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Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests

Monica G. Turner[a,1], Kristin H. Braziunas[a], Winslow D. Hansen[b], and Brian J. Harvey[c]

[a]Department of Integrative Biology, University of Wisconsin–Madison, Madison, WI 53706; [b]The Earth Institute, Columbia University, New York, NY 10025; and [c]School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195

Contributed by Monica G. Turner, April 15, 2019 (sent for review February 19, 2019; reviewed by Carissa D. Brown and Janet Franklin)

Subalpine forests in the northern Rocky Mountains have been resilient to stand-replacing fires that historically burned at 100- to 300-year intervals. Fire intervals are projected to decline drastically as climate warms, and forests that reburn before recovering from previous fire may lose their ability to rebound. We studied recent fires in Greater Yellowstone (Wyoming, United States) and asked whether short-interval (<30 years) stand-replacing fires can erode lodgepole pine (*Pinus contorta* var. *latifolia*) forest resilience via increased burn severity, reduced early postfire tree regeneration, reduced carbon stocks, and slower carbon recovery. During 2016, fires reburned young lodgepole pine forests that regenerated after wildfires in 1988 and 2000. During 2017, we sampled 0.25-ha plots in stand-replacing reburns (n = 18) and nearby young forests that did not reburn (n = 9). We also simulated stand development with and without reburns to assess carbon recovery trajectories. Nearly all prefire biomass was combusted ("crown fire plus") in some reburns in which prefire trees were dense and small (≤4-cm basal diameter). Postfire tree seedling density was reduced sixfold relative to the previous (long-interval) fire, and high-density stands (>40,000 stems ha^{-1}) were converted to sparse stands (<1,000 stems ha^{-1}). In reburns, coarse wood biomass and aboveground carbon stocks were reduced by 65 and 62%, respectively, relative to areas that did not reburn. Increased carbon loss plus sparse tree regeneration delayed simulated carbon recovery by >150 years. Forests did not transition to nonforest, but extreme burn severity and reduced tree recovery foreshadow an erosion of forest resilience.

wildfire | climate warming | Yellowstone National Park | Grand Teton National Park | *Pinus contorta*

Changing fire regimes have the potential to erode forest resilience (ability of a forest to absorb disturbance and maintain similar structure and function) (1, 2) in fire-prone landscapes. Fire is increasing in many forests worldwide as temperatures warm (3, 4), with profound consequences for forest ecosystems (5–10). In western North America, the number, size, and severity of fires have already markedly risen (11–17), and these trends are expected to accelerate in the 21st century. Fire frequencies in some forests may well exceed those documented over the past 10,000 y (18). In forests adapted to infrequent high-severity fires, more frequent fire increases the likelihood of compound disturbances (19), whereby two disturbances that occur in a short period of time have unexpected or synergistic ecological effects (20–23). Compound disturbances can cause a loss of ecological memory if the biological legacies that govern system responses to disturbance are diminished (22). However, empirical study of forest responses to novel fire regimes is challenging, because trees are long lived, the timing and location of fires are unpredictable, and forest responses unfold slowly across landscapes (23, 24).

Of particular concern is whether forest structure and function will shift fundamentally as fire activity increases and whether some forests could lose their capacity to recover (7, 19, 22, 25–30). Even forests well adapted to high-severity fire may be vulnerable (7, 22, 23, 29–31). Many forests characterized by stand-replacing fire regimes are dominated by obligate seeders and must rely on seedling recruitment to regenerate after fire (32, 33). Such forests span vast boreal forests of Eurasia and North America, conifer forests in Mediterranean regions, eucalypt forests of Australia, and subalpine forests of the Rocky Mountains and Pacific Northwest. Fire return intervals (FRIs) are typically long (e.g., centuries) (34) relative to the lifespan of the dominant trees, and whether these forests will be resilient to changing fire regimes remains unknown (10, 22, 35).

Increased frequency of stand-replacing fire can initiate profound shifts in forest structure if young forests reburn before recovering from previous fire (19, 22, 23). Short FRIs increase "immaturity risk" (36), because seed supply may be insufficient to regenerate a forest if young trees have not reached reproductive maturity (22, 37). Species that produce serotinous cones, which remain closed until heat triggers them to open and release their seeds, may be especially vulnerable to immaturity risk (32, 36, 38). The large canopy seedbank that ensures rapid and prolific postfire regeneration of serotinous tree species can take decades to develop (39). Reduced seedling regeneration after short-interval fires has been reported for *Pinus attenuata* in California, United States (36); *Picea mariana* in Yukon, Canada (40); and *Banksia hookeriana* in Australia (37), although not for conifers in a mixed evergreen forest in Oregon (41). Short-interval fires may also have different effects on young deciduous trees (e.g., trembling aspen *Populus tremuloides*) that can colonize burned conifer forests as seedlings and persist at low densities (42–44). Competition with conifers constrains aspen survival and growth in the Rocky Mountains (45–47), but colonists might benefit from short-interval fire if roots can survive and resprout (44).

Significance

Increased burning in subalpine and boreal forests dominated by obligate seeders and historically characterized by infrequent, stand-replacing fires has raised the specter of novel fire regimes in which young forests reburn before having recovered from previous fire. Empirical study of forest responses to such changing fire regimes is challenging; trees are long lived, the timing and location of fires are unpredictable, and forest responses unfold slowly. Short-interval stand-replacing fires in lodgepole pine forests of Greater Yellowstone led to substantial losses of biological legacies and reduced tree regeneration, which together delayed simulated recovery of aboveground carbon for >150 years. Results suggest profound changes in forest structure and function if short-interval fires become more common in a warmer world with more fire.

Author contributions: M.G.T. and B.J.H. designed research; M.G.T., K.H.B., W.D.H., and B.J.H. performed research; M.G.T. analyzed data; K.H.B. performed computer simulations; and M.G.T. wrote the paper.

Reviewers: C.D.B., Memorial University; and J.F., University of California, Riverside.

The authors declare no conflict of interest.

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Data deposition: Data have been deposited with the NSF-funded Environmental Data Initiative, https://portal.edirepository.org/nis/mapbrowse?packageid=edi.361.2.

[1]To whom correspondence should be addressed. Email: turnermg@wisc.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1902841116/-/DCSupplemental.

Published online May 20, 2019.

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Increased frequency of stand-replacing fire may also alter carbon (C) cycling, weakening C sinks if compound disturbances increase C losses and slow C recovery (48, 49). Forests store up to 80% of the total aboveground C in the terrestrial biosphere and 40% of that belowground C (50, 51), but C stocks are dynamic and vary considerably with stand age (52–54). During a fire, C is rapidly released to the atmosphere as foliage, twigs, branches, and soil organic horizons are combusted, but these immediate losses are usually a small fraction of total ecosystem C (54–56). Even in stand-replacing fires, relatively little downed coarse wood is combusted in long-interval fires (~8–16%) (41, 57), and most C in the fire-killed trees remains in the ecosystem as standing dead wood (54, 58, 59). Organic soil C represents only ~4.4% of total ecosystem C and <1% in recently burned stands (54), and fires in subalpine conifer forests typically do not burn deeply into mineral soil (60). After a fire, C stocks recover gradually as trees regenerate, and C storage is determined by the balance between C losses through decomposition and C gains through vegetation growth (52, 54, 61). Under historical fire regimes, forests recover their C long before burning again (e.g., 80% within 50 y and 90% within 100 y for subalpine forests in the Rocky Mountains) (54). Under projected future fire regimes, forests could reburn before C stocks are recovered (18), and fires could release even more C to the atmosphere if legacy wood is combusted (9, 59, 62). Effects on C stocks may be further compounded if tree regeneration is compromised such that postfire vegetation growth is reduced (63). Thus, short-interval fires may produce greater C losses to be recovered by a sparser forest (61, 64).

Opportunities to study effects of short-interval fires have been scarce. Strategically designed studies after natural disturbances—such as successive stand-replacing fires—can fill critical knowledge gaps, especially where long-term data are available (65–67) and confounding anthropogenic influences are minimal (68). Such "natural experiments" can yield timely insights into future forest dynamics (7, 22, 69) that inform stewardship of natural resources (31, 70), aid refinement of process-based models aiming to simulate novel future conditions (71, 72), and improve representation of vegetation dynamics in Earth system models (73–76). Recent fires in well-studied lodgepole pine (*Pinus contorta* var. *latifolia*) forests of Greater Yellowstone (Wyoming, United States) presented such an opportunity (*SI Appendix*, Movie S1).

Encompassing 80,000 km^2, Greater Yellowstone includes Yellowstone and Grand Teton National Parks and is one of the largest tracts of undeveloped land in the conterminous United States (77). This conifer-dominated landscape has long been shaped by fire. Large stand-replacing fires have occurred at 100- to 300-y intervals during warm, dry periods throughout the Holocene (78–82), and the biota are well adapted to such fires. Research after the large, severe 1988 Yellowstone fires documented remarkable forest resilience. The 1988 fires burned under extreme drought and high winds, primarily in forests that were >200 y old (39, 78), and the forests recovered rapidly (31, 83–91). Lodgepole pine recruitment was prolific but slightly reduced where FRI was <100 y and serotiny was prevalent (39). However, little area that burned in 1988 experienced the very short FRI (<30 y) projected for the mid- to late 21st century (18, 92, 93).

Fires in Greater Yellowstone that burned during summer 2016 created a natural experiment for evaluating effects of very short FRI on lodgepole pine forests. These fires included >18,000 ha of short-interval (16 and 28 y) fire ("reburns" hereafter), offering a preview of conditions likely to become more common (18, 93). Although forest responses will continue to unfold over time, early postfire measurements are critical to assess certain fire effects (63, 66). Burn severity and wood consumption cannot be measured reliably in later years, and tree seedling establishment after crown fires in lodgepole pine forests of Greater Yellowstone occurs almost entirely during the first year postfire (60) but shapes forest structure and function for centuries (54, 64, 89, 94, 95).

In this study, we asked whether short-interval stand-replacing fires can erode the resilience of subalpine lodgepole pine forests in Greater Yellowstone. We hypothesized that burn severity, early postfire tree regeneration, C stocks, and C recovery time would be markedly different relative to long-interval fire (Table 1). Field studies were conducted during summer 2017 at three sites where young postfire lodgepole pine forests had regenerated after fires in 1988 or 2000 (*SI Appendix*). At each site, we sampled nine 0.25-ha plots (six that reburned and three that did not reburn; $n=27$ total) (Table 2 and *SI Appendix*, Fig. S1). All reburned plots experienced stand-replacing fire (i.e., all trees and 100% of basal area were killed by the 2016 fires). Lodgepole pine density averaged 26,700 ± 7,300 stems ha^{-1} (range = 500–133,800 stems ha^{-1}) before the reburns (hereafter "prefire" within the reburned plots), typical of young postfire forests in Yellowstone (*SI Appendix*, Fig. S2), and stem density did not differ between plots that did or did not reburn (*SI Appendix*, *SI Text* and Table S1). We explored longer-term consequences of short-interval fire by using iLand, a process-based forest landscape model (96) recently parameterized for Greater Yellowstone (38, 97, 98). We simulated stand development and recovery of live, dead, and total aboveground C stocks for 150 y with and without the reburns and in the absence of additional confounding drivers (i.e., under historical climate and assuming no additional disturbance).

Results

Burn Severity. While all reburned plots experienced stand-replacing fire (per our study design), the short-interval fires included areas of more extreme burn severity than previously observed in Greater Yellowstone. Based on burn severity classes used for stand-replacing fire (60, 99), 3 plots were categorized as severe surface fire (Fig. 1*A*), and 15 were crown fire (Fig. 1*B*). However, four of the crown-fire plots burned with such complete biomass combustion (>95%) that we categorized them as crown fire plus (Fig. 1*C*), analogous to the definition of fourth-degree burns in the medical field in which the burned part is lost. A greater number and a greater proportion of stems were combusted when prefire trees were smaller (Fig. 2 and *SI Appendix*, Table S2). Where the proportion of stems combusted was >0.98 (crown fire plus plots), the prefire trees had been both densely packed (>47,000 stems ha^{-1}) and small (mean basal diameter was ≤4 cm) (Fig. 2*B*). Across all reburned plots, postfire stump density (charred stumps of trees alive at the time of the fire and for which the bole and branches were combusted entirely and absent) averaged 22,592 ± 844 stumps ha^{-1} (range = 33–106,467 stumps ha^{-1}), and the proportion of stems that were completely combusted averaged 0.41 ± 0.08 (range = 0.03–1.00).

Standard metrics of burn severity in the reburned plots were consistent with stand-replacing crown fire. Mean bole scorch was 98 ± 2%, proportion of tree height that was charred averaged 0.85 ± 0.06, and mean percentage cover of charred ground surface was 64 ± 6%. Metrics of burn severity increased as prefire tree density increased and mean basal diameter declined (*SI Appendix*, Table S2). As is typical for these forests, the shallow litter layer was largely combusted, and burning of soil was minimal. Ash depth averaged 7.4 ± 1.0 mm, and depth of soil char averaged 0.11 ± 0.06 mm among the reburned plots.

Postfire Tree Regeneration. First-year lodgepole pine seedlings were present in all reburned plots, but their density was much lower than the even-aged regeneration that followed the prior long-interval fire (*SI Appendix*, Table S3). Postfire lodgepole pine seedling density in the reburns averaged 6,450 ± 2,605 seedlings ha^{-1}, a sixfold reduction from mean prefire density (Fig. 3*A* and *SI Appendix*, Table S3). Postfire seedling density did not vary with bole scorch, proportion of tree height that was charred, percentage cover of charred surface, or measures of prefire stand structure. Furthermore, postfire seedling density did not vary with distance to or

Table 1. **Expectations related to indicators of forest resilience and evaluated after short-interval (<30-y) stand-replacing fires in lodgepole pine forests of Greater Yellowstone that are well adapted to historical long-interval (100- to 300-y) stand-replacing fires**

Response variable	Expectation with short-interval (<30-y) relative to long-interval (100- to 300-y) fire	Rationale
Burn severity	Typical of crown fires but increasing with density of young prefire lodgepole pines	Abundance and connectivity of canopy fuels increase with tree density, and dead surface fuels are abundant throughout the young forests (100)
Postfire tree regeneration	Reduced density of postfire lodgepole pine seedlings	Immaturity risk (36), as fires occur before trees have produced cones or built up a robust seed bank; increased exposure of cones to fire given the short stature of the trees (<3-m tall) (89) and proximity of the canopy to dead surface fuels (100)
Postfire tree regeneration	Increased relative abundance of aspens	Aspens that colonized from seed after the previous fire (42–44) can potentially resprout and thus, increase in relative abundance if conifer seedling density is substantially reduced (no mature aspen stands occurred in our study plots before the first or second fire)
Woody biomass and aboveground C stocks	Reduced coarse wood biomass and aboveground C stocks	A large volume of legacy-downed coarse wood (trees killed by the previous long-interval fires that have since fallen) was available to be burned
Recovery of aboveground C stocks	Delayed	C lost in the reburns as live trees and coarse wood are combusted will create a larger C debt and thus, delay recovery to C stocks typical of mature forests (54, 60)

height of the nearest unburned forest ($P > 0.20$). Variation in postfire lodgepole pine seedling density was explained only by a positive correlation with the density of cones remaining on fire-killed trees after the reburn ($r = 0.62$, $P = 0.0059$) (Fig. 4).

Dense young lodgepole pine stands were converted to sparse stands by short-interval fire, whereas sparse stands regenerated as sparse stands. Mean relative change in lodgepole pine density (from prefire stems to postfire seedlings) was −52% (*SI Appendix*, Table S3), and it was negatively correlated with prefire stem density ($r = -0.73$, $P = 0.0006$). Relative change in density varied with fire severity class ($r^2 = 0.66$, $P = 0.0003$). Density declined sharply in areas of crown fire and crown fire plus (−71 and −95%, respectively) and increased but remained sparse in areas of severe surface fire (+71.1%) that were sparsely treed in 2016.

Aspens were a minor component of these forests before and after the reburn. Prefire aspen density averaged 102 ± 38 stems ha^{-1} within the reburned plots, representing merely 1.4 ± 0.7% of the stems. Aspen density in nearby plots that did not reburn was higher (mean = 352 ± 138 stems ha^{-1}) than our reconstructions based on postfire stumps in the reburned plots, suggesting that over one-half of the young prefire aspens may have been killed by the 2016 fire. Postfire aspen stumps that resprouted in 2017 averaged 59 ± 25 stems ha^{-1} (Fig. 3*B*), representing 2.9 ± 1.2% of postfire stems.

Woody Biomass and Aboveground C Stocks.

Legacy downed coarse wood. Percentage cover of coarse wood in reburns was about one-half of what was measured in plots that did not reburn (7.3 vs. 15.5%, respectively) (Fig. 3*C*) and did not vary by site (*SI Appendix*, Table S4). Percentage cover of ghost

Table 2. **Prefire characteristics of young lodgepole pine forests that regenerated after fires in 2000 or 1988 and that did or did not reburn during 2016**

	Berry-Glade (16-y FRI)		Berry-Huck (28-y FRI)		Maple-North Fork (28-y FRI)	
Prefire attribute	Not reburned	Reburned	Not reburned	Reburned	Not reburned	Reburned
Stand structure and biomass						
Lodgepole pine density (stems ha^{-1})	21,267 (14,533)	18,833 (7,765)	6,655 (1,840)	13,539 (4,169)	63,189 (35,359)	76,511 (14,176)
Mean tree basal diameter (cm)	6.0 (1.2)	5.0 (0.7)	9.7 (1.3)	8.6 (1.5)	6.4 (1.2)	3.5 (0.6)
Lodgepole pine biomass (Mg ha^{-1})						
Foliage biomass	5.6 (1.9)	4.5 (1.6)	12.8 (2.3)	12.8 (1.7)	23.7 (2.9)	9.2 (1.0)
Bole biomass	17.3 (7.0)	14.0 (4.9)	30.6 (3.9)	33.3 (4.5)	68.1 (2.9)	31.8 (2.8)
Branch biomass	2.8 (0.8)	2.2 (0.8)	9.6 (2.4)	8.4 (1.3)	13.4 (3.8)	3.7 (0.7)
Total aboveground biomass	26.0 (9.7)	21.1 (7.4)	52.8 (8.2)	54.9 (7.2)	106.6 (8.5)	45.2 (4.5)
Aspen density (stems ha^{-1})	844 (174)	244 (75)	211 (78)	55 (55)	0 (0)	6 (6)
Cone supply						
Cone abundance (10^3 cones ha^{-1})	15.1 (83.9)	NA	12.9 (16.1)	NA	55.5 (35.4)	NA
Proportion of trees with one or more serotinous cones	0.06 (0.03)	NA	0.08 (0.04)	NA	0.20 (0)	NA
Downed coarse wood (>7.5 cm)						
Coarse wood cover (%)	14.7 (2.6)	11.5 (2.0)	16.6 (3.2)	11.6 (1.1)	15.3 (2.8)	11.1 (2.8)
Coarse wood volume (m^3 ha^{-1})	187.7 (29.8)	NA	294.2 (15.0)	NA	172.8 (27.2)	NA
Coarse wood biomass (Mg ha^{-1})	69.3 (10.1)	NA	109.0 (7.9)	NA	67.5 (11.0)	NA

For plots that did not reburn, $n = 3$; for reburned plots, $n = 6$. Values are mean (SE). NA, not applicable, as values could not be estimated within plots that reburned.

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A Severe-surface fire (n = 3)	Mean (SE)
Percent cover (%)	
Charred surface	33 (3)
Mineral soil	23 (8)
Live vegetation	29 (7)
Ghost logs	3 (1)
Proportion tree height charred	0.41 (0.11)
Proportion stems combusted	0.19 (0.10)

B Crown fire (n = 11)	Mean (SE)
Percent cover (%)	
Charred surface	61 (6)
Mineral soil	22 (5)
Live vegetation	29 (6)
Ghost logs	4 (1)
Proportion tree height charred	0.91 (0.04)
Proportion stems combusted	0.26 (0.05)

C Crown fire plus (n = 4)	Mean (SE)
Percent cover (%)	
Charred material	97 (1)
Mineral soil	47 (8)
Live vegetation	1 (0)
Ghost logs	6 (3)
Proportion tree height charred	1.00 (0.00)
Proportion stems combusted	0.99 (0.01)

Fig. 1. Short-interval stand-replacing fires (i.e., reburns) included areas of (*A*) severe surface fire, in which brown needles are still visible on fire-killed trees; (*B*) crown fire, in which needles were consumed in the fire; and (*C*) crown fire plus, in which combustion of stems, branches, and downed wood was nearly complete.

logs (logs that had been on the ground and were combusted in the fire) (visible in Fig. 1*C*) averaged 4.1 ± 0.8% in the reburns. Coarse wood volume and biomass varied among sites and between plots that did or did not reburn, with most variation due to burn status and no interaction with site (*SI Appendix*, Table S4). Coarse wood volume and biomass in reburns were less than one-half of those measured in nearby plots that did not reburn (volume: 92 vs. 218 $m^3\ ha^{-1}$, respectively; biomass: 29 vs. 82 Mg ha^{-1}, respectively) (Fig. 3*D*). Thus, about 58% of legacy coarse wood volume (126 $m^3\ ha^{-1}$) and 65% of coarse wood biomass (53 Mg ha^{-1}) were combusted during the short-interval fires. Nearly all wood was combusted in crown fire plus.

Aboveground C stocks. Reconstructed prefire aboveground C stocks averaged 59 ± 3.8 Mg C ha^{-1} across the reburned plots, including 40 ± 2.3 Mg C ha^{-1} in downed coarse wood and 19 ± 2.4 Mg C ha^{-1} in live lodgepole pine biomass (foliage, boles, and branches) (Fig. 5). After the reburn, aboveground C stocks averaged 24 ± 4.2 Mg C ha^{-1} (an average 62% loss of prefire aboveground C stocks) (*SI Appendix*, Table S3), with 15 ± 2.5 Mg C ha^{-1} remaining in downed coarse wood, 9.5 ± 2 Mg C ha^{-1} in standing fire-killed trees, assuming no bole or branch loss and no live tree C (Fig. 5). Relative losses of aboveground C varied from 32 to 96% among reburned plots (*SI Appendix*, Table S3) and were greater where lodgepole pines were smaller in diameter (correlation with mean tree basal diameter, r = –0.5, P = 0.0364). The absolute amount of C loss was unrelated to prefire stand density or biomass, but nearly all (92%) of aboveground C was lost in crown fire plus (Fig. 1*C* and *SI Appendix*, Table S4).

Simulated Recovery of Aboveground C Stocks. Short-interval fire alone delayed recovery of aboveground C stocks in simulated lodgepole pine stands by >150 y (Fig. 6). If the young forests had not reburned, aboveground C stocks would have recovered to the expected long-term average of 150 Mg C ha^{-1} well within 100 y assuming historical climate and no additional disturbance (Fig. 6). Accrual of aboveground C stocks after fire results from rapid tree growth and gradual recruitment of dead wood. With reburns, live tree C did recover within 60 y. However, dead wood C never reached prefire levels, and total aboveground C stocks never converged between stands that did and did not reburn (Fig. 6).

Discussion

Short-interval stand-replacing fires in lodgepole pine forests of Greater Yellowstone led to substantial losses of material legacies and likely will delay recovery of aboveground C stocks by >150 y. These results portend profound changes in the structure and

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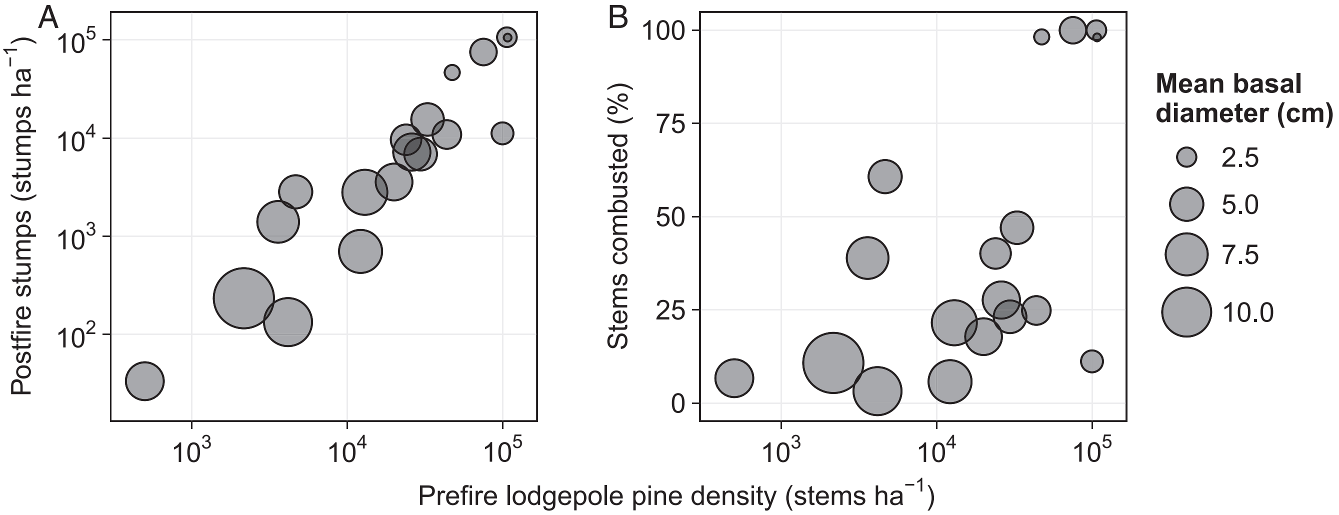

Fig. 2. Relationship between (*A*) postfire lodgepole pine stump density and (*B*) percentage of prefire lodgepole pine stems that were combusted in the 2016 short-interval fires vs. prefire density of lodgepole pines that regenerated after the 1988 or 2000 fires. Mean basal diameter of prefire lodgepole pines in each reburned plot (n = 18) is depicted by size of the bubble.

function of lodgepole pine forests in Greater Yellowstone if short-interval fires become more common. The 2016 fires clearly demonstrated that the short-interval high-severity fires implied by earlier projections based on statistical relationships between climate and fire (18) and supported by fuels data (100, 101) and regional analyses (102) are plausible. Disruptions of the disturbance–recovery cycle that transform forest structure and function are also likely to influence recovery from future disturbances.

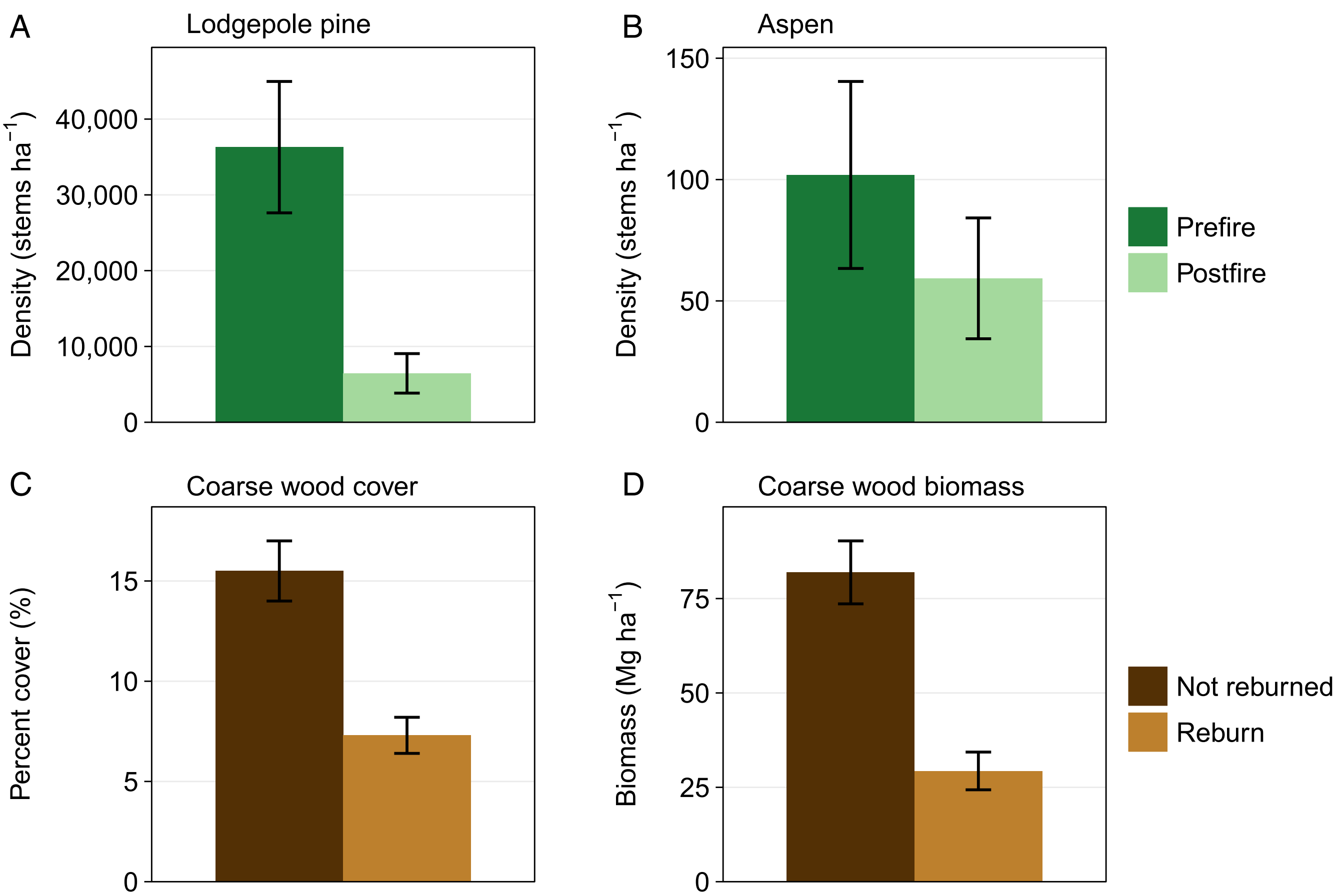

Fig. 3. (*A*) Prefire lodgepole pines and postfire first-year lodgepole pine seedlings in plots that reburned (n = 18). (*B*) Prefire aspens and postfire aspens that resprouted in plots that reburned (n = 18). (*C*) Surface cover of downed coarse wood (>7.5-cm diameter) in young stands that reburned (n = 18) and did not reburn (n = 9). (*D*) Biomass of downed coarse wood in young stands that reburned (n = 18) and did not reburn (n = 9). Error bars are ±1 SE.

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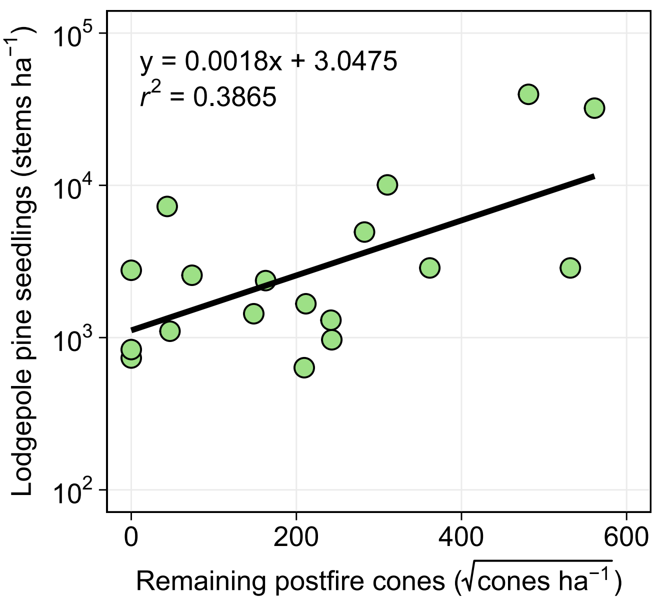

Fig. 4. Relationship between the density of first-year postfire lodgepole pine seedlings and the density of cones remaining on fire-killed trees within plots that had reburned (n = 18). Cones were primarily nonserotinous and charred but not combusted.

Burn Severity. Burn severity increased with lodgepole pine density as expected. Nonetheless, the areas of crown fire plus were surprising, as we had not observed this previously in Greater Yellowstone, even where young forests had reburned (e.g., 29-y FRI in the 2009 Bearpaw Fire and 24-y FRI in the 2012 Cygnet Fire). Lodgepole pines in our high-density stands were small (≤4-cm basal diameter), with a greater stem surface area to volume ratio than larger trees, and more combustible. Similar extreme burn severities were recorded in field notes after historical short-interval fires in the northern Rockies (e.g., portions of a 1910 fire in the Coeur d'Alene National Forest in Idaho "burned up all the trees" in an area burned 40 y prior) (103). Although it was likely rare historically, crown fire plus may become more common during the 21st century as fire frequency increases.

The conditions that produce areas of crown fire plus are not well understood, and we surmise that extreme burn severity resulted from an interaction of fuels and local fire weather or fire behavior. Burn severities were consistent with the potential for high-intensity fire when surface and canopy fuels are abundant and proximal to each other in young conifer stands (100, 101). The dense low-stature canopy conditions also reduce the wind speeds required for crown fire initiation and spread (101, 104). An extended period of smoldering combustion after passage of the main fire front also could have produced the areas of crown fire plus. Downed coarse wood was also abundant in all plots, which may promote ongoing combustion when weather is warm and dry (105). Finally, self-reinforcing internal dynamics of the fire (e.g., fire-induced winds that equal or exceed ambient winds) (106) also could have contributed. How weather and fuel profiles interact in young forests needs additional study. Crown fire plus was observed only in areas of high tree density, but not all high-density forests burned as crown fire plus.

Postfire Tree Regeneration. The substantial reduction in initial postfire recruitment of lodgepole pines in the reburns compared with the prior long-interval fires is consistent with immaturity risk and suggests that seed supply was the primary driver of recruitment density. The young stands that reburned were reproductively mature, and some trees had produced at least one serotinous cone prefire (Table 1). However, the prefire stands lacked the robust canopy seedbank that develops over 40–70 y (39), and in crown fire plus, there was complete loss of any in situ seed supply. Other studies have reported reduced postfire tree establishment for serotinous (36, 107) and semiserotinous conifers (40, 108) after similar short-interval severe fires, and the magnitude of reduction has varied widely. Reduced tree regeneration may result in a smaller canopy seedbank going forward (108), which could further reduce regeneration if another fire was to occur in <30 y (109). However, this feedback could be partially offset if trees in sparse stands grow faster and produce more cones per tree. Effects of short-interval fires on tree species that mature later (e.g., *Abies lasiocarpa*, *Picea engelmannii*, *Pseudotsuga menziesii*) would be even more severe (37). Establishment in reburns would then be limited by distance to unburned seed sources (110), but even the nearby seed supply may be scant for decades if the surrounding unburned forest is also young.

The fate of resprouting aspens after these short-interval fires is unclear. Seedling aspens grow slowly in Greater Yellowstone (43), largely because of competition with lodgepole pine (44), but resprouts can grow fast and even dominate early postfire succession (111–113). Our data suggest that up to two-thirds of the initial cohort of seedling aspens that established after the first fire were killed by the reburn, similar to effects on fire-tolerant *Eucalyptus puaciflora* in subalpine forests of Australia (114). Aspens also increased relative to conifers in boreal forests that reburned within 25 y of age (115). Surviving aspens could potentially increase in local dominance, as some reprouts were 1 m tall 2 y after the reburn.

Our data only quantified first-year tree regeneration, and long-term study is needed to ascertain the fates of the reburned stands. Postfire forest resilience could be further eroded if seedling survival or growth is limited by projected hotter, drier climate conditions (38, 116, 117) or competition with understory vegetation (e.g., *Calamagrostis rubescens* or *Calamagrostis canadensis*), which resprouted robustly in some of the reburns. Alternatively, although most lodgepole pine regeneration in these forests occurs during the first year or two, sparse stands should infill as initial recruits mature (95, 118) or aspens increase in density (44) as climate allows. Warmer temperatures and increased atmospheric CO_2 concentrations could also lead to increased rates of tree productivity in some locations (64, 119).

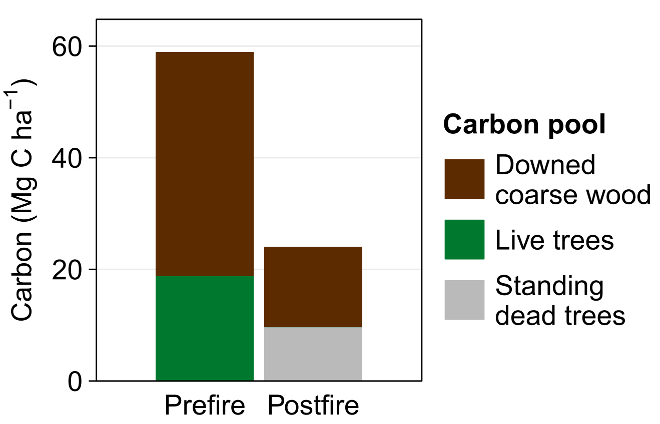

Fig. 5. Estimated aboveground C stocks in young lodgepole pine stands (n = 18) with and without short-interval (<30 y) fire. Prefire live C pool was reconstructed from estimates of prefire tree density, basal diameter, and site-specific allometric equations. Prefire dead C pool was estimated from nearby similar stands (n = 9) that did not reburn. Postfire C pools were calculated from field measurements in the reburned stands (n = 18). *SI Appendix*, Table S3 has additional details.

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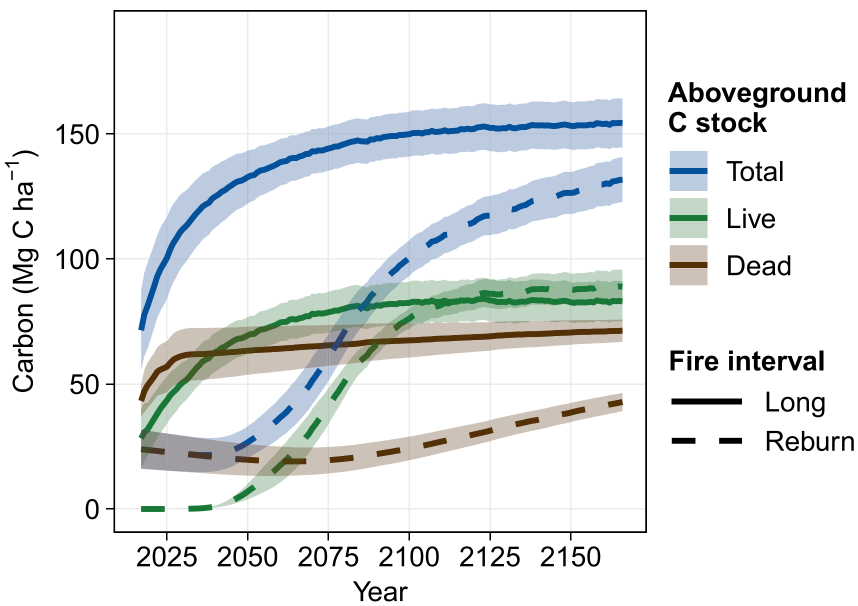

Fig. 6. Trajectories of live, dead, and total aboveground C stocks simulated for 150 y using iLand. Stand development of each plot sampled in this study (n = 18) was simulated for 150 y with (dashed line) and without (solid line) the 2016 reburn (assumed uninterrupted recovery from the prior long-interval fire). Lines are annual among-plot means (n = 18); shading indicates 95% confidence intervals around each line.

Understanding how multiple interacting drivers will shape stand development in the decades ahead is a critical research priority (8).

Woody Biomass and Aboveground C Stocks. We expected losses of woody biomass and C stocks with short-interval fire, but the magnitude of these losses was surprisingly high. Other studies in western US forests found reductions in woody surface fuels associated with reburns ranging from 15 (120) to 45% (59) compared with single burns. The large losses that we observed (>60%) were similar to reburns in boreal black spruce (*P. mariana*) forests (62), which are also short in stature. Short fire intervals also leave a lasting influence on dead wood; a near halving of dead wood mass in reburned stands in the Biscuit Fire (Oregon, United States) was expected to persist for at least 50 y until recruitment of new material begins, and to remain low for over a century (59). In Greater Yellowstone, effects on dead wood are likely to persist for over 150 y with cascading influences on wildlife habitat (121) and ecosystem processes, such as decomposition and nitrogen cycling (122, 123).

Replacement biomass is critical to sustaining ecosystem C stocks after stand-replacing fire, but the fire interval must equal or exceed the time required to recover C losses (53, 61, 63, 124, 125). Earlier simulation studies using the Century model found that the 1988 Yellowstone fires reduced total C stocks in lodgepole pine forests by only 12% from prefire levels, and 85% of that C was recovered in 100 y (124). FRIs < 90 y initiated a long-term decline in simulated total C stocks, and 30-y FRI reduced total ecosystem C stocks by 66% (124). Our field data are consistent with such declines, and our simulations reveal lengthy time lags for C stocks to rebuild. Repeated reburns could further reduce material legacies and ecological memory (22, 67), initiating a downward ratchet until trees do not regenerate and forest C stocks cannot recover (19, 23, 109).

Implications for Forest Resilience. Theoretical studies suggest that systems will recover more slowly from disturbance as they approach a critical transition (126–129). Our data demonstrate that postfire tree regeneration and rates of C recovery slowed with short-interval fire and could serve as early indicators of an erosion of forest resilience. Future ecosystem state is hard to predict when legacies are eliminated over large areas (130, 131), and increased extent of unusually high disturbance severity—such as crown fire plus—in which material and information legacies are lost could increase the likelihood of abrupt ecological change (22, 23, 109). Other drivers that reduce tree seedling survival, such as drought or competition, also could amplify the effects of a changing disturbance regime (107, 117, 118, 132, 133). However, negative feedbacks could develop between vegetation and fire that attenuate the effects of future fire (10). Although high-severity fire often begets high-severity fire, because live fuels recover quickly (100, 102, 134), conversion of dense stands to sparse stands or nonforest could alter fire spread or reduce burn severity. The absence of downed coarse wood for many decades also could deprive future fires of the fuels needed for extended periods of combustion, which may be a key factor in producing areas of crown fire plus. Our study underscores the need to understand mechanisms underpinning forest resilience and how feedbacks will evolve over time (69).

Future forest dynamics may diverge considerably from benchmarks of the past as climate and fire regimes continue to change (*SI Appendix*, Movie S1). Of course, consequences for forest landscapes will depend on the frequency, size, severity, and pattern of future fires and the suite of factors that control recovery. The recent short-interval fires in Greater Yellowstone did not transform the landscape, but they suggest that profound changes in forest structure and function are likely if short-interval fires become more common in a warmer world with more fire.

Materials and Methods

Study Area. We studied two fires in Greater Yellowstone (*SI Appendix*) that burned in subalpine forests during summer 2016 (*SI Appendix*, Fig. S1) and encompassed areas that we have studied previously (54, 83–92, 100). The Berry Fire in Grand Teton National Park began on July 27, 2016 and burned through mid-September, eventually encompassing ~8,500 ha. The Berry Fire reburned 28-y-old lodgepole pines that regenerated after the 1988 Huck Fire (90) and 16-y-old lodgepole pines that regenerated after the 2000 Glade Fire (86). The Maple Fire in Yellowstone National Park was reported on August 8, 2016 burning in dense 28-y-old lodgepole pine forests that had regenerated after the 1988 North Fork Fire (83, 84, 89). The Maple Fire continued burning through late October and encompassed ~21,000 ha. All of these burned forests were dominated by lodgepole pine. Small aspens that

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had established from seed after either the 1988 or the 2000 fire were also intermixed with the young conifers (42–44).

We established nine 0.25-ha (50 × 50-m) study plots at each of three sites (*SI Appendix*, Fig. S1). Two sites were in the Berry Fire [Berry-Glade (16-y FRI) and Berry-Huck (28-y FRI)], and one was in the Maple-North Fork (28-y FRI). At each site, six plots were established in areas of stand-replacing fire (i.e., all trees were killed). Because some variables (e.g., volume and mass of downed coarse wood, cone density, presence of serotinous cones, and density of aspens) could not be reconstructed with confidence in reburned plots, three plots were established in nearby young forests that did not reburn in 2016. In each reburned plot ($n = 18$), we measured prefire stand structure, burn severity, postfire tree regeneration, and downed coarse wood following protocols from our previous studies (14, 85, 89). In each plot that did not reburn ($n = 9$), we measured stand structure and downed coarse wood using the same procedures. Locations of each plot center (coordinates in Universal Transverse Mercator North American Datum 83 Zone 12N) and elevation were recorded with a GPS unit; plots were selected to have minimal slope and aspect (to avoid potential confounding effects), but both were measured in each plot.

Field Sampling. To quantify prefire stand structure and postfire tree regeneration, we tallied all prefire trees (live and fire killed) by species and all postfire tree seedlings and aspens (all of which were resprouts) in three 50 × 2-m belt transects in each plot (85, 86, 89). Transects were oriented to the north and generally separated by 25 m. However, in two plots in the Berry-Huck site, transects were separated by 15 m because of the configuration of reburned forest patches. Because prefire trees were fully combusted in some reburned plots (Fig. 1*C*), estimates of prefire tree density included burned stumps of lodgepole pines and aspens that were alive before the fire. At 5-m intervals along each transect, we located the nearest lodgepole pine and recorded its basal diameter (diameter at breast height if height > 1.4 m) and the number of cones present ($n = 25$ trees per plot). In plots that did not reburn, we also identified serotinous cones by their age (>3 y) and morphology (asymmetrical shape, acute angle of branch attachment, tightly closed, and weathered gray color) as in prior studies (39, 83, 87, 135). We computed the percentage of trees with cones, the percentage of trees with serotinous cones, and stand-level cone abundance (mean cones per stem × stem density).

Burn severity was quantified within a centrally located circular subplot of 30-m diameter following standard protocols (14). We measured the number and proportion of trees fully combusted; char height (meters), bole scorch (percentage of circumference), and fine branch consumption on dominant prefire live trees; ground cover (e.g., vegetation, mineral soil, litter, and charred material); depth of soil O horizon; and depth of soil charring.

The percentage cover, volume, and mass of downed coarse wood (>7.5-cm diameter) were quantified in each plot by sampling three 31.25-m Brown's transects per plot (136) oriented at azimuths of 0°, 120°, and 240° to avoid potential sample bias from nonrandom orientation of logs. In reburned plots only, we estimated percentage cover of "ghost logs" (log shadows indicating where downed wood had been consumed by the fire) by using the line intercept measurements along each Brown's transect.

Biomass and C Stock Calculations. Because most aboveground C is in the live trees and dead wood (54), we computed biomass and C stocks for these pools only. Foliage, bole, branch, and total aboveground live lodgepole pine biomass were estimated for each measured lodgepole pine by using allometric equations developed from destructive sampling of 60 24-y-old lodgepole pines within our study area (89, 137). Basal diameter was used to predict each response, and the models performed well (137). We multiplied biomass of the median tree in each plot by stem density to predict stand-level lodgepole pine aboveground biomass (megagrams hectare^{-1}) (54, 84, 89).

C stocks were estimated by applying empirically measured C content to foliage, live wood, and dead wood biomass pools (54). Because coarse wood biomass could not be reconstructed on reburned plots, we assumed that the mean coarse wood biomass at the three plots at each site that did not reburn represented the prefire values for the six reburned plots at each site. This is a reasonable assumption, because the 1988 and 2000 fires burned through mature lodgepole pine forests >150 y old, at which time stand density and biomass have generally converged (54, 94) and nearly all trees killed by the earlier fire had fallen (*SI Appendix* has more information). C losses were estimated by differences between prefire reconstructed C stocks and field measurements after the reburn.

Data Analysis. All data were analyzed at the plot level (138). Mean values are presented with one SE. All variables were tested for normality before analysis and transformed if necessary. Lodgepole pine densities (stems, stumps, and seedlings) were $\log_{10}$ transformed, cone density was square root transformed, and proportion data were arcsine square root transformed. Two-way ANOVA was used to test for differences in prefire stand structure among sites and between plots that did and did not reburn. Linear regression was used to assess relationships between response variables (burn severity, postreburn regeneration density) and prefire stand structure (lodgepole pine density, basal diameter, cone density, aboveground biomass). Predictor variables that were highly correlated ($|r| > 0.7$; e.g., lodgepole pine density and basal diameter) were not included in the same model, and the predictor with the strongest univariate correlation with the response variable was included. Model selection based on Akaike Information Criterion (AIC) was performed to identify models that were equally supported by the data (Δ AIC ≤ 2), and then, a top model was chosen based on parsimony (fewer variables) and adjusted r^2. Analyses were conducted in SAS version 9.4 (139).

Simulation Modeling. To explore longer-term consequences of short-interval fires on subsequent recovery of C stocks, we used the process-based forest simulation model iLand (96) to model aboveground live and dead lodgepole pine C stocks. iLand is an individual-based model that has been parameterized and performs well for the dominant conifer species in Greater Yellowstone (38, 97, 98). We used iLand to simulate development of stands (1 ha) of serotinous lodgepole pine, initializing each of the 18 reburned plots with (*i*) reconstructed prefire stand structure and downed coarse wood estimates, representing conditions had these areas not reburned, and (*ii*) postfire tree regeneration density, snag density, standing wood biomass, and coarse wood biomass (*SI Appendix*, Table S5 has initial conditions and drivers). Because prefire downed coarse wood biomass could not be directly measured in the reburned plots, we used the mean from the three plots at each site that did not reburn. Each 1-ha stand was simulated with and without the reburn for 150 y under historical climate (1980–2017) (140) without additional disturbance. Trees, saplings, and seedlings within a stand served as the only seed supply for subsequent regeneration, but stands infill readily, because lodgepole pines produce cones at young age (87, 141). Annual climate was drawn at random with replacement. Replicates ($n = 20$) were run for each simulation, and results were averaged by plot to avoid bias due to a particular climate sequence. Aboveground C dynamics (live tree C, standing dead snag C, and downed wood C) were then compared with and without the 2016 reburn and also compared among plots of different burn severity. We considered the stand to have recovered its aboveground C stock (live plus dead tree C) when it reached 150 Mg C ha^{-1} based on chronosequence data in this system (54).

ACKNOWLEDGMENTS. We thank the following people for their effort throughout our summer 2017 field season: Jacob Gold, Tyler Hoecker, Shauna Jacobs, Alexandra Orrego, Tanjona Ramiadantsoa, Saba Saberi, and Deirdre Turner. We also thank Diane Abendroth, Nathan Gill, Ann Olsson, Zak Ratajczak, Bill Romme, and Ron Steffens for assistance in the field and Bill Romme and Dan Donato for insightful discussions. We thank Michael Dillon and the University of Wyoming–National Park Service Research Station staff for logistical support and Yellowstone and Grand Teton National Parks for facilitating this study. Constructive comments from Dan Donato and Rupert Seidl improved this manuscript. Field sampling was conducted under National Park Service Research Permits YELL-2017-SCI-5238 and GRTE-2017-SCI-0021. Research was funded by NSF Grant DEB-1719905 and Joint Fire Science Program 16-3-01-4. M.G.T. acknowledges support from the University of Wisconsin–Madison Vilas Trust and the UW2020 initiative of the Wisconsin Alumni Research Foundation. W.D.H. acknowledges support from the Earth Institute at Columbia University and Columbia University's Center for Climate and Life.

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