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Sparse subalpine forest recovery pathways, plant communities, and carbon stocks 34 years after stand-replacing fire

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Abstract

Changing global climate and wildfire regimes are threatening forest resilience (i.e., the ability to recover from disturbance). Yet distinguishing areas of "no" versus "slow" postfire forest recovery is challenging, and consequences of sparse tree regeneration for plant communities and carbon dynamics are uncertain. We studied previously forested areas where tree regeneration remained sparse 34 years after the large, stand-replacing 1988 Yellowstone fires (Wyoming, USA) to ask the following questions: (1) What are the recovery pathways in areas of sparse and reduced forest recovery and how are they distributed across the landscape? (2) What explains variation in postfire tree regeneration density (total and by species) among sparse recovery pathways? (3) What are the implications of sparse recovery for understory plant communities? (4) How diminished are aboveground carbon stocks in areas of sparse postfire forest recovery? Tree densities and species-specific age distributions, understory plant communities, and carbon stocks were sampled in 55 plots during summer 2022. We detected three qualitatively distinct sparse recovery pathways (persistent sparse or non-forest, continuous tree infilling, and recent seedling and sapling establishment). Nearly half of the plots appeared "locked in" as persistently sparse or non-forest, while the remaining may be on a slow path to forest recovery. Plots with nearby upwind seed sources as well as in situ seed pressure from young postfire trees appear likely to recover to forest. Where trees were sparse or absent, plant communities resembled those found in meadows, capturing compositional changes expected to become more common with continued forest loss. However, forest-affinity species persisted in mesic locations, indicating mismatches between some plant communities and future forest change. Aboveground carbon stocks were low owing to minimal tree reestablishment. Almost all (96%) carbon was stored in coarse wood, a sharp departure from C storage patterns where forests are recovering. If not offset by future tree regeneration, decomposition of dead biomass will protract postfire aboveground carbon stock recovery. As global disturbance regimes

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and climate continue to change, determining the drivers of ecosystem reorganization and understanding how such changes will cascade to influence ecosystem structure and function will be increasingly important.

KEYWORDS
forest conversion, high-severity wildfire, lodgepole pine, resilience, subalpine fir, succession, whitebark pine, Yellowstone National Park

INTRODUCTION

Forest ecosystems, which make up 30% of the global land area (FAO, 2020) and sequester and store large amounts of carbon (C; Harris et al., 2021; Pan et al., 2011), are in a state of flux in many areas (McDowell et al., 2020). Anthropogenic climate change and novel disturbance regimes threaten forest resilience (Forzieri et al., 2022; Johnstone et al., 2016; Turner, 2010; Turner & Seidl, 2023), that is, the ability of a forest ecosystem to recover its structure and function after disturbance (Holling, 1973). With continued changes in climate and disturbance regimes (IPCC, 2023; Seidl et al., 2017), forest reorganization and regime shifts are increasingly likely (Falk et al., 2022; Millar & Stephenson, 2015; Seidl & Turner, 2022). However, if intrinsic post-disturbance forest recovery dynamics are slow, it may take decades to detect regime shifts and distinguish those from areas where forests may yet recover, with long-term trajectories uncertain (Coop et al., 2020). Studying successional pathways where previously closed-canopy forests have not recovered several decades after contemporary disturbances may indicate potentially eroded resilience and provide insight into the consequences of such future forest change.

Post-disturbance successional pathways and rates of forest recovery depend on ecological legacies, priority effects, and historical contingencies (Fukami, 2015; Johnstone et al., 2016; Meiners et al., 2015). For example, boreal forest composition after stand-replacing wildfire varies with the amount of soil organic layer combustion (Baltzer et al., 2021; Johnstone et al., 2010). Ex situ seed source distance, spatial arrangement, and species identity similarly influence forest recovery pathways (Downing et al., 2019; Peeler & Smithwick, 2020; Walker et al., 2023; Wu et al., 2020), as do in situ seed banks (Diaz-Perea et al., 2014; Keeley et al., 1999), topo-edaphic and climatic conditions (Anderson-Teixeira et al., 2013; Hadley, 1994; Herault & Piponiot, 2018), and disturbance history (Cole et al., 2014; Gauthier et al., 1996; Iglesias & Whitlock, 2020). Succession and recovery may be especially slow where disturbance patches are large and biotic dispersal rates are slow (sensu van de Leemput et al., 2018), such as in large patches of high-severity wildfire where fire-sensitive, obligate-seeding tree species dominate (Peet, 1981; Stahelin, 1943). Priority effects and nucleation processes may dictate pathways of recovery where biotic residuals are reduced and ex situ seed sources are far (Johnstone et al., 2016; Turner et al., 1998), leading to variable forest recovery pathways that can persist for decades to centuries (Braziunas et al., 2018; Buma & Wessman, 2011; Harvey & Holzman, 2014). If components of a disturbance regime fall within the historical range of variability (e.g., fire-return interval [FRI]; Kashian et al., 2005; Turner et al., 2016), convergence of initially disparate forest structure and function is still possible. However, the emergence of novel disturbance regime characteristics, such as size, frequency, and severity, are making this increasingly unlikely (Turner & Seidl, 2023).

Regime shifts from forest to sparse or non-forest are becoming more common as wildfire activity, an important disturbance agent of forests globally (Bowman et al., 2020; van Wees et al., 2021), increases with a warmer, drier climate. Larger burn patches (Dennison et al., 2014; Wang et al., 2022), greater area burned as stand-replacing fire (Collins et al., 2021; Parks & Abatzoglou, 2020; Tran et al., 2020), more frequent fire (Burrell et al., 2022; Sharples et al., 2016; Whitman et al., 2019), and longer fire seasons (Fill et al., 2019; Pimont et al., 2023; Westerling, 2016) are all linked to anthropogenic climate change (Abatzoglou & Williams, 2016; Duane et al., 2021). Increased fuel loads also play a key role in dry conifer forests adapted historically to frequent, low-severity fire (Agee & Skinner, 2005; Steel et al., 2015), but extreme fire weather driven by climate is more important in subalpine and boreal forests where fuels are seldom limiting (Bessie & Johnson, 1995; Harvey et al., 2016a). In western North America, recent sparse postfire tree regeneration has been attributed to hot and dry postfire climate (Crockett & Hurteau, 2023; Hankin et al., 2019; Stewart et al., 2021), lack of nearby ex situ seed sources (Gill et al., 2021; Harvey et al., 2016b; Rother & Veblen, 2016; Urza & Sibold, 2017), and reduced in situ canopy seed banks (Agne et al., 2022; Braziunas et al., 2023; Whitman et al., 2019). With continued climate warming and increasing fire size, postfire forest conversion is of growing concern (Coop et al., 2020; Stevens-Rumann et al., 2022) and extensive areas of forest may convert to

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sparse or non-forest by century's end (Rammer et al., 2021; Serra-Diaz et al., 2018; Tarancon et al., 2014). Detecting eroded resilience and potential conversion is a critical first step, but methods for distinguishing persistent forest conversion from slow forest recovery are absent, and effects of conversion on plant communities and ecosystem function remain largely unexplored.

While most current studies emphasize the trees (e.g., Coop et al., 2020; Stevens-Rumann et al., 2022), regeneration failure will have cascading effects on ground-layer vegetation (i.e., forbs, graminoids, and shrubs), which harbors the vast majority of temperate forest plant diversity (Gilliam, 2007). Plant community richness, diversity, and cover often increase soon after stand-replacing disturbances like wildfire (Hart & Chen, 2006; Swanson et al., 2011). Postfire communities typically include perennial species establishing from soil seed banks or resprouting from surviving roots and rhizomes as well as disturbance-affinity annuals and ruderals establishing from seed (Abella & Fornwalt, 2015; Archibold, 1979; Grime, 1977; Turner et al., 1997). Cover and diversity then decline with succession and forest recovery (Chipman & Johnson, 2002; De Grandpré et al., 1993; Romme et al., 2016) but may remain high in areas of sparse postfire tree regeneration and protracted canopy closure (Andrade et al., 2021; Coop et al., 2010). This dense layer of ground vegetation, including clump-forming graminoids and tall shrubs, competes with tree seedlings for resources (Decocq et al., 2004; North et al., 2019; Ridding et al., 2020; Stahelin, 1943) and may preclude subsequent forest recovery. Community composition in high-light environments may shift toward more species adapted to warmer, drier conditions (i.e., thermophilization; De Frenne et al., 2015; Stevens et al., 2015) and species common to open meadows, shrubland, and steppe (Coop et al., 2016; Guiterman et al., 2018; Savage & Mast, 2005). Current plant community dynamics where postfire tree regeneration is sparse may offer insight into the effects of widespread forest conversion, with understory communities as potentially important early indicators of change.

A shift to sparse or non-forest following fire may similarly influence ecosystem services such as C storage. Global forest C stocks account for ~67% of the total CO_2 sequestered by terrestrial ecosystems (Gower, 2003) and are integral to offsetting anthropogenic C inputs to the atmosphere (Running, 2008). In temperate and boreal forest ecosystems like those in western North America, stand-replacing wildfires temporarily reduce aboveground C by combusting live and dead biomass and increasing the amount of dead wood available for decomposition (Chapin III et al., 2006; Dore et al., 2008, 2012). These areas typically recover aboveground C within the fire-free interval as trees reestablish, aboveground biomass accumulates, and mineral soil C stocks remain stable (Kashian et al., 2006; Rothstein et al., 2004; Seedre et al., 2011). However, disruption of the disturbance-recovery cycle can prevent recovery of C stocks lost to combustion, with sparse postfire tree regeneration or forest conversion to non-forest reducing aboveground C stocks (Bowman et al., 2021; Kashian et al., 2006; Yang et al., 2018). Understanding how aboveground C storage varies among areas of sparse tree regeneration is essential for determining the implications of future forest loss.

We studied effects of sparse postfire tree regeneration on subalpine forest recovery pathways, plant community composition, and aboveground C stocks 34 years after the 1988 Yellowstone fires in the Greater Yellowstone Ecosystem (GYE), Wyoming, USA. Subalpine forests in the GYE have experienced large, infrequent, stand-replacing fires throughout the Holocene (Higuera et al., 2011; Romme & Despain, 1989; Whitlock et al., 2008). In 1988, drought, lightning, and high winds drove extensive wildfires that burned ~570,000 ha of subalpine forest (Romme et al., 2011). Serotiny in populations of lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) contributed to rapid, dense tree regeneration across much of the burned landscape (Turner et al., 2004). However, some areas dominated prefire by obligate ex situ seeders, including non-serotinous lodgepole pine, Engelmann spruce (*Picea engelmannii* Parry ex Engelm. var. *engelmannii*), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt. var. *lasiocarpa*), contained 0 stems ha^{-1} by 24 years postfire (Turner et al., 2016). Landsat satellite imagery and the Normalized Difference Vegetation Index (NDVI) subsequently revealed ~41,000 ha of previously closed-canopy forest exhibited sparse (relative to recovering stands) and reduced (relative to prefire stands) stem densities three decades postfire, much of which was found at higher elevations, on steeper slopes, and further from ex situ seed sources (Kiel & Turner, 2022). Such protracted postfire forest recovery is common in relatively mesic, high-elevation subalpine forests where seed dispersal distances of dominant tree species often diminish beyond 150 m (Greene & Johnson, 1996; Harvey et al., 2016b; Kemp et al., 2016; Littlefield, 2019) and historically long (200–400-year) FRIs provided sufficient time for forests to recover before burning again (Higuera et al., 2014; Schoennagel et al., 2003; Sibold et al., 2006). However, wildfire distributions are changing such that more high-elevation forests are burning (Alizadeh et al., 2021; Schwartz et al., 2015), which may trigger plant community change (Wilson et al., 2024) and drive extensive conversion of high-elevation subalpine forest to sparse or non-forest (Rammer et al., 2021). To characterize current areas of reduced postfire tree

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regeneration and inform the future of these burned landscapes, we asked the following questions:

1. *Detecting pathways of recovery: What are the current recovery pathways in areas of sparse and reduced forest recovery and how are they distributed across the landscape?* We expected to detect several pathways of forest recovery depending on total stem densities and the relative abundance of old versus young stems, with both persistent conversion to sparse or non-forest and slowly recovering forest pathways distinguishable more than three decades after stand-replacing fire. We expected areas with the lowest likelihood of recovering to forest (hereafter, persistent sparse) to be at higher elevations; further, upwind, and/or uphill of ex situ seed sources; and with few to no cone-bearing trees as in situ seed sources. Among areas with the potential to recover, we expected ex situ seed sources and in situ nucleation processes to drive different stand structures and tree age distributions (Turner et al., 1998), and thus variable recovery pathways. We expected slowly recovering areas that were closer, downwind, and/or downhill of ex situ seed sources and with few cone-bearing trees to possess a relatively equal distribution of stem ages (hereafter, continuous infilling). Alternatively, we expected slowly recovering areas with relatively more young than old stems (hereafter, recent establishment) to have lower ex situ seed pressure, possess more cone-bearing trees, and be at lower elevations where lodgepole pine, which typically mature within 5–10 years in open stands (Alexander, 1974), is more abundant and can contribute to in situ seed pressure.
2. *Tree regeneration density: What explains variation in postfire tree regeneration density (total and by species) among sparse recovery pathways?* Across all pathways, we expected overall stem densities to be greater at lower elevations; with moister topo-edaphic conditions such as on northeast-facing aspects, gentler slopes, in soils with greater clay content, and with greater spring moisture availability; and closer, downwind, and/or downhill of ex situ seed sources. However, we also expected tree species to respond individualistically to drivers, with greater densities of fire-sensitive species (Engelmann spruce and subalpine fir) at higher elevations, in areas of greater ex situ seed pressure, and where potential forest recovery is driven by continuous infilling, while lodgepole pine densities would be greater at lower elevations and in plots exhibiting a recent pulse of stem establishment. We expected drivers of whitebark pine (*Pinus albicaulis* Engelm.) densities to be like those of Engelmann spruce and subalpine fir, except nearby seed pressure would likely matter less owing to its dispersal by Clark's Nutcracker (*Nucifraga columbiana*; Tomback, 1982). Young and old stems for all species may respond differently to broad environmental gradients in part because climate has warmed since 1988 (Hostetler et al., 2021), contributing to greater sensitivity of seedlings and saplings of all species to topo-edaphic and climatic factors than trees. Additionally, primary seed sources may shift from ex situ to in situ as young trees that established soon after the 1988 fires mature.
3. *Understory plant communities: What are the implications of sparse recovery for understory plant communities?* Though areas of poor forest recovery, by definition, lack a closed canopy, we refer to the non-tree plant community (i.e., herbaceous forbs and graminoids and woody shrubs) as the understory, especially given many of the plants present immediately following the 1988 fires were resprouting individuals present before the fire (Anderson & Romme, 1991; Turner et al., 1997). As such, we expected understory plant communities to contain a mix of forest-affinity perennials that were present in closed-canopy forests prefire, as well as annuals and meadow-affinity species more common early in succession and in adjacent treeless meadows (e.g., Debinski et al., 2010). However, the relative abundance of meadow-affinity species, as well as overall community richness and diversity, will decrease with increasing stem density. Community composition will similarly vary across broad topo-edaphic and climatic gradients, with community richness and diversity increasing in moister topo-edaphic conditions and decreasing with shrub and graminoid cover.
4. *Carbon stocks: How diminished are aboveground carbon stocks in areas of sparse postfire forest recovery?* We expected C stocks to be substantially lower than in those areas where forests recovered following the 1988 fires. As a result, we expected the amount of C stored in downed coarse wood to be larger than either that stored in live stems or understory plant communities. We also expected the proportion of C stored in sound versus rotten coarse wood, and thus total coarse wood C, to increase with elevation because of slower decomposition rates (Acker et al., 2013; Brown et al., 1998; Kueppers et al., 2004) and older prefire forests dominated by large Engelmann spruce, subalpine fir, and whitebark pine. The amount of C stored in live stems will respond similarly to environmental drivers as stem density. Finally, plant community C stocks may either increase with community diversity because of complementarity in resource acquisition and thus biomass accumulation (Allan et al., 2011; Cardinale et al., 2007) or decrease

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with diversity because of increased biomass of dominant competitors (e.g., graminoids; Wasof et al., 2018).

STUDY AREA AND METHODS

Study area

The GYE is an ~8.9-million-ha landscape containing Yellowstone and Grand Teton National Parks (YNP and GTNP, respectively) and surrounding national forests. At the southern end of the Northern Rockies ecoregion (Hostetler et al., 2021), the GYE's climate is characterized by mild summers and cold, snowy winters, with daily average minimum/maximum temperatures of −17.1°/−4.2°C in January and 5.3°/22°C in July, and average annual precipitation of ~531 mm from 1981 to 2010 (Lake Yellowstone, Wyoming, station #485345; Western Regional Climate Center, 2021). However, the average 21st century (2001–2020) temperature has met or exceeded historical (~20,000 year) maximums and average annual snowfall (1950–2020) has declined by 8.9 cm decade^{-1} because of anthropogenic climate warming (Hostetler et al., 2021). Conifer-dominated forests occupy most of the GYE between 1800 and 2900 m above sea level (asl). Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco) is most abundant in lower montane forests; lodgepole pine dominates YNP's forested plateaus; and Engelmann spruce, subalpine fir, and whitebark pine are most common at high elevations (Baker, 1986; Despain, 1990). Lower montane and lodgepole pine-dominated subalpine forests are largely underlain by volcanic-derived, relatively infertile rhyolitic substrates, whereas volcanic-derived andesitic soils underlie higher elevation forests (Despain, 1990; Whitlock, 1993).

Field sampling

Our study was conducted during summer 2022, 34 years after the 1988 Yellowstone fires. Sampling occurred solely within the ~41,000 ha of area that burned as stand-replacing fire in 1988 (relativized differenced normalized burn ratio ≥ 675; Harvey et al., 2016a; Miller & Thode, 2007), was forested at the time of the fire, and exhibited poor forest recovery as of 30 years postfire (Kiel & Turner, 2022). Plots ($n = 55$) were well distributed across a wide geographic range and were stratified across elevation and distance from unburned forests (putative ex situ seed source; Figure 1). Although we initially planned extensive sampling that included areas of poor forest recovery in the northeast corner of YNP (Figure 1), historic spring flooding in 2022 prohibited access. As such, sampling locations were augmented elsewhere based on access and safe backcountry travel. Because most potential sampling locations were remote, plots were grouped geographically for access by trail, but were separated by ≥250 m. Plots also varied in aspect, slope (<20°), and direction and slope from mature live forest that did not burn in 1988 (Table 1).

Postfire stem characteristics and densities, coarse wood, and understory plant communities were sampled in 30-m × 30-m plots oriented due north following established methods (Braziunas et al., 2023; Romme et al., 2016; Turner et al., 2019; see Appendix S1: Figure S1 for plot design). Live trees (≥1.37 m height) were tallied by species in three parallel, evenly spaced 4-m × 30-m belt transects (360 m^2) oriented north–south, while live tree seedlings (≤1 year old) and saplings (>1 year old and <1.37 m height) were tallied by species in three 2-m × 30-m belt transects (180 m^2). Tree density was measured across the whole plot for one stand in which belt transects were not representative of plot-level stem densities. We recorded the basal diameter (in centimeters), dbh (in centimeters), and height (in meters) of all trees rooted in the belt transect; for seedlings and saplings, we recorded the basal diameter and height of the nearest seedling or sapling rooted in the belt transect at 3-m intervals ($n \leq 30$ plot^{-1}). For all measured stems, we recorded the presence and abundance of cones and counted branch whorls and terminal bud scars as a nondestructive proxy for tree age (Urza & Sibold, 2013). We verified our nondestructive estimate of tree age with basal tree cores taken from lodgepole pine trees ($n = 9$) of varying size outside of our plots but within areas burned as stand-replacing fire in 1988. Whorl counts consistently overestimated tree age ($m = 1.24$; intercept forced through 0), but the relationship was strongly linear ($R^2_{adj} = 0.988$), suggesting our nondestructive age estimates via whorl and terminal bud scar counts were comparable across tree ages and appropriate as a relative estimate of tree age distributions among plots (Appendix S1: Figure S2).

Understory plant communities were assessed in 0.25-m^2 quadrats placed at 5-m intervals along each 30-m transect ($n = 15$ quadrats plot^{-1}). Percent cover by species was measured in each quadrat and total species richness was measured via a 15 min whole plot sweep. The 15 quadrats did not include all plant species present in the plot, and thus, the timed sweep allowed us to tally additional species missed in the quadrats (Appendix S1: Figure S3). Although timed surveys can underestimate richness in speciose communities, our richness estimates were not biased by the number of species recorded (Appendix S1: Figure S3, Table S1). In addition, the understory vegetation was not dense (~30% cover; see *Results*), making it less likely for a species to go undetected. Nonetheless, we recognize our plot-level richness value is still an estimate.

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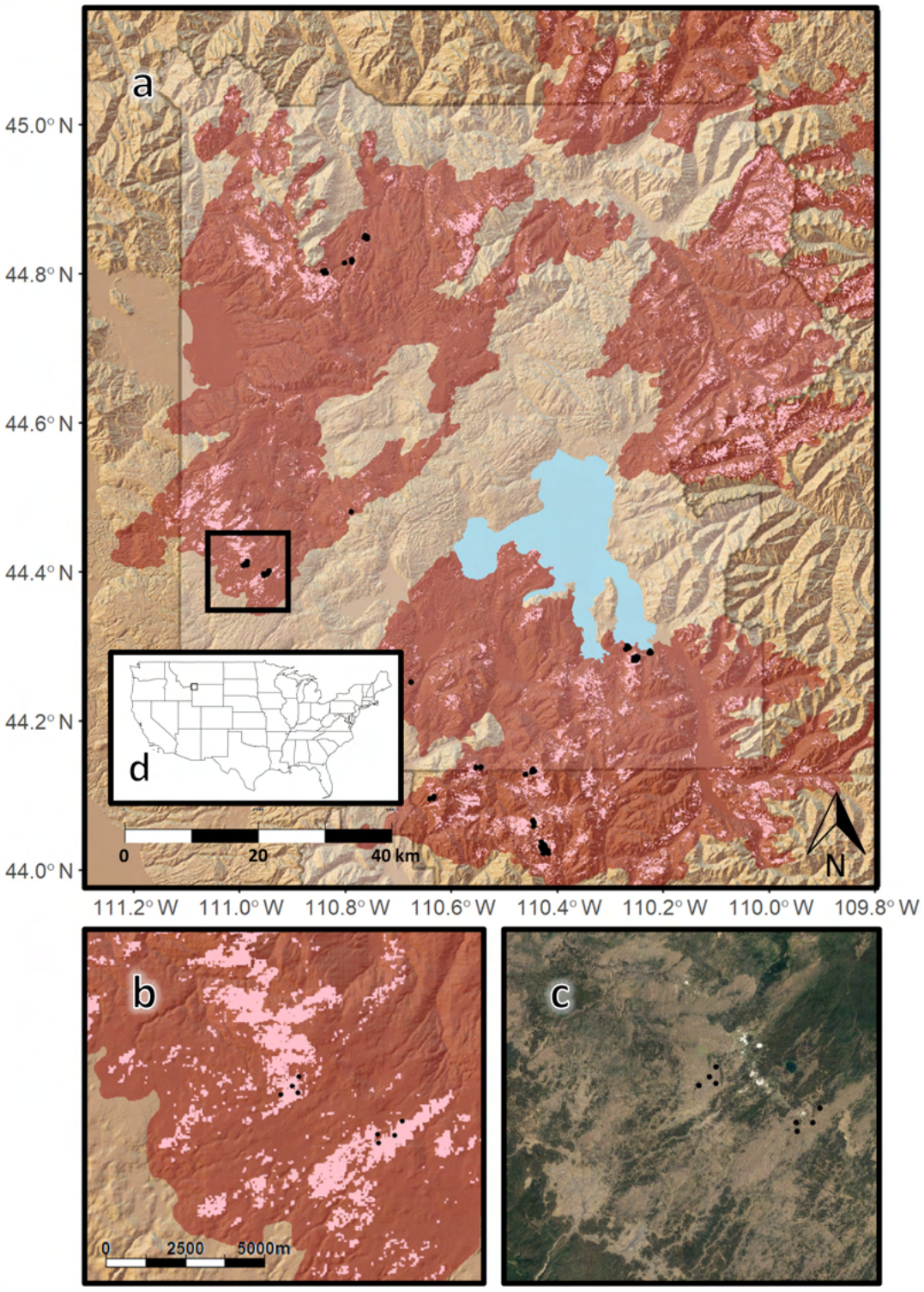

FIGURE 1 Study area and plot locations for assessing forest recovery pathways, plant communities, and aboveground carbon stocks 34 years after stand-replacing fire in the Greater Yellowstone Ecosystem (Wyoming, USA). (a) Distribution of plots (black points; $n = 55$) within areas of sparse forest recovery (pink) sampled 34 years after stand-replacing fire (red) during the 1988 Yellowstone fires in and around Yellowstone National Park (light tan). (b) Subset of plots showing placement within an area of sparse recovery. (c) The same subset of plots as in (b) but showing sparse recovery with Google Earth satellite imagery. (d) Location of study area within the continental United States.

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TABLE 1 Biotic and abiotic characteristics for plots ($n = 55$) in areas exhibiting sparse and reduced forest recovery sampled 34 years after the 1988 Yellowstone fires in the Greater Yellowstone Ecosystem, Wyoming, USA.

Biotic and abiotic characteristic	Mean ± SE	Median	Range
Elevation (m)	2525 ± 20	2554	2237–2801
Aspect (°)	178 ± 12	159.5	14–338
Slope (°)	7.5 ± 0.6	7.2	0–18.2
Soil clay content (%)	9.9 ± 0.6	9.9	4.4–26.4
30-year winter snow water equivalent (mm)	1351 ± 21	1341	1044–1633
30-year summer water deficit (mm)	283 ± 3	283	250–326
Local seed source abundance (m^2)	3317 ± 735	310	0–19,960
Seed source direction (°)	181 ± 15	157	0–358
Cone-bearing tree abundance (stems ha^{-1})	100 ± 14	83	0–472

Note: 30-year (1989–2018) snow water equivalent and summer water deficit data were derived from 4-km-resolution TerraClimate data (Abatzoglou et al., 2018). Plots also varied in their slope to nearest ex situ seed source, which was coded as a categorical variable (up, down, or even with seed source).

Four soil cores (5-cm diameter and 30-cm depth) were collected throughout the plot and composited in the field. Soils were homogenized in the laboratory and then analyzed for soil texture using the hydrometer method (Bouyoucos, 1962) and for percent carbon using a Thermo Flash EA 1112 analyzer (see *Question 4: Carbon stocks*). Finally, coarse wood was measured using four, 10-m Brown's planar intersect transects (Brown, 1974) oriented 30° clockwise off each cardinal direction. We measured both sound and rotten coarse wood (≥7.6 cm, 1000-h fuel). Standing dead tree stems (snags) were rare by three decades postfire (~3 $plot^{-1}$; Kiel, Romme, et al., 2023) and therefore not sampled.

Data analyses

Analyses for question 1 focus on detecting variable forest recovery pathways and determining drivers of their distribution. Questions 2–4, which focus on the effects of variable recovery for tree regeneration, understory plant communities, and aboveground C stocks, respectively, are then addressed with two complementary approaches. First, we determined how each response variable (i.e., tree density, plant community composition, and carbon stocks) varied among the three recovery pathways. Next, we identified which potentially relevant topo-edaphic and biotic predictors explained variation in our response variable among all plots regardless of recovery pathway. In so doing, we could both quantify differences among recovery pathways and identify drivers of tree regeneration, plant community composition, and carbon stocks across all areas of sparse and reduced forest recovery. All analyses were conducted in R (R Core Team, 2023) using the below packages, and the results were visualized with the rayshader and ggplot2 packages (Morgan-Wall, 2021; Wickham, 2016).

Question 1: Detecting pathways of recovery

To assign each plot to one of three recovery pathways, we used plot-level (i.e., all conifer tree species) whorl and bud scar frequency distributions (Figure 2). We could not estimate the ages of quaking aspen (*Populus tremuloides* Michx.) stems in our plots, but abundance was low ($n = 6$ stems), so it did not meaningfully contribute to total stem densities. Persistent sparse recovery was defined as any plot with <500 total stems ha^{-1} (i.e., all seedlings, saplings, and trees) or plots with ≥500 stems ha^{-1} possessing a negatively skewed whorl distribution indicating many older and few younger stems. Lodgepole pine forests converge to ~1200 stems ha^{-1} after two centuries of stand development (Kashian et al., 2005), so our threshold of <500 stems ha^{-1} represents the sparse end of possible forest recovery pathways and is at least an order of magnitude lower than stem densities where forests are recovering following the 1988 fires (Turner et al., 2016). Continuous infilling was defined as any plot with ≥500 stems ha^{-1} and little to no skewness in its whorl distribution indicating roughly equal number of older and younger stems. Recent establishment was defined as any plot with ≥500 stems ha^{-1} and a strong positively skewed whorl distribution indicating many younger and few older stems. The latter two pathways, with ≥500 stems ha^{-1}, capture those plots that may yet recover to forest either from ex situ or in situ seed sources (as young postfire trees begin to produce cones) given enough time, but different proportions of older versus younger stems indicate differences in stand structure (Figure 2) and potential drivers of recovery.

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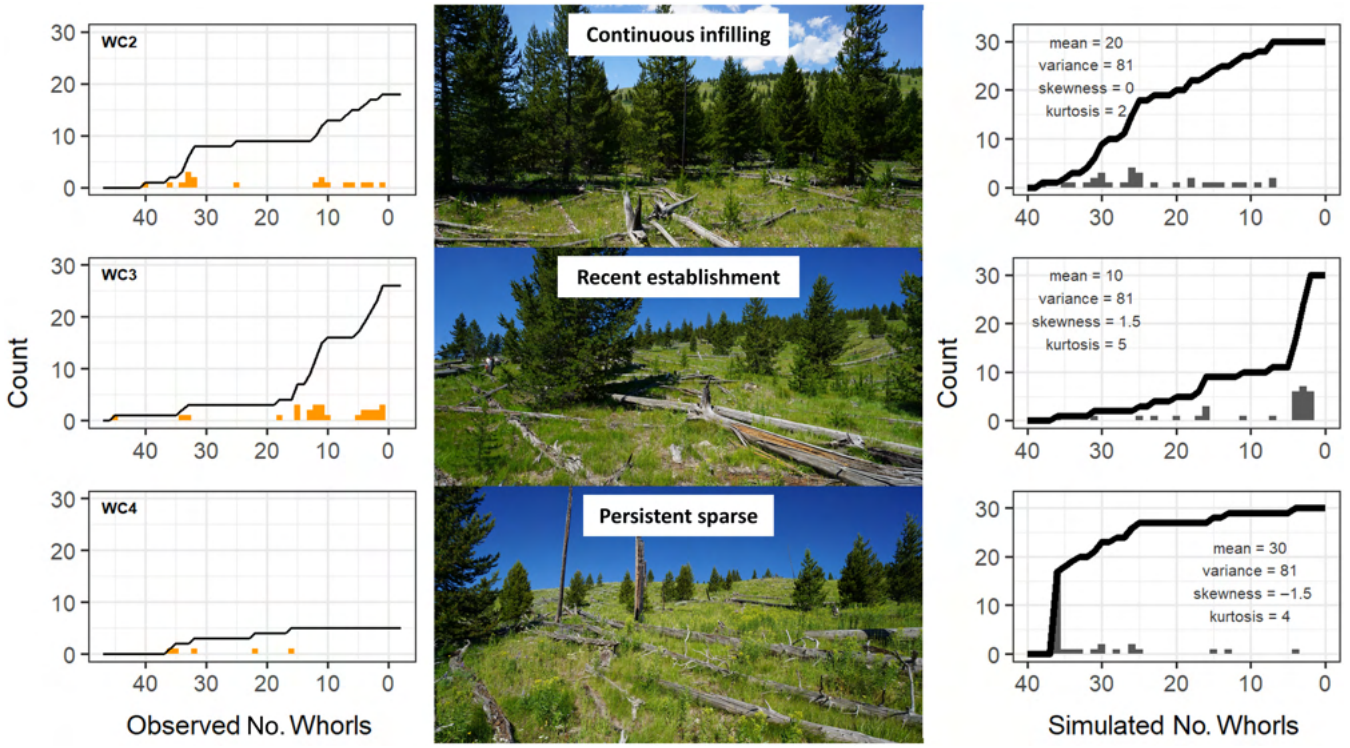

FIGURE 2 Example frequency distributions of observed (left) and simulated (right) estimates of tree ages from each potential forest recovery pathway 34 years after the 1988 Yellowstone fires in Greater Yellowstone, Wyoming, USA. Continuous infilling are those plots with ≥500 stems ha^{-1} and relatively equal amounts of older and younger stems; recent establishment are those plots with ≥500 stems ha^{-1} and relatively more younger than older stems; and persistent sparse are those plots with <500 stems ha^{-1} and/or relatively more older than younger stems. Black lines represent cumulative frequency distributions. The presented plots (Winter Creek [WC] 2, 3, and 4) were sampled in the same geographic area and contained only lodgepole pine (orange bars). All photos were taken facing west; photos by Nathan G. Kiel.

One-thousand distributions were simulated for each pathway using the PearsonDS package (Becker & Klößner, 2022), with the distribution moments (i.e., mean, variance, skewness, and kurtosis) varying between pathways to capture representative distributions (Figure 2). To assign a recovery pathway to plots with ≥500 stems ha^{-1} ($n = 32$), we tested for differences between observed and simulated whorl distributions using the Kolmogorov–Smirnov test (e.g., observed whorl and bud scar distributions in hypothetical "Plot One" by simulated persistent sparse distributions; $n = 96{,}000$ tests). We then tallied the number of simulated distributions for each pathway that did not differ ($\alpha > 0.05$) from each observed distribution and calculated the average p-value and D statistic across all observed-by-simulated distribution combinations for each pathway. The pathway for which the most simulated distributions did not differ from the observed whorl, and bud scar distribution was assigned to that observed distribution.

To explain the occurrence of each of the three recovery pathways, we used two sequential classification trees. A first classification tree analysis was conducted to identify drivers of persistent sparse versus potentially recovering pathways (continuous infilling and recent establishment pathways combined), and a second classification tree analysis within the potentially recovering pathways was used to distinguish continuous infilling from recent establishment. Sequential analyses were conducted because different characteristics distinguished each category (i.e., stem densities and age distributions separated persistent sparse from both continuous infilling and recent establishment versus only stem age distributions separated continuous infilling from recent establishment). Potential predictors were chosen to capture several aspects of seed pressure, including elevation (which closely corresponds to dominant tree species distributions in the region; in meters); the abundance of trees with cones (as a proxy for in situ seed source; stems per hectare); and local ex situ seed source abundance (area [in square meters] of live mature forest not burned in 1988 within a 150-m radius of plot center; Appendix S1: Figure S4), direction (cosine-transformed; 0 = southwest [plot downwind], 2 = northeast [plot upwind]; Western Regional Climate Center, 2002), and slope (uphill, downhill, or even) from to plot center. Classification trees were fit and visualized using the rpart

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and rpart.plot packages, respectively (Milborrow, 2022; Therneau & Atkinson, 2022). Classification trees were pruned to minimize the cross-validation mean error.

Question 2: Tree regeneration density

We first assessed how postfire conifer stem densities varied among the three forest recovery pathways by age class (seedlings and saplings vs. trees) and species using multivariate ANOVA (MANOVA) and post hoc Tukey's tests. We then fit a multilevel model (Gelman & Hill, 2007) to quantify differences in overall as well as species- and age-specific stem densities across gradients in topography, soil, climate, and seed pressure among all recovery pathways. In addition to the seed pressure predictors used above, we included topographic moisture index (TMI; cosine-transformed aspect as a measure of southwest- vs. northeast-facing aspects; Beers et al., 1966), plot slope (in degrees), soil texture (% clay), and 4-km-resolution 30-year normal (1989–2018) winter snow water equivalent (SWE; in millimeters) and summer water deficit (WD; in millimeters; Abatzoglou et al., 2018) in our model to capture site-specific seedling establishment conditions (e.g., moisture availability). While burn severity can also influence postfire stem densities (Turner et al., 1997, 1999), it was not considered here because all plots burned as severe, stand-replacing crown fire. Similarly, climate immediately following fire (≤3 year postfire), though increasingly implicated in variable tree regeneration densities (Crockett & Hurteau, 2023; Hankin et al., 2019; Stewart et al., 2021), is likely less important than long-term climate where slow recovery dynamics and seedling establishment can occur over several decades (Coop et al., 2010; Peet, 1981; Stahelin, 1943).

Predictor variables in our multilevel model were *z*-transformed prior to analyses so that the magnitude of coefficient estimates could be compared, and the variance inflation factor (VIF) was <4 for all predictors (tested for using the car package; Fox & Weisberg, 2019). Douglas-fir and quaking aspen were removed prior to model fitting because they were each present in ≤3 plots. While Engelmann spruce stems were present in 29% of plots, it was also excluded to avoid model overfitting because of low total abundance (24 trees and 14 seedlings and saplings). Thus, our multilevel model included seedlings, saplings, and trees of lodgepole pine, whitebark pine, and subalpine fir. Model fit was assessed with R^2_{pred}, a measure of explained variance derived from observed versus predicted model residuals (Ives, 2018). Stem densities were treated as count data, and model residuals were not over-dispersed (dispersion = 0.627, $p = 0.504$; tested using the DHARMa package; Hartig, 2022), so a Poisson distribution was used. Significant ($\alpha = 0.05$) fixed effects were interpreted as the effect of that predictor on overall stem densities. Significant ($\alpha = 0.05$) random effects were interpreted as the effect of that predictor on species- and age-specific stem densities and were identified using likelihood-ratio tests. The abundance of trees with cones in each plot was only considered as a fixed effect due to few trees of species other than lodgepole pine possessing cones across all plots (four for subalpine fir). We considered the sum of a predictor's fixed and random effects for a given stem category as ecologically meaningful if $>|0.20|$ (Romme et al., 2016).

Question 3: Understory plant communities

We calculated three complementary metrics of community composition: species richness; Simpson's diversity, which ranges from zero to one and captures the likelihood two individuals from a community are of different species (Simpson, 1949; calculated in the vegan package; Oksanen et al., 2022); and a community-weighted habitat index. For the community-weighted habitat index, each species was assigned a habitat value from one to five based on their preference for treeless meadows, grasslands, and steppe, or closed-canopy subalpine forest (Whipple, 2015, unpublished; Appendix S1: Table S7). The relative abundance of each species within a plot was then multiplied by that species' habitat value and summed across the community to create a community-weighted index ranging from one (preference for open meadows and grasslands) to five (preference for closed-canopy forest). Differences in these three metrics among forest recovery pathways were tested using MANOVA and post hoc Tukey's tests.

Next, we fit several models to determine the drivers of plant community composition across all plots. First, multiple regression models were fit to identify potential abiotic and biotic predictors of community-weighted habitat index and Simpson's diversity. Plot-level biotic, topo-edaphic, and climate predictors included total stem density (all seedlings, saplings, and trees; stems per hectare), soil texture (% clay), elevation (in meters), slope (in degrees), TMI, and 30-year normal SWE and WD as proxies for climate and seasonal moisture availability known to be important for high-elevation plant communities (Kiel, Braziunas, et al., 2023; Möhl et al., 2023). For Simpson's diversity, we also included percent cover of graminoids and shrubs as potential interspecific competitors for space (Decocq et al., 2004; Lieffers et al., 1993; Stahelin, 1943) and light (North et al., 2019; Ridding et al., 2020), respectively.

We then fit a multilevel model to species-level data to identify drivers of understory plant community

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composition and individual species distributions among the above predictors (Jackson et al., 2012). A binomial distribution was used for predicting species presence, and fixed and random effects for each predictor were determined. Significant ($\alpha = 0.05$) fixed effects captured predictors' effects on whole plant community richness, whereas significant ($\alpha = 0.05$) random effects indicated species-specific effects of that predictor. Additional species-by-predictor fixed-plus-random effects $>|0.20|$ represent important species responses to that predictor. Only taxa present in >5% of plots ($n = 59$) and identified at least to genus were included in the final multilevel model and some congeneric taxa were considered only at the genus level (e.g., *Aquilegia*, *Trifolium*). As discussed above, multiple regression and multilevel model predictors were *z*-transformed prior to analyses and the VIF for all model coefficients was <4.

Question 4: Carbon stocks

We estimated live tree, sapling, and ground layer plant community aboveground biomass from stem densities and percent cover using previously derived, regionally specific allometric equations (Brown, 1978; Callaway et al., 2000; Copenhaver & Tinker, 2014; Ter-Mikaelian & Korzukhin, 1997; Turner et al., 2004; Appendix S2). Quaking aspen was excluded due to low abundance across all plots ($n = 6$ stems). Live-tree and sapling biomass was calculated by averaging the predicted dry mass for trees or saplings measured along each belt transect then multiplying by the number of trees or saplings tallied within that transect. Transect-level tree and sapling biomass estimates were then averaged by plot and scaled to Mg per hectare. Understory plant biomass was predicted by species based on mean percent cover in each plot, summed across species, and scaled to Mg per hectare. For species without allometric equations, an equation from another species with comparable form was used (Appendix S2). Downed coarse wood biomass was computed following Brown (1974) with a correction for plot slope (in degrees).

Aboveground carbon (in megagrams of C per hectare) stocks were calculated from biomass by applying field-derived percent carbon of each respective pool (Kashian et al., 2013). Lodgepole pine sapling and tree percent carbon for foliage and wood were used for all conifers (Kashian et al., 2013), and dbh < 1 cm for Engelmann spruce ($n = 3$) was rounded to 1 to permit natural-log-transformation (Brown, 1978; Ter-Mikaelian & Korzukhin, 1997). To quantify mineral soil carbon pools (0–30 cm), soils were sieved (2 mm) and homogenized; then 45-mg samples from each plot were processed in a Thermo Flash EA 1112 analyzer (Jackson Lab, University of Wisconsin-Madison, Madison, WI). One plot was excluded from analyses because of repeated failed carbon content analyses. We assumed a constant soil bulk density of 0.83 kg L^{-1} (Smithwick et al., 2009) to estimate the soil carbon stock size (in megagrams of C per hectare) for each plot.

While we applied the best available methods for estimating C stocks in our region, uncertainty in field measurements and allometric equations can introduce uncertainty in ecosystem-level C stocks (Yanai et al., 2010, 2018). For example, regional field estimates of bulk density vary (0.6–1.0 kg L^{-1}; Griffin et al., 2011, 2013; Turner et al., 2019) and are consistently lower than those derived from the U.S. Department of Agriculture's Web Soil Survey. As such, we explored the sensitivity of our estimates of biomass and carbon stock sizes to allometric equations and parameters (Appendix S2).

Differences in aboveground C stocks among pathways were tested using a MANOVA and post hoc Tukey's tests, while important topo-edaphic predictors of C stocks among all plots were identified with regression analyses. Given we did not expect mineral soil C to vary between recovery pathways (and it did not; Appendix S1: Table S2), it was not included in our MANOVA. Separate multiple linear regression models were fit for stem, plant community, coarse wood, and mineral soil C stocks, and models included *z*-transformed slope (in degrees), elevation (in meters), soil texture (% clay), and TMI (VIF <4) for each plot. We also regressed the proportion of C stored in sound versus rotten coarse wood against elevation to determine whether slower decomposition rates at higher elevations contributed to variable C storage patterns and used simple linear regression to determine whether understory plant diversity influenced C storage across plots.

RESULTS

Plots spanned a wide range of environmental conditions (Table 1). Postfire tree (≥1.37-m tall) density (±SE) averaged only 322 ± 32 trees ha^{-1} (median = 222), well below the threshold of 1000 trees ha^{-1} used to identify areas of poor postfire forest recovery from satellite imagery (Kiel & Turner, 2022) and confirming sparse forest recovery after the 1988 fires (Table 2). Two plots exceeded 1000 trees ha^{-1} (Figure 3) because of whitebark pine stems clustered closely together likely due to seed caching by Clark's Nutcracker (Tomback, 1982). The density of seedlings and saplings (<1.37-m tall) exceeded that of trees, averaging 1022 ± 274 stems ha^{-1} (median = 333; Table 2) but varying widely across plots (Figure 3). Lodgepole pine was most abundant, making up 51% and 82% of tree and seedling/sapling densities, respectively (Table 2). Densities of

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TABLE 2 Species-specific stem densities (stems per hectare) across plots of sparse and reduced forest recovery ($n = 55$) sampled 34 years after the 1988 Yellowstone Fires in the Greater Yellowstone Ecosystem, Wyoming, USA.

	Trees (≥1.37-m tall)		Seedlings and saplings (<1.37-m tall)	
Species	**Mean ± SE**	**Median**	**Mean ± SE**	**Median**
Lodgepole pine	165 ± 23	139	839 ± 267	167
Whitebark pine	121 ± 27	28	99 ± 23	0
Subalpine fir	25 ± 7	0	59 ± 18	0
Engelmann spruce	12 ± 4	0	14 ± 4	0
Quaking aspen	2 ± 1	0	3 ± 2	0
Douglas-fir	0	0	8 ± 6	0
Total	322 ± 38	222	1022 ± 274	333

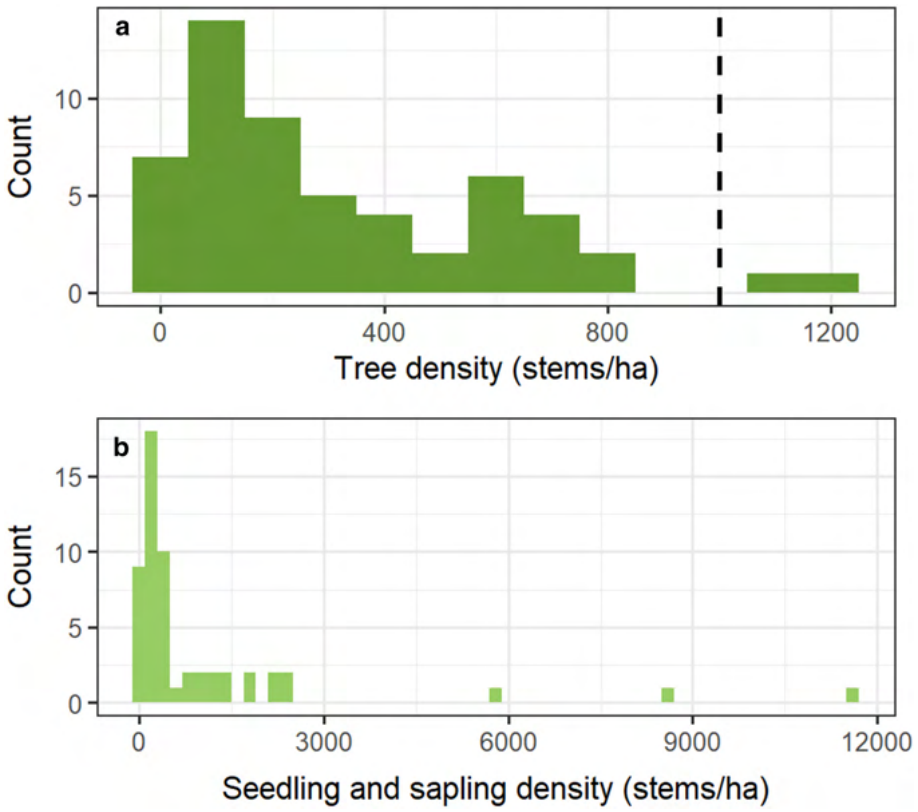

FIGURE 3 Distribution of tree (≥1.37-m tall; a) and seedling plus sapling densities (<1.37-m tall; b) across plots of sparse and reduced forest recovery ($n = 55$) sampled 34 years after the 1988 Yellowstone fires in the Greater Yellowstone Ecosystem, Wyoming, USA. The vertical dashed line at 1000 trees ha^{-1} is the previously defined threshold of sparse and reduced postfire forest recovery (Kiel & Turner, 2022), below which were all but two plots.

seedlings and saplings exceeded those of trees for all species except whitebark pine (Table 2).

Detecting pathways of recovery

All three forest recovery pathways were observed among our plots. Nearly half (42%, $n = 23$) were persistently sparse with <500 total seedlings, saplings, and trees ha^{-1} (Appendix S1: Figure S5). Slightly fewer (38%, $n = 21$) were classified as continuous infilling (Appendix S1: Figure S6) and 20% (11) were classified as recent establishment (Appendix S1: Figure S7) based on Kolmogorov–Smirnov tests between observed and simulated age distributions (Appendix S1: Table S3). All distribution moments except variance differed among recovery pathways as expected, supporting our classifications ($F_{2,49} = 4.7$, Pillai = 0.6, $p = 7.2 \times 10^{-5}$; Appendix S1: Tables S4 and S5). Mean

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whorl counts were five to six whorls lower in plots categorized as recent establishment, distribution skewness was strongly positive in recent establishment plots, and distribution kurtosis was 25%–50% lower in persistent sparse plots than either continuous infilling or recent establishment plots (Appendix S1: Table S4). Distribution skewness also varied with elevation, with lower elevation plots exhibiting more positively skewed distributions and higher elevation plots exhibiting negatively skewed distributions ($F_{1,50} = 9.088$, $R^2_{adj} = 0.14$, $p = 0.004$; Appendix S1: Figure S8).

Areas of persistent sparse recovery were distinguished from areas potentially recovering to forest via either continuous infilling or recent establishment by the scarcity of cone-bearing trees, ex situ seed source direction, and elevation (cross-validation error rate = 38.2%; Figure 4a). Plots in potentially recovering pathways had ≥153 cone-bearing trees ha^{-1} (Figure 4a). Of plots with <153 cone-bearing trees ha^{-1}, persistently sparse plots tended to be upwind of live mature forest (i.e., had low ex situ seed pressure) or, if downwind of potential seed source, had <14 cone-bearing trees ha^{-1} (Figure 4a). Persistently sparse plots also tended to be at lower elevations (<2487 m) than potentially recovering plots among those with 14–153 cone-bearing trees ha^{-1} and located relatively downwind of potential seed source (Figure 4a). Plots potentially recovering via continuous infilling were more likely at higher elevations than those potentially recovering via a recent pulse of establishment (cross-validation error rate = 34.4%; Figure 4b).

Tree regeneration density

Regeneration densities (stems per hectare) varied by species and age class among recovery pathways ($F_{2,52} = 6.2$,

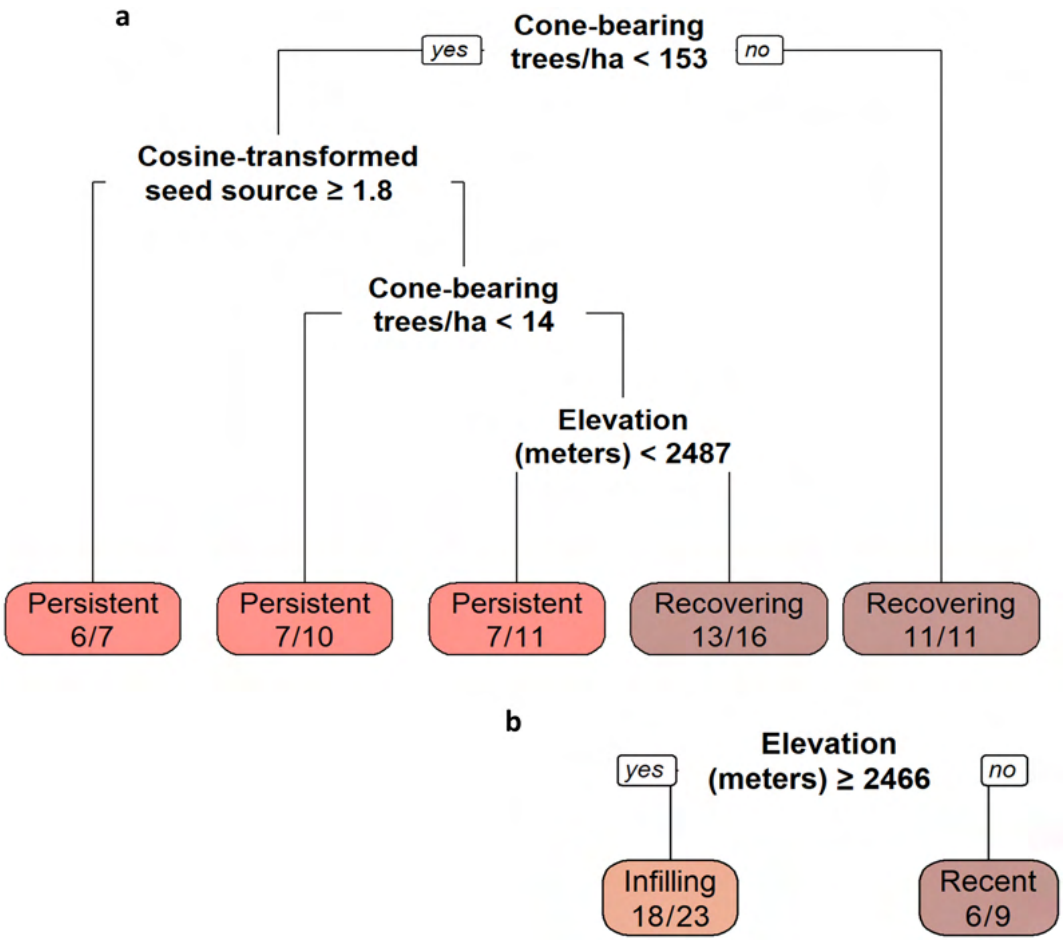

FIGURE 4 Sequential classification trees of current sparse and reduced forest recovery pathways 34 years after burning as stand-replacing fire in the 1988 Yellowstone fires (Wyoming, USA). (a) Plots in the "persistent" category are those identified as persistently sparse; those in the "recovering" category are those identified as either (b) continuous infilling ("infilling") or recent establishment ("recent"). Higher cosine-transformed seed source direction corresponds to plots that are upwind of nearby seed source. Numbers within each box are the number of plots in that category divided by the total number meeting that criterion (e.g., nine potentially recovering plots were <2466 m above sea level, of which six exhibited a recent pulse of establishment).

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Pillai = 1.1, $p = 1.7 \times 10^{-9}$; Table 3a, Appendix S1: Table S6). Plots in the persistently sparse pathway had roughly an order of magnitude lower densities of Engelmann spruce seedlings and saplings, all whitebark pine stems (i.e., trees, seedlings, and saplings), and all lodgepole pine stems than potentially recovering pathways (Table 3a). Recent establishment plots had ~3.5 times greater lodgepole pine seedling and sapling densities than continuous infilling plots, while all other stem densities did not differ (Table 3a).

Total stem densities increased with soil clay content, the abundance of cone-bearing trees, and presence of an uphill seed source, which were all significant as fixed effects in our multilevel model ($R^2_{pred} = 0.37$; Table 4). These and all other variables (elevation, slope, TMI, 30-year SWE and WD, local seed source abundance, and seed source direction) were significant as random effects, indicating species- and age-specific stem densities responded differently from one another to dominant topo-edaphic, climatic, and seed pressure drivers.

Lodgepole pine seedling and sapling densities decreased with elevation and local seed source abundance but increased with uphill seed source and greater winter snowfall (SWE; Table 5). Lodgepole pine tree densities also decreased with elevation and increased with winter snowfall but increased with local seed source abundance. Whitebark pine stem densities (both trees and seedlings/saplings) increased with elevation, plot slope, soil percent clay, and uphill seed source while decreasing with local seed source abundance. Whitebark pine tree densities also decreased with greater winter snowfall and on northeast-facing aspects. Subalpine fir

TABLE 3 Variation in (a) tree regeneration densities (stems per hectare), (b) plant community composition, and (c) aboveground carbon stocks (in megagrams of C per hectare) among postfire forest recovery pathways (persistent sparse, continuous infilling, and recent establishment) within areas burned as stand-replacing fire in the 1988 Yellowstone fires (Wyoming, USA) and exhibiting sparse and reduced forest recovery 34 years postfire.

	Persistent sparse	Continuous infilling	Recent establishment	*p*
(a) Q2: Tree regeneration density (mean ± SE stem density; stems ha^{-1})				
Lodgepole pine				
Tree (≥1.37 m)	$62^{a} \pm 12$	$269^{b} \pm 47$	$167^{ab} \pm 34$	**0.0001**
Seedling + sapling (<1.37 m)	$82^{a} \pm 15$	$733^{a} \pm 272$	$2626^{b} \pm 1097$	**0.0012**
Whitebark pine				
Tree (≥1.37 m)	$18^{a} \pm 6$	$224^{b} \pm 57$	$141^{ab} \pm 47$	**0.0015**
Seedling + sapling (<1.37 m)	$14^{a} \pm 9$	$159^{a} \pm 44$	$162^{b} \pm 61$	**0.0051**
Subalpine fir				
Tree (≥1.37 m)	5 ± 4	42 ± 2	35 ± 10	0.052
Seedling + sapling (<1.37 m)	31 ± 13	71 ± 40	91 ± 43	0.43
Engelmann spruce				
Tree (≥1.37 m)	1 ± 1	20 ± 10	20 ± 10	0.098
Seedling + sapling (<1.37 m)	$2^{a} \pm 2$	$16^{ab} \pm 7$	$35^{b} \pm 14$	**0.010**
Douglas-fir				
Seedling/sapling (<1.37 m)	5 ± 3	0 ± 0	30 ± 30	0.19
(b) Q3: Understory plant communities (mean ± SE)				
Richness	33 ± 2	34 ± 2	35 ± 3	0.86
Simpson's diversity	0.70 ± 0.03	0.73 ± 0.02	0.72 ± 0.04	0.74
Habitat preference	$2.86^{a} \pm 0.07$	$3.19^{b} \pm 0.07$	$3.39^{b} \pm 0.13$	**0.00033**
(c) Q4: Carbon stocks (mean ± SE Mg C ha^{-1})				
Live conifer	$0.8^{a} \pm 0.2$	$2.6^{b} \pm 0.5$	$2.0^{ab} \pm 0.6$	**0.0082**
Coarse wood	59.4 ± 4.7	66.4 ± 6.7	67.5 ± 8.7	0.61
Understory	1.0 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.11

Note: Letters distinguish significant differences among pathways for individual categories and bolded *p*-values are those <0.05, our threshold for statistical significance. Overall MANOVAs for each section were significant. (a) $F_{2,52} = 6.2$, Pillai = 1.1, $p = 1.7 \times 10^{-9}$; pairwise *p*-values following Tukey's post hoc tests in Appendix S1: Table S5. (b) $F_{2,52} = 2.94$, Pillai = 0.29, $p = 0.011$; Appendix S1: Table S8. (c) $F_{2,52} = 2.59$, Pillai = 0.26, $p = 0.23$; Appendix S1: Table S10.

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TABLE 4 Summary of the multilevel model for abundance of trees and seedlings/saplings of lodgepole pine, whitebark pine, and subalpine fir across areas of sparse and reduced forest recovery 34 years after the 1988 Yellowstone fires in the Greater Yellowstone Ecosystem, Wyoming, USA, showing standardized coefficient estimates for fixed and random effects of each predictor.

Model coefficient (overall model)	Effect (*p*-value)	
	Fixed	Random
Intercept	0.613 (0.170)	**1.175 ($<2 \times 10^{-16}$)**
Elevation (m)	0.202 (0.257)	**0.155 (1.5×10^{-14})**
Slope (°)	0.130 (0.229)	**0.054 (0.002)**
Topographic moisture index (TMI; unitless)	−0.058 (0.588)	**0.055 (1.4×10^{-5})**
Soil clay content (%)	**0.302 (0.024)**	**0.099 ($<2 \times 10^{-16}$)**
30-year winter snow water equivalent (SWE; mm)	0.179 (0.221)	**0.097 (3.6×10^{-7})**
30-year summer water deficit (WD; mm)	0.207 (0.123)	**0.070 (0.002)**
Abundance of cone-bearing trees (stems ha^{-1})	**0.368 ($<2 \times 10^{-16}$)**	...
Seed source slope (down, even, up)	**0.226 (0.018)**	**0.044 ($<2 \times 10^{-16}$)**
Local seed source abundance (m^2)	−0.105 (0.521)	**0.148 ($<2 \times 10^{-16}$)**
Seed source direction (cosine-transformed; unitless)	−0.109 (0.187)	**0.030 (0.005)**

Note: $R^2_{pred} = 0.37$. Seed source slope is categorical (uphill, even, and downhill) and seed source direction is cosine-transformed (0 = southwest, 2 = northeast) and unitless. Bolded values are significant ($p < 0.05$) fixed and random effects of the overall model.

stem densities across age classes similarly increased with elevation and percent clay content, as well as with greater summer aridity and local seed source abundance. However, subalpine fir tree densities decreased on northeast-facing aspects and when seed source was downwind but increased with winter snowfall, while seedling and sapling densities were greater on northeast-facing aspects and with uphill seed source.

Understory plant communities

We identified 118 plant species across all plots (in addition to six tree species; Appendix S1: Table S7). Plot sweeps contained an average of 33.6 ± 1.2 species (median = 35), and percent cover of understory vegetation in quadrats averaged 30.9 ± 1.6%. Native perennial species dominated, with only 0.25 ± 0.05% annual and 0.21 ± 0.05% non-native cover across plots. None of the eight non-native species (*Cirsium arvense* (L.) Scop., *Crepis tectorum* L., *Hieracium aurantiacum* L., *Rumex acetosella* L., *Taraxacum officinale* F.H. Wigg., *Tragopogon dubius* Scop., *Trifolium repens* L., and *Trifolium pratense* L.) were new to the regional flora. More than half (15.9 ± 1.3%) of the plant community cover was graminoid, whereas shrub cover was low (3.5 ± 0.6%).

Among metrics of community composition, community-weighted habitat index was lower (i.e., greater relative abundance of meadow-affinity species) in persistently sparse plots ($F_{2,52} = 2.94$, Pillai = 0.29, $p = 0.011$; Table 3b, Appendix S1: Table S8). Species richness and Simpson's diversity were both relatively high (~34 species $plot^{-1}$ and $H \sim 0.73$) and did not differ among recovery pathways (Table 3b). Forest-affinity species became relatively more abundant with increasing stem density, soil clay content, and on northeast-facing aspects ($F_{7,47} = 9.03$, $R^2_{adj} = 0.51$, $p = 5.22 \times 10^{-7}$; Figure 5a). Though Simpson's diversity did not differ among pathways, it decreased with stem density (stems ha^{-1}) and graminoid cover (%), the latter having roughly twice as strong of an effect ($F_{9,45} = 15.6$, $R^2_{adj} = 0.71$, $p = 3.74 \times 10^{-11}$; Figure 5b).

Understory plant community richness decreased with stem density and elevation but increased on northeast-facing aspects and with greater winter snowfall and summer aridity ($R^2_{pred} = 0.54$; Table 6). Individualistic species responses to several predictors, including soil clay content, elevation, slope, and winter snowfall (Table 6), manifested in species-level fixed-plus-random effects (Appendix S1: Table S9). Elevation was an important predictor for the most taxa ($n = 48$), with 30-year SWE ($n = 44$), soil clay content ($n = 41$), and slope ($n = 38$) important for sequentially fewer taxa. One-third of taxa responding to elevation (16 of 48) were more likely to occur at higher elevations, while most (28 of 38) taxa responding to slope were more likely to occur on steeper (up to 20°) slopes. Nearly all (38 of 44) taxa responding to 30-year SWE were more likely to occur in areas of greater winter snowfall, and most (63%) taxa responding to soil clay content were more likely to occur with greater clay content (Appendix S1: Table S9).

Among functional groups, most forbs were more likely to occur with greater winter snowfall (29 of 33), higher soil clay content (18 of 31), at lower elevations (24 of 35), and on steeper slopes (20 of 29; Appendix S1: Table S9). *Calyptridium umbellatum* (Torr.) Greene, *Collinsia parviflora* Lindl., *Hieracium gracile* Hook. var. *gracile*, and *Sibbaldia procumbens* L. were the only forbs less likely to occur in areas of greater winter snowfall

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TABLE 5 Summary of the multilevel model for abundance of trees and seedlings/saplings of lodgepole pine, whitebark pine, and subalpine fir across areas of sparse and reduced forest recovery 34 years after the 1988 Yellowstone fires in the Greater Yellowstone Ecosystem, Wyoming, USA, showing fixed effects plus species-by-predictor random effects.

Random effects coefficients after fixed effects have been added	Elevation (m)	Slope (°)	TMI	Clay (%)	30-year winter SWE	30-year summer WD	Seed source slope	Local seed source abundance (m^2)	Seed source direction
Lodgepole pine									
Tree (≥1.37 m)	**−0.295**	0.002	0.037	−0.197	**0.359**	−0.064	−0.138	**0.234**	−0.089
Seedling + sapling (<1.37 m)	**−0.297**	0.121	−0.192	−0.015	**0.479**	0.184	**0.470**	**−0.469**	−0.134
Whitebark pine									
Tree (≥1.37 m)	**0.395**	**0.239**	**−0.310**	**0.561**	**−0.310**	−0.092	**0.347**	**−0.604**	0.153
Seedling + sapling (<1.37 m)	**0.508**	**0.496**	0.044	**0.331**	0.198	**0.315**	**0.201**	**−0.314**	−0.049
Subalpine fir									
Tree (≥1.37 m)	**0.290**	−0.148	**−0.224**	**0.438**	**0.380**	**0.348**	0.193	**0.229**	**−0.346**
Seedling + sapling (<1.37 m)	**0.598**	0.054	**0.307**	**0.621**	−0.045	**0.537**	**0.276**	**0.296**	−0.185

Note: Bolded values are those group-by-predictor fixed-plus-random effects that are >|0.20| and thus ecologically significant.

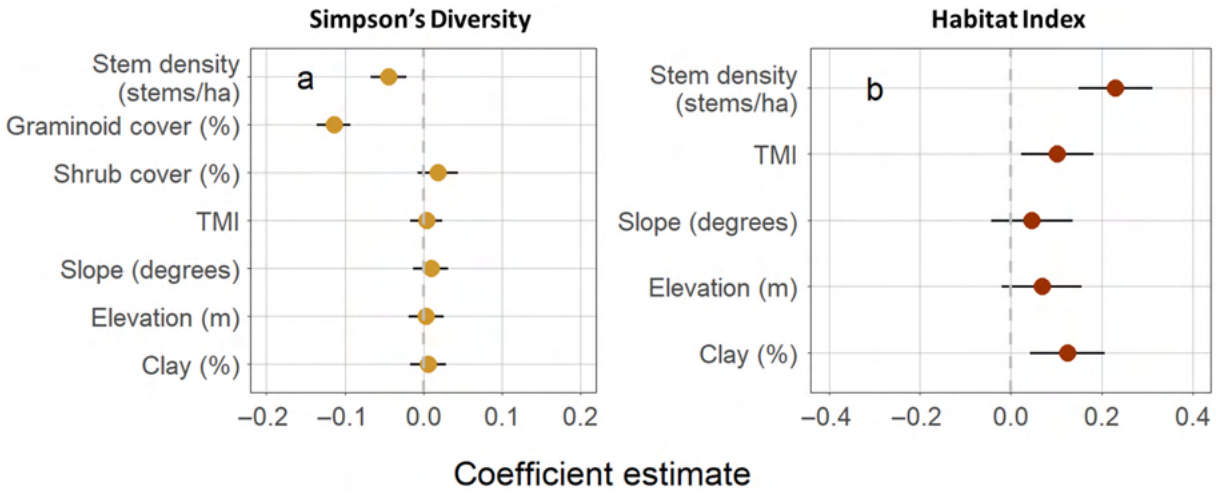

FIGURE 5 Drivers of plant community composition in areas of sparse and reduced forest recovery 34 years after the 1988 Yellowstone fires in the Greater Yellowstone Ecosystem, Wyoming, USA. (a) Standardized coefficient estimates of community-weighted habitat index, which increased with stem density (stems per hectare), plot northeasterliness (topographic moisture index [TMI]; unitless), and soil clay content (in percentage). (b) Standardized coefficient estimates of plant community Simpson's diversity, which declined with stem density (stems per hectare) and graminoid cover (in percentage).

(Appendix S1: Table S9), none of which were forest-affinity species (habitat class >3; Appendix S1: Table S7). Of the 11 forbs more likely to occur at higher elevations, only one (*Hieracium albiflorum* Hook.) was a forest-affinity species (habitat class >3; Appendix S1: Table S7), with the rest either meadow-affinity species or capable of persisting in both forests and meadows. Non-native taxa identified to species in our multilevel model (*Ci. arvense*, *Ta. officinale*, and *Tr. dubius*) were all forbs and were more likely to occur on steeper slopes. Two of nine graminoids (*Calamagrostis rubescens* Buckley and *Carex rossii* Boott) were more likely to occur in areas of greater winter snowfall, with *Elymus elymoides* (Raf.) Swezey the only graminoid less likely to occur on steeper slopes (Appendix S1: Table S9). Two of five graminoids were less likely with greater soil clay content (Appendix S1: Table S9), both of which (*E. elymoides* and *Koeleria macrantha* (Ledeb.) Schult.) are meadow-affinity species (habitat class <3; Appendix S1: Table S7).

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TABLE 6 Fixed and random effects of multilevel model for plant species present in >5% of plots across areas of sparse and reduced forest recovery 34 years after the 1988 Yellowstone fires in the Greater Yellowstone Ecosystem, Wyoming, USA.

Model coefficient	Effect (*p*-value)	
	Fixed	Random
Intercept	**−1.66 (1.3×10^{-10})**	**3.49 ($<2 \times 10^{-16}$)**
Stem density (stems ha^{-1})	**−0.34 (0.001)**	0.13 (0.057)
Soil clay content (%)	0.13 (0.200)	**0.33 (8.7×10^{-8})**
Elevation (m)	**−0.26 (0.042)**	**0.64 ($<2 \times 10^{-16}$)**
Slope (°)	0.14 (0.132)	**0.26 (2.5×10^{-6})**
Topographic moisture index (unitless)	**0.26 (1.7×10^{-5})**	0.02 (0.306)
30-year winter snow water equivalent (mm)	**0.50 (0.001)**	**0.63 (6.0×10^{-16})**
30-year summer water deficit (mm)	**0.38 (0.0001)**	0.02 (0.782)

Note: $R^2_{pred} = 0.54$. See Appendix S1: Table S9 for species-level responses to predictors.

Shrub species responded consistently to all environmental factors except elevation, tending to become more likely with greater winter snowfall, higher soil clay content, and on steeper slopes (Appendix S1: Table S9). Only *Vaccinium scoparium* Leiberg ex Coville was more likely at higher elevations, whereas *Lonicera utahensis* S. Watson, *Spiraea betulifolia* Pall., and *Vaccinium membranaceum* Douglas ex Torr. were more likely at lower elevations (Appendix S1: Table S9).

Carbon stocks

Total aboveground carbon in areas of sparse and reduced forest recovery averaged 66.3 ± 3.6 Mg C ha^{-1} and varied considerably among plots (28.0–131.4 Mg C ha^{-1}), driven by differences in the abundance of downed coarse wood (Table 7). Nearly all (96%) aboveground C was stored in coarse wood, with only 2.5% of aboveground C stored in live conifer trees, seedlings, and saplings. Mineral soil C (0–30 cm) stocks were comparable with total aboveground C (75.9 ± 5.7 Mg C ha^{-1}) and made up >50% of total ecosystem C (142.6 ± 7.3 Mg C ha^{-1}) but varied considerably more among plots (14.4–262.8 Mg ha^{-1}).

For aboveground C stocks, only live conifer C varied among recovery pathways ($F_{2,52} = 2.59$, Pillai = 0.26, $p = 0.023$), with two to three times more C stored in potentially recovering plots compared with persistently sparse plots (Table 3c, Appendix S1: Table S10). Live conifer C stocks also decreased with elevation ($F_{4,49} = 3.836$, $R^2_{adj} = 0.18$, $p = 0.0086$; Appendix S1: Table S11). Carbon in understory plant communities did not vary across plots ($F_{4,49} = 0.796$, $R^2_{adj} = -0.02$, $p = 0.53$; Appendix S1: Table S11) but declined with Simpson's diversity ($F_{1,53} = 29.69$, $R^2_{adj} = 0.35$, $p = 1.3 \times 10^{-6}$). Coarse wood C also did not vary among recovery pathways and was not predicted at the plot level by the variables considered here (Appendix S1: Table S11). However, the proportion of coarse wood C stored in sound versus rotten wood increased with elevation ($F_{1,53} = 20.35$, $R^2_{adj} = 0.26$, $p = 3.6 \times 10^{-5}$). Mineral soil C increased on northeast-facing slopes and decreased with soil clay content ($F_{4,48} = 4.072$, $R^2_{adj} = 0.19$, $p = 0.0064$; Appendix S1: Table S11).

TABLE 7 Carbon stocks in plots ($n = 55$) of sparse and reduced forest recovery sampled 34 years after the 1988 Yellowstone fires in the Greater Yellowstone Ecosystem, Wyoming, USA.

C stock	Mean ± SE Mg C ha^{-1}	Range
Live conifers	1.7 ± 0.3	0–8.4
Live ground layer (forb, graminoid, shrub)	0.9 ± 0.05	0.2–1.8
Downed coarse wood	63.7 ± 3.6	27.0–130.0
Total aboveground	66.3 ± 3.6	28.0–131.4
Mineral soil (0–30 cm)	75.9 ± 5.7	9.4–262.8
Total ecosystem	142.6 ± 7.3	60.9–342.3

DISCUSSION

We detected three recovery pathways among areas of sparse and reduced forest recovery, with both "slow" and "no" recovery present 34 years after large, stand-replacing wildfire. Nearly half of the plots showed patterns consistent with regime shifts and persistent conversion to sparse or non-forest. Other areas appeared to be on a slow path to forest recovery either via continuous infilling or a recent pulse of seedling and sapling establishment owing to seed pressure from both ex situ and in situ sources. Ecosystem components (i.e., understory plant communities and aboveground C stocks) varied in their resilience. Understory richness remained high and non-native species cover low, but community composition shifted toward meadow-affinity species where trees were sparse or absent. However, forest-affinity species persisted with greater postfire stem densities and in topo-edaphically mesic conditions,

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implicating factors like microclimate in the magnitude community change. Regardless of compositional changes, ground cover of meadow species and graminoids in all three recovery pathways may be a stabilizing feedback that constrains additional tree seedling establishment. The conifers in our study region germinate and establish on bare mineral soil, and such feedbacks could entrain forest conversion or greatly slow recovery rates. Finally, disruption of historical disturbance-recovery processes qualitatively and quantitatively altered C storage patterns, with nearly all aboveground C stored in downed coarse wood biomass. If C losses from initial combustion and continued decomposition are not offset by C sequestration via tree establishment and growth, areas of sparse recovery may fail to recover C stocks before burning again.

Detecting pathways of recovery and their drivers

The presence of few to no seedlings and saplings in persistently sparse plots suggest these areas have undergone a regime shift that will persist for some time. In contrast, areas with continuous infilling and recent seedling and sapling establishment may be only temporarily restructured as sparse forest (Seidl & Turner, 2022). Assuming additional establishment coupled with seedling and sapling survival, these areas are likely in a transient restructuring phase prior to eventual forest recovery (Falk et al., 2022). However, continued changes to climate and wildfire regimes in Greater Yellowstone may impede these slow recovery pathways via poor establishment conditions and more frequent fire (Hansen & Turner, 2019; Turner et al., 2022), instead maintaining slowly recovering forest as sparse or non-forest and reinforcing already converted areas into non-forest states (Falk et al., 2022). Importantly, these alternative recovery pathways were only detectable several decades after succession was initiated, and the methods used here, though field intensive, are readily applicable to other areas and ecosystems. Long-term postfire recovery pathways among areas of inhibited resilience are difficult to predict (Coop et al., 2020), so recovery pathways should be continually tracked in the decades following disturbance (Abella et al., 2021; Lecina-Diaz et al., 2024; Stevens-Rumann et al., 2022).

Both ex situ and in situ seed pressure were important for distinguishing pathways of sparse postfire forest recovery, with in situ pressure from cone-bearing trees and ex situ seed source direction differing among pathways. Nearly all (96%) cone-bearing trees across plots were lodgepole pine, suggesting this species is primarily responsible for recent pulses of seedling and sapling establishment up to 34 years postfire. Lodgepole pine can mature within a decade in open growing conditions (Alexander, 1974) and began producing cones following the 1988 fires earlier at lower (<2300 m) elevations (Turner et al., 2007). This may have also driven the elevational differences between continuous infilling and recent establishment, as lodgepole pine densities declined with elevation. Somewhat surprisingly, local seed source abundance (i.e., the area of unburned forest within 150 m of plot center) did not differ among pathways. This may in part be explained by our focus on areas that have remained sparse or non-forest for more than three decades postfire. Locations burned as stand-replacing fire with high local seed source abundance upwind or uphill are not likely to have exhibited persistent sparse and reduced forest recovery and instead may already be recovering to forest.

Species- and age-specific stem densities were variably influenced by both the spatial arrangement and local abundance of seed sources, highlighting the importance of considering several metrics of seed pressure when identifying drivers of tree regeneration (Peeler & Smithwick, 2020). For the wind-dispersed species in our region, most seeds disperse <150 m away from mature trees (Greene & Johnson, 1996; Harvey et al., 2016b; Kemp et al., 2016; Littlefield, 2019). However, rare long-distance (~400 m) dispersal events may be important for forest recovery (Horn et al., 2001), especially in large patches of stand-replacing fire (Laughlin et al., 2023). While lodgepole pine tree and subalpine fir stem densities increased with local seed source abundance, this effect became negative for lodgepole pine seedling and sapling densities, which were instead driven by in situ cone-bearing trees and uphill seed sources. Importantly, seed production varies annually (Alexander, 1974, 1987), and the observed seedling and sapling densities may in part be driven by interannual variation in both seed abundance and climate. While some young stems will likely fail to survive, the lack of canopy cover should allow many to persist, assuming climate conditions remain suitable. Conversely, declining whitebark pine stem densities with local seed source abundance likely relates to its dispersal ecology, with Clark's Nutcracker capable of dispersing seeds of several species, including whitebark pine, considerable distances (Hutchins & Lanner, 1982; Vander Wall & Balda, 1977).

Plot-level establishment conditions were similarly important in shaping postfire tree regeneration and forest recovery. Greater stem densities with higher winter snowfall, an important driver of seasonal moisture availability, have been observed elsewhere in western North America (Andrus et al., 2018; Lubetkin et al., 2017) and were found for lodgepole pine and subalpine fir among our plots. Higher elevation tree species (i.e., subalpine fir and whitebark pine) also appeared to benefit from warmer summer growing conditions, but continued climate warming may exceed temperature thresholds for

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establishment of dominant tree species in the region (Hansen & Turner, 2019; Kueppers et al., 2017). In such cases, mesic topographic positions may act as refugia for seedling establishment in drought conditions (Harvey et al., 2016b). Temperatures in YNP increased by ~2.5°C from 1982 to 2015 while winter snowpack has declined (Notaro et al., 2019), which may have influenced establishment across our plots (Appendix S1: Figures S4–S6). However, because of our nondestructive estimate of stem ages, we are limited in our ability to determine the climate conditions associated with years of high versus low seedling establishment. Future work relating interannual climate variability with species-specific establishment in sparsely forested areas would further understanding of slow postfire forest recovery dynamics.

Sparse, slowly recovering postfire pathways may exemplify "precocious" forests (Donato et al., 2012) that skip the stem-exclusion stage of standard forest succession (Oliver, 1981) and develop a more complex vertical structure like that of old forests (Franklin & Van Pelt, 2004; Halpern & Spies, 1995; Qian et al., 2009). The variation in tree ages among slow pathways would likely lead to much greater variation in tree heights and crown widths relative to high-density, even-aged stands where trees are of similar size (e.g., Turner et al., 2004, 2016). Precocious stand development has been observed elsewhere in temperate forests via mixed-severity fire regimes (Keeton & Franklin, 2005; Meigs et al., 2017; Tepley et al., 2013), but we suggest precocity is possible in areas burned solely as severe, stand-replacing fire where tree regeneration is slow. However, the development of precocious forests with old-growth attributes assumes adequate time for forest succession and recovery prior to reburning, a prospect increasingly unlikely with changing climate and wildfire activity in the region (Hostetler et al., 2021; Rammer et al., 2021; Westerling et al., 2011).

Other potential drivers of postfire forest recovery dynamics not included in our analyses warrant consideration in this and other contexts. The species identity of surrounding unburned forest acting as putative ex situ seed source can influence postfire forest recovery pathways (e.g., Walker et al., 2023). Though not quantified for our study, unburned forest composition varies with elevation (Baker, 1986; Despain, 1990), which was an important driver of stem densities for the three most abundant tree species. Postfire stem densities also vary with prefire abundance of serotinous cones in populations of lodgepole pine (Turner et al., 1997, 2003), which could not be determined in our plots more than three decades postfire. However, the average elevation of our sampling locations was >2500 m, with most plots well above the elevation at which levels of serotiny sharply decline (~2400 m; Schoennagel et al., 2003; Tinker et al., 1994). Non-serotinous cones that are not combusted during stand-replacing wildfire can contribute to early postfire lodgepole pine seedling establishment, especially in stands burned as severe-surface as opposed to severe-crown fire (Turner et al., 1997). However, the positive relationship between lodgepole pine tree densities and local seed source abundance, as well as relatively high whitebark pine tree densities in our plots, suggests ex situ seed pressure was more important for establishment after the 1988 fires than in situ canopy seed banks. Finally, herbivory can alter post-disturbance forest recovery trajectories (Andrus et al., 2020). Among canopy trees in our study, quaking aspen is preferred as browse (Romme et al., 1995), particularly by elk (*Cervus canadensis*) in their winter ranges. We observed only six quaking aspen stems across all plots and did not document any browse on conifer seedlings or saplings, suggesting this mechanism may be of minimal importance for maintaining sparse and reduced postfire forest recovery in our study area.

Understory plant communities

Understory plant communities contained a mix of meadow- and forest-affinity species across all recovery pathways but were increasingly composed of meadow-affinity species where tree densities remained low. The abundance of species adapted to drier, sunnier conditions often increases in high light environments, leading to community thermophilization (De Frenne et al., 2015; Stevens et al., 2015). While we did not test for potential thermophilization per se, species more common to montane and subalpine meadows, by definition, prefer high light conditions, which may correlate with other indices of community thermophilization. The persistent lack of canopy closure in areas of sparse and reduced forest recovery also contributed to high relative graminoid cover, similar to findings elsewhere in Greater Yellowstone (Andrade et al., 2021). Increased graminoid abundance where tree densities are low has implications for subsequent tree seedling establishment and potential forest recovery, as rhizomatous graminoids (e.g., *Calamagrostis canadensis* (Michx.) P. Beauv. and *Ca. rubescens*) often compete with conifer seedings in temperate and boreal forests (Lieffers et al., 1993; Petersen, 1988). Such competitive effects of understory plant species on tree seedlings likely overwhelm any potential facilitative effects (e.g., as nurse plants; Gómez-Aparicio et al., 2004) given dominant tree species in the region preferentially establish on mineral soil (Alexander, 1974, 1987).

Despite these shifts, forest-affinity species remained relatively abundant and non-native species cover was conspicuously low, likely because surviving native perennial species resprouted shortly after the fire and

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subsequently seeded in (Anderson & Romme, 1991; Romme et al., 2016; Turner et al., 1997). Increased postfire abundance of non-native plant species is spatially variable and short-lived in the region (Romme et al., 2016; Wright & Tinker, 2012) even after anomalously short FRIs (Kiel, Braziunas, et al., 2023). Our study indicates non-native species did not invade even where trees remain sparse or absent more than three decades after fire. The greater relative abundance of forest-affinity species with soil clay content and on northeast-facing aspects also suggests more mesic topo-edaphic conditions can act as microrefugia (sensu Maclean et al., 2015) and buffer community change where trees do not recover. Further, the heterogeneous light environment where trees are present but sparse may maintain more shade-tolerant species (e.g., Drever & Lertzman, 2003). However, whether populations of forest-affinity species will persist where tree densities remain low is not known, especially as temperatures continue to rise. Forest canopy cover affects understory plant phenology, flowering, and performance (Lindh, 2005; Lorer et al., 2024; Scanga, 2014), and how such effects vary among forest- and meadow-affinity species and potentially drive temporal change in community composition where forests fail to recover warrants investigation.

Plant communities in areas of sparse forest recovery may be more sensitive to climate change without the buffering capacity of a forest canopy (De Frenne et al., 2019; De Lombaerde et al., 2022), as continued warming is expected to drive understory community change elsewhere in temperate forests (Braziunas et al., 2024). Alternatively, plant communities where forests have converted to sparse or non-forest may be better adapted than those beneath forest canopies where differences in macro- and microclimate are amplified (Perez-Navarro et al., 2024; Richard et al., 2021). Regardless of local forest cover, shifts in understory plant communities in Greater Yellowstone will likely continue with changing climate. For example, while most understory species were more likely to occur in areas of greater winter snowfall, annual snowpack has already declined by 25% since 1950, a trend that is likely to continue (Hostetler et al., 2021). Areas of sparse recovery may also be important for maintaining locally high understory richness and diversity, which decline with canopy closure (Halpern & Spies, 1995; Romme et al., 2016; Schoonmaker & McKee, 1988). However, more diverse communities in areas of sparse forest recovery did not store more C, likely due to the dominance of high-biomass clump-forming graminoids, indicating potential trade-offs in important ecosystem services. Monitoring these and other changes in understory plant community cover and composition with forest reorganization or conversion will continue to be critical to understand the future of temperate forest ecosystems (Landuyt et al., 2019).

Aboveground carbon stocks

Our results indicate that aboveground C stocks will be reduced for a long time where postfire tree regeneration is sparse, in strong contrast to the rapid recovery of C stocks where tree regeneration is dense (Kashian et al., 2013; Turner et al., 2004, 2016). With sparse tree regeneration, only 4% of aboveground C was stored in live vegetation. Even this small proportion is likely an overestimate because we did not measure fine surface fuels or litter, both of which contribute to aboveground biomass and C (Braziunas et al., 2023; Nelson et al., 2016). Live tree C was roughly an order of magnitude lower than that in 16–28-year-old postfire recovering lodgepole pine forests (Turner et al., 2019). Understory C stocks were comparable with national estimates derived from U.S. Department of Agriculture Forest Inventory and Analysis plots (Johnson et al., 2017) but were ~ 34% greater than those in recovering forests 24 years after the 1988 fires (Turner et al., 2016). Notably, the understory C stock size was of comparable magnitude to that stored in live conifers, a sharp departure from postfire stands with high tree densities. Thus, understory vegetation may be of greater relative importance for C cycling where tree regeneration is low (e.g., Coop et al., 2020; Powers et al., 2013). Additionally, biomass turnover is high in forest understories (Gilliam, 2007; Muller, 2014), so its role in materials cycling may be outsized relative to what its standing stock size would suggest (Moore et al., 2007; Yarie, 1980).

The amount of C stored in coarse wood in our study area was 1.5–10 times higher than other young (16–35-year-old) subalpine forests in Greater Yellowstone (Kashian et al., 2013; Nelson et al., 2016; Turner et al., 2019). We sampled generally higher elevation areas dominated prefire by old Engelmann spruce and subalpine fir forests (Despain, 1990) which often attain greater individual sizes and total stand wood volumes than lodgepole pine (Alexander, 1974, 1987). This can lead to greater postfire coarse wood abundance (Nelson et al., 2016) that may also persist for a longer time given slow rates of wood decay at high elevations (Acker et al., 2013; Brown et al., 1998; Kueppers et al., 2004). Nonetheless, continued decomposition without concomitant tree regeneration will protract C recovery (Kashian et al., 2006) and potentially amplify projected declines in subalpine forest ecosystem C with continued climate change (Kueppers & Harte, 2005).

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Conclusions

Leveraging 34 years of succession following a large, natural disturbance, we detected both "no" and "slow" forest recovery pathways primarily driven by variable seed pressure. Persistently sparse areas appear to have experienced a regime shift, with little to no evidence of eventual forest recovery in the form of young tree seedlings and saplings. If applied to the total area of sparse and reduced recovery three decades after the 1988 Yellowstone fires (Kiel & Turner, 2022), our results suggest upward of 18,000 ha of previously forested area may have experienced conversion. In contrast, slightly more than half of our plots are in a transient restructuring phase and slowly recovering to forest, as occurred historically in these high-elevation subalpine forests (Peet, 1981; Stahelin, 1943). However, long-term forest recovery in these areas remains uncertain given changes in both climate and wildfire. Tree seedling establishment in high-elevation subalpine forests is sensitive to climate and microsite availability (Elliot, 2011, 2012; Hansen & Turner, 2019), and expected warming, drying trends will likely affect tree regeneration (Conlisk et al., 2017; Kueppers et al., 2017; Smithers et al., 2021). Continued monitoring of potential forest recovery is needed for a mechanistic understanding of slow recovery dynamics in an era of rapid global change.

In the absence of a closed canopy among areas of poor postfire forest recovery, plant communities were increasingly dominated by meadow species. These understory communities may be exhibiting "adaptive community dynamics" sensu Carroll et al. (2023), and their more rapid response capacities may make them useful indicators of environmental change. However, the persistence of forest-affinity species in relatively mesic areas suggests both the importance of microrefugia and the potential for increasing mismatches of plant communities with changing climate (i.e., climatic debt; Bertrand et al., 2016). The dominance of graminoids in areas of sparse recovery and their potential to constrain tree seedling establishment and reinforce conversion raises questions about long-term trajectories and future C stocks. In areas not managed as wilderness, areas of sparse tree recovery might be targeted for planting if a goal is to enhance C assimilation. However, this must be balanced with other ecosystem services like floral and faunal diversity that may increase where sparse or non-forest predominates.

Changing global drivers, including climate and disturbance regimes, are reshaping the world's forests, with myriad implications for Earth system functioning and biodiversity (Ellison et al., 2024; Harris et al., 2021; Seidl et al., 2017; Trumbore et al., 2015). Wildfire is changing globally (Bowman et al., 2020; Cunningham et al., 2024; Pausas & Keeley, 2021), and with it the forests that burn. Additional field studies in diverse fire-prone regions are critical for both distinguishing transient postfire forest reorganization from regime shifts and elucidating how, where, and why forests are changing. As government agencies and wildland managers grapple with whether to resist, accept, or direct ecosystem change (Lynch et al., 2021; Schuurman et al., 2022), understanding the nature of ecosystem transformations will reveal the consequences of accepting ecosystem change.

AUTHOR CONTRIBUTIONS

Nathan G. Kiel and Monica G. Turner designed the study. Nathan G. Kiel and Eileen F. Mavencamp collected data. Nathan G. Kiel analyzed data with contributions from Eileen F. Mavencamp. Nathan G. Kiel and Monica G. Turner wrote the paper with contributions from Eileen F. Mavencamp.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kiel et al., 2024) are available in the Environmental Data Initiative EDI Data Portal at https://doi.org/10.6073/pasta/4740d3b18c56f0f426b7b3eaa2cf0800.

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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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