live and dead branch biomass into fuel size classes (i.e., 1-, 10-, 100-, 1000-h) using accumulative proportion equations based on species, dbh, and height (Brown, 1978; Snell & Little, 1983). This approach was developed by Brown and Johnston (1976) and is used in common modeling tools for fuel and fire management including FuelCalc (Reinhardt, Lutes, & Scott, 2006) and the Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS; Rebain, 2010). For shade-intolerant species (Appendix S1: Table S5), we used separate branch size proportion equations for individual trees in dominant versus intermediate canopy positions. We assigned canopy position based on a tree's height relative to other trees within each stand: if tree height was above the 60th percentile for the stand, a tree was considered dominant (i.e., among the tallest 40% of trees); otherwise it was considered intermediate (Rebain, 2010).

Available canopy fuel load is the portion of canopy biomass that would be consumed in a crown fire and includes the sum of foliage, dead 1-h branches, and half of live 1-h branches (Reinhardt, Scott, et al., 2006). We created vertical canopy fuel profiles for each stand by evenly distributing available canopy fuel in 0.25-m bins along the crown length of each canopy tree and summing by bin (Donato, Harvey, et al., 2013; Simard et al., 2011). Canopy bulk density is the mean volume of available fuel within the canopy and was defined as the maximum 3-m running mean across the vertical canopy fuel profile (Reinhardt, Scott, et al., 2006). Canopy base height represents the height at which there is enough available fuel for fire to travel vertically through the canopy (Scott & Reinhardt, 2001) and was defined as the lowest height at which canopy bulk density exceeded 0.04 kg m^{-3} (Cruz et al., 2004; Donato, Harvey, et al., 2013; Sando & Wick, 1972).

Statistical analysis

We compared mean aboveground biomass carbon and fuel profiles across strata using generalized linear models with plot as the sample unit. Model structure was consistent for all response variables, predicting each nonnegative continuous response as a function of categorical pre-fire stand age and burn severity. Responses were modeled by a gamma distribution with log link function and included an intercept-only zero-inflation parameter to account for sampling zeros. We considered adding a random effect of fire to control for variability among sites but did not include this term in the final models due to limited df, similarity of coefficient estimates with and without the random effect term, and convergence failure warnings for several response variables when the random effect term was included. To compare the relative strength of pre-fire stand age and burn severity as drivers of post-fire legacies, we computed pairwise differences in predicted means (i.e., marginal comparisons) for each response across all levels of pre-fire stand age and burn severity. Mean effect size for each predictor was obtained by taking the average of the absolute differences across levels. Analyses and visualizations were performed in R Statistical Software version 4.4.0 (see Appendix S1 for packages; R Core Team, 2024). Results are reported for outputs with $p < 0.05$.

RESULTS

Post-fire aboveground biomass carbon

The majority of aboveground biomass carbon (hereafter "carbon") persisted through fire. On average, burned stands had at least 67% of the total carbon in unburned stands, the majority of which (>95%) was in woody biomass (Appendix S2: Table S1). Pre-fire stand age was the dominant driver of total carbon, with 2–3 times the effect of burn severity on the major carbon components, including all standing trees and down woody debris (Figure 3). In general, post-fire carbon increased with pre-fire stand age (Figure 4). Compared to young stands, mid- and late-seral stands had 223% and 299% more post-fire total carbon, respectively (Appendix S2: Tables S3 and S8). Burn severity drove conversion from live to dead carbon but did not override the effect of pre-fire stand age on post-fire total carbon (Figure 3). Compared to unburned stands, post-fire live carbon was similar in low-severity stands but 99% less in high-severity stands. Both low- and high-severity stands had 49% and 321% more post-fire dead carbon, including 0.3 Mg C ha^{-1} more charred wood, respectively (Figure 4; Appendix S2: Tables S3 and S8).

Post-fire fuel profiles

Surface fuels

Pre-fire stand age was the dominant driver of post-fire surface fuel profiles, with 3× the effect of burn severity on the major surface fuel components, including coarse and fine woody debris (Figure 3). In general, post-fire dead surface fuels increased—and live surface fuels decreased—with pre-fire stand age (Figure 5). Compared to young stands, mid- and late-seral stands had 197% and 554% more coarse and 37% and 59% more fine woody debris post-fire, respectively (Appendix S2: Tables S4 and S8). However, burn severity was the dominant driver of post-fire fuel depths and live surface fuels, with 2–3× the effect of pre-fire stand age on duff, litter, and live vegetation (Figure 3), though these components comprise a minor portion of the post-fire total surface fuel profile (Figure 5). This effect was unique to each burn severity class; fuel depths and live surface fuels were distinct for unburned, low-, and high-severity stands. In general, post-fire surface fuels decreased with burn severity (Figure 5). Compared to unburned stands, low- and high-severity stands had 57% and 89% less duff, 33% and 67% less litter, and 79% and 50% less live surface fuel post-fire, respectively (Appendix S2: Tables S4 and S8).

Canopy fuels

Burn severity was the dominant driver of post-fire canopy fuel profiles, with 2–5× the effect of pre-fire stand age on available canopy fuels and canopy bulk density (Figure 3). This burn severity effect was driven primarily by high-severity stands; post-fire canopy fuel profiles

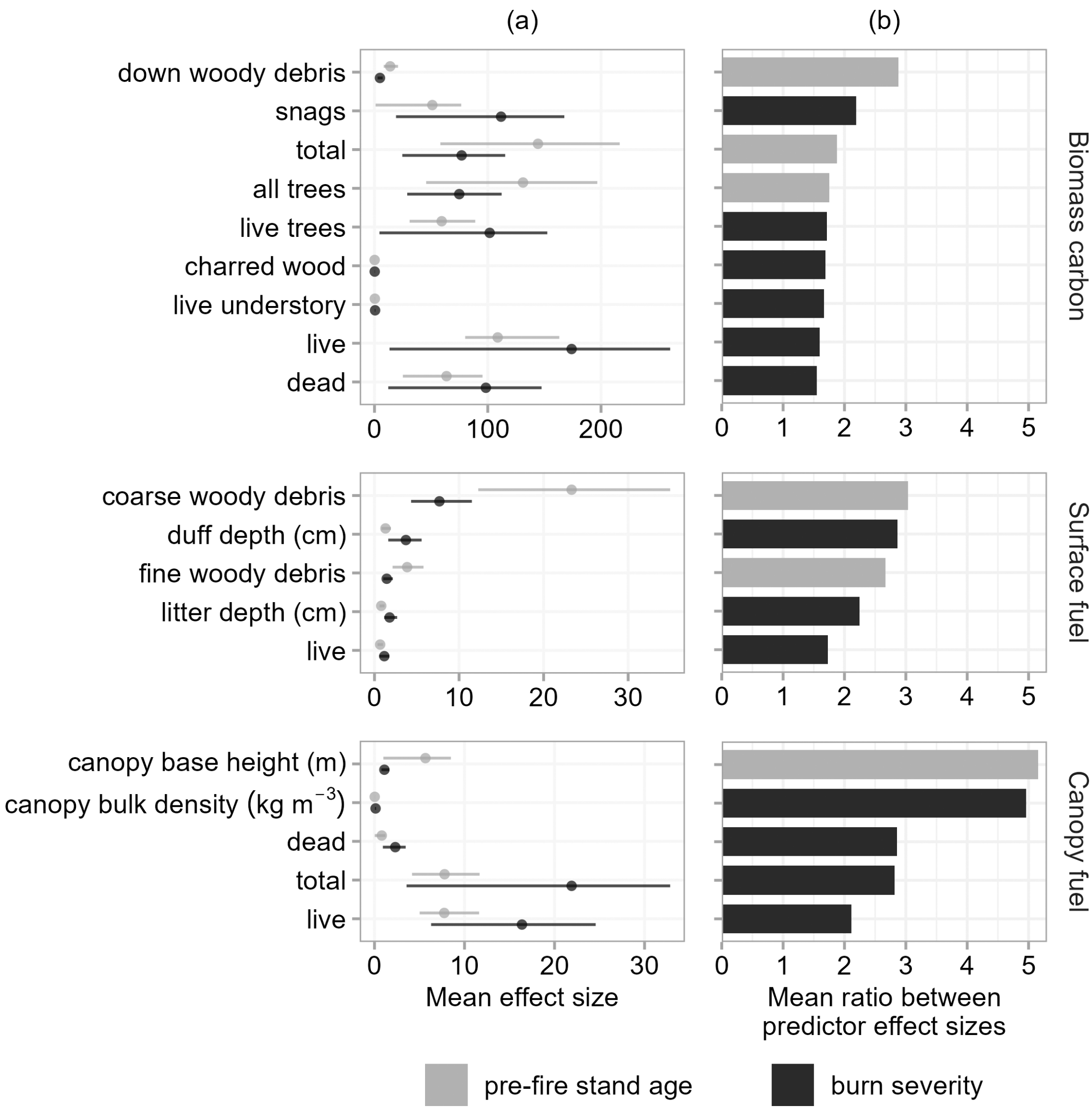

FIGURE 3 Relative effects of pre-fire stand age and burn severity on initial post-fire aboveground biomass carbon and fuel profiles. (a) Marginal comparisons in mean effect sizes. Points and lines are the mean and range (min–max) of absolute differences in predicted means for pairwise comparisons across all predictor levels, on the response scale (in megagrams per hectare, unless otherwise indicated). Wider ranges indicate larger differences in a single predictor level compared to the other levels. (b) Ratio in mean effect sizes relative to the dominant predictor. See Appendix S2 for marginal comparison summaries and additional response variables.

were largely indistinguishable between unburned and low-severity stands. In general, post-fire total and live fuels decreased—and dead fuels increased—with burn severity (Figure 5). Compared to unburned and low-severity stands, high-severity stands had 86% less post-fire total available canopy fuel, and 82% and 75% less canopy bulk density, respectively. Both low- and high-severity stands had 11% and 98% less live and 163% and 213% more dead post-fire available canopy fuel than unburned stands, respectively (Appendix S2: Tables S5 and S8). However, pre-fire stand age had 5× the effect of burn severity on post-fire canopy base height (Figure 3), driven primarily by mid-seral stands. In general, post-fire canopy fuels increased with pre-fire stand age (Figure 5). Compared to young stands, mid- and late-seral stands had 86% and 117% more post-fire total available canopy fuel, respectively. Mid-seral stands also had 669% taller post-fire canopy base height than young stands (Appendix S2: Tables S5 and S8).

DISCUSSION

By testing how multiple drivers affect post-fire legacies of aboveground biomass carbon and fuel profiles, our study demonstrates the importance of the pre-disturbance ecosystem state in dictating many aspects of initial post-disturbance

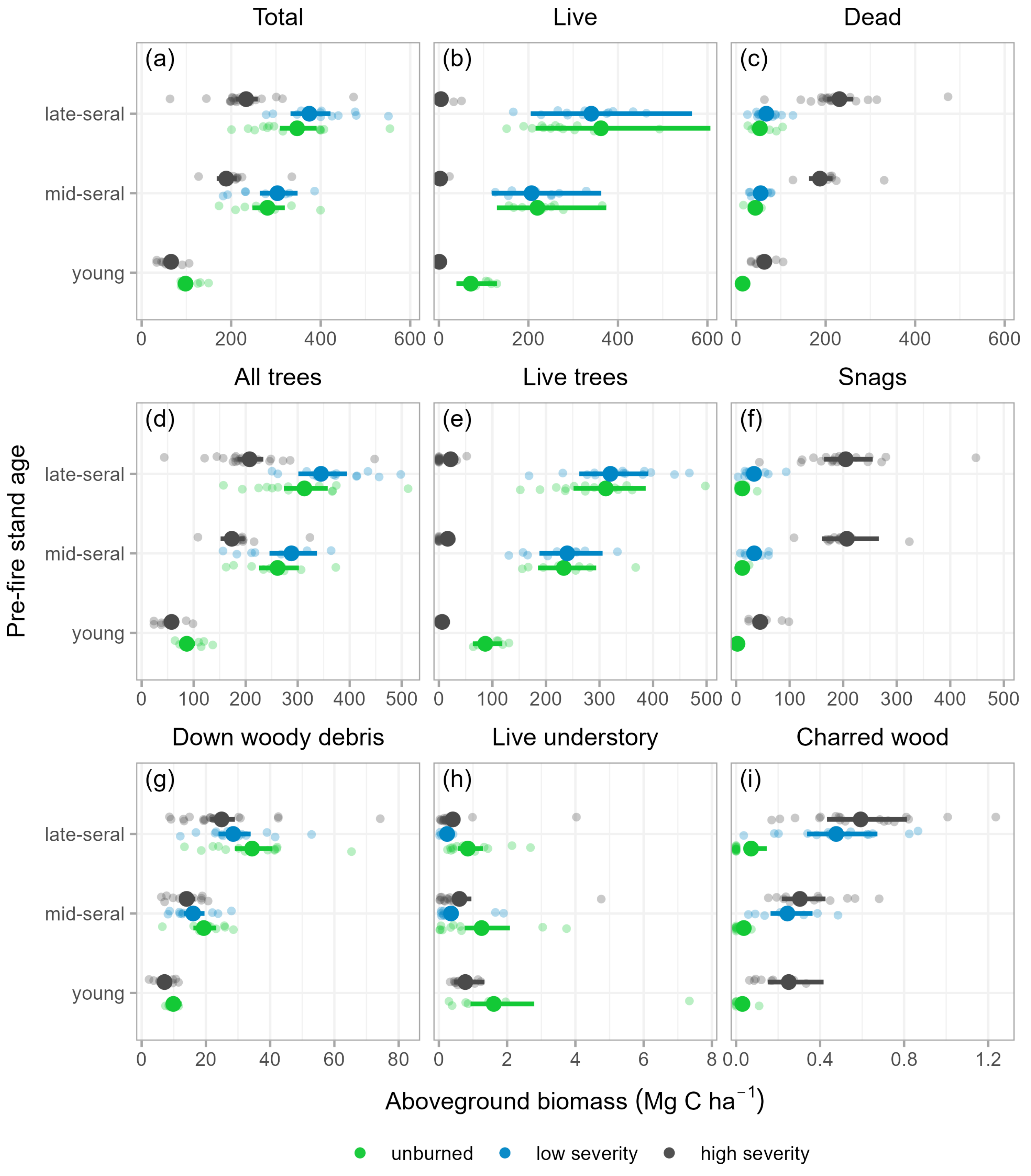

FIGURE 4 Initial post-fire aboveground biomass carbon. Bold points and lines are model-predicted means and 95% CIs for each stand age class, colored by burn severity. Translucent points show plot-level values. See Appendix S2 for model summaries.

structure and function. This work builds understanding of the mechanisms behind disturbance-mediated change and feedbacks in systems shaped by long intervals between severe disturbances, with notable implications for managing post-fire recovery trajectories in some of Earth's most productive and high-biomass forests.

Pre-fire stand age drives variability in total post-fire legacies

Pre-fire stand age was the dominant driver of initial patterns in total legacies after fire. Within each burn severity class, stands that were older at the time of

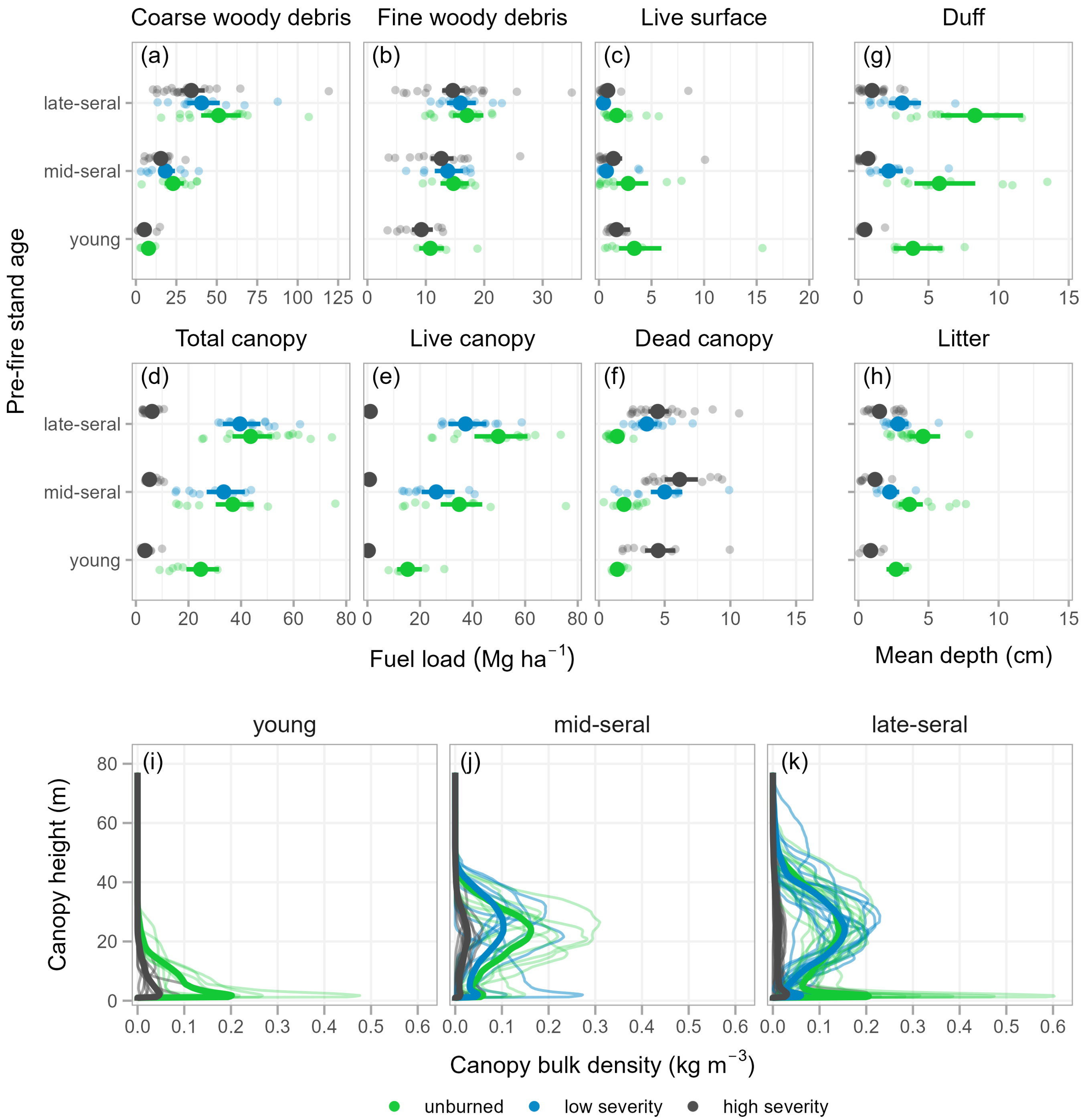

FIGURE 5 (a–c) Initial post-fire surface, (d–f) available canopy, (g–h) forest floor, and (i–k) vertical fuel profiles. Bold points and lines are model-predicted means and 95% CIs (a–h) or simple means (i–k) for each stand age class, colored by burn severity. Translucent points (a–h) and lines (i–k) show plot-level values. See Appendix S2 for model summaries.

fire had greater post-fire total aboveground biomass carbon, total tree mass, and down woody debris than younger stands, corresponding to trends in biomass with succession in wet temperate forests in northwestern Cascadia (Agee & Huff, 1987; Gray et al., 2016; Spies et al., 1988) and globally (Burrascano et al., 2013; Pregitzer & Euskirchen, 2004). Most biomass present pre-fire persisted post-fire, supporting regional trends (Campbell et al., 2007; Donato, Fontaine, et al., 2013; Fahnestock & Agee, 1983) and suggesting that high-carbon pre-fire stands lead to high-carbon post-fire stands (and vice versa), regardless of burn severity. Woody biomass, particularly within larger trees, accounted for most of the remaining carbon, reflecting expected patterns of combustion (Agee, 1993).

These findings suggest that, when burned, late-seral stands may have greater potential than younger stands to support several ecosystem functions, due to greater abundance of post-fire legacies. Retention of legacies, especially woody biomass, is important for supporting critical post-disturbance functions (e.g., nutrient cycling, wildlife habitat, microsite diversity), particularly following stand-replacing disturbances (Franklin et al., 2002). Persistence of legacy biomass on site, even as it decays following high-severity fire, will buffer total ecosystem carbon storage as live carbon recovers over time. Accordingly, alterations to pre-disturbance ecosystem state will have lasting effects on post-fire function and recovery potential (Seidl et al., 2014), underscoring the importance of considering stand ages present on a landscape when managing for desired post-disturbance conditions.

Burn severity moderates the condition of post-fire legacies

Burn severity moderated the condition of legacies, driving initial patterns in live and dead aboveground biomass carbon and canopy fuel profiles after fire. In stands burned at high severity, >95% of the total post-fire aboveground biomass carbon was in dead material, and very little (<15% of unburned) canopy fuel remained. Given these stands experienced predominantly crown fire, which consumes the majority of available fuels (Agee, 1993), and are composed of several tree species with few adaptations to resist fire (Minore, 1979; Stevens et al., 2020), these findings are in line with expectations from similar systems (Kauffman et al., 2019). Lack of fire-resistant traits—coupled with smaller tree stature, higher tree density, and abundant fine surface fuels—may also predispose young stands to severe fire effects due to low fire resistance and high fuel availability and connectivity. This pattern has been observed throughout the region (Busby et al., 2023; Evers et al., 2022) and may underlie our difficulty in finding young stands burned at low severity within the study area. By contrast, in unburned and low-severity stands, >70% of total post-fire aboveground biomass carbon was stored in live material and canopy fuel profiles were similar. This is likely due to low-severity stands experiencing predominantly surface fire behavior which, compared to crown fire, has less influence on vegetation structure and does little to alter available canopy fuels in these systems (Bassett et al., 2017).

These findings have different implications following low- and high-severity fire, both of which can play important roles in forest dynamics of wet temperate systems with relatively long intervals between stand-replacing fires. Retention of mostly live legacies and similarity to unburned stands suggests greater continuity of structure and function pre- and post-fire in low-severity stands compared to high-severity stands. Low-severity stands may also help facilitate recovery of more severely burned areas by providing a live seed source for dispersal into nearby high-severity patches (Donato, Fontaine, et al., 2009; Laughlin et al., 2023). Yet, this role may be limited by delayed tree mortality which can shift landscape patterns of burn severity (Reilly et al., 2023) and reduce live seed sources (Dyer et al., 2025). In contrast, retention of mostly dead legacies and rapid growth of non-tree vegetation suggests protracted regeneration timelines and a wider range of potential stand development pathways in high-severity stands compared to low-severity stands (Tepley et al., 2013). Accordingly, high-severity stands can facilitate the development of structurally complex early-seral ecosystems, promoting increased biodiversity and unique ecosystem functions (Swanson et al., 2011), and the restoration of the most contemporarily underrepresented and ephemeral landscape condition in the region (Donato et al., 2020).

Implications for future forest dynamics and management

Initial patterns of post-fire legacies have implications for carbon trajectories, reburn potential, and climate-adaptive management. While pre-fire stand age was the dominant driver of initial post-fire total carbon dynamics in these stands, burn severity will define carbon trajectories over longer timescales. Long-term post-fire carbon trajectories are a function of the balance between carbon lost through biomass consumption and decomposition of fire-killed vegetation, and carbon gained through vegetation regrowth (Pugh et al., 2019), influenced by the distribution of stand structures and ages across the burned landscape (Kashian et al., 2006). Total aboveground biomass carbon remained high in burned stands, though most initial post-fire carbon was stored in live biomass for low-severity stands and dead biomass for high-severity stands. This suggests post-fire carbon trajectories in low-severity stands are likely to be similar to unburned stands and follow expected trends with later successional stages (Janisch & Harmon, 2002). In contrast, high-severity stands are likely to remain carbon sources for several decades post-fire until net primary production exceeds decomposition losses (Law et al., 2004), though dead wood can be an effective long-term carbon store, taking several decades to centuries to fully decompose (Harmon et al., 1986). Given that regional projections of future fire activity generally forecast an increased number of fires, greater area burned by large fires, shorter fire return intervals, and longer fire seasons (Dye et al., 2024), increased fire frequency may substantially reduce total carbon through the conversion of older stands to younger stands (Harmon et al., 1990; Seidl et al., 2014) and less persistent large woody legacies due to more frequent combustion (Donato et al., 2016; Raymond & McKenzie, 2012).

Our findings suggest that fire, regardless of severity, can promote long-term carbon storage in wet temperate forests via char formation. Black carbon within charred wood biomass is a particularly persistent form of dead carbon that is resistant to decay (Bird et al., 2015). Both low- and high-severity stands had a quarter to more than half a metric ton of charred wood biomass carbon per hectare. This mechanism of long-term carbon storage produced values comparable to other systems that have observed similar amounts of black carbon generated from a range of burn severities (Campbell et al., 2007; Volkova et al., 2022). However, many unknowns have yet to be addressed about the role of black carbon (Santín et al., 2016), and additional aspects of the carbon cycle—including belowground carbon storage and plant, microbial, and soil carbon fluxes—were not addressed by this study, but are important processes influencing carbon dynamics following fire (e.g., Hudiburg et al., 2023).

Fire occurrence in high-productivity wet temperate forests may increase the risk of reburning in a subsequent fire due to initial fire effects on post-fire legacies, meaning major fires may effectively occur in episodes of burn–reburn sequences (Agee, 1993; Gray & Franklin, 1997). Reburn potential appears greater in stands burned at high severity due to rapid regeneration of more flammable live surface vegetation within the first several years post-fire (Landesmann et al., 2021; Thompson et al., 2007) as well as reduced live overstory canopy and likely microclimatic shifts toward warmer and drier conditions (Chen et al., 1993, though see Cawson et al., 2017). Yet, despite possible differences in reburn potential as a function of burn severity, initial post-fire fuel profiles may be sufficient to support fire in all stands. For example, reburn potential may be similar between low-severity and unburned stands because canopy fuels are largely unchanged, and reductions in surface fuels are incremental. In combination with the high ecosystem productivity in the study area, our results suggest fuel reduction from fire is a short-lived or insignificant limitation on the occurrence and potential behavior of subsequent fires, though additional research is needed to disentangle the relative importance of structural versus weather drivers of reburn potential in this system.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Morris, 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.17538352.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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