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Influences on vegetation structure 55 years after clearcutting and broadcast burning, and wildfire in a western larch forest

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Abstract

Background Experimental forests present unrivaled opportunities to understand the factors influencing vegetation structure many decades after silvicultural treatments or natural disturbances. In this study, we use the western larch-dominated moist mixed-conifer forests at Miller Creek Demonstration Forest (Miller Creek) to better understand the relationship between current vegetation structure, 55 years after two forms of high-intensity disturbance (clearcutting plus broadcast burning, and a high-severity wildfire) and characteristics of the site, the disturbance, and pre-disturbance vegetation. We also utilize measurements of fire intensity to test the hypothesis that moderate intensity fires promote greater fine-scale vegetation spatial heterogeneity, many decades disturbance, than low or high fire intensities.

Results Fifty-five years after high-intensity disturbance, forest cover has returned to all sample sites at Miller Creek. Further, these sites support the full suite of tree species common to this forest type; although western larch is generally dominant in the overstory, its more shade-tolerant associates are abundant in the understory. Our results suggest that fire intensity and heat load index, used as summaries of disturbance and site characteristics, respectively, are associated with current overstory vegetation. By contrast, our data implies that understory vegetation at Miller Creek is more strongly influenced by a variety of site factors. Our results provide no evidence of a relationship between fire intensity and spatial heterogeneity.

Conclusions Our findings suggest that characteristics of both the initiating disturbance and the site influence vegetation structure at Miller Creek. Moreover, five-plus decades post-disturbance, the understory plant community is more closely aligned with habitat type than is the overstory. However, while western larch is likely to maintain overstory dominance at Miller Creek for many decades, our findings suggest that perpetuating this species alongside a diverse understory may call for future moderate- to high-intensity harvests with overstory retention and broadcast burning.

The findings and conclusions in this report are those of the author(s) and should not be construed to represent any official USDA or U.S. Government determination or policy.

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Resumen

Antecedentes Los bosques experimentales presentan oportunidades inmejorables para entender los factores que influencian su estructura varias décadas luego de haberles realizado tratamientos silviculturales o de disturbios naturales. En este estudio usamos el bosque mixto semi-húmedo de coníferas dominado por el alerce del oeste (*western larch*) en el bosque demostrativo de Miller Creek (Miller Creek), para entender mejor la relación entre la estructura actual de la vegetación, luego de 55 años después de habérsele realizado dos tipos de tratamientos (disturbios) de alta intensidad (tala rasa más quema de broza y residuos, y un incendio de alta severidad), y las características del sitio, los disturbios, y la vegetación pre-disturbio. Utilizamos asimismo mediciones de la intensidad del fuego para probar la hipótesis que de fuegos de moderada intensidad promueven la heterogeneidad de la vegetación a escala fina, muchas décadas después que fuegos tanto de alta como de muy baja intensidad.

Resultados Después de 55 años del incendio de alta intensidad, la cobertura forestal retornó a todas las áreas de muestreo de Miller Creek. Además, esos sitios contuvieron a todas las categorías de especies forestales comunes en este tipo de bosque; aunque el alerce del oeste es generalmente dominante en el dosel superior de este bosque, las especies asociadas más tolerantes a la sombra también fueron abundantes en el sotobosque. Nuestros resultados sugieren que la intensidad del fuego y el índice de carga de calor (*heat load index*), usados como resumen de los disturbios y de las características del sitio, respectivamente, están asociadas con la vegetación del dosel actual. Contrastando con esto, nuestros datos implican que la vegetación del sotobosque en Miller Creek está más influenciada por una variedad de factores del sitio. Estos resultados, entonces, no proveen de evidencia sobre una relación entre la intensidad de los incendios y la heterogeneidad espacial.

Conclusiones Nuestros resultados sugieren que tanto el disturbio iniciador como las características del sitio influencian la estructura de la vegetación en Miller Creek. Además, cinco décadas después de los disturbios, la comunidad de plantas del sotobosque se asemejan más al tipo de hábitat que su estrato superior. Aparte de ello, mientras que el alerce del oeste parece mantener la dominancia del dosel superior del bosque en Miller Creek, nuestros resultados sugieren que la perpetuación de esta especie junto a un sotobosque diverso puede resultar de futuras cortas de moderada a alta intensidad junto con la retención de algunos árboles del dosel superior y la quema superficial del sotobosque.

Introduction

Understanding the patterns of recovery and reorganization following disturbance has been a cornerstone of ecological research from the beginnings of ecosystem science (Clements 1916; Odum 1969; Christensen 2014). Far from a theoretical exercise, research on the nature of post-disturbance ecosystem development and the controls on this process has long provided a foundation for ecosystem management, including forest stand dynamics (e.g., Seymour and Hunter 1999; Franklin et al. 2002; Ashton and Kelty, 2018). As we progress further into an era of rapid and unpredictable changes in the abiotic environment, biological systems, and the socio-economic context for natural resource management (e.g., Tilman and Lehman 2001; Millar et al. 2007; Trumbore et al. 2015), knowledge of the controls on secondary succession is increasingly salient to deriving management responses to these changes.

The controls on vegetation development following disturbance may be grouped into abiotic (e.g., climate, topography, the edaphic environment) and biotic (e.g., species presence, fitness, biological interactions) factors (e.g., Hobbs and Norton 2004; Poorter et al. 2024; Van Breugel et al. 2024). These controls may influence ecosystem dynamics interactively and at varying scales (e.g., Huston 1999; Belote et al. 2015; Kraft et al. 2015; Cadotte and Tucker 2017). For example, climate may act as a top-down control at large spatial scales to determine in-situ species viability (Poff, 1997; Mittelbach 2012; Janečková et al. 2024), while bottom-up site resources and inter- and intra-specific interactions influence fine-scale patterns of plant community composition and structure (Connell, 1978; Wiens and Rotenberry 1981; Forrester 2014).

In this study, we focus on three important controls on secondary succession, characteristics of (i) the pre-disturbance plant community, (ii) the initiating disturbance, and (iii) the site. Using data collected in 2023 from the Miller Creek Demonstration Forest (Miller Creek), a long-term research site in northwest Montana, we sought to determine whether the influence of these controls on ecosystem structure can still be detected more than five decades after managed and natural disturbances—clearcutting followed by various applications of broadcast burning, and high-severity wildfire. In combination, clearcutting followed by broadcast burning is a high-intensity disturbance, but at Miller Creek the broadcast burn treatments ranged from low to moderately high fire

intensity. Meanwhile, the wildfire at Miller Creek was a high-intensity disturbance. Thus, Miller Creek provides an excellent opportunity to examine plant community development after disturbances that caused extremely high levels of overstory mortality but span a range of fire intensities and different fire origins. In returning to Miller Creek 55 years after disturbance, our study builds on the detailed picture of early-seral plant community development at Miller Creek reported in previous research over the first two decades post-disturbance (DeByle 1981; Stickney 1990; Shearer and Stickney 1991).

Of the three controls on secondary succession that we investigate, pre-disturbance vegetation influences community development by providing most of the compositional building blocks for post-disturbance regrowth (Stickney 1986, 1990; Halpern 1989). Interactions between the traits of these pre-existing species and disturbance characteristics heavily influences survival, growth, and seed supply (Shorohova et al. 2009; Stevens et al. 2021; Barrett et al. 2023). While colonization by off-site species may supplement the in situ species pool, especially for high-severity disturbances (Stickney 1990; Myers and Harms 2009; Halpern and Antos 2022), plant community development is often a story of changes in the relative abundance of the pre-disturbance species rather than dramatic compositional shifts through successive colonization (Stickney 1986, 1990; Halpern 1989).

Second, disturbance characteristics directly and indirectly affect ecosystem re-assembly by modifying the physical site, resource availability, and the pre-existing vegetation (e.g., Pickett and White 1985; Lorimer 1989; Agee 1993). This includes changes to the edaphic environment that alter seedbed characteristics and the availability of moisture and critical nutrients (Roberts 2004; Certini et al., 2005; Nave et al. 2011). For example, overstory mortality creates physical growing space, alters environmental gradients, contributes organic matter for decomposition, and modifies the germination substrate (e.g., Harmon et al. 1986; Taylor 1990); Hansen and Lorimer, 2007; Kern et al. 2019). Through such changes, disturbances alter and potentially diversify niche space for subsequent plant establishment and growth (Harpole and Tilman 2007; Kern et al. 2013).

And third, site attributes, such as topography and climate, directly shape post-disturbance vegetation development over various timeframes, and may have important indirect effects by amplifying or attenuating the disturbance (Ruth and Yoder 1953; Whitman et al. 2018; Merschel et al. 2024). Implicit in classifications of site potential vegetation is that the relative importance of these site characteristics increases through time, such that they eventually become the dominant control on vegetation in the absence of further disturbance (Daubenmire 1952; Margalef 1968; Christensen and Peet 1984).

Past research at Miller Creek identified disturbance characteristics and their interaction with pre-disturbance vegetation as central to early-seral community dynamics following high-intensity wildfire, or clearcutting followed by various applications of broadcast burning (Stickney 1990; Shearer and Stickney 1991). Specifically, the amount of duff combusted during burning was posited as a primary influence on early-seral plant community development (initially herbaceous vegetation, and later shrubs and tree seedlings). Duff consumption served as a proxy for fire intensity and soil burn severity and directly influenced survivorship of existing vegetation, persistence of dormant seedbanks, and the properties of the post-disturbance seedbed. Traits possessed by pre-disturbance vegetation mediated these effects of fire intensity (Stickney 1990). Site characteristics exerted an influence on early-seral community development by amplifying the effect of weather conditions on seedling establishment, growth, and survival. These findings accord with the role of soil burn severity in shaping post-fire community dynamics in many other temperate and boreal forests (e.g., Johnstone and Chapin 2006; Halpern and Antos 2022; Bushey et al. 2023). However, there have been few previous analyses of the controls on plant community structure in communities that have transitioned out of the early-seral stage following disturbances of known/measured characteristics. In the only such study that we are aware of, Halpern et al. (2024) observed relatively weak effects of burn characteristics on community composition (including herbs, shrubs, and trees) in a moist temperate forest, four decades post-disturbance. The legacy of past research at Miller Creek makes this site well suited to examining the longer-term effects of disturbance on plant communities.

Although fire intensity was determined to be an important influence on early-seral plant community development at Miller Creek, the effects of fire intensity on vegetation spatial pattern (i.e., spatial heterogeneity in vegetation physical structure) were not evaluated. Vegetation spatial pattern is now of widespread interest for its role in ecosystem function (e.g., Franklin et al. 2002; Larson and Churchill 2012; Hessburg et al. 2015). At stand-scales, the mixed-severity fire regime typical of the moist mixed-conifer forests at Miller Creek produces a coarse-grained spatial mosaic (Arno et al. 1997; Clyatt et al. 2016; Hood et al. 2021). At sub-stand scale, heterogeneity in the spatial pattern of post-fire community development should emerge from heterogeneity in the effects of fire on the physical environment and existing vegetation (i.e., spatial heterogeneity in mortality and survival), which results in spatial heterogeneity in

germination substrate and resource availability (Johnstone and Chapin 2006). An analogy can be drawn with the theory of "niche dimensionality" (Hutchinson 1957), which suggests that diversification of access to essential resources (niche partitioning) should promote high levels of biodiversity (Harpole and Tilman 2007; Harpole et al. 2016). High-intensity fires overcome soil moisture constraints to duff consumption, leaving little intact duff and killing a high proportion of above- and belowground meristematic plant tissues (belowground meristems are common in northern Rocky Mountain herbs and shrubs, and are often located at various depths in the duff layer) and the soil seedbank (Stickney 1986, 1990; Stephan et al. 2010; Agbeshie et al. 2022). In the northern Rocky Mountains, such conditions may lead to the establishment of dense thickets of lodgepole pine (*Pinus contorta*) in uniform, high-light environments with abundant mineral soil exposure (Lotan and Perry, 1983; Lotan et al. 1985; Berkey et al. 2021). Meanwhile, during low-intensity fires when fuel moisture is high, duff may fail to ignite and mortality of buried plant tissues is likely to be low, enabling rapid regrowth of existing vegetation (Shearer and Stickney, 1991; Stickney, 1990; Roberts 2004; Varner et al. 2016; Agbeshie et al. 2022). These low- and high-intensity fire scenarios exemplify limited spatial partitioning of resource availability and the physical germination substrate. Moderate intensity fires, by comparison, may provide more scope for spatial variability in the outcome of interactions between fire, physical microsite conditions (including heterogeneity in pre-fire duff depth), and plant tissues, promoting heterogeneous establishment conditions and, hence, vegetation spatial pattern (Lee 2004; Greene et al. 2005; Kreye et al. 2014). Over post-disturbance timeframes of many decades, this heterogeneity is most likely to persist in the physical location of long-lived woody shrubs and trees. We are not aware of previous research that addresses the influence of fire intensity on long-term spatial heterogeneity of vegetation at fine (microsite to tree neighborhood (tens of meters)) spatial scales.

In this study, we use recent empirical data from Miller Creek to:

(1) Evaluate the controls on vegetation structure and composition, 55 years following high-severity disturbance. Specifically, we hypothesize that disturbance characteristics more strongly influence vegetation structure and composition, five decades post-disturbance, than do site characteristics or pre-existing vegetation;
(2) Examine the relationship between fire intensity and heterogeneity in the horizontal and vertical distribution of understory and overstory vegetation (i.e., spatial heterogeneity in vegetation physical structure) five decades post-disturbance. Specifically, we hypothesize that, across the range of fire intensities at Miller Creek, moderate intensity fire is associated with greater spatial heterogeneity in vegetation physical structure than either low- or high-intensity fires.

Methods

Site description

Miller Creek Demonstration Forest (Miller Creek) is a 1984-ha research demonstration forest located on the Flathead National Forest in northwest Montana and represents a hub of collaboration between the U.S. Forest Service management and research personnel. The site is the location of a pioneering multi-disciplinary study, initiated in 1966, into the effects of clearcutting and broadcast burning on wide-ranging natural resource outcomes, from smoke production and hydrological impacts, to ecological and silvicultural consequences (DeByle 1981; Latham et al. 1998; Williams et al. 2023a).

Miller Creek experiences a cool, moist climate, with a short, relatively dry growing season. Average daily minimum temperatures range from −9.1 °C in January to 6.2 °C in August, while the mean daily maximums range from −1.6 to 24.8 °C (PRISM Climate Group, Oregon State University n.d). Total annual precipitation averaged 652 mm over the last 30 years, two thirds of which typically falls as snow. Elevation ranges from 1250 to 1550 m, while slopes average 35% but face all cardinal aspects as a series of ridgelines cut across the site (Table 1). Soils are classed as Andic Cryoboralfs with an organic horizon typically ranging from 2.5 to 7.5 cm depth, above silt and gravelly loam (Beaufait et al. 1975).

Vegetation at this mid-elevation site falls in the *Abies lasiocarpa*/*Clintonia uniflora* (ABLA/CLUN) habitat type (Pfister et al. 1977) in which subalpine fir (*Abies lasiocarpa*) is the dominant late-seral species. Western larch (*Larix occidentalis*) is an important and long-lived pioneer in the ABLA/CLUN habitat type in northwestern Montana and was characteristic of the 250-year-old old-growth stands that covered the Miller Creek drainage before experimental treatments. This older forest still forms a matrix around treatment areas and, in addition to western larch, Engelmann spruce (*Picea engelmannii*), Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and subalpine fir are major overstory species, while lodgepole pine and black cottonwood (*Populus balsamifera* subsp. *trichocarpa*) are locally important. Three phases of the ABLA/CLUN habitat type occur at Miller Creek. The *Xerophyllum tenax* phase ("ABLA/CLUN – XETE" or simply "XETE"), which occupies cold, dry sites that are typically also the most exposed to solar insolation

Table 1 Summary data on 2023 vegetation, treatment, and site characteristics for the 13 Experimental Burn Units (EBUs) at Miller Creek that were included in this study. Habitat type phases: CLUN – *Abies lasiocarpa/Clintonia uniflora – Clintonia uniflora*, MEFE – *Abies lasiocarpa/Clintonia uniflora – Menziesia ferruginea*, XETE – *Abies lasiocarpa/Clintonia uniflora – Xerophyllum tenax*

EBU	2023 total BA (m^2/ha)	2023 av. tree Ht. (m)	2023 herb cover (%)	2023 shrub cover (%)	2023 tree cover (%)	Disturbance type	Burn month	Aspect	Elevation (m)	Habit type phase
MC10	36.5	11.4	27	5	211	Cut-burn	June	North	1510	MEFE
MC11	23.9	8.4	23	7	203	Cut-burn	Oct	North	1450	CLUN
MC12	24.6	9.5	48	22	123	Cut-burn	May	South	1490	XETE
MC15	35.4	11.5	11	8	196	Cut-burn	Sept	North	1490	MEFE
MC17-1	25.4	10.5	38	25	97	Cut-burn	July	West	1430	XETE
MC17-3	28.0	10.5	38	23	177	Cut-burn	Oct	West	1400	XETE
MC18	34.9	11.5	28	4	265	Cut-burn	Sept	North	1490	MEFE
MC20	19.0	11.0	28	7	178	Cut-burn	Sept	West	1430	XETE
MC21-1	45.2	12.1	38	0	233	Cut-burn	Oct	East	1430	MEFE
MC21-3	37.5	10.4	58	2	175	Cut-burn	Oct	East	1430	XETE
MC22-1	38.2	13.4	15	5	159	Wildfire	August	South	1400	XETE
MC22-3	25.4	13.6	32	17	188	Wildfire	August	South	1390	XETE
MC23	28.9	10.7	16	23	261	Wildfire	August	West	1310	XETE

during the warm summer months, and the *Menziesia ferruginea* phase ("MEFE"), which occurs on relatively cold and moist sites, are the dominant phases. The *Clintonia uniflora* phase ("CLUN") is found on warmer and moist sites, but is a small component of Miller Creek (Table 1).

Study design and sampling

The complete experiment at Miller Creek involved different applications of clearcutting followed by broadcast burning, with variation in the season of broadcast burning (spring, summer, fall), the number of years between clearcutting and burning (0–2), and site aspect (north, east, south, west) (Table 1). Treatment units—termed Experimental Burn Units (EBUs)—were 4 ha in area, square in shape, and distributed across the demonstration forest within the matrix of older forest (Fig. 1). In 1967, a wildfire burned some or all of 16 of the 60 EBUs in the complete Miller Creek experiment. At the time of burning, some of these units had already received their assigned clearcut and burn treatment, while others were mid-treatment or untreated. In most affected EBUs, the fire burned at high severity, causing extremely high levels of overstory mortality and severe soil burning. A subset of EBUs at Miller Creek were subsequently included in a planting study, but most units, including those studied here, regenerated naturally via seed rain from surrounding old-growth forest. Because of the relatively small size of EBUs and their staggered, longitudinal distribution within the demonstration forest (Fig. 1), the maximum seed dispersal distance from unharvested forest to the edges of EBUs was approximately 100 m. Dispersal from nearby forest was supplemented by seed from any unburned cones in snags and serotinous seeding from lodgepole pine (especially in wildfire-affected stands).

The Plant Succession Study that is the subject of the current research originally focused on 16 of the EBUs at Miller Creek (Stickney and Campbell, 2000). Of these 16 EBUs, only 13 could be reliably relocated and remeasured in 2023 for the current study. Three of these EBUs were burned by the 1967 wildfire, while the remaining units were clearcut and broadcast burned (i.e., no EBUs experienced both wildfire, and clearcut plus broadcast burning). Hence, for the purpose of our analysis and previously published findings from the first two decades of the Plant Succession Study at Miller Creek (e.g., Stickney 1981; Shearer and Stickney 1991), the wildfire constitutes another variation on the disturbance (i.e., treatment) that initiates secondary succession. Vegetation sampling for the current research took place in 2023, but we also make use of pre-treatment measurements gathered by the study originators in 1966.

The Plant Succession Study involved measurement of herbs, shrubs, and trees (Stickney and Campbell, 2000). Sampling was conducted on two transects per EBU using a nested, fixed-area plot design. Transects measuring 5×25 m were generally oriented in the same direction in each EBU and situated adjacent to one another, short end-on. Plot design and sampling protocols are described in detail in Stickney and Campbell, 2000. In brief, vegetation was inventoried in different plot sizes according to lifeform, height, and habit (Fig. 1). Trees and shrubs with height ≥ 2.5 m were sampled in five 5×5 m ($25\ m^2$)

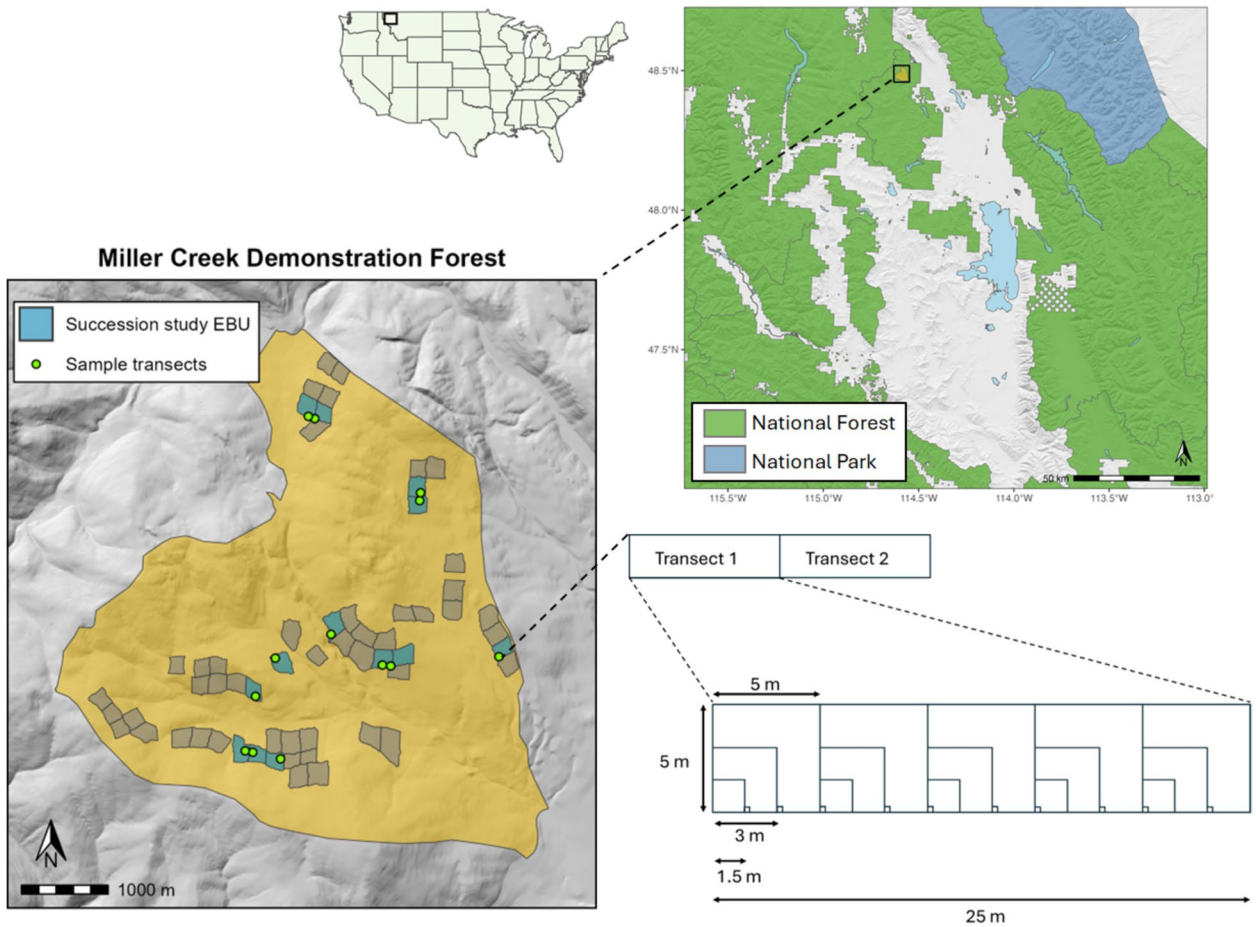

Fig. 1 The Miller Creek Demonstration Forest is located on the Flathead National Forest in northwest Montana. Multi-disciplinary research into the effects of clearcutting and broadcast burning commenced in 1966 on 60 4-ha Experimental Burn Units (EBUs; shown as polygons in the local map (lower left image). The Plant Succession Study involved 16 of these EBUs, 13 of which (teal shading) were relocated and sampled in 2023 using the original Plant Succession Study protocols. Sampling was conducted on two adjacent transects in each EBU (locations of the midpoint of the two transects shown as green points in the lower left image). In each transect (close-up shown in the lower right image), fixed area plots ranging from 0.5 × 0.5 m (the smallest squares on the lower right image) to 5 × 5 m were used to inventory plants according to height and lifeform

overstory plots located immediately adjacent to each other along the transect. All stems in each plot were identified to species, and total height (or path length, for leaning stems), diameter at breast height (DBH, 1.37 m), and crown diameter in two dimensions (axis one at the widest point in the crown, and axis two orthogonal to axis one) were measured. Shrubs and saplings with 1.5 m < height < 2.5 m, and 0.5 m < height < 1.5 m, were similarly inventoried (minus DBH measurement) in subplots measuring 3 × 3 m (9 m^2) and 1.5 × 1.5 m (2.25 m^2), respectively, each of which was located at the leading downslope corner of an overstory plot. All herbs, and shrubs and tree seedlings less than 0.5 m height, were sampled in ten 0.5 × 0.5 m (0.25 m^2) microplots, which were systematically located along each transect, two per overstory plot (Fig. 1). In each microplot, species occurrence was recorded. Cover was then estimated to the nearest 1/6th microplot and height to the nearest 5 cm for (i) all individual species accounting for at least 1/6th of a microplot, and (ii) on aggregate for all miscellaneous species that did not meet the 1/6th threshold. When estimating cover, we recognized vegetation in multiple strata in each microplot, i.e., cover of overtopped plants was also estimated even if these individuals could not be seen when looking down on the plot from above.

Data analysis

Response and explanatory variables

Sample data collected in 2023 were converted into metrics of composition, structure, and spatial heterogeneity

for use as response variables in data visualization and statistical modeling (see Supplement 1 for detailed description of aggregation procedures). Basal area per hectare was computed, on aggregate and per species, from stems ≥ 5 cm DBH. Understory plant richness was converted into an index of frequency of detection, expressed at the scale of sample transects (data provided in Supplement 2). This frequency of detection index was also calculated after grouping species by fire life history categories. These categories describe distinct modes of landscape-scale persistence with respect to fire (Table 2) and were used by the original researchers on the Plant Succession Study as a lens through which to view early-seral dynamics (Stickney 1986; Stickney and Campbell, 2000). Five metrics of spatial complexity were calculated: the coefficient of variation (CV) of herb cover, CV of shrub cover, CV of tree cover, Shannon Diversity Index (H`) of tree height, and CV H` tree height. Metrics involving the CV were calculated per EBU based on values of the underlying variable in sample plots along transects. H` tree height has long been used as a metric of vertical heterogeneity of foliage structure in forests, often because of the theoretical relationship between heterogeneity in the vertical distribution of vegetation and the diversity of microhabitats available for forest biota (e.g., MacArthur and MacArthur 1961; Staudhammer and LeMay 2001; McElhinny et al. 2005). Partnered with visualization of tree locations along sample transects, and when summarized into a CV of H` tree height along transects, H` tree height yields useful information on spatial heterogeneity in vertical structure of vegetation. We calculated H` tree height using 3-m height bins, initially computing the index across all trees in each EBU to obtain H` tree height per EBU, and then across all trees in each overstory plot in each EBU to obtain CV H` tree height. A variety of approaches exist for selecting height bins to calculate H` tree height, including aligning bins with different plant life habits as a coarse surrogate for differences in resource utilization by forest biodiversity (MacArthur and MacArthur 1961). In this study, our immediate interest was in quantifying vegetation physical structure, and as maximum tree height in sample EBUs was relatively low we adopted relatively narrow, fixed height intervals.

To examine the influence of characteristics of (i) the initiating disturbance, (ii) the site, and (iii) the pre-disturbance vegetation, on 2023 vegetation structure and composition, we identified a single explanatory variable representing each of these three categories of controls. The final set of variables was as follows: water loss from a metal can embedded at the duff—mineral soil interface before burning (selected to integrate characteristics of the disturbance), Heat Load Index (HLI, a generalized estimate of the heat derived from incoming solar radiation experienced at a given location based on geographic and topographic information; McCune and Keon 2002; McCune 2007) (integrating characteristics of the site), and pre-disturbance overstory basal area (in total or by species) or pre-disturbance frequency of detection of understory species by life history category (all representing pre-disturbance vegetation, depending on the response variable). More detailed rationale for and calculation of these explanatory variables is provided in Supplement 1. We limited the number of response variables in our analysis to one per category (of control) because of the small sample size (13 EBUs) at this single-forest study.

Analytical procedures

Research question 1: overstory vegetation We used generalized linear mixed models (GLMM) with a Tweedie error distribution to evaluate the influence of characteristics of the disturbance (*water_loss*, in the equation below), site *(HLI*), and pre-disturbance vegetation (*PD_BA*) on

Table 2 The four fire life history classes used to categorize vegetation at Miller Creek by different approaches to persisting in the presence of fire. Classification and descriptions are based on the work of Peter Stickney at Miller Creek and other sites in the northern Rocky Mountains (e.g., Stickney and Campbell, 2000). * The avoider category was not defined by Peter Stickney or used in earlier work at Miller Creek, but is defined here to include species previously described as "accidental survivor." The term avoider was used for consistency with other published examples of fire life history classifications (e.g., Rogers et al. 2015; Williams et al. 2023b)

Life history class	Description	Example species
Avoiders*	Species with low tolerance of fire that persist by inhabiting sites or microsites in which fire is rare but are typically killed when fire does occur	*Taxus brevifolia* (Pacific yew)
Survivors	Species that persist via adaptations that enable aboveground or belowground meristematic tissues to survive fire. For shrubs and herbaceous vegetation, this strategy typically involves resprouting following top-kill	*Xerophyllum tenax* (common beargrass)
Residual colonizers	Species that colonize the site after a fire from seed contained in aerial or soil seedbanks within the fire perimeter	*Pinus contorta* (lodgepole pine)
Offsite colonizers	Species that colonize sites from seed traveling into the site from offsite sources	*Chamerion angustifolium* (fireweed)

2023 basal area of individual species and total basal area. The sample size of the Plant Succession Study—13 EBUs, 26 sample transects—presents undoubted statistical challenges when attempting to explore relationships between multiple explanatory variables and the response variable. Using a multilevel GLMM with a Tweedie error distribution provides a robust but flexible framework for modeling our response variables as a function of three explanatory variables while accounting for the nested data structure and frequent "zero" observations. Five tree species were sufficiently widespread to permit modeling of individual species basal area (Douglas-fir, Engelmann spruce, lodgepole pine, subalpine fir, and western larch), resulting in a total of six GLMM of the form:

$$y_{ijk} \sim Tweedie(\mu_{ijk})$$

$$log\left(\mu_{ijk}\right) = \eta_{ijk}$$

$$\eta_{ijk} = \beta_0 + \beta_1 water\_loss_{ijk} + \beta_2 HLI_{ijk} + \beta_3 PD\_BA_{ijk} + a_k + a_{j|k} + \varepsilon_{ijk}$$

$$a_k \sim N\left(0, \sigma_k^2\right)$$

$$a_{j|k} \sim N\left(0, \sigma_j^2\right)$$

$$\varepsilon_{ijk} \sim N\left(0, \sigma^2\right)$$

where y_i is the predicted value of the ith observation in the jth transect (for $j = 1, 2$) and the kth EBU (for $k = 1, 2, \ldots, 13$) for the response variable, a_k is the random intercept allowing for variation between EBUs, $a_{j|k}$ is the random intercept allowing for variation between transects nested in EBUs, ε_{ijk} is the random error term, and $\beta_0 - \beta_3$ are parameters to be estimated.

Visual outputs and formal statistical tests were used to evaluate the distribution of residuals, and the presence of zero-inflation and over/under dispersion. The model for 2023 lodgepole pine basal area was strongly underdispersed and also contained many zeros, the latter contributing to the former. Adjusting for this underdispersion while accounting for the zero-inflated distribution required refitting the GLMM using a zero-inflated gamma distribution. The fixed and random effect structures for the conditional (gamma) and zero-inflated components of this model were identical to those of the Tweedie distribution used for other response variables. Use of the zero-inflated model for lodgepole pine alters the interpretation of the model outputs. Model means and confidence intervals reported in Fig. 2 for lodgepole pine represent the estimated relationship between the explanatory variables and 2023 lodgepole pine basal area for those EBUs

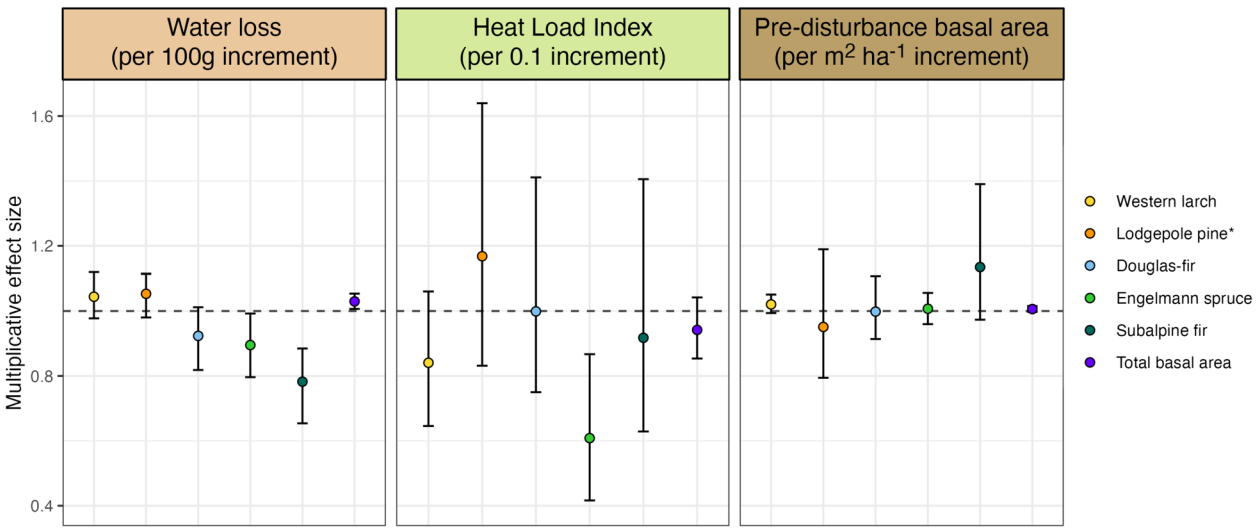

Fig. 2 Multiplicative effect size and 95 percent confidence intervals for water loss (disturbance characteristics) (left panel), Heat Load Index (HLI, site characteristics) (center panel), and pre-disturbance basal area (pre-disturbance characteristics) (right panel). For ease in interpretation, effect sizes for water loss and HLI variables have been converted from the original units—per 1 g for water loss, per 1 unit for HLI—to per 100 g and per 0.1 pt increments, respectively. Note that the results for 2023 lodgepole pine basal area apply to EBUs in which lodgepole pine was present, rather than the complete set of EBUs

in which lodgepole pine was present in 2023 (i.e., the conditional component of the model), rather than across the entire population of EBUs. Likelihood ratio tests were used to evaluate the significance ($\alpha < 0.05$) of covariates in the zero-inflated component of the model (Zuur et al. 2009) because profile confidence intervals (a more reliable approach than simple linear approximation for GLMMs) failed to converge on a solution.

We used 95% profile confidence intervals around parameter estimates to evaluate statistical relationships between response and explanatory variables. Model means and confidence intervals were converted back (from the log scale) to the scale of the response variable for interpretation (Fig. 2) and, as such, effect sizes are expressed in multiplicative not additive terms.

Research question 1: understory vegetation We used NMDS to examine potential drivers of 2023 understory community structure. The input community matrix consisted of species' frequency of detection per sample transect, with Bray–Curtis distances used for the distance matrix. We specified a maximum of 300 iterations during model convergence, and 40 repetitions for ordinations with $k = 1, 2, \ldots 7$ dimensions. A $k = 3$ ordination provided a suitable balance between low stress (0.07) and interpretability.

Graphical overlays were used to highlight relationships between disturbance, site, and pre-disturbance vegetation characteristics and ordination space. Points representing sample transects in ordination space were colored according to their "treatment" – clearcut + broadcast burn or wildfire – convex hull polygons were used to visualize the degree of clustering of sample transects according to site aspect, and a centroid overlay was used to depict the central location of ordination space occupied by sample transects on different habitat type phases (XETE, MEFE, CLUN—noting that CLUN is represented by only two transects). We then used vector overlays to examine the correlation of water loss, HLI, and pre-disturbance frequency of detection of the four fire life history classes with the ordination axes.

A second NMDS ordination was conducted, as described above, on an input community matrix composed of 2023 frequency of detection per life history classes in sample transects.

PerMANOVA (Anderson, 2001) was used to compare groups of transects corresponding to different fire origins (broadcast burn versus wildfire), different aspects, and different habitat type phases. PerMANOVA was conducted on the Bray–Curtis distance matrix of 2023 understory species frequency of detection. Differences between groups were considered significant using an α of 0.05.

Research question 2: spatial heterogeneity We used linear regression models to assess the influence of fire intensity on 2023 vegetation spatial heterogeneity. For each of the five response variables, CV herb cover, CV shrub cover, CV tree cover, H` tree height, and CV H` tree height, we constructed a second-order polynomial regression model of the form.

$$y_i = \beta_0 + \beta_1 x_i + \beta_2 x_i^2 + \varepsilon_i \quad \text{for } i = 1, 2 \ldots 13 \text{ and } \epsilon\, N(0, \sigma^2)$$

where y_i is the predicted value of response variable in the ith EBU, x_i is water loss (g), and ε_i is the random error term. We did not examine higher order polynomial models as our hypothesized relationship between fire intensity and spatial heterogeneity was quadratic in form. Model validation was completed as previously described. A confidence interval for the x^2 term that did not include 0, accompanied by a positive effect size, were interpreted as indicative of moderate-intensity fire contributing to greater spatial complexity (for the given explanatory variable) than low- or high-intensity fires.

As an additional tool for visualizing spatial pattern, we plotted the location of all trees along sample transects in each EBU. Although tree locations within each plot were not mapped during fieldwork, the two sample transects in each EBU are located adjacent to one another, effectively forming a 50-m sample length divided into ten continuously located plots. Tree locations are thus approximations, and plotting locations against tree height creates an informative, though fuzzy, rendering of both horizontal distribution and vertical forest structure along sample transects.

All data analysis was conducted in the R programming environment (R Core Team, 2024) using the packages, DHARMa (Hartig 2024), ggfortify (Tang et al. 2016), ggh4x (Van den Brand 2024), ggpubr (Kassambara 2023), ggresidpanel (Goode 2019), glmmTMB (Brooks et al. 2017), grid (R Core Team, 2024), here (Müller 2020), MuMIn (Bartoń, 2024), performance (Lüdecke et al. 2021), tidyverse (Wickham et al. 2019), and vegan (Oksanen et al. 2024).

Results

Research Question 1—controls on 2023 vegetation structure

Overstory basal area in 2023 was more strongly associated with characteristics of the disturbance and the site than characteristics of the pre-disturbance vegetation. Ninety-five percent confidence intervals for fire-induced water loss indicate a negative relationship between fire intensity and 2023 basal area of subalpine fir and Engelmann spruce (Fig. 2). When species are arranged in order of shade tolerance, estimates and confidence intervals show a general trend from positive to negative effects of

water loss on 2023 basal area with increasing shade tolerance (Fig. 2). However, confidence intervals around the estimated multiplicative effect size for 2023 western larch, lodgepole pine, and Douglas-fir basal area narrowly included 1, indicating insufficient evidence of a statistically significant effect. Total basal area in 2023 was positively associated with water loss, reflecting the contribution of western larch to the total basal area in most EBUs. Basal area of Engelmann spruce was strongly negatively associated with heat load index (HLI), our summary variable for site characteristics (Fig. 2), but confidence intervals for all other response variables included 1 and were often extremely wide. By contrast, pre-disturbance vegetation was not significantly associated with 2023 basal area for any individual species, or for total basal area. Given that confidence intervals for GLMM are approximations, the results for western larch and total basal area in 2023 could be interpreted as suggestive of a weak positive relationship with pre-disturbance western larch or total basal area (Fig. 2), respectively, but the effect sizes are sufficiently small to be immaterial in ecological terms. The zero-inflated component of the lodgepole pine GLMM suggested that an increase in water loss was associated with a reduction in the odds of lodgepole pine absence (i.e., "structural zeros") (likelihood ratio p-value 0.012 – Table S1, Supplement 1). In numerical terms, HLI and pre-disturbance basal area were also inversely correlated with the odds of lodgepole pine absence, but the relationship was not statistically significant (likelihood ratio test p-values of 0.10 and 0.13, respectively).

Site characteristics again emerged as a potential driver of understory community composition in 2023. When using a species-level community matrix as the input for NMDS analysis, sample transects on different aspects generally occupy distinct regions of ordination space, with modest overlap between south and west aspects (Fig. 3a). Similarly, the centroids of the two dominant habitat type phases represented at Miller Creek, MEFE and XETE, were located on opposing sides of ordination space (Fig. 3a), MEFE being proximal to north aspects and XETE to south and west aspects. Plant community composition of wildfire EBUs (i.e., the EBUs with highest water loss/fire intensity) was also coincident with the region of ordination space occupied by the XETE habitat type phase, and hence the south and west aspects. Vector overlays of disturbance-, site-, and pre-disturbance vegetation-related variables implied a relatively well-defined linear relationship between both HLI (R^2: 0.61), and pre-disturbance survivors (R^2: 0.54), and ordination space (axes 1 and 2). HLI, in particular, was strongly correlated with regions of ordination space occupied by south and west-facing sample transects and the XETE habitat type phase (Fig. 3a).

Results of PerMANOVA analysis are consistent with the importance of site characteristics in the species-level NMDS ordination. P-values from permutation-based F-tests indicate that sample transects representing different aspects and fire origin (broadcast burn versus wildfire—a differentiation that reflects the significantly higher fire intensity of the wildfire than broadcast burning) differ in understory vegetation composition (Table 3). The marginal effect of habitat type phase—i.e., the effect of habitat type phase after accounting for fire origin and aspect—was not significant, although conducting the same PerMANOVA using sequential variable addition revealed that habitat type phase was significant when included in isolation.

In general, the relationships between understory community composition and disturbance, site and pre-disturbance factors that were observed in the species-level NMDS analysis were not evident when aggregating input data by fire life history class (Fig. 3B). With the exception of water loss, which was again associated with southern aspects, most categorical and continuous explanatory variables were less readily clustered or exhibited weaker relationships with the life history space defined in this ordination.

Research Question 2—spatial heterogeneity

Counter to our hypothesis on the effects of moderate intensity fire on spatial structure, the second-order term for water loss was not significant in polynomial regression models for the coefficient of variation (CV) of herb,

(See figure on next page.)

Fig. 3 Non-metric multi-dimensional scaling (NMDS) ordinations using a species-level community matrix (**A**) and a fire life history class community matrix (**B**). Graphical overlays depict the location of sample transects; the color of points illustrates the amount of fire-induced water loss, a measure of fire intensity; colored convex hull polygons display different aspects; and colored crosses show the centroids of habitat types. Vector overlays of continuous explanatory variables are presented as colored arrows. The length of arrows indicates the strength of correlation with ordination space, as do R^2 values (the square of the correlation). Vector overlay descriptions: *avoiders*—pre-disturbance frequency of detection of species with an avoider fire life history strategy; *survivors*—pre-disturbance frequency of detection of species with a survivor fire life history strategy; *offsite colonizers*—pre-disturbance frequency of detection of species with an offsite colonizer fire life history strategy; *HLI*—Heat Load Index; *water loss*—fire-driven water loss from metal cans placed on site before burning. Overlays are only presented for relationships in which the R^2 value exceeded 0.20

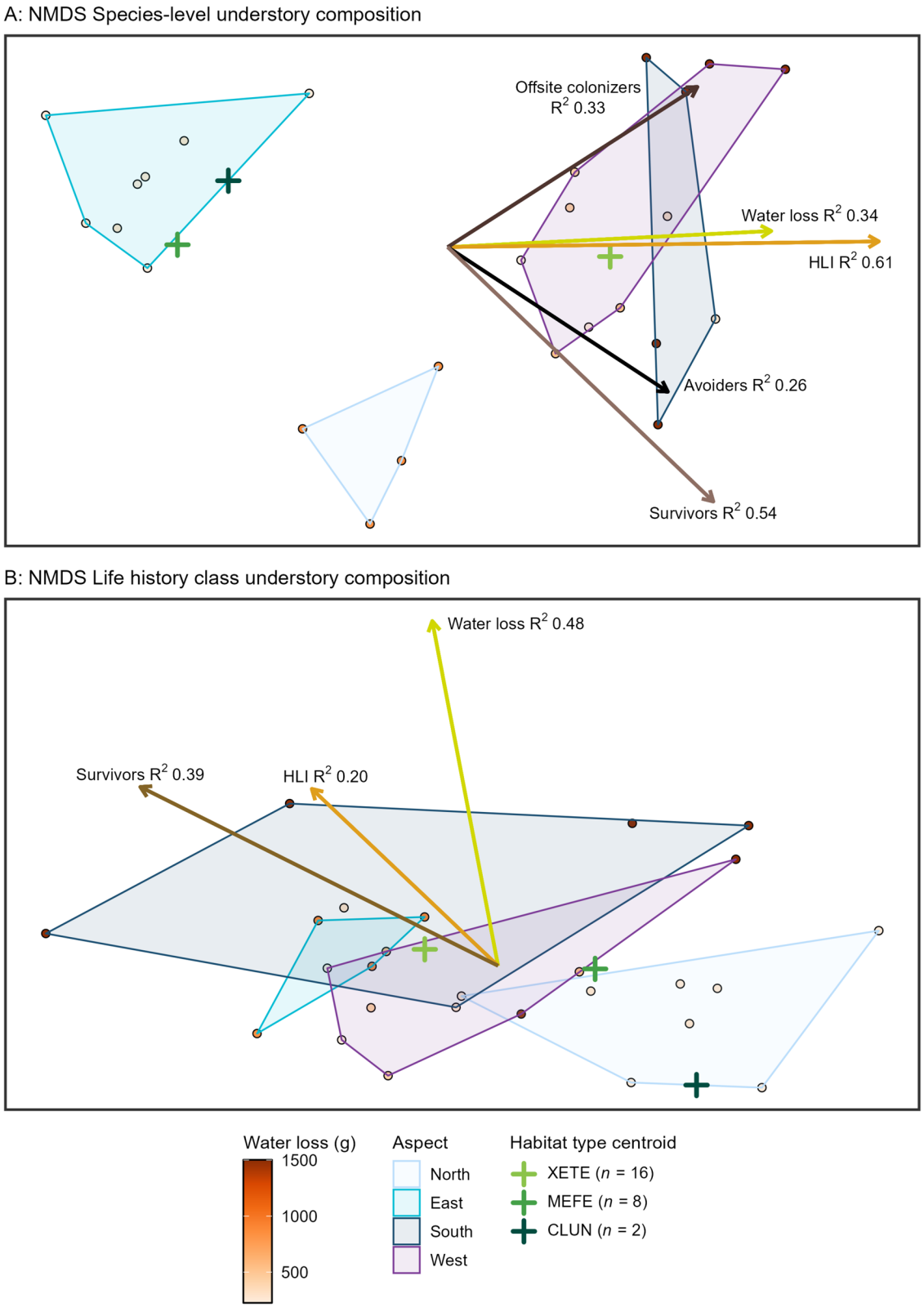

Fig. 3 (See legend on previous page.)

Table 3 Statistical outputs from a PerMANOVA test of the marginal effects (i.e., effects when other variables are held constant) of key categorical variables associated with disturbance and site characteristics

Variable	Permutation-based F-statistic	Permutation-based *P*-value
Fire origin	4.165	0.001[a]
Habitat type phase	1.094	0.344
Aspect	3.394	0.001[a]

[a] Indicates statistical significance against an α of 0.05

shrub, or tree cover, or with H` tree height or CV H` tree height (Table 4). Indeed, most polynomial models exhibited higher AICc scores than their equivalent first order linear models (results not shown), implying that the more parsimonious models offered superior fit. Therefore, our results do not provide evidence that any of the metrics of spatial heterogeneity examined here peak at moderate fire intensities.

Visual inspection of tree heights along sample transects in each EBU yields important information on long-term post-disturbance forest development (Fig. 4). Consistent with expectations, the overstory in most EBUs is dominated by larch and/or lodgepole pine, species with low shade tolerance, and rapid early growth. Lodgepole pine was common only in EBUs in which wildfire occurred, and here it competes with and sometimes overtops larch (for example, MC22-1, and MC23). Shade tolerant subalpine fir and Engelmann spruce form the lower canopy, extending into the midstory, in most EBU's that were clearcut and subsequently broadcast burned. Where these shade-tolerant species were particularly abundant underneath a larch-dominated overstory, H` tree height values were often high and CV H` tree height were relatively low (e.g., MC10, MC15, MC21-1). Although tree locations in Fig. 4 are approximations of their precise location, there are clear differences in stem density and the amount of "whitespace" or "gappiness" in the canopy, especially the upper canopy, between EBUs. Relatively higher CV H` tree height values typically corresponded to sample transects with lower stand density (MC20, MC22-1, for example), or those with clear canopy gaps (e.g., MC17-3, MC12). In this limited sample, the EBU with the highest CV H` tree height value (MC20) was also that with the greatest mixing of species with different shade tolerance and fire life history strategies in the upper canopy.

Table 4 Parameter estimates and 95 percent confidence intervals for first- and second-order terms in polynomial regression models for five metrics of spatial heterogeneity. Ninety-five percent confidence intervals that do not include 0 are indicative of a relationship between response and explanatory variables. Reported effect sizes are for increments of 1 g water loss

Variable	Model R^2	Coefficient	Estimate	Lower CI	Upper CI
CV herb cover	0.072	Intercept	0.887	0.401	1.374
		Water loss	−0.001	−0.003	< 0.000
		Water loss^2	< 0.000	− < 0.000	< 0.000
CV shrub cover	0.259	Intercept	0.832	0.060	1.603
		Water loss	< −0.000	−0.003	0.002
		Water loss^2	< 0.000	− < 0.000	< 0.000
CV tree cover	0.025	Intercept	0.327	0.099	0.556
		Water loss	< 0.000	< −0.000	0.001
		Water loss^2	< −0.000	− < 0.000	< 0.000
H` tree height	−0.193	Intercept	1.621	1.152	2.090
		Water loss	< 0.000	−0.001	0.002
		Water loss^2	< −0.000	− < 0.000	< 0.000
CV H` tree height	−0.193	Intercept	0.478	−0.135	1.091
		Water loss	< −0.000	−0.002	0.002
		Water loss^2	< 0.000	− < 0.000	< 0.000

Discussion

Our findings build on the dedication to understanding patterns and mechanisms of post-disturbance plant succession that led past researchers at Miller Creek to collect annual data and photographs for over two decades following a variety of clearcut and broadcast burn treatments, and high-severity wildfire (Stickney 1986; Stickney and Campbell, 2000; Williams et al. 2023a).

Post-disturbance recovery

Fifty-five years after high-severity disturbance, all EBUs have regained forest cover and transitioned to the stem exclusion phase of stand development. With much attention currently devoted to identifying management options for increasing ecological resilience and aiding recovery following uncharacteristically severe disturbance in many dry forests in the western U.S. (e.g., Halofsky et al. 2018; Stevens-Rumman and Morgan, 2019; Abatzoglou et al. 2021; Stevens et al. 2021; Larson et al. 2022), an important take-home message from our study is that the moist mixed-conifer forests at Miller Creek have naturally regenerated following common high-severity disturbances in these systems. Moreover, forest regeneration at Miller Creek was successful irrespective of the intensity and origin of burning, the site characteristics, and a challenging post-disturbance environment that included poor seed years, harsh weather conditions, and intense seed predation and disease (Shearer 1981).

The natural disturbance regime of mid-elevation, moist mixed-conifer forests in the northern Rocky Mountains

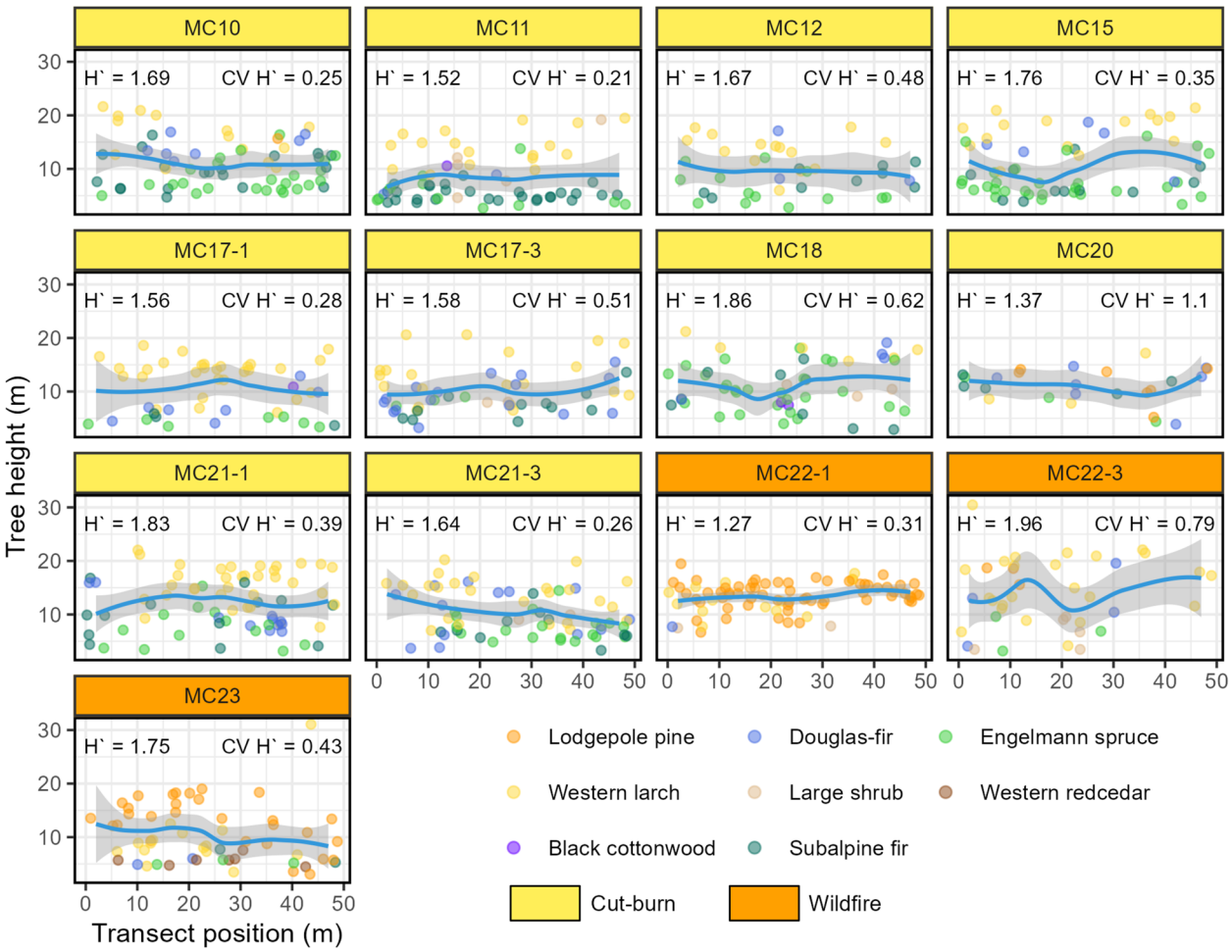

Fig. 4 Approximate locations of trees along sample transects in 13 Experimental Burn Units (EBU) at Miller Creek, representing "clearcut + broadcast burn" and "wildfire" treatments. Two 25-m-long transects are located adjacent to one other in each EBU, so for visualization the combined 50-m-long transect is depicted on the *x*-axis as a continuous length. Trees were sampled in 5 × 5 m plots located contiguously along transects. Because the exact distance of trees within plots was not measured, trees were assigned the midpoint location within each plot and the precise position "jittered" randomly by 2 m to remove the artificial centering of tree locations in plots and improve visibility. Hence, this graphic should be viewed as an approximation of tree locations that illustrates the horizontal structure of plots, rather than as showing the precise location of each tree. Blue lines are a loess smoothing function (with grey shading for one standard error) of changes in tree height along the combined 50-m transect. Inset statistics are the Shannon Diversity Index of tree height (*H`*), and coefficient of variation of H` of tree height (*CV H`*)

is thought to include mixed- to high-severity wildfire, depending on site and location (Barrett et al. 1991; Arno and Fischer 1995; Arno et al. 1997), while clearcutting has been among the primary regeneration harvest methods in managed western larch forests (DeByle 1981; Burns 1983). Western larch and lodgepole pine are widespread disturbance-dependent pioneer species adapted to wildfire and with the potential for extremely high juvenile growth rates in high light conditions (Schmidt et al. 1976; Agee 1993; Cobb et al. 1993; Harper et al. 2009). Resampling 13 EBUs at Miller Creek in 2023 shows that these pioneer species are now dominant in the overstory of almost all units, with western larch widespread and lodgepole pine common in EBUs that experienced a high-intensity wildfire. Less expected is that EBUs treated with a variety of clearcutting plus broadcast burn applications already possess an understory comprised primarily of shade-tolerant subalpine fir and Engelmann spruce, as well as mid-tolerant Douglas-fir. Our results, therefore, illustrate that these young stands have not only regained forest cover within 55 years of high-severity disturbance, but are already species mixtures with relatively complex vertical structure.

Controls on vegetation structure five decades post-disturbance

Our findings build on results from the first two decades of study at Miller Creek that illustrated the important

role of fire intensity in shaping secondary succession (Stickney 1990; Shearer and Stickney 1991). Early work at Miller Creek identified the proportion of duff consumed during fire as an important determinant of early-seral community composition, cover, and rates of colonization via its effects on the sub-surface meristematic tissues of pre-disturbance vegetation, and on the germination substrate (Stickney 1990; Shearer and Stickney 1991). While our analysis was a point-in-time snapshot of ecosystem structure, our results show that the effects of differences in fire intensity (and hence soil burn severity) on overstory vegetation structure are still apparent, more than five decades post-disturbance.

The primary tree species found in northern Rocky Mountain moist mixed-conifer forests exhibit widely varying fire tolerances (Belote et al. 2015; Hood et al. 2018; Stevens et al. 2020), and our results imply that the interaction of fire intensity with these life history traits can have long-term implications for overstory structure. Subalpine fir and Engelmann spruce possess thin bark and other characteristics rendering these species extremely vulnerable to moderate-intensity surface and crown fires (Uchytil 1991a, b and references within; Agee 1993; Hood et al. 2018). This is especially true for the advanced regeneration left behind after clearcutting at Miller Creek (Shearer and Stickney 1991). The negative relationship between fire intensity and subalpine fir and Engelmann spruce basal area that we observed, 55 years post-disturbance, is consistent with the silvics of these species, which have a fire avoider life history strategy (Alexander et al. 1990; Agee 1993; Rogers et al. 2015; Harvey et al. 2016).

Although lodgepole pine also has low fire resistance (Minore 1979; Hood et al. 2021), natural regeneration of serotinous and semi-serotinous lodgepole pine is heavily dependent on fire. Confidence intervals from our GLMM results do not support a statistically significant relationship between lodgepole pine and fire-induced water loss, but this result only applies to those EBUs in which lodgepole pine was present in 2023. Visual inspection of estimated water loss and 2023 lodgepole pine basal area in the complete sample of 13 EBUs strongly implies a positive relationship between these variables. This conclusion is supported by the inverse correlation between water loss and the odds of lodgepole pine absence in the zero-inflated component of the model for this species. Also relevant to these observations are differences in the type of disturbance between sample EBUs, specifically clearcutting (before broadcast burning) compared to high-severity wildfire. Clearcutting practices at Miller Creek removed most or all of the overstory before broadcast burning, leaving behind primarily smaller, generally younger trees that typically have lower cone-bearing capacity than the mature overstory trees that existed before high-severity wildfire. Hence regeneration in stands affected by wildfire typically benefitted from a larger aerial seedbank than in clearcut plus broadcast burn stands. These results are consistent with the silvics of lodgepole pine and the species' occurrence in the northern Rocky Mountains (Arno 1980; Turner et al. 1998; McKenzie and Tinker 2012). Indeed, research over the first two decades of succession at Miller Creek documented vigorous establishment of lodgepole pine in wildfire-affected EBUs (sites that experienced higher intensity burning than other EBUs) which allowed this species to overtop competing herbs and shrubs within a decade of fire (Shearer and Stickney 1991; Latham et al. 1998).

Unlike lodgepole pine, the positive correlation that we observed between western larch basal area and fire intensity was not statistically significant. Resource competition with co-occurring lodgepole pine undoubtedly constrained western larch basal area development on the EBUs at the upper end of the fire intensity spectrum. Western larch may also display sufficient flexibility in its seedbed preferences to blunt the observed relationship with fire-intensity at Miller Creek, given that all sites were burned. Within its range, natural regeneration of western larch is associated with early-seral conditions and burned sites (Steed and Goeking 2020; Veiera et al., 2024), and the mineral soil and ash seedbeds created by high-intensity fire often appear to favor western larch establishment (Boyd and Deitschman 1969; Schmidt 1969; Schmidt et al. 1976; Urza and Sibold 2017). However, some studies have documented a more complex regeneration niche (Ferguson et al. 1986; Oswald and Neuenschwander 1993; Steed and Goeking 2020), and once established, western larch attains its highest growth rates on sites that retain some soil organic material (Graham et al. 1995). Our findings almost certainly reflect some of this complexity, while at the same time illustrating western larch's general affinity for a wide range of burned sites and high light conditions that allow it to dominate the current young forest at Miller Creek.

Halpern et al. (2024) observed positive effects of broadcast burning on the development of early-seral tree species, and negative effects on late-seral species, in moist, low- to mid-elevation forests in the western Cascades (Halpern et al. 2024). While these authors did not evaluate the effects of fire intensity on tree species basal area, their survey of plant succession 40 years after clearcutting and burning is the only study that we are aware of to document responses to controlled experimental burning over similarly long post-treatment timeframes to those at Miller Creek. In their analysis, Halpern et al. (2024) note the potential for highly localized responses to broadcast burning stemming from interactions between the burning treatment, the site, and pre-disturbance vegetation

characteristics. Despite this variability, the positive effects of burning on fire-tolerant, shade-intolerant tree species, and negative effects on fire-intolerant, shade-tolerant tree species at Miller Creek and in the western Cascades suggest these trends may be broadly generalizable across forest types.

Based on the metrics that we examined, the relationships between disturbance characteristics and understory vegetation at Miller Creek, more than five decades post-disturbance, were relatively muted. In the coarsest terms, differences in 2023 understory community structure between EBUs that experienced a high-intensity fire and those that experienced lower-intensity fire are visible in NMDS outputs; EBUs affected by the high-intensity fire (the wildfire) are tightly clustered along axis 1 of ordination space (although are widely dispersed along axis 2), while EBUs that experienced low- and moderate-intensity fire (all broadcast burns) are located throughout ordination space. However, water loss was only weakly related to NMDS ordination space, suggesting that fire intensity, which was a key control on understory vegetation in the early-seral phase at Miller Creek (Stickney 1990; Shearer and Stickney 1991), is no longer a major influence. Over short post-disturbance timeframes, shifts in understory dominance by certain species or groups of species with similar traits or disturbance responses have been documented in many forest types in response to broadcast burning (e.g., Whittle et al. 1997; Lee 2004; Knapp et al. 2009; Halpern and Antos 2022), although see Bushey et al. (2023), Hood et al. (2024). However, while some studies have documented the effects of alternative broadcast burning strategies on certain aspects of understory plant community structure more than one decade post-disturbance (Shearer and Stickney 1991; Zald et al. 2020), the only study of longer post-disturbance timeframes that we are aware of detected only a faint imprint of broadcast burning on understory vegetation (Halpern et al. 2024). Therefore, evidence points to a diminution in the influence of disturbance characteristics on understory community dynamics through time, and an increase in the importance of other factors.

At Miller Creek, our results suggest that site characteristics are now the foremost of these other factors. Research during the first two decades at Miller Creek (Stickney 1981, 1990; Shearer and Stickney 1991) described site characteristics as a moderating influence on the pace of transition from bare ground to herb and then shrub or tree dominance. For example, poor seedbed conditions created by a Spring burn were exacerbated by a south-facing aspect and a warm, dry summer following the fire, resulting in extended herb dominance (Shearer and Stickney 1991). Variations in climate over fine spatial scales in the rugged terrain of the northern Rocky Mountains may have a profound effect on vegetation (Larsen 1930; Pfister et al. 1977; Habeck 1987). Although this is perhaps most visible in low- and high-elevation vegetation types (Arno and Hammerly 1984), mid-elevation forests possess tree species with sufficient differences in temperature, moisture, growing season length optima, and frost tolerance to generate spatial variability in species occupancy and dominance in response to biophysical gradients (Minore 1979; Arno and Hammerly 1984; Burns and Honkala 1990). Using heat load index to summarize site characteristics, we found that Engelmann spruce is currently less dominant on drier, exposed sites than on sites with greater moisture availability, after accounting for the effect of initial disturbance. This is consistent with observed site preferences of this species, which is commonly found in draws and riparian areas at mid to high elevations in the northern Rocky Mountains (Pfister et al. 1977; Alexander and Shepperd, 1990) and references within). Subalpine fir was not statistically associated with heat load index because of wide confidence intervals around the model mean. Although this species is highly shade-tolerant, subalpine fir is the dominant late-seral species across all habitat type phases present at Miller Creek, indicating broad tolerance for the range of conditions at this site.

For understory vegetation, site characteristics appear to be an even more important influence on community structure, five decades after disturbance at Miller Creek. The relationship between sample plots in NMDS ordination space and aspect, heat load index, and habitat type phase, indicates that understory composition and relative dominance are now broadly consistent with expectations based on the physical character of the site (Pfister et al. 1977). This conclusion is strengthened by the mutual consistency of these three site attributes in ordination space; understory composition on west- and south-facing slopes overlapped with the area of ordination space occupied by the most xeric habitat type phase present at Miller Creek, and was also correlated with higher heat load index. An important caveat is that 55 years (post-disturbance) is far short of the timeframes required for development of mature or old-forest structure in these mid-elevation forests. Dispersal-limited understory species that were locally extirpated during clearcutting, broadcast burning, or wildfire are unlikely to have recolonized EBUs that are suitable habitat (Stickney 1981; Shearer and Stickney, 1991; Halpern and Spies 1995; Halpern et al. 2024). Hence, it is unlikely that the current species composition yet approaches the late-successional site potential, as delineated in regional habitat type classifications (Pfister et al. 1977).

Our results highlight an interesting difference in the extent to which trees and understory plants reflect

site-driven versus disturbance-driven controls at Miller Creek. As the preceding discussion highlights, overstory species dominance in 2023 appears to be significantly influenced by characteristics of both the initiating disturbance and the site. Understory composition, on the other hand, appears to be more heavily controlled by attributes of the site. To the extent that convergence on a common species assemblage for a given site type exists in ecosystems (Margalef 1968; Christensen and Peet 1984; Turner et al. 1998), the understory in 2023 is further along this path than the overstory. Demographic rates and vegetation dynamics in trees differ markedly from those of shrubs and, particularly, herbaceous vegetation. Although changes in overstory structure alter the environment at the forest floor (Ellum 2009; Von Arx et al. 2013; Dobrowski et al. 2015), potentially favoring certain understory species over others (Whitney and Foster 1988; Halpern and Spies 1995; Halpern and Lutz 2013), mechanisms such as long-distance aerial dispersal of small seeds, annual seed production, and shorter generation times that enable more rapid turnover of growing space, may conceivably create opportunities for understory plant succession toward a composition aligned with site characteristics on a much shorter timeframe than might be expected for trees.

In all but the most severe natural disturbances, vegetation existing pre-disturbance typically provides a majority of the genetic material to begin the new sere, resulting in a high degree of continuity from pre- to post-burn communities (Stickney 1986; Halpern 1989; Roberts 2004; Halpern et al. 2024). This was the case at Miller Creek during the first two decades of community development after disturbance (Stickney 1981). Despite this, we did not detect a strong relationship between vegetation on site 55 years post-disturbance and that which existed before disturbance. It is possible that offsite colonization has since blunted these antecedent effects. Sampling and analytical methods may also have limited our ability to detect any relationships that do exist. Developing concise numerical summaries of the many dimensions of pre-disturbance vegetation that could influence long-term successional trajectories is extremely challenging. It is possible that our attempts to distil this information into a single response variable for statistical modeling were insufficiently comprehensive. Relatedly, our analysis necessarily aggregated data from across the 13 EBUs at Miller Creek to derive conclusions across the range of disturbance and site characteristics that exist. This pooling undoubtedly obscures detailed site-specific relationships between pre- and post-disturbance vegetation that may have been detected by treating each EBU as a case study. Thus, while our results do not highlight any meaningful influence of pre-disturbance vegetation on long-term successional trajectories, other sampling or analytical approaches may offer different perspectives.

Fire intensity and spatial pattern

Our results do not support the idea that moderate fire intensity promotes more complex fine-scale spatial patterns of vegetation development than either low or high fire intensities at relatively long post-disturbance timeframes. Although each of the metrics of spatial heterogeneity that we evaluated displayed variation between EBUs—a property that was supported by anecdotal visual observations of vegetation structure during fieldwork—peak heterogeneity was not associated with moderate-intensity burning across the range of fire intensities present in this dataset. This could be interpreted as a sign that the fine-scale spatial patterns—patterns emerging at the microtopographic to neighborhood scale (< 1 m to tens of meters)—so important to seedling establishment, survival, and growth (e.g., Taylor, 1990; Davies et al. 2020; Hill and Ex 2020), are no longer present, i.e., spatial homogenization. However, structural data from our EBUs points to continued recruitment of shade-tolerant tree species in the understory of many EBUs, and small-scale features may remain important to recruitment in multi-aged forest types (e.g., Kern et al. 2019; Allogio et al., 2021). Hence, it is also possible that forces other than the initiating disturbance may contribute to spatial pattern as time since the initial disturbance increases.

It is also possible that methodological factors affected our ability to detect a relationship between fire intensity and vegetation spatial pattern that does exist. For continuity with past work at Miller Creek, our sampling used the original Plant Succession Study transects established in 1966, but these 5 × 25 m transects (two per EBU) and 1.5 × 1.5 m—5 × 5 m nested plots were not designed for detecting spatial pattern in vegetation. A key assumption in our fire intensity hypothesis is that moderate fire intensities produce a more heterogeneous soil burn mosaic than low- and high-intensity fire. If this is the case, then detecting this heterogeneity may require a higher within-EBU sampling density (more transects) than provided for in the 1966 study design. Another possibility is that, for 50-year-old overstory trees in particular, spatial pattern resulting from differences in establishment locations and rates may emerge over spatial scales larger than our sample transects and nested plots (Clyatt et al. 2016; Churchill et al. 2017). Therefore, for many reasons, the legacy sampling design that we used may have been mis-matched with our fire intensity – spatial pattern research hypothesis.

Disturbance characteristics are now regarded as a contributor to forest spatial pattern at multiple spatial scales through their interaction with a range of other

biophysical factors (Hessburg et al. 2015, 2019), and it is conceivable that such multi-scale interactions mediate the relationship between fire intensity and vegetation spatial pattern that we sought to identify. For example, despite the gradient in environmental conditions that exist at Miller Creek, the habitat type phases present here are all relatively productive, by regional standards (Pfister et al. 1977), and tree, shrub, and herb species in this forest type exhibit a wide range of traits and environmental preferences (Stickney 1986; Burns and Honkala 1990; Stickney and Campbell, 2000). Thus, it may be that on this relatively benign site, post-disturbance substrates and environmental conditions are rarely a barrier to complete growing space occupancy (inhibiting the development of fine-scale spatial pattern) by one species or another beyond the first few decades of succession, regardless of fire intensity. By contrast, on harsher sites to which fewer species are adapted—for example, the sites with low moisture availability, temperature extremes, and poor edaphic conditions that lodgepole pine occupies in parts of the Northern Rocky Mountains and Pacific Northwest (Pfister et al. 1977; Arno and Hammerly 1984; Agee 1993)—relationships between fire intensity and fine-scale spatial pattern of vegetation structure may be more likely, or more enduring.

Beyond spatial scope, another sampling consideration is the approach to quantifying spatial pattern. In the absence of stem-mapping of trees or other true spatial data, we calculated structural metrics for individual plots along transects and used the variability in these metrics as a measure of spatial heterogeneity. This relatively coarse, indirect approach may have lacked the precision required to capture spatial heterogeneity that did exist.

Finally, we lack direct estimates of heterogeneity of soil burning (for example, percent cover of different soil burn severity classes in subplots along transects) immediately after disturbance, which is essential to verifying the assumption that moderate fire intensities produce more complex mosaics of microsite conditions than low- or high-intensity burns. Even high-severity fires with little to no overstory tree survival typically leave some variability in soil burn severity, if only minor (Stickney 1986; Whittle et al. 1997; Hollingsworth et al. 2013). Hence, it is possible that sufficient post-fire microsite heterogeneity existed in low- and high-intensity burns to blur any link between moderate fire intensity and spatial pattern.

Limitations

Resampling a network of plots that has previously yielded important findings on early-seral plant community development allows us to relate current vegetation structure to changes documented in the past. However, it is not without challenges. By contemporary standards, our 13 EBUs (26 sample transects) are a small sample for statistical analysis. Similarly, the 20 0.25 m × 0.25 m sample plots per EBU (ten per transect) that were used to sample herbs, small shrubs, and seedlings is less intensive than the sampling approaches now used in studies of herb and seedling populations. Another experimental legacy that reduced our analytical options was an imbalanced sample, relative to the experimental factors in the original Miller Creek Study design (DeByle 1981). As a result of the 1967 wildfire and the original 1960s selection of EBUs to include in the Plant Succession Study, the number of EBUs representing each factor level of burn season, slope direction, and time between clearcutting and broadcast burning was not equal. A second consequence of the wildfire is that disturbance type (clearcutting plus burning versus wildfire) varies between EBUs in the Plant Succession study. Natural disturbances typically have different—often more complex—effects on the biotic and abiotic components of the ecosystem than anthropogenic disturbances of similar magnitude. Identifying and separating these effects from those of other disturbance, site, and pre-disturbance vegetation factors at a distance of 55 years post-disturbance, especially with a small sample size, is non-trivial. While we are confident that the unique nature of the Miller Creek experiment merits overcoming such sampling limitations, these legacy effects inevitably influenced our analytical freedom and must be considered when interpreting our findings.

Management implications

Long-term research sites, such as the Miller Creek Demonstration Forest and the network of USDA Forest Service Experimental Forests and Ranges (Adams et al. 2008), provide invaluable opportunities for the study of ecosystem dynamics (Turner et al. 2003). In forested systems, the kind of operational-scale manipulative experiments implemented many decades ago at sites like Miller Creek are now challenging to fund, but continue to yield valuable insights into treatment outcomes and implications across the long timeframes relevant to forestry (e.g., Crotteau et al. 2018; Graham et al. 2019; Kern et al. 2021).

Our sample of vegetation at Miller Creek, 55 years post-disturbance, presents an encouraging message about the resilience of mid-elevation, moist-mixed conifer forests of the northern Rocky Mountains. Moderate- and high-severity wildfire, such as the 1967 fire at Miller Creek, is central to the natural disturbance regime of these forests and to the ecology of western larch (Barrett et al. 1991; Arno et al. 1997; Hood et al. 2021). The clearcut regeneration harvests that are widely used in managed western larch stands are now understood to incompletely imitate the effects of high-severity wildfire,

which may have important consequences for many forest processes and functions (Franklin et al., 2007, 2018). Nevertheless, at Miller Creek, recovery of forests following clearcutting and broadcast burning, and high-severity wildfire has been prompt. Moreover, after 55 years, the young forests here contain the complete suite of overstory tree species found in the pre-disturbance forests. Our findings indicate a resilience to common natural and managed disturbances in these moist mixed-conifer forests, at least in the absence of major climatic change.

The ecological effects of a changing climate and associated changes in disturbance regimes are becoming increasingly apparent and have wide-reaching implications for forest managers (e.g., Vose et al. 2016; Halofsky et al. 2018; USGCRP, 2023) that are not accounted for in this study. Regeneration of forests at Miller Creek overcame hot, dry summers, several years of poor cone crops, and high levels of seed predation immediately after disturbance (DeByle et al., 1981). However, changes in environment and disturbance processes over the coming century are likely to threaten the persistence of some species. This is particularly true of subalpine fir and Engelmann spruce, the least drought- and fire-tolerant species in the moist mixed-conifer forest type (Hansen and Phillips, 2015; Parks and Abatzoglou 2020; Keane et al. 2018), but concerns also exist about western larch, especially on drier sites (Rehfeldt and Jaquish 2010; Crotteau et al. 2019, although see Vieira et al. 2024). This is a cautionary note for the interpretation of our findings, which illustrate forest regeneration before the onset of more recent climate warming.

Our results do, however, illustrate the value of seed source retention for ecological continuity and as an adaptative strategy. At Miller Creek, the presence of mature lodgepole pine in EBUs affected by wildfire was undoubtedly a contributor—alongside the high fire intensity—to prompt lodgepole pine regeneration on these sites. These structural legacies promoted continuity of species from pre- to post-disturbance environments. A related property of the EBUs at Miller Creek was the proximity of intact forest to all harvest units; with relatively small EBUs (4 ha) at Miller Creek, microsites were rarely more than 100 m from the nearest unharvested mature forest edge (Fig. 5). This is especially important in obligate-seeding conifers, for which distance to seed source is a major determinant of regeneration success following high-severity disturbance (e.g., Stevens-Rumman and Morgan, 2019; Peeler and Smithwick 2020; Coop, 2022). Because of this seed source proximity, forest regeneration at Miller Creek is unlikely to be reflective of recovery following large, high-severity disturbances that leave scarce residual on-site seed sources.

Allied with earlier work at Miller Creek, our results support the use of prescribed burning following clearcutting for maintaining early-seral species on the landscape. Halpern et al. (2024), in a study of the effects of clearcutting and broadcast burning on vegetation more than four decades post-disturbance, proposed broadcast burning after regeneration harvest as a means of promoting early-seral vegetation. Our findings are consistent with this assessment. Early-seral herbaceous species were widely documented shortly after disturbance in all EBUs in the Plant Succession Study, and especially in EBUs affected by high-intensity fire (Shearer and Stickney 1991). Meanwhile, EBUs at Miller Creek that were clearcut but not burned (not part of the Plant Succession Study) retained a largely intact understory containing advanced regeneration of late-seral tree species (Latham et al. 1998). In 2023, however, understory plant communities are more consistent with expectations based on habitat type than a pioneer community, and tree cover has returned across the site. Together, these findings suggest that broadcast burning after harvest helps create the conditions for a biologically diverse early-seral flora (Swanson et al. 2011, 2014) but does not impede to transition to closed-canopy forest conditions over management-relevant timeframes. Moreover, at larger spatial scales the intermixing of unharvested stands and stands at various stages of development following harvesting and burning should produce a range of successional conditions to increase landscape-wide pyrodiversity (e.g., Jones and Tingley 2022).

Finally, our snapshot of stand dynamics at Miller Creek reveals useful information for designing regeneration harvests to perpetuate western larch in these moist, mixed-conifer forests. Inventory data from 13 EBUs highlighted the dominance of western larch across varying disturbance and site types. Western larch is an ecologically and silviculturally important species (Schmidt et al. 1976; Arno and Hammerly 1984; Crotteau et al. 2019), is extremely long-lived (Arno and Hammerly 1984; Arno 2021), is more disturbance-tolerant than any other tree of the moist-mixed conifer forest type (Hood et al. 2018; Stevens et al. 2020), and is matched only by western white pine (*Pinus monticola*) and Engelmann spruce in maximum height potential (Earle 2023). These silvical traits suggest that maintenance of western larch as a major overstory component in young forests such as that at Miller Creek is unlikely to be a problem for many decades to centuries, notwithstanding uncertain climate implications on drier sites. However, the lower canopy at Miller Creek is already heavily dominated by more shade-tolerant species. This implies that management interventions over the remainder of the rotation or sere that fail to create high light conditions at the forest floor and do not eliminate advance regeneration via slashing or burning are likely to expedite transition away from western larch dominance. Conversely,

Fig. 5 A 1967 image (upper image) shows a broadcast burn being conducted in one of the Experimental Burn Units at Miller Creek, and illustrates the matrix of unharvested old-growth forest adjacent to harvest units. The lower image shows a mixed herb, shrub, and tree community developing several decades after clearcutting and burning. Image credits: USDA Forest Service

moderate- to high-intensity harvests that incorporate dispersed retention of large trees plus aggregated retention of undisturbed forest, followed by broadcast burning, are likely to perpetuate western larch in the overstory, create the conditions for regenerating larch in the understory (dependent on the amount of dispersed retention), could enhance spatial complexity and reduce fire hazard, and will avoid the long-term loss of seed sources for late-successional understory vegetation.

Supplementary Information

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Supplementary Material 1.

Supplementary Material 2.

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Authors' contributions

NGW, JSC, and DKW designed the study and collected data. NGW conducted statistical analysis and developed the initial manuscript draft. NGW, JSC, and DKW reviewed and edited drafts of the manuscript. JSC secured research funding for NGW.

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Data availability
All data developed and used in this study will be made publicly available on the USDA Forest Service, Research Data Archive (https://www.fs.usda.gov/rds/archive/). A DOI to the study location in the Research Data Archive will be included in the published manuscript.

Declarations

Competing interests
The authors declare that they have no competing interests.

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