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Less fuel for the next fire? Short-interval fire delays forest recovery and interacting drivers amplify effects

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Abstract

As 21st-century climate and disturbance dynamics depart from historic baselines, ecosystem resilience is uncertain. Multiple drivers are changing simultaneously, and interactions among drivers could amplify ecosystem vulnerability to change. Subalpine forests in Greater Yellowstone (Northern Rocky Mountains, USA) were historically resilient to infrequent (100–300 year), severe fire. We sampled paired short-interval (<30-year) and long-interval (>125-year) post-fire plots most recently burned between 1988 and 2018 to address two questions: (1) How do short-interval fire, climate, topography, and distance to unburned live forest edge interact to affect post-fire forest regeneration? (2) How do forest biomass and fuels vary following short-interval versus long-interval severe fires? Mean post-fire live tree stem density was an order of magnitude lower following short-interval versus long-interval fires (3240 vs. 28,741 stems ha^{-1}, respectively). Differences between paired plots were amplified at longer distances to live forest edge. Surprisingly, warmer–drier climate was associated with higher seedling densities even after short-interval fire, likely relating to regional variation in serotiny of lodgepole pine (*Pinus contorta* var. *latifolia*). Unlike conifers, density of aspen (*Populus tremuloides*), a deciduous resprouter, increased with short-interval versus long-interval fires (mean 384 vs. 62 stems ha^{-1}, respectively). Live biomass and canopy fuels remained low nearly 30 years after short-interval fire, in contrast with rapid recovery after long-interval fire, suggesting that future burn severity may be reduced for several decades following reburns. Short-interval plots also had half as much dead woody biomass compared with long-interval plots (60 vs. 121 Mg ha^{-1}), primarily due to the absence of large snags. Our results suggest differences in tree regeneration following short-interval versus long-interval fires will be especially pronounced where serotiny was high historically. Propagule limitation will also interact with short-interval fires to diminish tree regeneration but lessen subsequent burn severity. Amplifying driver interactions are likely to threaten forest resilience under expected trajectories of a future fire.

KEYWORDS
aspen, biomass, burn severity, fire frequency, forest resilience, Greater Yellowstone, lodgepole pine, self-regulation, tree regeneration, US Northern Rocky Mountains

INTRODUCTION

Changes in disturbance regimes threaten the fate of contemporary ecosystems. Disturbances can spur rapid change in ecosystem structure and resource availability (White & Pickett, 1985), ecosystem processes such as biogeochemical cycling (Wan et al., 2001), and species diversity (Collins et al., 1998; Connell, 1978). Ecosystems are resilient, meaning they can absorb disturbance without shifting to a qualitatively different structural or functional state (Holling, 1973), when aligned with historical disturbance frequency, size, and severity (Johnstone et al., 2016). Ecosystem recovery is the process of returning to this initial state (Ghazoul & Chazdon, 2017). Although ecosystems may be resilient to changes in a single driving process such as increasing disturbance frequency, interacting drivers can push systems past thresholds where recovery is inhibited and resilience is no longer possible (Barnosky et al., 2012; Ratajczak et al., 2018; Turner et al., 2020). Interactions are amplifying when they increase the magnitude or likelihood of change, such as the effects of blowdown and fire on forest recovery (Kleinman et al., 2019); disease, predation, cyclones, and bleaching events on coral reefs (De'Ath et al., 2012; Haapkylä et al., 2013); and pathogens and pesticides on bee populations (Doublet et al., 2015). Anticipating how interacting drivers affect resilience is critical because simultaneous driver change will be the norm, not the exception, in the coming decades (Seidl et al., 2017).

Anticipating resilience is especially important in forests (Millar & Stephenson, 2015; Pugh et al., 2019; Reyer et al., 2015; Trumbore et al., 2015). Forests store approximately half of the world's terrestrial carbon (Bonan, 2008), sequester twice as much carbon as they emit (Harris et al., 2021), and provide ecosystem services such as wildlife habitat, clean water, building materials, and scenic beauty (MEA, 2005). Fire is a dominant forest disturbance, and fire activity is expected to increase across much of the globe with warmer and drier 21st-century climate (Bowman et al., 2020). Fire-adapted traits of tree species (e.g., thick bark, serotinous seed banks, resprouting, and long-distance dispersal; Baker, 2009; Pausas & Keeley, 2014), together with residual post-fire structures such as dead wood and nearby live seed sources, confer resilience and enable forests to persist or recolonize burned areas (Franklin et al., 2000). However, these disturbance legacies may be lost or diminished under expected changes in fire and climate, especially when fires are stand-replacing (Johnstone et al., 2016). For example, more frequent fires may recur before a forest can replenish its former carbon stocks or reach reproductive maturity (Keeley et al., 1999; Turner et al., 2019), larger fires may impair regeneration by increasing distances to seed sources (Harvey et al., 2016b), and more severe fires may facilitate changing post-fire tree species composition by altering soil seedbeds (Johnstone et al., 2010). Tree seedlings are particularly vulnerable to climate change because they tolerate a narrow range of temperature and moisture stress relative to mature trees (Dobrowski et al., 2015; Hansen & Turner, 2019; Jackson et al., 2009). Simultaneous changes in fire, climate, and vegetation may interact to erode resilience by amplifying reductions in post-fire forest recovery.

Projections of future fire often incorporate only climate drivers, but post-fire forest and fuel recovery also affect subsequent fire behavior. In many western USA forest landscapes, increasing fire frequency is expected to regulate future fires by decreasing fuel loads, thereby reducing fire spread rates and burn severity (Parks et al., 2014, 2015; Prichard et al., 2017; Stevens-Rumann et al., 2016). These negative feedbacks could counteract the influence of climate on fire at landscape scales (Coop et al., 2020), but may not limit regional climate-driven increases in burning (Abatzoglou et al., 2021). Further, self-regulation after a single severe fire is short-lived in many forest types. For example, lodgepole pine (*Pinus contorta* var. *latifolia*) forests recover fuels rapidly after fire and can burn at similar or higher severity as mature forests within 10–12 years (Braziunas et al., 2022; Harvey et al., 2016a; Nelson et al., 2016, 2017).

Short-interval fires (i.e., fires that burn forests at a short fire return interval relative to historical intervals, hereafter referred to as "reburns") are occurring more often, yet understanding of forest and fuel recovery following reburns under a wide range of post-fire climate conditions remains unresolved. In the United States Northern Rocky Mountains, 138,061 ha of forest burned twice within a 26-year period (1984–2010), with more than one-third of reburns occurring in subalpine forests (i.e., 0.5% of total subalpine forest area in this region burned twice over 26 years; Harvey et al., 2016a). High-severity fires in subalpine forests historically recurred every 100–300 years, driven by rare combinations of drought and high wind (Higuera et al., 2011; Romme & Despain, 1989; Whitlock et al., 2008), and forests recovered rapidly (Turner et al., 1999). However, area burned is already increasing with warmer and drier climate (Abatzoglou & Williams, 2016; Littell et al., 2009; Westerling, 2016), and climatically based fire rotations could shorten to <30 years over the 21st century (Westerling et al., 2011). In this study, we used field data from paired short-interval and long-interval post-fire plots in Greater Yellowstone most recently burned between 1988 and 2018 to ask: (1) How do short-interval fire, climate, topography, and distance to unburned live forest edge interact to affect post-fire forest regeneration? We expected post-fire tree stem densities to be lower in short-interval (<30-year) compared with long-interval (>125-year) plots and drier post-fire climate to amplify differences between paired plots (Whitman et al., 2019). We further expected lower post-fire stem density with warmer–drier topographic conditions and greater distance to live forest edge (Hoecker et al., 2020; Stevens-Rumann & Morgan, 2019). (2) How do forest biomass and fuels vary following short-interval versus long-interval severe fires? We expected lower loads and delayed recovery of live and dead biomass and fuels following short-interval relative to long-interval fire (Donato et al., 2016; Stevens-Rumann et al., 2020; Turner et al., 2019). In all plots, we expected large fuels (1000-h downed wood or >7.6 cm diameter snags) to comprise the majority of dead woody biomass. For both questions, we considered long-interval plots the reference condition for resilient post-fire recovery compared with paired short-interval plots.

METHODS

Study area

The Greater Yellowstone Ecosystem (GYE) comprises 89,000 km^2 (YNP, 2017) of mostly federally managed land centered on Yellowstone and Grand Teton National Parks (Figure 1). Greater Yellowstone has cold, snowy winters and mild summers, with most annual precipitation falling as snow. Average summer temperature (1981–2010) is 12.3°C, and annual precipitation averages 644 mm at centrally located Old Faithful in Yellowstone National Park (WRCC, 2021). The region is expected to get warmer and drier over the 21st century, with lengthening fire seasons and harsher conditions for germination and establishment of young tree seedlings (Romme & Turner, 2015; Westerling et al., 2011). Since 1950, Greater Yellowstone has warmed +1.3°C, and annual snowfall has decreased by 25% (Hostetler et al., 2021). Soils are primarily derived from highly infertile, volcanic rhyolite; slightly less infertile andesite; or sedimentary parent materials (Despain, 1990).

Subalpine forests cover much of the GYE between ~1500–3000 m elevation and historically recovered rapidly after infrequent severe fire due to prevalent serotinous lodgepole pine with its fire-stimulated canopy seed bank (Turner et al., 1999). Stand-level percent serotiny of lodgepole pine is highest at lower elevations (up to ~2300–2400 m) and ranges widely (0 to more than 85% of trees with serotinous cones; Schoennagel et al., 2003; Tinker et al., 1994). Approximately one-third of 1984–2010 area burned in United States Northern Rocky Mountains subalpine forests was stand-replacing (Harvey et al., 2016a), and 19%–25% of 1984–2020 short-interval area burned in Northwest United States forests was stand-replacing in both the initial and subsequent fire (Harvey et al., 2023). Mean aboveground biomass in lodgepole pine-dominated forests averages 139 Mg ha^{-1} (live tree) and 98 Mg ha^{-1} (dead woody) across a 300-year chronosequence, and stand density stabilizes to approximately 1200 stems ha^{-1} after 200 years of stand development (Kashian et al., 2013; Kashian, Turner, & Romme, 2005).

Other tree species in the subalpine zone include Douglas fir (*Pseudotsuga menziesii* var. *glauca*) and quaking aspen (*Populus tremuloides*) at lower elevations, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at higher elevations, and whitebark pine (*Pinus albicaulis*) near upper treeline (Baker, 2009). Douglas fir, Engelmann spruce, subalpine fir, and non-serotinous lodgepole pine rely on wind dispersal from nearby live seed sources, and most seeds fall within 50 m of a live tree (Gill et al., 2021; McCaughey & Schmidt, 1987). Whitebark pine and quaking aspen can disperse over longer distances (Lorenz et al., 2011; Turner et al., 2003), and aspen can also resprout after fire (Baker, 2009).

Reburn and plot selection

We identified recent, large fires (1994–2018; ≥404 ha) that severely burned subalpine forests at both short (<30-year; $n = 16$ reburns) and long (>125-year) intervals (Figure 1a; Appendix S1; Eidenshink et al., 2007). In 2021, we sampled 22 plot pairs (1–2 pairs per reburn) each consisting of a 0.25-ha short-interval plot burned twice as stand-replacing fire and a topographically similar, nearby 0.25-ha long-interval plot burned as stand-replacing in the same recent fire (Figure 1c). These data were augmented with paired short-interval and long-interval post-fire plot data collected in 2000, 12 years after the 1988 fires (Braziunas et al., 2023;

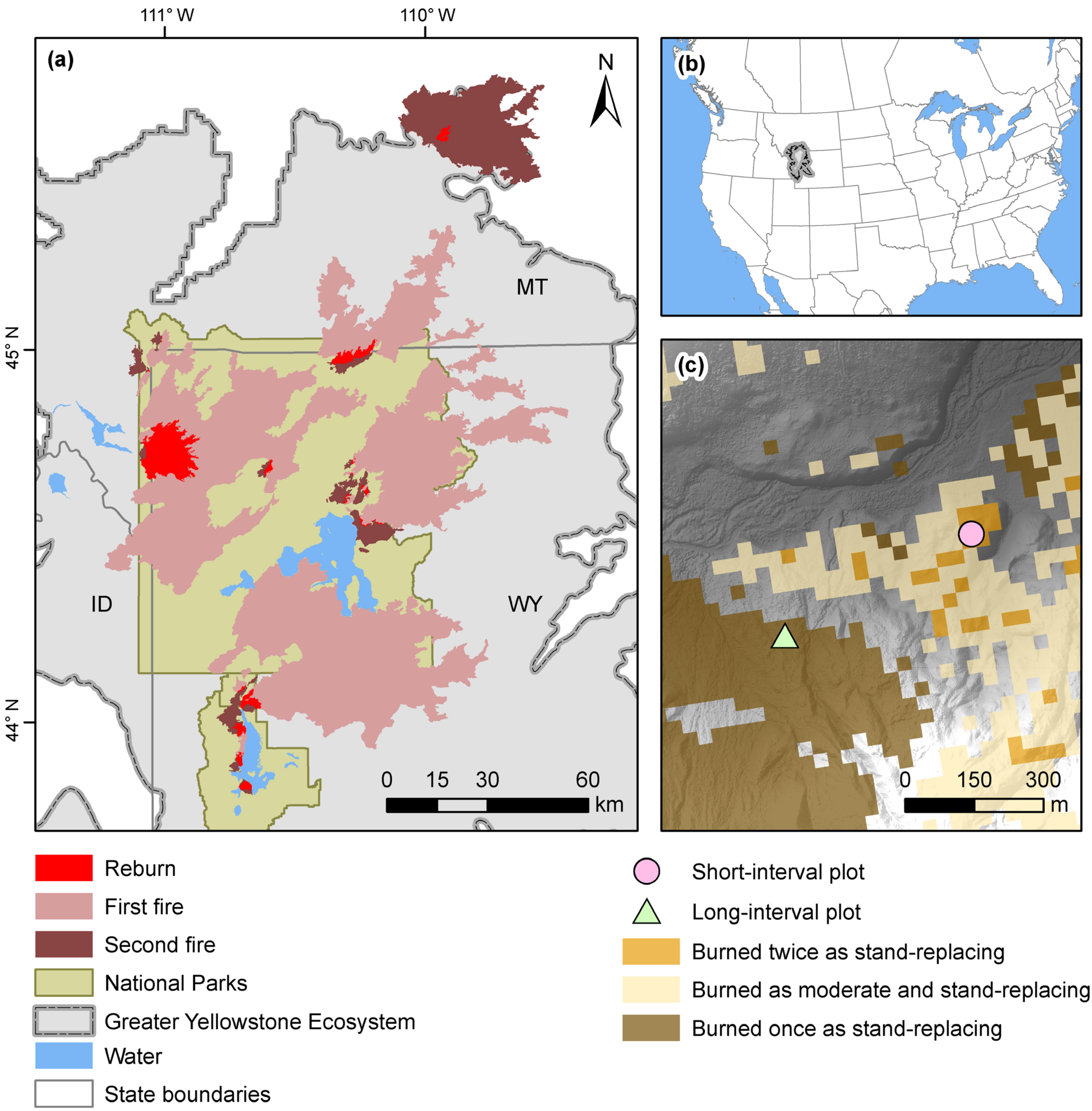

FIGURE 1 (a) Reburns sampled in 2021 in the Greater Yellowstone Ecosystem (GYE). Different shades show perimeter of first fires, second fires (long-interval), and reburned areas (short-interval overlap of first and second fires). (b) Location of GYE within the USA. (c) Example paired plot site in the 2016 Berry Fire reburn of the 2000 Wilcox Fire, Grand Teton National Park (44.0° N, 110.7° W). Short-interval plots burned twice as stand-replacing fire and long-interval plots only burned as stand-replacing in the most recent fire. Shading shows underlying topography.

Schoennagel et al., 2003). Together, these datasets included 33 plot pairs ($n = 66$ plots) in 27 reburns widely distributed throughout the GYE and representing 7–28-year short fire return intervals, 3–27 years since most recent fire, 1798–2769 m in elevation, 0–356° aspect, and 0–25° slope (Figure 1; Appendix S2: Table S1 and Figure S1).

Field data collection

Forest recovery and fuels were sampled in 0.25-ha plots following standard methods (Nelson et al., 2016; Turner et al., 2019). Seedling (<2 years old), sapling (>2 years old and <1.4 m height), tree (≥1.4 m height), and standing dead (≥1.4 m height) stem density were tallied in three parallel 2-m × 50-m belt transects. At 5-m intervals, we measured height, crown base height, and diameter at breast height (dbh) of the closest live tree by species; height and dbh of the closest standing dead snag; height of the closest sapling by species; and cover and average height of shrubs by species in 0.25-m^2 quadrats ($n = 25$ quadrats for 6.25-m^2 per plot). Downed woody and forest floor fuels were quantified with five 20-m Brown's planar intersect transects (Brown, 1974) oriented randomly from plot center (total length = 100 m per plot). We recorded 1-h (<0.64 cm diameter) and 10-h (0.64–2.54 cm) fuels along the first 3 m, 100-h (2.54–7.60 cm) fuels along the first 10 m, and sound and rotten coarse woody debris (≥7.6 cm diameter, 1000-h fuel) along the entire 20 m. Litter and duff depth were recorded at 2-m intervals at three locations per transect ($n = 15$ measurements per plot). At plot center we measured aspect, slope, and distance to unburned live forest edge. If live edge was not visible or too far to measure in the field, this distance was estimated in ArcGIS Desktop 10.6 from aerial imagery and burn severity perimeters. Field data from 2000 included live stem densities by species counted in four parallel 2-m × 50-m belt transects spaced 25 m apart (Schoennagel et al., 2003).

Biomass and fuels calculations

We derived live tree, dead snag, lodgepole pine sapling, and shrub aboveground biomass using allometric equations (Appendix S1). Snag biomass was summarized by size classes corresponding to downed wood (i.e., 1-, 10-, 100-, and 1000-h based on dbh). Canopy fuel load and bulk density were estimated from conifer tree crown biomass. Dead woody fuel biomass was computed for 1-, 10-, 100-, and 1000-h pools following Brown (1974) and correcting for slope. Litter and duff biomass were quantified based on average depth and bulk densities for lodgepole pine forest types (Brown et al., 1982; Nelson et al., 2016).

Question 1: Effects of interacting drivers on forest regeneration

We tested whether live stem densities (including all seedlings, saplings, and trees) were lower in short-interval versus long-interval fire with a one-sided, paired Wilcoxon signed rank test ($n = 33$ pairs, lower densities expected in reburns). Differences were also evaluated by species. For lodgepole pine, which was present in all plots, a two-sided, paired Wilcoxon signed rank test was used. For other species, which were absent from many plots and exhibited high variance relative to mean values, differences in presence and density between pairs were tested with zero-inflated negative binomial regression models adjusted for matched data (Abadie & Spiess, 2022; McElduff et al., 2010). Simulated model residuals were evaluated to determine that these distributions appropriately represented underlying data (Appendix S2: Figures S2 and S3). Subsequent analyses only used live conifer stem densities (i.e., excluding aspen).

Post-fire climate was characterized with water-year (October–September) climate water deficit and summer (June–August) vapor pressure deficit (VPD; Davis et al., 2019; Harvey et al., 2016b; Stevens-Rumann et al., 2018). We used 4-km resolution climate data (TerraClimate; Abatzoglou et al., 2018) and summarized 30-year normal (1989–2018) and 3-year post-fire anomaly (z-score relative to normal; Appendix S2: Figures S4–S7). We assessed whether differences in conifer stem density were associated with warmer–drier climate using Spearman's rank correlations because pairwise bivariate distributions were not normal.

The relative importance of drivers of post-fire stem density was tested with multiple linear regression models ($n = 66$ observations). Predictors included climate (climate water deficit normal and post-fire summer VPD anomaly), short-interval versus long-interval fire, lower (<2350) versus higher elevation as a proxy for stand-level serotiny, topography (heat load index and topographic position index; Appendix S1), and distance to live edge. Continuous predictors were not strongly correlated (Pearson's $|r| < 0.5$) and were rescaled to have a mean of 0 and a standard deviation of 1. Conifer stem density was $\log_{10}$ transformed to meet assumptions of linearity, normality, and equal variance, which were assessed with residual and quantile–quantile plots (Appendix S2: Figures S10 and S11). We fit a full model, including interactions between each predictor and short-interval versus long-interval fire. We used exhaustive model selection to identify the most important factors based on model Bayesian Information Criterion (BIC), retaining all models with differences in BIC <2 (see Appendix S2: Table S2 for additional models).

Question 2: Forest biomass and fuels after short-interval versus long-interval fires

We assessed whether total live and dead tree biomass was lower in short-interval versus long-interval fire with one-sided, paired t-tests ($n = 22$ pairs for live and $n = 21$ for dead fuels, lower biomass expected following reburns). Individual fuel pool differences were tested using either two-sided, paired t-tests or two-sided, paired Wilcoxon signed rank tests. Fuels were transformed as needed to meet normality based on quantile–quantile plots (Appendix S2:

Figure S12), and a Wilcoxon test was used if transformations did not result in normal distributions. Trees (≥1.4 m height), canopy fuels, and 1-h and 10-h snags were absent from >40% of plots and were not tested for differences. Finally, biomass pools were averaged over 0–10, 10–20, and 20–30 years since fire to explore trajectories of biomass change and recovery following short-interval versus long-interval fires.

All analyses and visualizations were performed in ArcGIS Desktop 10.6 and R 4.1.3 (R Core Team, 2022). See Appendix S1 for supplemental detail on methods and R packages.

RESULTS

Question 1: Effects of interacting drivers on forest regeneration

Live stem densities were an order of magnitude lower following short-interval compared with long-interval fire (mean 3240 vs. 28,741 stems ha^{-1}, median 2000 vs. 5000 stems ha^{-1}, respectively; Figure 2). Tree species presence did not differ between plot pairs, but conifer densities were 68%–92% lower following short-interval reburns (Table 1). In contrast, aspen density was more than 500% higher in short-interval plots (Table 1; Appendix S2: Figure S13). Differences in long-interval minus short-interval conifer stem density were strongly positively correlated with climate water deficit normal ($\rho = 0.67$, $p = 0.00002$, $n = 33$; Figure 3a) and weakly positively correlated with summer VPD anomaly ($\rho = 0.34$, $p = 0.05$, $n = 33$; Figure 3b).

Higher post-fire stem densities were best explained by long fire return intervals, higher climate water deficit normal (i.e., warmer–drier conditions), and interactions of fire interval with both distance to unburned live edge and deficit (Figure 3c,d; Table 2). Following short-interval fire, stem densities declined at farther distances from live edge and diverged from long-interval densities with warmer–drier climate. However, stem densities increased with warmer–drier climate after both short-interval and long-interval fire; although not in the top models, this was also the case for post-fire summer VPD anomaly (Appendix S2: Table S2). The main effects of fire interval and climate water deficit explained most variation in stem densities (adjusted $R^2 = 0.23$ for the model without interactions, adjusted $R^2 = 0.27$–0.29 for models with interactions).

Question 2: Forest biomass and fuels after short-interval versus long-interval fires

Short-interval plots had more than seven times less aboveground live tree/shrub biomass and half as much dead woody biomass compared with long-interval plots (mean 1.72 vs. 12.73 Mg ha^{-1} live and 60.19 vs.

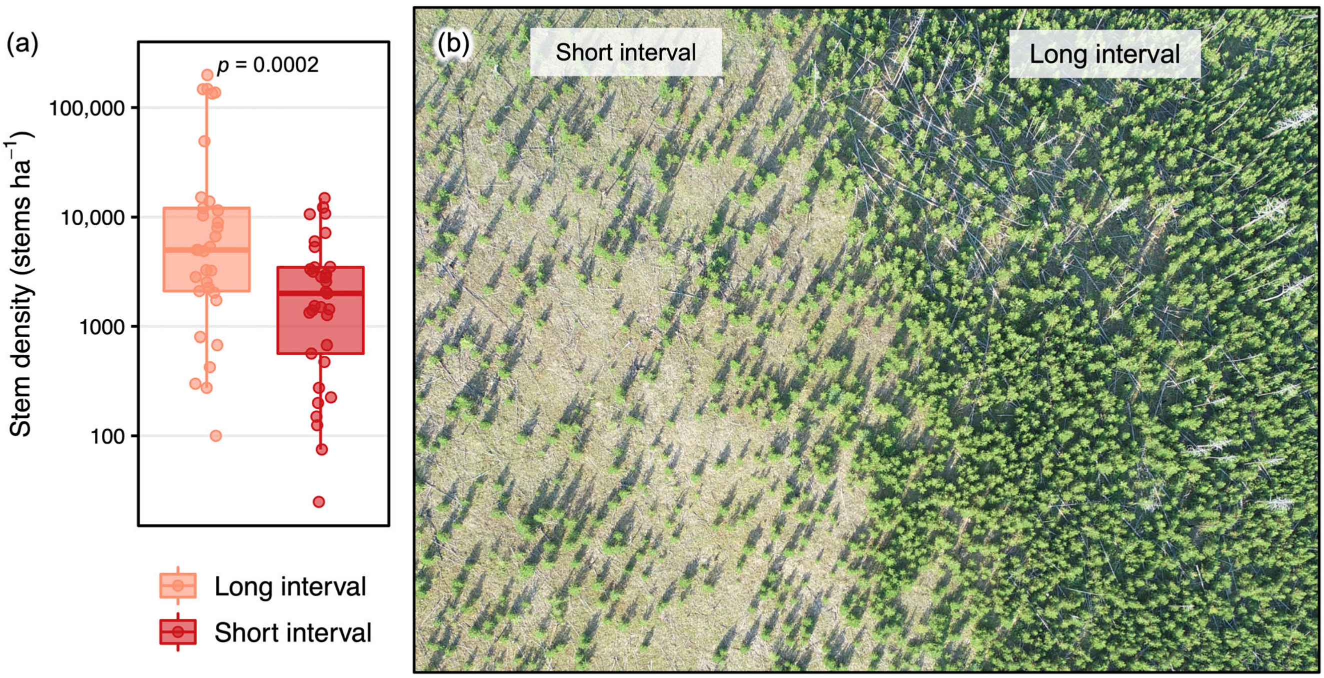

FIGURE 2 (a) Total live stem density boxplots for long-interval and short-interval plots. Jittered points show raw data. Differences are significant at $p = 0.0002$ based on a one-sided, paired Wilcoxon signed rank test (test statistic $V = 478$, $n = 33$ pairs). (b) Aerial view of forest recovery and variation in fuels following the 2006 Derby Fire, which reburned the 1990 Iron Mountain Fire as short-interval fire (left) and burned older forest as long-interval fire (right). Location: 45.6° N, 109.9° W. Photograph credit: Kristin Braziunas.

TABLE 1 Presence (proportion of plots) and live stem density (stems ha^{-1}) by species in long-interval and short-interval plots ($n = 33$ of each).

Species	Presence proportion		Test statistic	p	Live stem density mean (SE) range		Test statistic	p
	Long	Short			Long	Short		
ABLA	0.27	0.21	0.77	0.45	97 (53) 0–1667	13 (6) 0–167	−7.45	$\mathbf{2 \times 10^{-8}}$
PIAL	0.18	0.09	1.74	0.09	77 (40) 0–1133	20 (14) 0–433	−2.26	**0.03**
PICO	1.00	1.00	…	…	28,189 (9560) 33–197,433	2790 (663) 25–14,825	490	$\mathbf{7 \times 10^{-5}}$
PIEN	0.42	0.30	1.42	0.16	286 (174) 0–5667	23 (10) 0–300	−8.14	$\mathbf{3 \times 10^{-9}}$
POTR	0.24	0.36	−1.60	0.12	62 (37) 0–1200	384 (164) 0–4300	3.16	**0.003**
PSME	0.24	0.09	1.86	0.07	31 (13) 0–267	10 (8) 0–267	−0.22	0.83

Note: Differences in lodgepole pine density were tested with a two-sided, paired Wilcoxon signed rank test (test statistic = V). Presence and density for all other species were tested with zero-inflated negative binomial regression models adjusted for matched data (test statistic = t, df = $n - 1$). Bold p-values are significant at $p < 0.05$.

Abbreviations: ABLA, Subalpine fir; PIAL, Whitebark pine; PICO, Lodgepole pine; PIEN, Engelmann spruce; POTR, Quaking aspen; PSME, Douglas fir.

121.25 Mg ha^{-1} dead, respectively; Table 3; see illustrative plot photos in Appendix S2: Figure S13). Differences in live biomass were reflected in tree biomass, available canopy fuel load, canopy bulk density, and lodgepole pine sapling biomass. Live shrub biomass was low and similar between plot pairs (Table 3).

Individual snag and downed woody pools were highly variable and mostly did not differ between short-interval and long-interval plots (Table 3). Large, 1000-h (≥7.6 cm diameter) snags were the primary driver of lower dead woody fuel loads in short-interval plots (Figure 2b; Table 3). Although the majority (>80%) of dead woody fuels were in 1000-h pools in all plots, the proportion of dead wood in 100-h fuels increased from 2% to 15% following short-interval reburns (Appendix S2: Figure S14). Litter and duff loads did not differ between plot pairs.

Total live plus dead biomass increased over time following long-interval fire and allocation shifted among standing dead, downed wood, and live pools; in contrast, total live plus dead biomass changed little during the first 30 years after short-interval fire (Figure 4). Live tree biomass accumulated more rapidly following long-interval compared with short-interval stand-replacing fire. Long-interval plots had much higher snag biomass immediately after fire, which increased the accumulation of downed wood over time.

DISCUSSION

Our study revealed interactions between short-interval fire and other drivers of subalpine forest regeneration. Mean post-fire stem density was an order of magnitude lower following short-interval versus long-interval fires, and differences were amplified farther from unburned live forest edge. Surprisingly, warmer–drier climate was associated with increases in conifer regeneration even after short-interval fire. Despite the pace of climate change in this region, seedling physiological tolerance thresholds appear not to have been crossed across a wide range of recently reburned areas. Relationships with climate highlight the importance of stand-level lodgepole pine percent serotiny, which is highest at lower elevations where climate is warmer and drier. Greater differences in regeneration density between short-interval and long-interval fires in warmer–drier areas indicate that young forests are reburning before recovering their serotinous seed bank. Our results suggest that forest change due to short-interval fire will be especially pronounced in historically high-serotiny areas, shifting recovery from a high-density to a low-density pathway and potentially leading to forest restructuring (sensu Seidl & Turner, 2022). Furthermore, conifer regeneration in subalpine forests with previously robust serotinous seed banks becomes more reliant on ex situ seed sources after short-interval fire, and propagule limitation interacts with short-interval fire to threaten subalpine forest resilience.

Differences in post-fire biomass between short-interval and long-interval plots highlight nuanced feedbacks between developing fuels and subsequent fire. Although many short-interval reburns had abundant downed wood, they had minimal additional input from snags and a higher proportion of fuels in smaller size

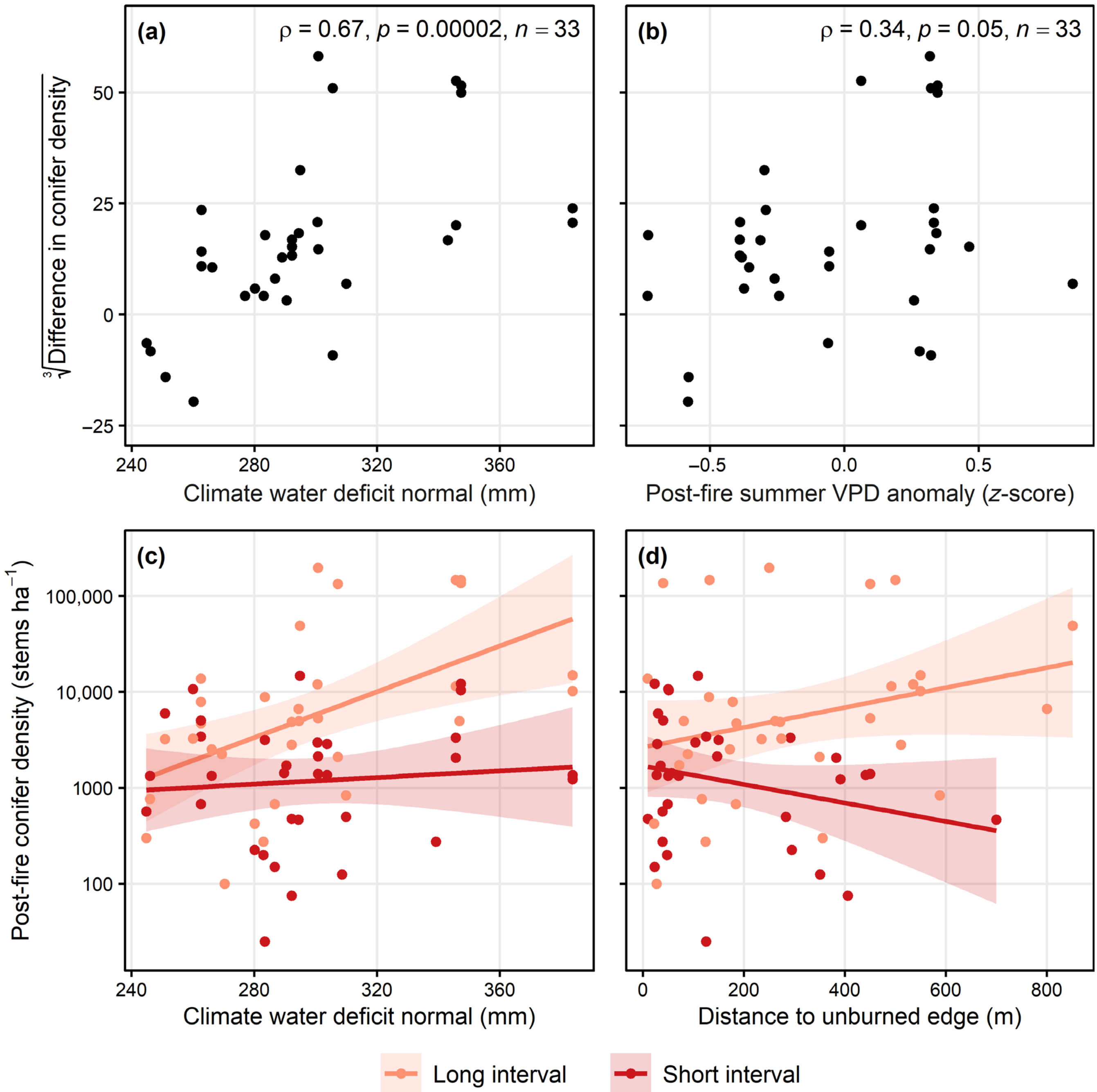

FIGURE 3 Pairwise relationships between (a) climate water deficit normal (1989–2018) or (b) 3-year post-fire summer vapor pressure deficit (VPD) anomaly and differences in live conifer stem density in long-interval minus short-interval paired plots ($n = 33$). Differences in conifer density have been cube-root transformed for plotting. Interactions between fire interval and (c) climate water deficit normal or (d) distance to unburned live forest edge explained post-fire live conifer stem density ($n = 66$). Points and lines are colored by long-interval (light peach) or short-interval (dark red) fire. *Y*-axis is on a $\log_{10}$ scale. Lines are linear fits and shading is standard error.

classes that could decompose quickly or burn readily if fire recurred. In contrast with rapid recovery after long-interval fire, live biomass and canopy fuels remained low nearly 30 years after short-interval fire, suggesting delayed recovery of pre-fire biomass and prolonged self-regulation of future burn severity (Figure 5).

Interacting drivers amplify effects on forest regeneration

Independent effects of short-interval reburns and long distances to live forest on post-fire conifer densities are well documented (Stevens-Rumann & Morgan, 2019), and here

TABLE 2 Multiple linear regression models predicting stem density (log_{10} transformed) from multiple factors and potential interactions with short-interval fire.

Model	ΔBIC	Adjusted R^2	Predictor	Estimate	SE	t	p
Model 1	0	0.28	(Intercept)	3.70	0.13	29.01	**2×10^{-37}**
			Fire interval (short)	−0.74	0.18	−4.03	**0.0002**
			Climate water deficit normal	0.28	0.09	3.02	**0.004**
			Distance to unburned:Fire interval (short)	−0.34	0.16	−2.19	**0.03**
			Distance to unburned:Fire interval (long)	0.12	0.12	0.96	0.34
Model 2	0.7	0.27	(Intercept)	3.74	0.12	30.60	**4×10^{-39}**
			Fire interval (short)	−0.67	0.17	−3.87	**0.0003**
			Climate water deficit normal	0.43	0.12	3.55	**0.0008**
			Climate water deficit normal:Fire interval (short)	−0.37	0.17	−2.12	**0.04**
Model 3	1.1	0.23	(Intercept)	3.74	0.13	29.77	**8×10^{-39}**
			Fire interval (short)	−0.67	0.18	−3.77	**0.0004**
			Climate water deficit normal	0.25	0.09	2.81	**0.007**
Model 4	1.7	0.29	(Intercept)	3.72	0.13	29.17	**4×10^{-37}**
			Fire interval (short)	−0.74	0.18	−4.01	**0.0002**
			Climate water deficit normal	0.40	0.13	3.09	**0.003**
			Distance to unburned:Fire interval (short)	−0.28	0.16	−1.72	0.09
			Climate water deficit normal:Fire interval (short)	−0.24	0.19	−1.30	0.20
			Distance to unburned:Fire interval (long)	0.07	0.12	0.59	0.56

Note: Exhaustive model selection and Bayesian Information Criteria (ΔBIC <2) were used to identify models that best represented the relative importance of predictors. Continuous predictors were standardized to have a mean of 0 and a standard deviation of 1. Bold p-values are significant at $p < 0.05$.

we found amplifying interactions. This is particularly concerning in western United States forests, where current trends in area burned and stand-replacing fire indicate that these two conditions will co-occur with increasing likelihood (Buma et al., 2020; Harvey et al., 2016a, 2023; Westerling, 2016). Climate-driven increases in other agents of tree mortality, such as bark beetles, wind, drought, and pathogens (Anderegg et al., 2020; Seidl et al., 2017), could further reduce seed source availability throughout forest landscapes and exacerbate impacts on post-fire regeneration (Coop et al., 2020). Interactions among drivers alter the likelihood of crossing thresholds and the rate of ecosystem transformation (Ratajczak et al., 2018; Scheffer & Carpenter, 2003). Our findings suggest that historically fire-resilient forests could experience much slower rates of recovery or be vulnerable to surprising forest change where interacting drivers overlap (Figure 5).

Contrary to our expectations, warmer–drier sites and drier post-fire conditions were associated with higher conifer seedling densities, as well as greater differences between short-interval and long-interval plots. This in part reflects the higher prevalence of lodgepole pine serotiny (Tinker et al., 1994) and longer growing seasons at lower elevations, which explains how warmer–drier sites could buffer tree regeneration even after short-interval fires that occur before forests recover their serotinous seed banks. Stevens-Rumann et al. (2018) similarly found that 30-year climate water deficit was positively associated with post-fire forest replacement before 2000, but after 2000 this relationship switched to negative. The warmer–drier conditions represented in our study were apparently still favorable for tree seedling regeneration, but post-fire droughts have exceeded seedling tolerance thresholds in many forests across the western USA over the past 20 years (Davis et al., 2019; Stevens-Rumann & Morgan, 2019). Future research should prioritize areas that burned as short-interval fire followed by extreme drought and disentangle the role of warmer–drier climate from serotiny. Other changing drivers not considered in this study may also affect post-fire regeneration densities and could be included in future research (e.g., height of live forest edge, because young forests are shorter and disperse seeds less far into burned patches; Gill et al., 2021). Overall, post-fire conifer regeneration densities were lower and less variable across a broad environmental gradient after short-interval versus long-interval fire. These initial regeneration densities dictate stand development for decades to centuries, with important implications for

TABLE 3 Fuels and biomass pools in long-interval and short-interval plots ($n = 22$ each of short and long plots unless otherwise noted); due to time constraints, fuels data were not measured in one plot pair and shrubs were not measured in two plot pairs.

Biomass or fuel characteristic	Long-interval mean (SE) range	Short-interval mean (SE) range	Test or trans.	Test statistic	*p*
Live tree aboveground (all species)	10.25 (4.01) 0–63.64	1.46 (0.70) 0–15.32	…	…	…
Canopy fuels (conifers only)					
Available canopy fuel load	3.57 (1.39) 0–23.71	0.52 (0.26) 0–5.62	…	…	…
Canopy bulk density (kg m^{-3})	0.20 (0.10) 0–2.14	0.03 (0.01) 0–0.30	…	…	…
Dead aerial fuels					
1-h snag size class	…	0.00 (0.00) 0–0.01	…	…	…
10-h snag size class	0.01 (0.00) 0–0.10	0.29 (0.21) 0–4.50	…	…	…
100-h snag size class	0.41 (0.20) 0–4.48	1.98 (0.72) 0–13.36	Wilcoxon	48	0.11
1000-h snag size class	53.88 (8.41) 0–133.92	3.19 (0.98) 0–18.78	Cube root	9.81	$\mathbf{3 \times 10^{-9}}$
Total snag	54.29 (8.41) 0–134.16	5.46 (1.28) 0–20.45	Square root	9.03	$\mathbf{1 \times 10^{-8}}$
Live surface fuels					
Sapling aboveground (lodgepole pine)	2.40 (1.54) 0–34.18	0.19 (0.06) 0–0.93	Wilcoxon	214	**0.003**
Shrub ($n = 20$)	0.08 (0.01) 0.01–0.22	0.08 (0.02) 0–0.46	Cube root	0.70	0.49
Dead surface fuels ($n = 21$)					
Litter	3.84 (0.80) 0.03–16.20	2.62 (0.66) 0.17–11.41	Wilcoxon	168	0.07
Duff	12.01 (2.46) 0–45.52	9.14 (2.54) 0–45.34	Wilcoxon	110	0.12
1-h	0.16 (0.04) 0.01–0.72	0.10 (0.02) 0–0.34	Wilcoxon	162	0.11
10-h	1.68 (0.26) 0.09–5.02	1.37 (0.25) 0–4.42	No trans.	0.79	0.44
100-h	3.66 (0.52) 1.00–11.98	4.86 (0.68) 1.21–12.79	Wilcoxon	58	0.08
Sound 1000-h	45.86 (7.73) 5.67–154.30	32.10 (6.59) 0–105.30	Wilcoxon	151	0.23
Rotten 1000-h	17.64 (5.53) 0–95.75	16.14 (2.92) 0.31–56.92	Cube root	−1.29	0.21
Total live aboveground (tree + sapling + shrub)	12.73 (4.98) 0.06–91.14	1.72 (0.73) 0.02–16.27	Log_{10}	3.82	**0.0005**
Total dead woody (snags + downed wood, $n = 21$)	121.25 (7.92) 58.97–203.50	60.19 (7.80) 20.15–153.54	No trans.	7.48	$\mathbf{2 \times 10^{-7}}$

Note: All loads are in Mg ha^{-1} unless otherwise noted. Differences between plot pairs were tested with one-sided, paired *t*-tests (total live and total dead, test statistic = *t*), two-sided paired *t*-tests (test statistic = *t*, df = $n - 1$), or Wilcoxon signed rank tests (test statistic = *V*). The Test or transformation (trans.) column indicates whether a Wilcoxon test was used or whether a transformation was used with a *t*-test (No trans. = data were not transformed). Snag and woody surface fuel size classes: 1-h, <0.64 cm diameter; 10-h, 0.64–2.54 cm; 100-h, 2.54–7.60 cm; and 1000-h, ≥7.6 cm diameter. Bold *p*-values are significant at $p < 0.05$.

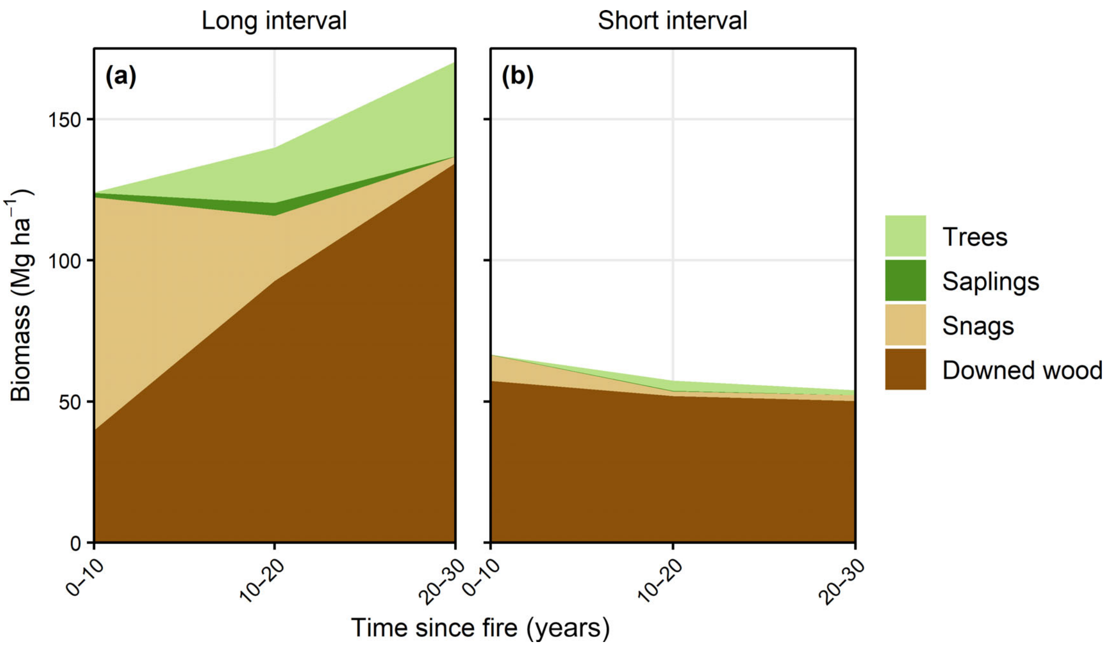

FIGURE 4 Aboveground live and dead biomass pool trajectories following (a) long-interval and (b) short-interval fire. Plots cover a range of 3–27 years since most recent fire. Pools are averaged in 10-year bins (0–10 years since fire, $n = 11$ plot pairs; 10–20, $n = 8$; and 20–30, $n = 2$).

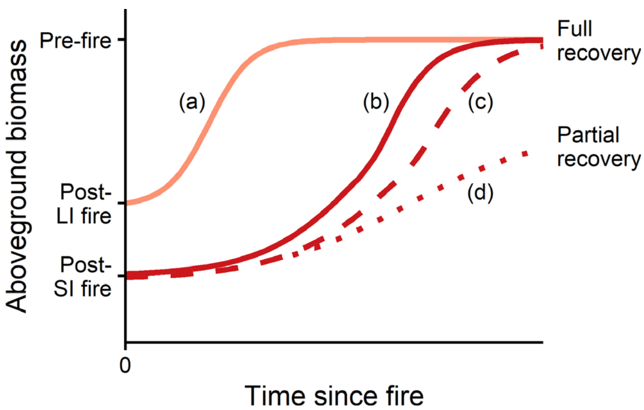

FIGURE 5 Conceptual framework of potential recovery trajectories for aboveground biomass (live plus dead) after stand-replacing long-interval or short-interval fire. The starting point for each trajectory is the residual dead woody biomass after the fire. Following long-interval fire (a, light peach), biomass recovers rapidly to pre-fire levels. Following short-interval fire (b, solid dark red), biomass recovery is delayed and slower due to lower initial levels of dead biomass and tree regeneration. Average regeneration densities are sufficient so that full biomass recovery is likely in the absence of subsequent disturbance. Amplifying effects of long distances from seed source or other drivers could further delay biomass recovery (c, dashed dark red) or potentially result in only partial biomass recovery if post-fire tree density is insufficient for self-replacement (d, dotted dark red). If stand-replacing fires reburn forests before they have recovered to pre-fire conditions, forests may be vulnerable to sustained reductions in biomass. LI, long interval; SI, short interval.

ecosystem structure, function, and services (Braziunas et al., 2018; Kashian, Turner, Romme, & Lorimer, 2005; Turner et al., 2016).

Quaking aspen emerged as a potential winner in a more fiery future, although regeneration density after a single short-interval fire often remained much lower than conifer density. Aspen effectively colonizes recently burned areas from seed via long-distance dispersal (Turner et al., 2003). Once established, aspen resprout successfully and in abundance after short-interval reburns (e.g., Eisenberg et al., 2019; this study) or short intervals between bark beetle outbreaks and fire (e.g., Andrus et al., 2021). Aspen is a keystone species of global importance for biodiversity (Rogers et al., 2020), and warmer climate is associated with inhibited growth and dieback of aspen in the Rocky Mountains (Hanna & Kulakowski, 2012). Our results highlight a potentially positive effect of climate-driven increases in short-interval fire, which may enable aspen expansion by reducing competition with conifers and facilitating aspen regeneration. Similarly, severe fire has catalyzed transitions from conifer to deciduous dominance in boreal forests (Johnstone et al., 2010; Mack et al., 2021).

Reburns alter fuel recovery trajectories and potential future burn severity

Delayed recovery of live canopy fuels following short-interval stand-replacing fire suggests a lower likelihood of crown fire for 30 years or more following reburns. Average canopy bulk density in long-interval plots was already above an active crown fire threshold of 0.10 kg m^{-3} (Cruz et al., 2005), whereas average short-interval bulk density was well below. Self-regulating effects of past fires on future fire spread and burn severity are often short-lived (Buma et al., 2020; Parks et al., 2015), especially in subalpine forests (Harvey et al., 2016a), but our data show that regulation of canopy burn severity could be lengthened following short-interval fire.

Surface fire spread relies on fine surface fuels, which did not differ between plot pairs, suggesting future surface fire spread may be unaffected by reburns. Although we did not quantify herbaceous fuels, Schoennagel et al. (2004) found that herb and grass cover did not differ 12 years after short-interval versus long-interval fire in this region. Coarse woody debris does not contribute substantially to fire spread rates, but higher loadings can increase residence time, burn severity, and resistance to fire control (Graham et al., 2004; Sikkink & Keane, 2012). Downed coarse wood loads of 22–67 Mg ha^{-1} balance high ecological benefits with low-to-moderate fire hazard in cool-climate, post-fire forests (Brown et al., 2003). Average loadings following short-interval fire were within this range, but average long-interval loadings including large snags were much higher. Thus, short-interval reburns may reduce future surface burn severity even if they do not limit spread. Alternatively, more open forest canopies result in drier fuels and higher windspeeds, which could enable rapid fire spread and high tree mortality given sufficient surface fuel loads (van Wagtendonk, 1996).

Implications for forest resilience and change

Overall, our results suggest that some characteristics of forest resilience remain intact after short-interval fire, while others are diminished or lost. All plots had tree regeneration and average densities in reburned areas were sufficient for self-replacement (1200 stems ha^{-1} in 200-year-old stands; Kashian, Turner, & Romme, 2005), indicating that forest regeneration could be considered resilient even after two severe fires within a few decades (Figure 5). In terms of material disturbance legacies, downed coarse wood, which provides regeneration microsites, energy, nutrients, and carbon in post-fire environments (Franklin et al., 2007; Harmon et al., 1986), remained high following short-interval fire. In contrast, large standing snags, which serve as a critical wildlife habitat for several bird species (Hutto, 1995), were virtually absent in reburns. Total live and dead biomass was also much lower in reburns, and biomass accumulation was dampened relative to long-interval fire. These results suggest that short-interval fires weaken forest contributions to climate regulation via carbon sequestration. These diminished capabilities could be long-lasting and further amplified if stands reburn again within a few decades (Figure 5; Hayes & Buma, 2021; Turner et al., 2019). However, negative feedbacks on burn severity from reduced fuel loads could still mitigate future fire effects, and transitions to deciduous species could enhance carbon uptake and increase albedo (Beck et al., 2011; Mack et al., 2021).

Our results apply to other forests facing simultaneous changes in multiple interacting drivers, including North American boreal (Baltzer et al., 2021; Whitman et al., 2019), European temperate (Albrich et al., 2022; Senf & Seidl, 2021), pantropical (Brando et al., 2019), and Mediterranean forests (Batllori et al., 2019). Historically resilient forests may experience restructuring or reassembly following disturbance (Seidl & Turner, 2022) if species traits become misaligned with changing disturbance regimes (Johnstone et al., 2016). Results of this study underscore the importance of considering amplifying interactions among drivers, the need for quantifying recovery over time scales long enough to detect trends, and the power of paired design to improve causal inferences from observational data. Short-interval fire diminished and delayed forest recovery and, coupled with interacting drivers, could lead to rapid, surprising changes in forest resilience during the 21st century.

AUTHOR CONTRIBUTIONS

Kristin H. Braziunas and Monica G. Turner designed the study; Kristin H. Braziunas, Nathan G. Kiel, and Monica G. Turner collected data; Kristin H. Braziunas analyzed data; and Kristin H. Braziunas and Monica G. Turner wrote the paper with contributions from Nathan G. Kiel.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and novel code (Braziunas et al., 2023) are available in the Environmental Data Initiative's EDI Data Portal at https://doi.org/10.6073/pasta/97bacd7594c89104536d4d2288d93572.

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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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Less fuel for the next fire?

Short-interval fire delays forest recovery and interacting drivers amplify effects

Kristin H. Braziunas, Nathan G. Kiel, and Monica G. Turner

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Appendix S1: Supplemental detail on methods

Methods

Reburn and plot selection

As part of our reburn selection process, we excluded prescribed fires, fires without high-severity reburns of previous severe fire, and areas where management altered recovery trajectories (e.g., timber harvest, salvage, or planting; USDA Forest Service 2019). Burn severity was classified using relative differenced Normalized Burn Ratio (RdNBR; Miller and Thode 2007) and regionally calibrated breakpoints (Harvey et al. 2016a). Classes included: unburned (RdNBR < 0), low severity (< 50% basal area killed by fire, 0-288 RdNBR), moderate severity (50-92.5% basal area killed, 288-675 RdNBR), and high or stand-replacing severity (≥ 92.5% basal area killed, 675-2000 RdNBR). Extremely high values with > 2000 RdNBR were excluded (Harvey et al. 2016a). RdNBR performs well in this region and appropriately represents field-measured burn severity across a range of stand ages (Abendroth 2008; Harvey 2015; Saberi 2019). For fires before 1983, when satellite-derived RdNBR was unavailable, stand-replacing fire was hand-digitized using historical imagery from Google Earth Pro Version 7.3.

Plot-pair sites were identified based on close (within 1 km) proximity of short- and long-interval burned patches, and short-interval plot locations were randomly selected. Short-interval plots had burned twice at stand-replacing severity and were located > 30 m from the edge of a burned patch, which was defined as an area of stand-replacing severity in one fire that burned at moderate or stand-replacing severity in the other fire (see Figure 1c). The most topographically similar long-interval plot at that site was identified based on propensity scores accounting for aspect, elevation, and slope (Butsic et al. 2017). Aspect was transformed to deviation from northeast (Beers et al. 1966). In the field, we verified that plots represented short- or long-interval fire, were stand-replacing, and shared similar topographic conditions within pairs. Plots were moved if needed to meet these criteria. Most paired plots were < 375 m apart and all were < 1200 m apart.

Biomass and fuels calculations

Species- and tree size-specific allometric equations for live trees ≥ 1.4 m height were used to calculate biomass in live crown, dead crown, and stem compartments (Brown 1978; Gholz et al. 1979; Ker 1984; Ter-Mikaelian and Korzukhin 1997). For lodgepole pine saplings, total aboveground biomass was quantified with regionally developed equations (Turner et al. 2004; Copenhaver and Tinker 2014). Sapling biomass of other species was omitted because > 96% of saplings were lodgepole pine. Individual snag volumes were calculated from diameter at breast height and height (Cole 1971) and multiplied by 0.405 g cm^{-3}, the wood density of lodgepole pine coarse woody debris assuming decay class 1 or 2 (Harmon and Sexton 1996). Shrub biomass was derived from cover using separate equations for shorter shrubs (< 0.5 m height, equation based on *Vaccinium scoparium*; Turner et al. 2004) and taller shrubs (≥ 0.5 m height, equation based on *Ceanothus velutinus*; Means et al. 1996).

To calculate canopy fuel load (CFL) and bulk density, conifer crown biomass was first allocated to foliage and branchwood compartments (Brown 1978). Available CFL was the sum of live foliage, 50% of live 1-h branchwood, dead foliage, and 100% of dead 1-h branchwood

(Reinhardt et al. 2006; Donato et al. 2013). CFL was then distributed evenly in 0.25-m bins along the crown length of each individual tree, and bins were summed to create a vertical canopy fuel profile. Canopy bulk density was the maximum 4-m running mean fuel load, consistent with the Fire and Fuels Extension of the Forest Vegetation Simulator (Rebain 2010) and other studies in this region (Simard et al. 2011; Donato et al. 2013; Nelson et al. 2016).

Question 1: Effects of interacting drivers on forest regeneration

We focused on climate water deficit and summer (June-August) vapor pressure deficit because both synthesize temperature and precipitation variability and anticipate patterns of conifer regeneration (Harvey et al. 2016b; Stevens-Rumann et al. 2018; Davis et al. 2019). Climate water deficit is the cumulative difference between potential and actual evapotranspiration, and higher values indicate higher water stress. Both climate drivers exhibit a general warming-drying trend over the past three decades, but also show distinct year-to-year trends (Appendix S2:Figures S4-S7). Both actual and relative differences in stem density between plot pairs were calculated, and both exhibited generally consistent relationships with climate variables (Appendix S2:Figures S8-S9).

Each of the plot pairs sampled in 2021 fell within the same 4-km TerraClimate grid cell (i.e., the short- and long-interval plots within each respective pair shared the same climate). Some plot pairs sampled in 2000 differed in climate grid cell (all but 1 pair differed by < 5% in the value of a given climate driver); for these plot pairs, climate variables were averaged for comparison with differences in regeneration density.

Topographic predictors of post-fire conifer stem density included head load index and topographic position index. Heat load index quantifies potential annual direct incident radiation and was calculated from latitude and field-measured aspect and slope (McCune and Keon 2002).

Topographic position index quantifies relative position (i.e., lower versus higher, valley versus ridge; Weiss 2001) from a 30-m digital elevation model (US National Elevation Dataset).

Following model selection, we tested whether forced inclusion of time since fire would alter the importance of other predictors, because time since fire is associated with changes in stem density over post-fire stand development. Inclusion of time since fire did not alter the strength of other predictors in the top model, and it was not a significant predictor of post-fire conifer stem density in short- or long-interval plots (Appendix S2:Table S3). This is likely because our plots covered a wide range of site conditions, including areas with high initial regeneration densities followed by self-thinning (e.g., lower elevation areas with high pre-fire serotiny) and areas with low initial stem densities and opportunities for infilling (e.g., higher elevation areas with lower dominance of serotinous lodgepole pine).

R packages

Analyses were performed in R 4.1.3 (R Core Team 2022) primarily used the car (Fox and Weisberg 2019), DHARMa (Hartig 2022), corrplot (Wei and Simko 2021), cowplot (Wilke 2020), ggpubr (Kassambara 2020) , glmmTMB (Brooks et al. 2017), gridExtra (Auguie 2017), leaps (Lumley and Miller 2020), lmtest (Zeileis and Hothorn 2002), MatchIt (Ho et al. 2011), openxlsx (Schauberger and Walker 2021), plotrix (Lemon 2006), pscl (Zeileis et al. 2008), raster (Hijmans 2022), rgdal (Bivand et al. 2021), rgeos (Bivand and Rundel 2021), RNetCDF (Michna and Woods 2022), sandwich (Zeileis et al. 2020; Zeileis 2006), sf (E. Pebesma 2018), sp (E. J. Pebesma and Bivand 2005), tidyverse (Wickham et al. 2019), and tmap (Tennekes 2018) packages.

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Less fuel for the next fire?

Short-interval fire delays forest recovery and interacting drivers amplify effects

Kristin H. Braziunas, Nathan G. Kiel, and Monica G. Turner

Journal: Ecology

Appendix S2: Supplemental tables and figures

Table S1. Short-interval fires included in this study. Fire names from Yellowstone National Park database or Monitoring Trends in Burn Severity. First fire names not available for all records.

Fire return interval	# plot pairs	First fire	First fire year	Second fire	Second fire year	Sample year	Time since fire (years)
7	1	Witch	1981	Red	1988	2000	12
7	1	Forest Lake	1981	Snake	1988	2000	12
7	1	-	1981	Red-Shoshone	1988	2000	12
9	1	-	1979	North Fork	1988	2000	12
9	1	Beaver Heart	1979	Red	1988	2000	12
9	1	Gallatin	1979	North Fork	1988	2000	12
9	1	-	1979	Red-Shoshone	1988	2000	12
12	1	Pelican	1996	Le Hardy	2008	2021	13
13	1	Astringent	1981	Tern	1994	2000	6
13	1	Astringent	1981	Tern	1994	2021	27
15	1	Clover	1988	East	2003	2021	18
15	1	Rathbone	2003	Bacon Rind	2018	2021	3
16	2	Iron Mountain	1990	Derby	2006	2021	15
16	1	Wilcox	2000	Berry	2016	2021	5
16	2	Glade	2000	Berry	2016	2021	5
19	1	North Fork	1988	Owl	2007	2021	14
20	1	Clover	1988	Le Hardy	2008	2021	13
24	2	North Fork	1988	Cygnet	2012	2021	9
24	1	Clover	1988	Dewdrop	2012	2021	9
26	1	Waterfalls	1974	Moran	2000	2021	21
27	1	Madison River	1961	North Fork	1988	2000	12
28	1	Central Plateau	1960	North Fork	1988	2000	12
28	1	-	1960	North Fork	1988	2000	12
28	2	Mystic	1981	Bearpaw Bay	2009	2021	12
28	2	Huck	1988	Berry	2016	2021	5
28	2	North Fork	1988	Maple	2016	2021	5
28	1	Hellroaring	1988	Buffalo	2016	2021	5

Table S2. Additional multiple linear regression models predicting stem density (log10-transformed) from multiple factors and potential interactions with short-interval fire.

Model rank	ΔBIC	Formula (predictors)
5	2.1	3.75 + 0.25 (Climate water deficit normal) + 0.34 (Summer VPD anomaly) - 0.79 (Fire interval Short) - 0.37 (Distance to unburned:Fire interval Short)
6	3.2	3.70 + 0.12 (Distance to unburned) + 0.28 (Climate water deficit normal) - 0.74 (Fire interval Short) - 0.46 (Distance to unburned:Fire interval Short)
7	3.3	3.75 + 0.38 (Climate water deficit normal) + 0.30 (Summer VPD anomaly) - 0.67 (Fire interval Short) - 0.36 (Climate water deficit normal:Fire interval Short)
8	3.4	3.74 + 0.29 (Climate water deficit normal) - 0.78 (Fire interval Short) - 0.38 (Distance to unburned:Fire interval Short) + 0.28 (Summer VPD anomaly:Fire interval Short)
9	3.6	3.76 + 0.53 (Summer VPD anomaly) - 0.66 (Fire interval Short)
10	3.7	3.75 + 0.20 (Climate water deficit normal) + 0.31 (Summer VPD anomaly) - 0.67 (Fire interval Short)
11	4.0	3.75 + 0.37 (Climate water deficit normal) + 0.33 (Summer VPD anomaly) - 0.76 (Fire interval Short) - 0.29 (Distance to unburned:Fire interval Short) - 0.27 (Climate water deficit normal:Fire interval Short)
12	4.0	3.74 + 0.43 (Climate water deficit normal) - 0.74 (Fire interval Short) - 0.30 (Distance to unburned:Fire interval Short) - 0.34 (Climate water deficit normal:Fire interval Short) + 0.45 (Summer VPD anomaly:Fire interval Short)
13	4.1	3.90 - 0.40 (Elevation High) - 0.66 (Fire interval Short)
14	4.5	3.74 + 0.30 (Climate water deficit normal) - 0.78 (Fire interval Short) + 0.27 (Elevation High:Fire interval Short)
15	4.5	3.74 - 0.08 (Time since fire) + 0.26 (Climate water deficit normal) - 0.67 (Fire interval Short)
16	4.7	3.73 - 0.66 (Fire interval Short)
17	5.2	3.74 - 0.07 (Time since fire) + 0.44 (Climate water deficit normal) - 0.76 (Fire interval Short) - 0.28 (Distance to unburned:Fire interval Short) - 0.28 (Climate water deficit normal:Fire interval Short)
18	5.5	3.72 + 0.07 (Distance to unburned) + 0.40 (Climate water deficit normal) - 0.74 (Fire interval Short) - 0.35 (Distance to unburned:Fire interval Short) - 0.24 (Climate water deficit normal:Fire interval Short)
19	5.5	3.72 + 0.10 (Distance to unburned) + 0.23 (Climate water deficit normal) + 0.32 (Summer VPD anomaly) - 0.75 (Fire interval Short) - 0.46 (Distance to unburned:Fire interval Short)
20	6.8	3.73 - 0.14 (Heat load index) - 0.67 (Fire interval Short)
21	7.3	3.73 - 0.73 (Fire interval Short) - 0.20 (Distance to unburned:Fire interval Short)
22	10.4	3.40 + 0.25 (Climate water deficit normal)
23	11.9	3.51 - 0.52 (Elevation High:Fire interval Short)
24	12.2	3.43 + 0.53 (Summer VPD anomaly)
25	12.5	3.57 - 0.40 (Elevation High)

Note (Table S2): Exhaustive model selection (maximum 5 predictors x 5 models evaluated per number of predictors, for a total of $n = 25$ models) and Bayesian Information Criteria BIC < 2 were used to identify models that best represented the relative importance of predictors, which are included in the main manuscript. Continuous predictors were standardized to have a mean of 0 and standard deviation of 1.

Table S3. Multiple linear regression model 1 predicting stem density (log10-transformed) when time since fire is also included (see manuscript Table 2).

Adj. R^2	**Predictor**	**Estimate**	**SE**	**t**	**p**
0.28	(Intercept)	3.70	0.13	28.93	**2×10^{-16}**
	Fire interval (short)	-0.74	0.18	-4.00	**0.0002**
	Climate water deficit normal	0.29	0.09	3.04	**0.004**
	Distance to unburned:Fire interval (short)	-0.34	0.16	-2.15	**0.04**
	Distance to unburned:Fire interval (long)	0.12	0.12	1.00	0.32
	Time since fire	-0.07	0.09	-0.84	0.40

Figure captions

Figure S1. Histograms showing general characteristics of plots sampled in 2021 (*n* = 44, this study) and 2000 (*n* = 22) including elevation, aspect where 0 is southwest and 2 is northeast, slope, short fire interval, time since most recent fire, and year of most recent fire. Short fire interval is only summarized for short-interval plots.

Figure S2. Residual and quantile-quantile plots overlayed with results of Kolmogorov-Smirnov, dispersion, outlier, and uniformity tests to determine whether zero-inflated negative binomial models appropriately represented species count data in paired plots. For assumption checks, models were fit with the glmmTMB package and model residuals were simulated (*n* = 100 repetitions) and tested with the DHARMa package in R (see citations in Appendix S1). ABLA: Subalpine fir, PIAL: Whitebark pine, PIEN: Engelmann spruce.

Figure S3. Residual and quantile-quantile plots overlayed with results of Kolmogorov-Smirnov, dispersion, outlier, and uniformity tests to determine whether zero-inflated negative binomial models appropriately represented species count data in paired plots. For assumption checks, models were fit with the glmmTMB package and model residuals were simulated (*n* = 100 repetitions) and tested with the DHARMa package in R (see citations in Appendix S1). POTR: Quaking aspen, PSME: Douglas-fir.

Figure S4. Climate water deficit normal (30-year, 1989-2018; mm) for the Greater Yellowstone Ecosystem at 4-km resolution. Calculated based on water-year (e.g., 1989 deficit is summed across October 1988 through September 1989) because most precipitation falls as snow. Points show location of field plots sampled in 2000 and 2021.

Figure S5. Climate water deficit anomaly (z-score) for the Greater Yellowstone Ecosystem for 1988-2021.

Figure S6. Summer (June-August) vapor pressure deficit normal (30-year, 1989-2018; kPa) for the Greater Yellowstone Ecosystem at 4-km resolution. Points show location of field plots sampled in 2000 and 2021.

Figure S7. Summer vapor pressure deficit anomaly (z-score) for the Greater Yellowstone Ecosystem for 1988-2021.

Figure S8. Pairwise relationships between 1989-2018 summer vapor pressure deficit normal (kPa) and 3-year post-fire climate water deficit anomaly (z-score) and differences in paired long- minus short-interval live conifer stem density (n = 33). Differences in conifer density have been cube-root transformed for plotting. Plots show the strength of pairwise relationships (Spearman's rank correlation) and significance (p-value). VPD = vapor pressure deficit, norm = normal, anom = anomaly.

Figure S9. Pairwise relationships between climate variables and relative differences in paired long- and short-interval live conifer stem density (n = 33). Plots show the strength of pairwise relationships (Spearman's rank correlation) and significance (p-value). VPD = vapor pressure deficit, norm = normal, anom = anomaly.

Figure S10. Residual and quantile-quantile plots to evaluate assumptions of linearity, normality, and equal variance for multiple linear regression models predicting conifer stem density. Assumptions were assessed for the full model and all top models (see manuscript Table 2). This figure includes the full model and models 1-2.

Figure S11. Residual and quantile-quantile plots to evaluate assumptions of linearity, normality, and equal variance for multiple linear regression models predicting conifer stem density. Assumptions were assessed for the full model and all top models (see manuscript Table 2). This figure includes models 3-4.

Figure S12. Quantile-quantile plots to evaluate the assumption of normality for fuel and biomass pools tested with t-tests.

Figure S13. Illustrative photos of long- and short-interval plot pairs highlighting differences in live woody biomass and associated conifer regeneration density, dead woody biomass and fuels, and aspen regeneration density. Photo credit: Kristin Braziunas

Figure S14. Biomass of dead woody fuels by size class, including standing dead snags and downed woody debris.

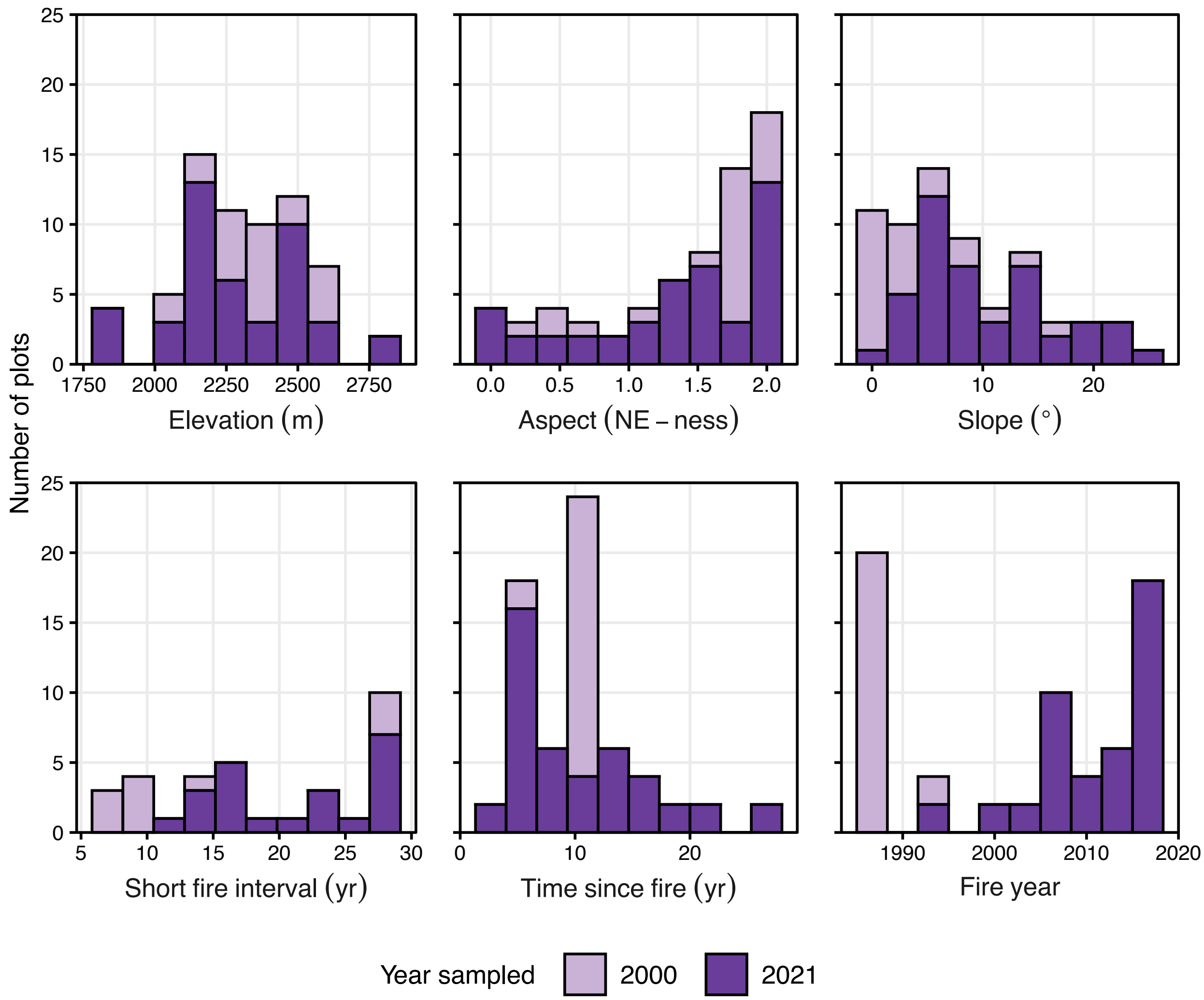

Number of plots
25
20
15
10
5
0
1750
2000
2250
2500
2750
Elevation (m)
0.0
0.5
1.0
1.5
2.0
Aspect (NE – ness)
0
10
20
Slope (°)
5
10
15
20
25
30
Short fire interval (yr)
0
10
20
Time since fire (yr)
1990
2000
2010
2020
Fire year
Year sampled
2000
2021

Figure S1

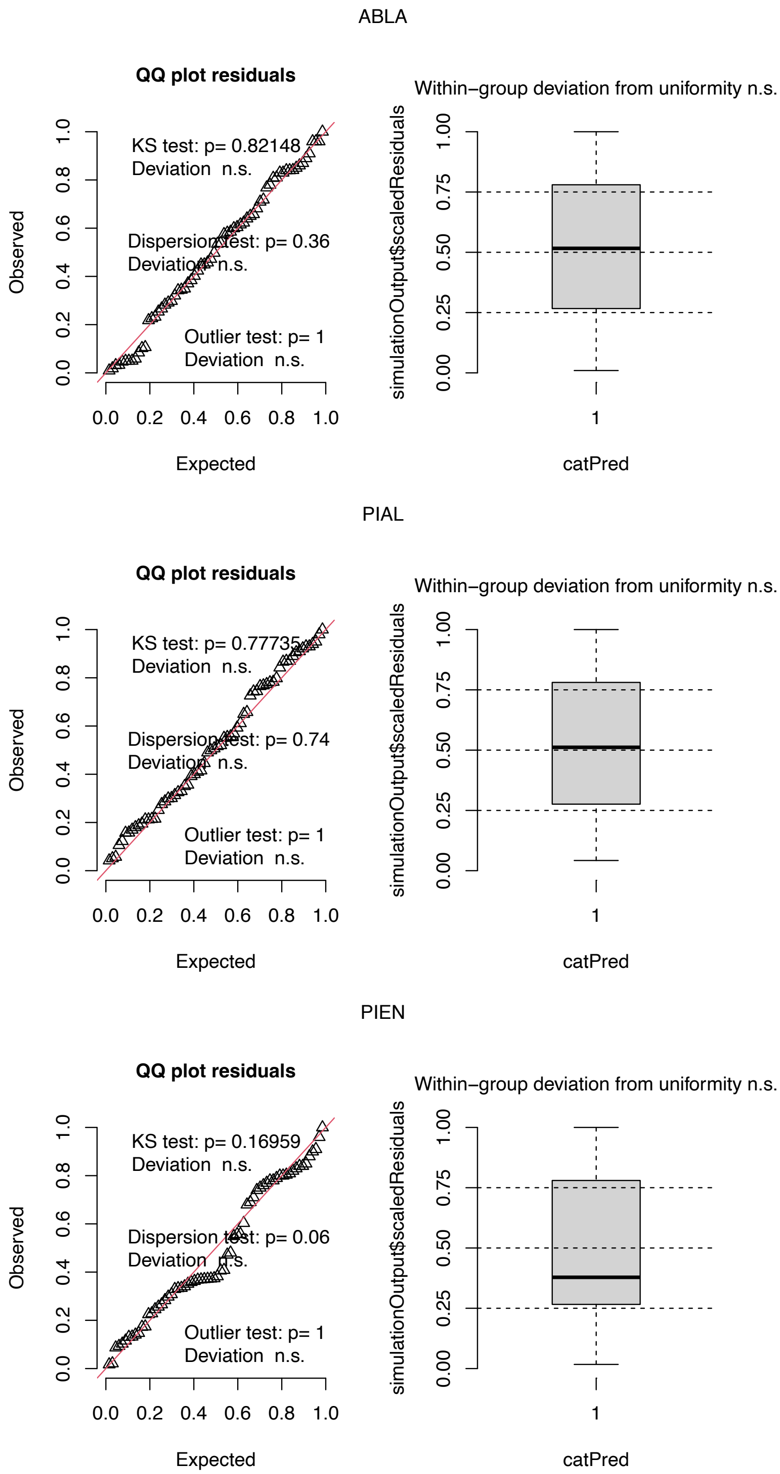

ABLA
QQ plot residuals
KS test: p= 0.82148
Deviation n.s.
Dispersion test: p= 0.36
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Within−group deviation from uniformity n.s.
simulationOutput$scaledResiduals
catPred
PIAL
QQ plot residuals
KS test: p= 0.77735
Deviation n.s.
Dispersion test: p= 0.74
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Within−group deviation from uniformity n.s.
simulationOutput$scaledResiduals
catPred
PIEN
QQ plot residuals
KS test: p= 0.16959
Deviation n.s.
Dispersion test: p= 0.06
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Within−group deviation from uniformity n.s.
simulationOutput$scaledResiduals
catPred

Figure S2

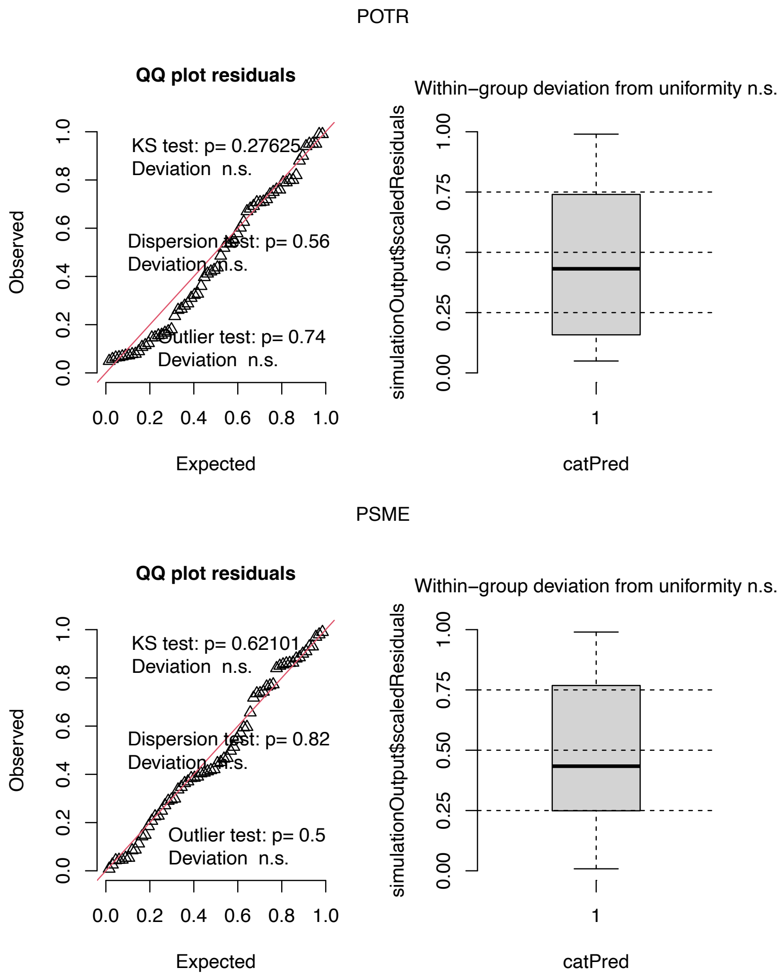

POTR
QQ plot residuals
KS test: p= 0.27625
Deviation n.s.
Dispersion test: p= 0.56
Deviation n.s.
Outlier test: p= 0.74
Deviation n.s.
Observed
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Expected
Within−group deviation from uniformity n.s.
simulationOutput$scaledResiduals
0.00 0.25 0.50 0.75 1.00
1
catPred
PSME
QQ plot residuals
KS test: p= 0.62101
Deviation n.s.
Dispersion test: p= 0.82
Deviation n.s.
Outlier test: p= 0.5
Deviation n.s.
Observed
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Expected
Within−group deviation from uniformity n.s.
simulationOutput$scaledResiduals
0.00 0.25 0.50 0.75 1.00
1
catPred

Figure S3

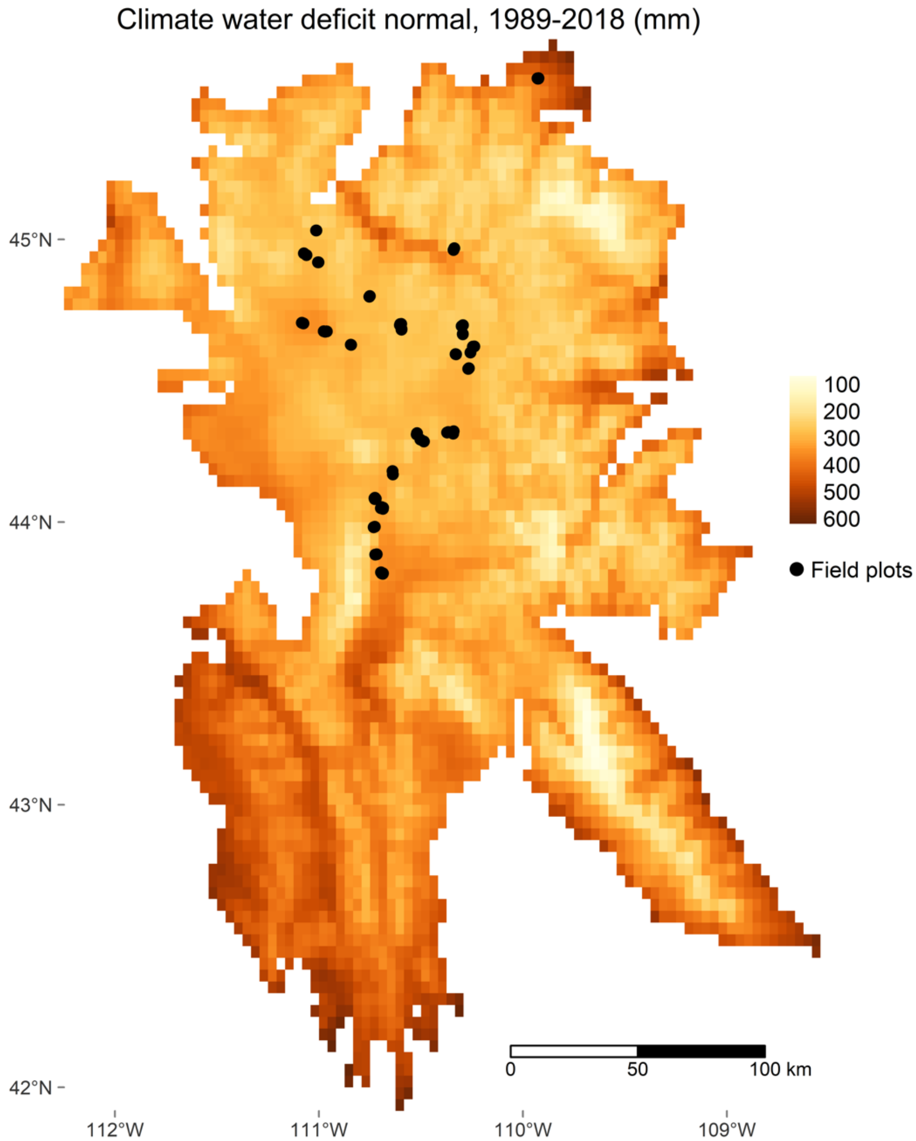

Climate water deficit normal, 1989-2018 (mm)
45°N
44°N
43°N
42°N
112°W
111°W
110°W
109°W
100
200
300
400
500
600
Field plots
0
50
100 km

Figure S4

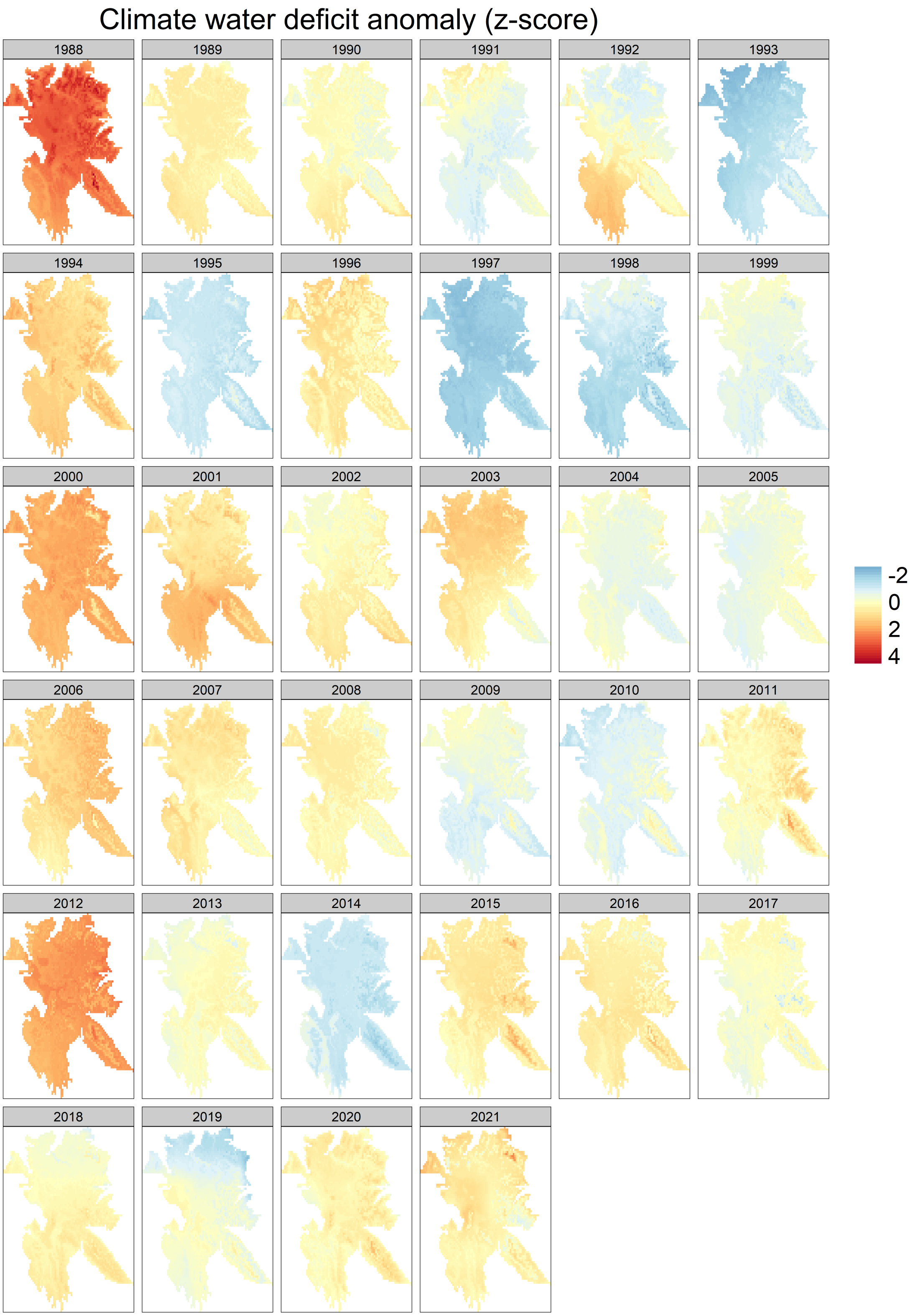

Climate water deficit anomaly (z-score)
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
2021
-2
0
2
4

Figure S5

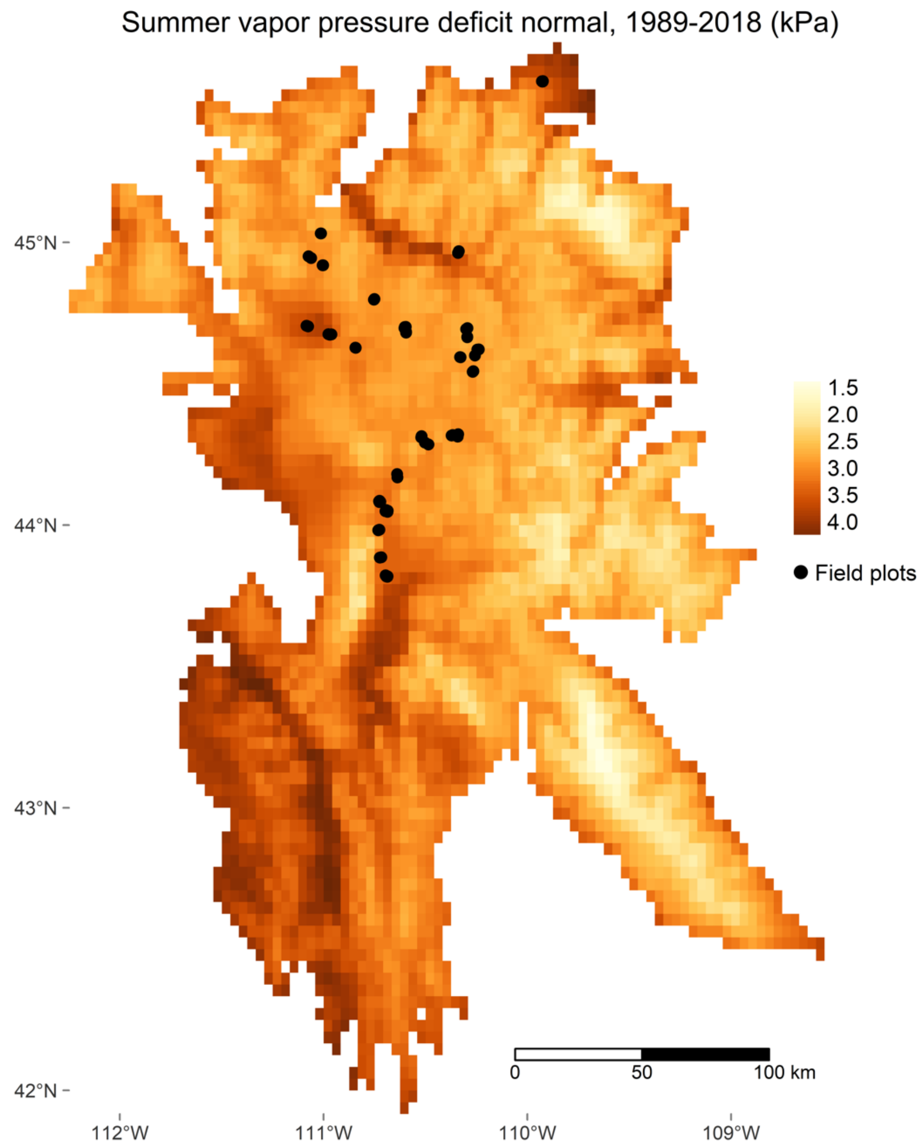

Summer vapor pressure deficit normal, 1989-2018 (kPa)
45°N
44°N
43°N
42°N
112°W
111°W
110°W
109°W
1.5
2.0
2.5
3.0
3.5
4.0
Field plots
0
50
100 km

Figure S6

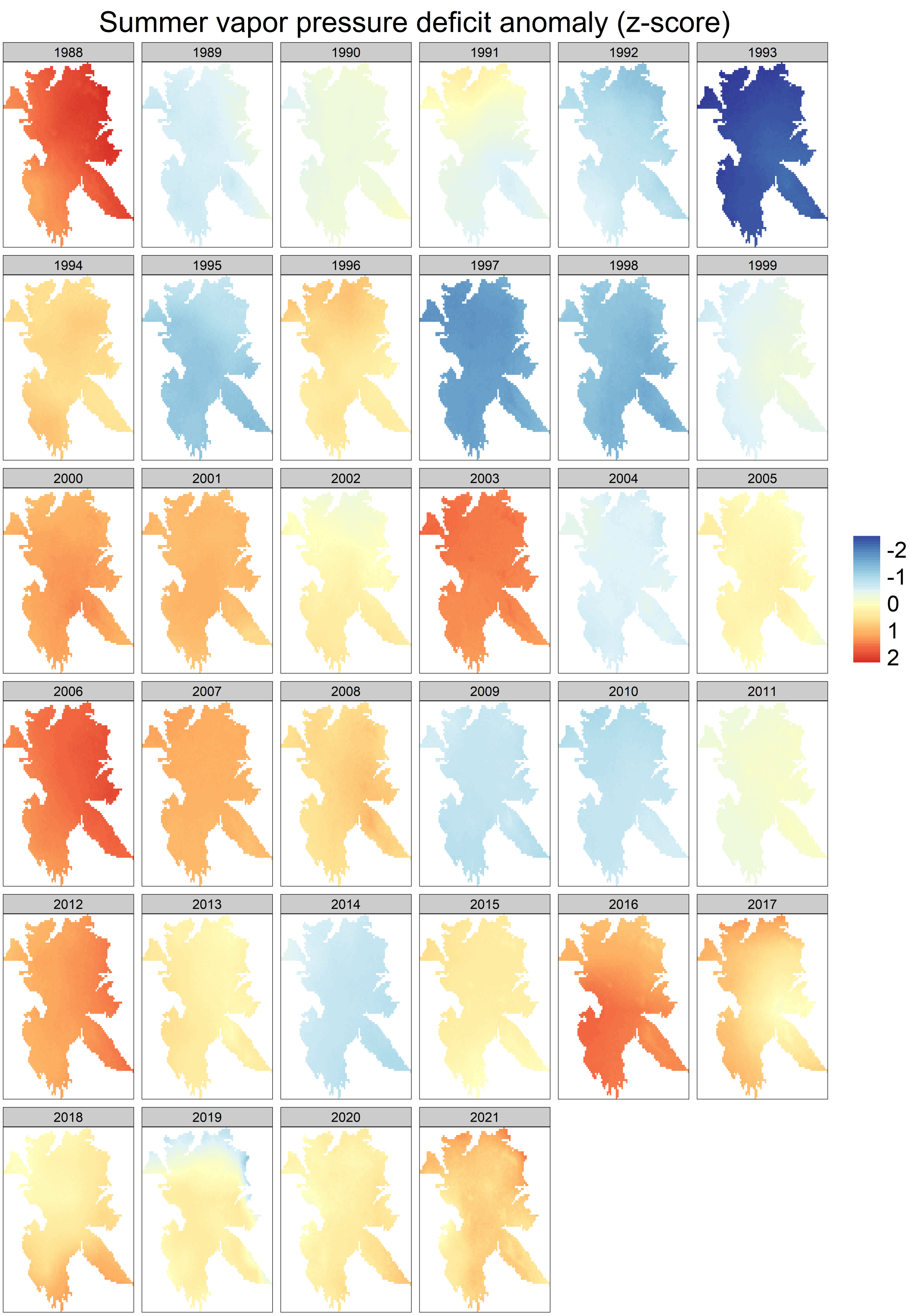
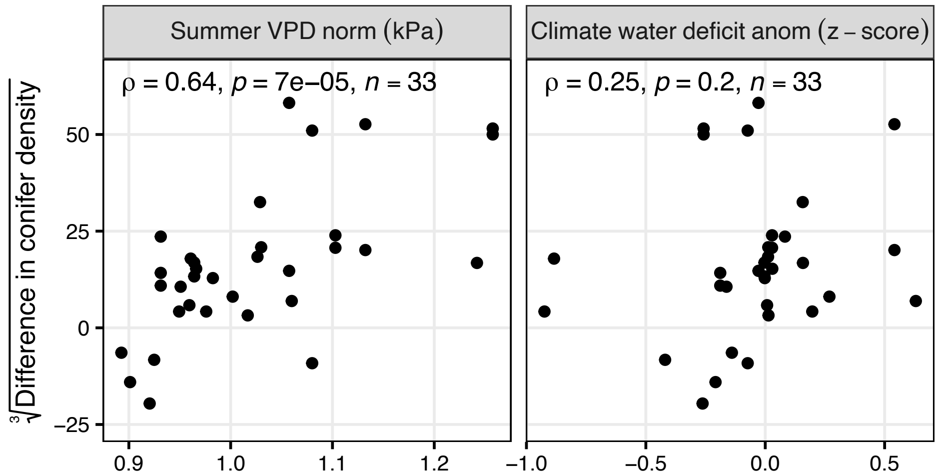

Summer vapor pressure deficit anomaly (z-score)
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
2021
-2
-1
0
1
2

Figure S7



Summer VPD norm (kPa)
Climate water deficit anom (z – score)
ρ = 0.64, p = 7e–05, n = 33
ρ = 0.25, p = 0.2, n = 33
∛Difference in conifer density
50
25
0
–25
0.9
1.0
1.1
1.2
–1.0
–0.5
0.0
0.5

Figure S8

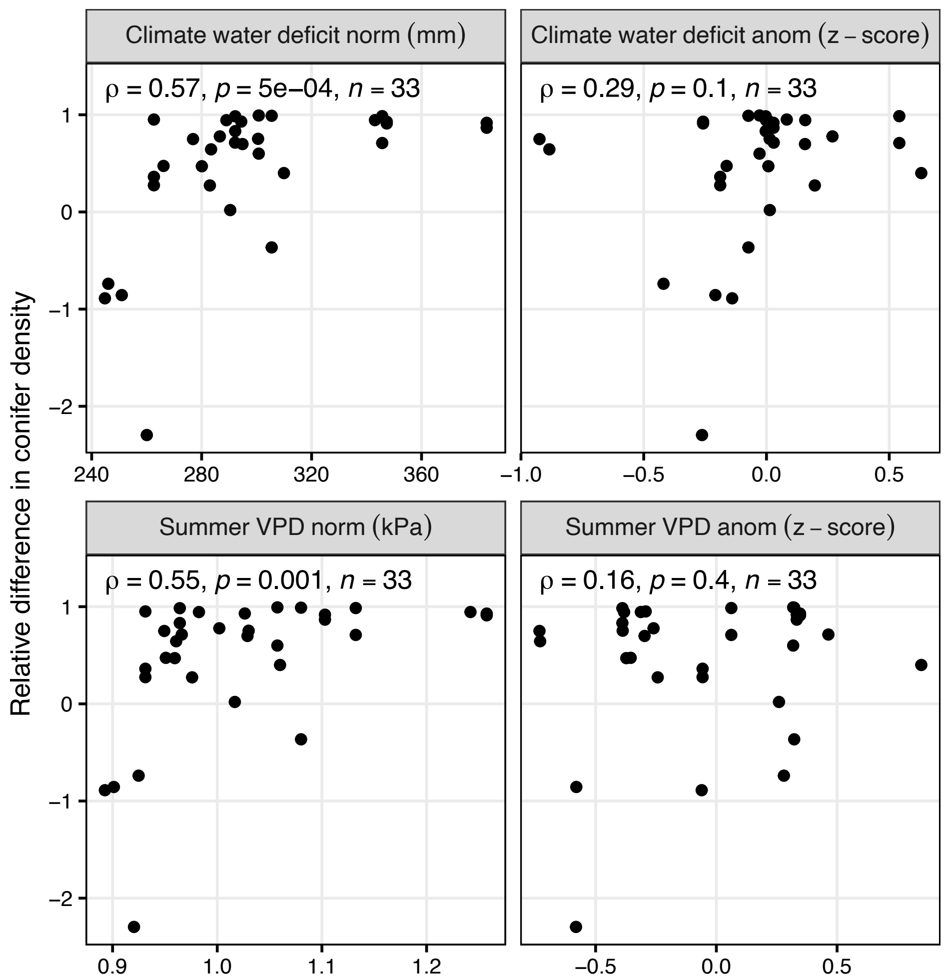
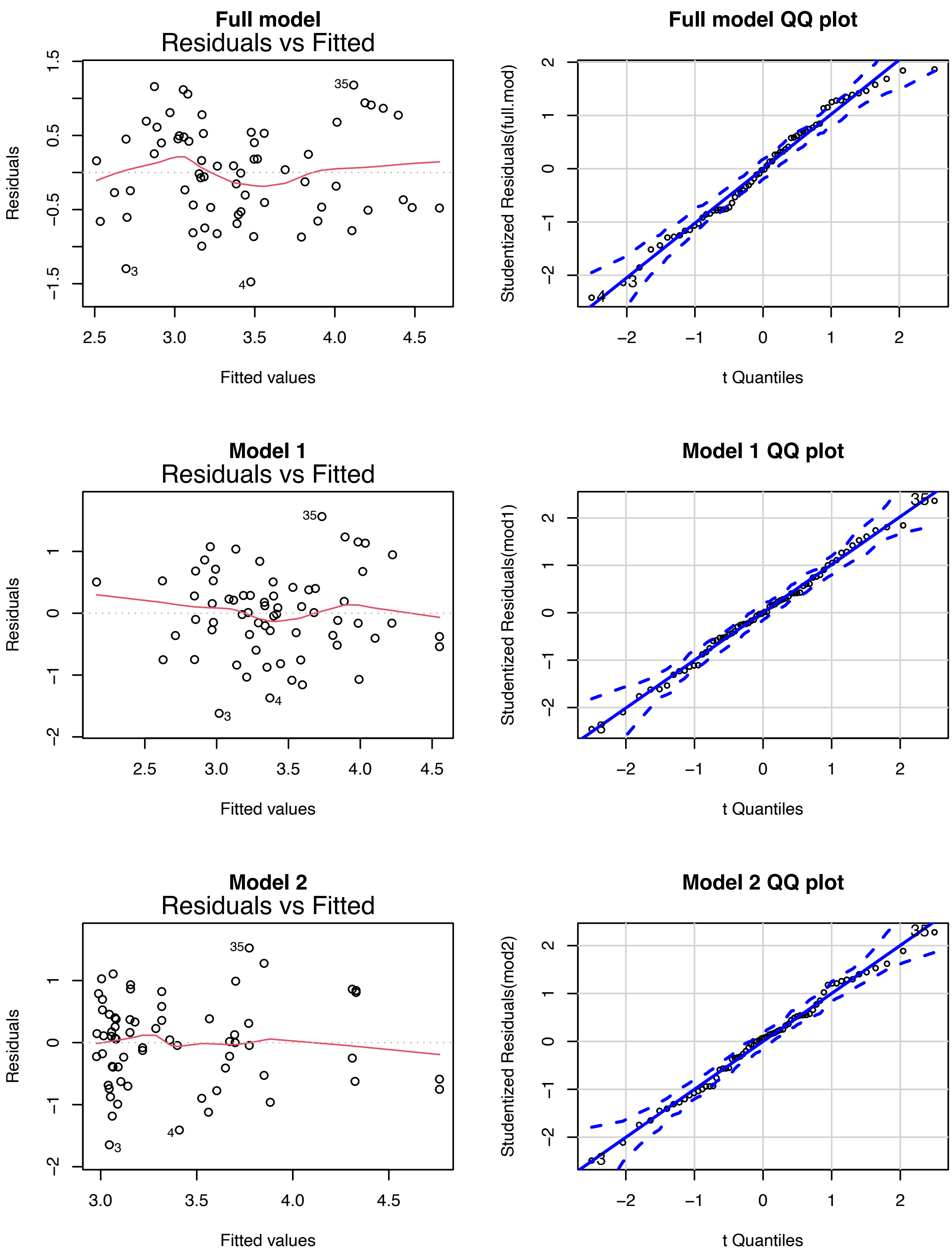

Climate water deficit norm (mm)
Climate water deficit anom (z – score)
ρ = 0.57, p = 5e–04, n = 33
ρ = 0.29, p = 0.1, n = 33
Summer VPD norm (kPa)
Summer VPD anom (z – score)
ρ = 0.55, p = 0.001, n = 33
ρ = 0.16, p = 0.4, n = 33
Relative difference in conifer density
1
0
–1
–2
240
280
320
360
–1.0
–0.5
0.0
0.5
0.9
1.0
1.1
1.2

Figure S9



Full model
Residuals vs Fitted
Residuals
Fitted values
Full model QQ plot
Studentized Residuals(full.mod)
t Quantiles
Model 1
Residuals vs Fitted
Model 1 QQ plot
Studentized Residuals(mod1)
Model 2
Residuals vs Fitted
Model 2 QQ plot
Studentized Residuals(mod2)

Figure S10

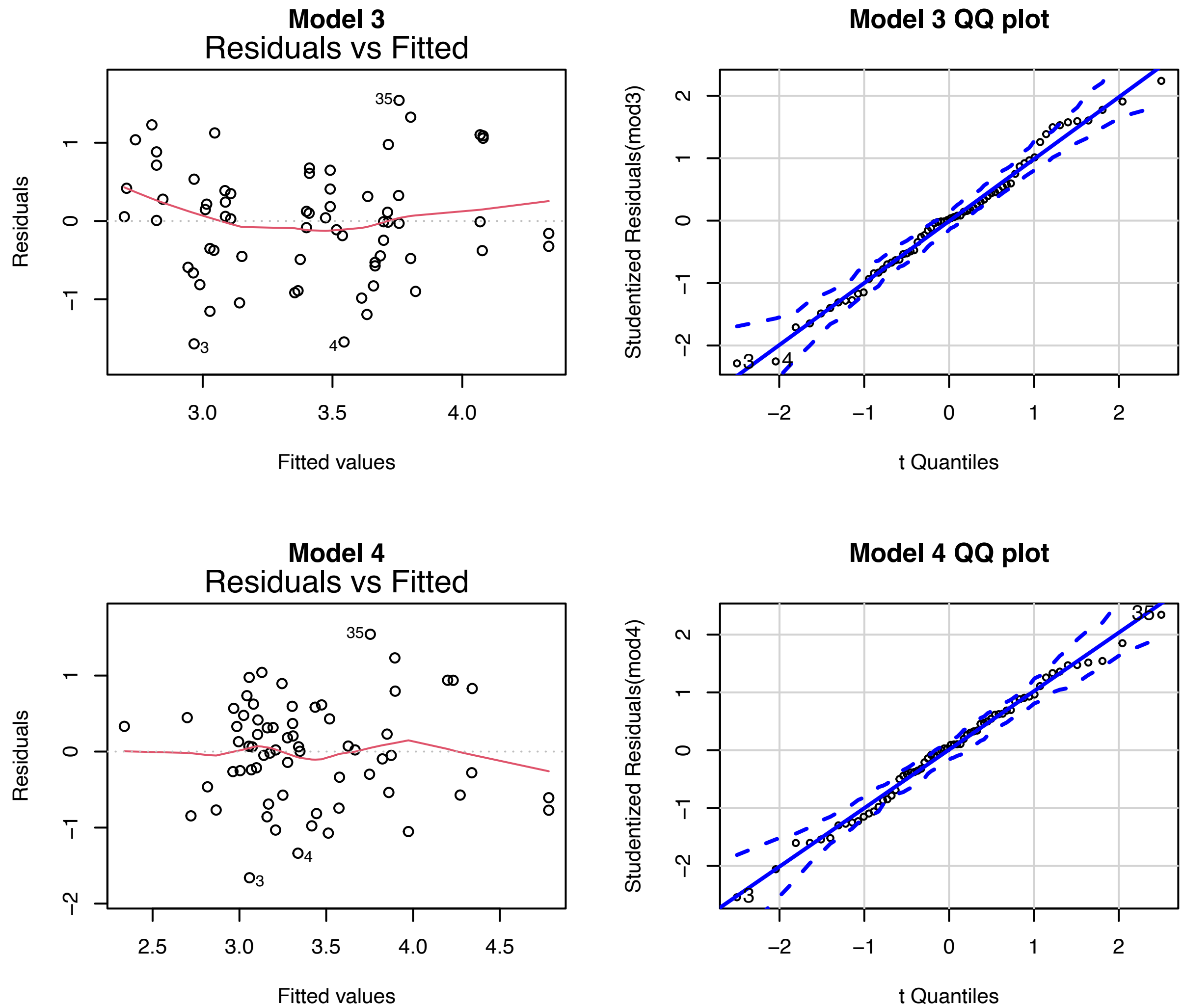

Model 3
Residuals vs Fitted
Residuals
Fitted values
Model 3 QQ plot
Studentized Residuals(mod3)
t Quantiles
Model 4
Residuals vs Fitted
Residuals
Fitted values
Model 4 QQ plot
Studentized Residuals(mod4)
t Quantiles

Figure S11

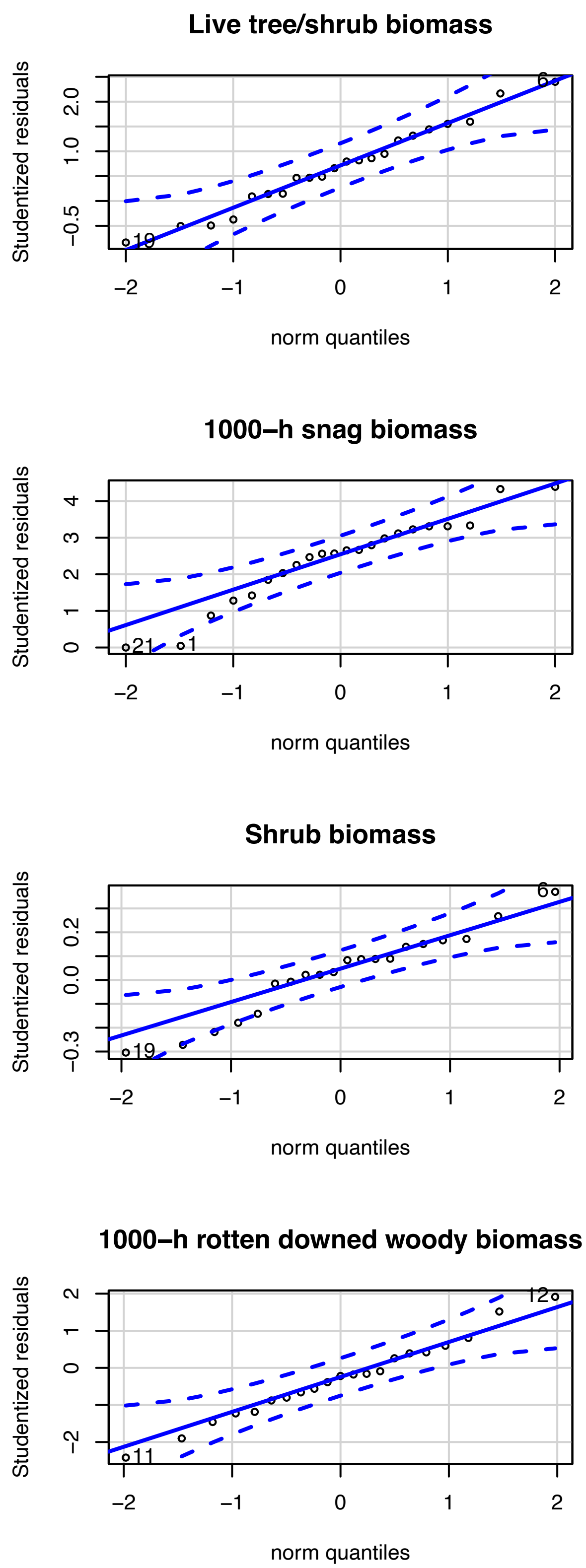

Live tree/shrub biomass
Dead woody biomass
1000–h snag biomass
Total snag biomass
Shrub biomass
10–h downed woody biomass
1000–h rotten downed woody biomass
Studentized residuals
norm quantiles

Figure S12

Compared to long-interval plots, short-interval paired plots had…

…seven times less live tree/shrub biomass.

…half as much dead woody biomass.

…five times higher aspen density.

Figure S13

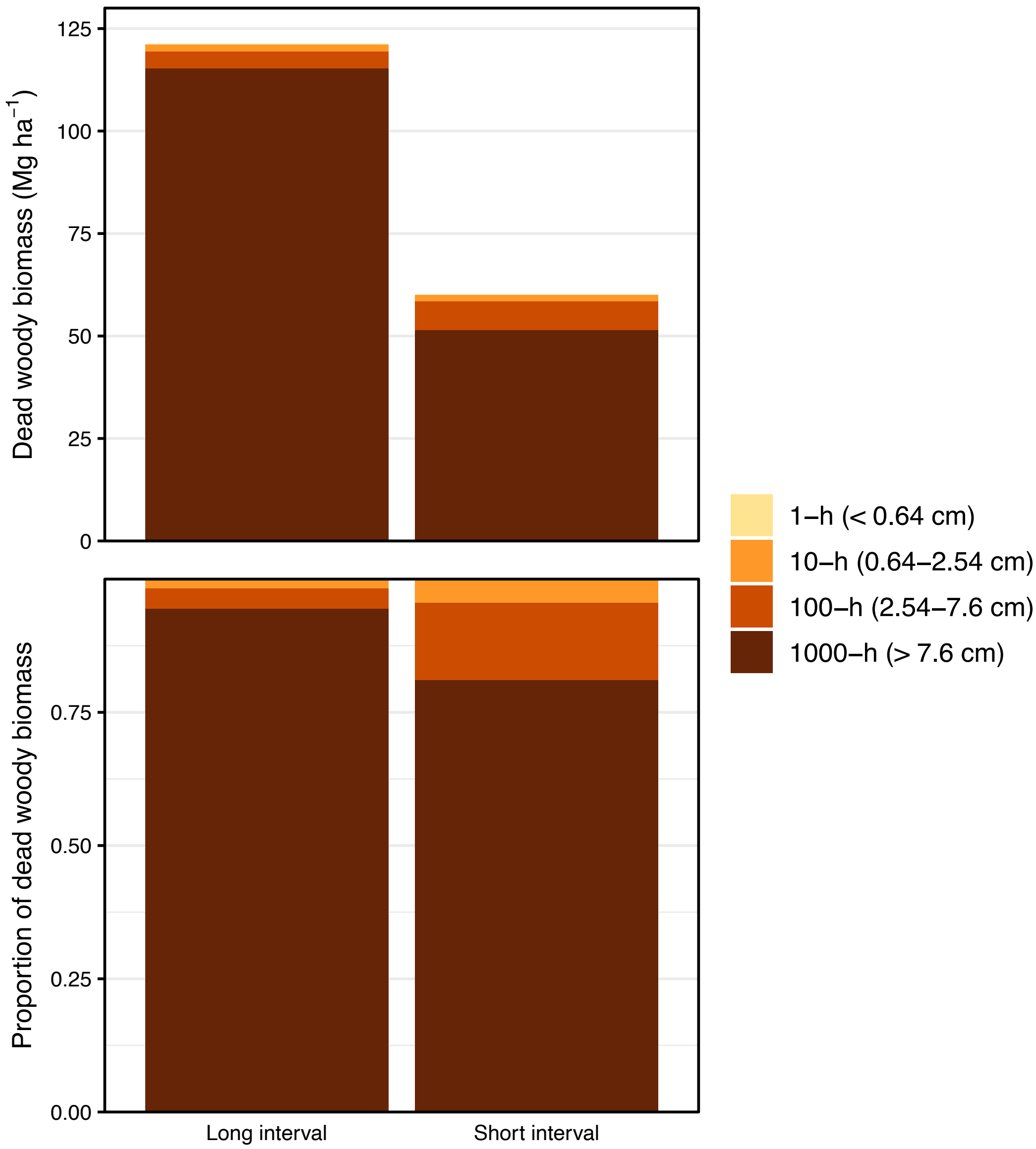

125
100
75
50
25
0
Dead woody biomass (Mg ha^{-1})
0.75
0.50
0.25
0.00
Proportion of dead woody biomass
Long interval
Short interval
1–h (< 0.64 cm)
10–h (0.64–2.54 cm)
100–h (2.54–7.6 cm)
1000–h (> 7.6 cm)

Figure S14