

Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function?

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Abstract. Disturbance and succession have long been of interest in ecology, but how landscape patterns of ecosystem structure and function evolve following large disturbances is poorly understood. After nearly 25 years, lodgepole pine (*Pinus contorta* var. *latifolia*) forests that regenerated after the 1988 Yellowstone Fires (Wyoming, USA) offer a prime opportunity to track the fate of disturbance-created heterogeneity in stand structure and function in a wilderness setting. In 2012, we resampled 72 permanent plots to ask (1) How have postfire stand structure and function changed between 11 and 24 yr postfire, and what variables explain these patterns and changes? (2) How has landscape-level (among-stand) variability in postfire stand structure and function changed between 11 and 24 yr postfire? We expected to see evidence of convergence beginning to emerge, but also that initial postfire stem density would still determine trajectories of biomass accumulation. After 24 yr, postfire lodgepole pine density remained very high (mean = 21,738 stems/ha, range = 0–344,067 stems/ha). Stem density increased in most plots between 11 and 24 yr postfire, but declined sharply where 11-yr-postfire stem density was >72,000 stems/ha. Stems were small in high-density stands, but stand-level lodgepole pine leaf area, foliage biomass, and live aboveground biomass increased over time and with increasing stem density. After 24 yr, mean annual lodgepole pine aboveground net primary production (ANPP) was high (mean = 5 Mg·ha⁻¹·yr⁻¹, range = 0–16.5 Mg·ha⁻¹·yr⁻¹). Among stands, lodgepole pine ANPP increased with stem density, which explained 69% of the variation; another 8% of the variation was explained by environmental covariates. Early patterns of postfire lodgepole pine regeneration, which were contingent on prefire serotiny and fire severity, remained the dominant driver of stand structure and function. We observed mechanisms that would lead to convergence in stem density (structure) over time, but it was landscape variation in functional variables that declined substantially. Stand structure and function have not converged across the burned landscape, but our evidence suggests function will converge sooner than structure.

Key words: biomass; disturbance; productivity; Rocky Mountains; subalpine forest; succession; wildfire; Yellowstone National Park.

INTRODUCTION

Disturbance and succession have long been of interest in ecology (Peters et al. 2011, Christensen 2014), but how landscape patterns of ecosystem structure and function evolve following large disturbances is not well understood. Natural disturbances create complex landscape patterns (Foster et al. 1998, Turner 2010) that set the stage for succession and influence ecosystem dynamics long into the future (Kashian et al. 2005a,b, Tepley et al. 2013). Long-term study of ecosystems regenerating after major disturbance events can provide insights into processes of recovery (Lindenmayer et al. 2010). Successional dynamics are key for carbon storage, wildlife habitat,

and many forest ecosystem services (Turner et al. 2013), but spatial heterogeneity in ecosystem structure and function within early successional systems is not well studied (Swanson et al. 2011, Donato et al. 2012).

Forest age is a primary driver of forest structure and function, yet variation in post-disturbance regeneration among stands of the same age may confound simple age-based relationships (Bradford et al. 2008). Further, the magnitude of spatial variation within a given early successional stage may approach the amplitude of temporal change in average stand characteristics during succession (Turner 2010), with key implications for carbon balance over the disturbance cycle (Kashian et al. 2006, Smithwick et al. 2009). How spatial variation in structure and function evolves through time is poorly known, yet understanding variability in ecological responses to disturbance can provide novel insights about disturbance effects and mechanisms (Kashian

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et al. 2005a,b, Fraterrigo and Rusak 2008). In particular, assessing deviations from a measure of central tendency (e.g., coefficient of variation) can reveal effects missed or obscured by averaging (Kashian et al. 2005a, Fraterrigo and Rusak 2008) and provide a more complete assessment of landscape function.

Increased understanding of early seral forests is especially important in the northern Rocky Mountains, where stand-replacing fires burned >1.15 million ha between 1984 and 2010, accounting for 34% of total area burned and 5% of the region's forested area (Harvey 2015). As the frequency and size of stand-replacing fires increase with warmer temperatures, earlier snowmelt, and longer fire seasons (Westerling et al. 2006, Morgan et al. 2008), young forests occupy more of the landscape. Stand-replacing fires dominate the disturbance regime of many northern coniferous forests (Johnson 1992, Turner and Romme 1994, Schoennagel et al. 2004), and fire frequency and size are expected to increase in coming decades (Westerling et al. 2011, Barbero et al. 2015). Knowledge of postfire stand development is essential for anticipating the future of these forest landscapes and their role in regional carbon budgets (Stephens et al. 2013, Kishchuk et al. 2015, Trumbore et al. 2015).

The 1988 fires in Yellowstone National Park (USA) created opportunities to study postfire forest structure and function at an unprecedented scale in a wilderness setting (Romme et al. 2011, Turner et al. 2016). The fires burned under extreme drought and high winds, affected ~600 000 ha in Greater Yellowstone, and produced a complex landscape mosaic of patches that varied in size, shape and burn severity (Turner et al. 1994). Plant re-establishment was rapid and spatially variable (Turner et al. 1997, 1999). Although serotinous lodgepole pines (*Pinus contorta* var. *latifolia*) are known for regenerating in dense, even-aged stands following stand-replacing fire, the range of lodgepole pine densities measured after the 1988 fires, from 0 to >500 000 stems/ha, was surprising (Turner et al. 1997, 1999, 2003, 2004). This variation was largely due to two contingent effects, the proportion of prefire lodgepole pines bearing serotinous cones and local fire severity, rather than topoedaphic conditions (Turner et al. 1997, 1999). Heterogeneity in postfire stem density also generated a functional mosaic in which landscape patterns of leaf area index (LAI) and aboveground net primary production (ANPP) varied widely with stem density (Turner et al. 2004, 2009, Schoennagel et al. 2008, Turner 2010).

After nearly 25 yr, the forests that regenerated after the 1988 fires offer a prime opportunity to track the fate of disturbance-created heterogeneity in stand structure and function. Lodgepole pine density and growth rates converge during the multi-century interval between fires (Kashian et al. 2005a), but pathways to structural and functional convergence remain unresolved. Self-thinning is widely reported in lodgepole pine stand development (Peet and Christensen 1980), but the balance between mortality and ongoing tree recruitment is not well

understood. Young lodgepole pines are very productive, reaching maximum rates of ANPP between 24 and 60 yr (Pearson et al. 1987, Ryan et al. 1997, Kashian et al. 2013). Stands regenerating from the 1988 fires are approaching peak ANPP and could be nearing transitions in structure and function.

We resampled permanent plots 24 yr after the 1988 Yellowstone fires to ask (1) How have postfire stand structure and function changed between 11 and 24 yr postfire, and what variables explain these patterns and changes? (2) How has landscape-level (among-stand) variability in postfire stand structure and function changed between 11 and 24 yr postfire? We expected to see evidence of convergence beginning to emerge. For stand structure, we expected mean postfire stem density and among-stand variation in postfire stem density to have declined substantially through density-dependent mortality in most stands and gradual tree recruitment in low-density stands. We expected aboveground live lodgepole pine biomass, LAI, and ANPP to have increased because these even-aged early seral forests are aggrading (Ryan et al. 1997). In contrast, we expected herbaceous ANPP to have declined over time because of increasing competition with the rapidly growing trees. Among stands at postfire year 24, we expected stem density to remain a "master variable" determining trajectories of biomass accumulation. We expected lodgepole pine ANPP to be highest in stands of intermediate density; low-density stands would have too few trees to reach high ANPP, and high-density stands would have experienced intense intra-specific competition. Finally, we expected environmental variability (elevation, soils, growing season precipitation) to have a secondary but detectable influence on ANPP because, although these gradients did not drive initial postfire stem density (Turner et al. 1997, 1999), they influence growing season length and drought stress.

STUDY AREA AND METHODS

Study area

Yellowstone National Park encompasses 9000 km² on a high-elevation (~2050–2650 m) forested plateau in northwest Wyoming, USA. Approximately 80% of the park is dominated by lodgepole pine forest, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelm.) may be locally abundant at higher elevations (Despain 1990). Our study area was the forested subalpine plateau that covers most of Yellowstone (Fig. 1) and encompasses dry, infertile, rhyolitic substrates as well as more mesic and slightly less infertile andesitic and former lake-bottom substrates. The climate is generally cool and dry, but the summer of 1988 was the driest on record since 1886 (Renkin and Despain 1992).

Large, stand-replacing fires have occurred at 100–300 yr intervals during warm, dry periods throughout the

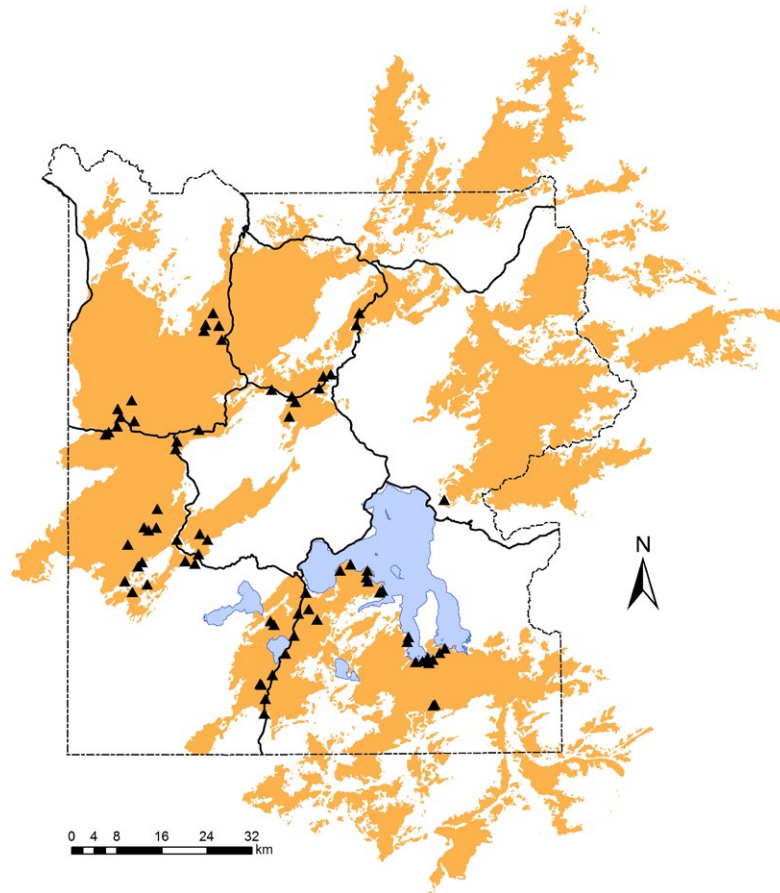


FIG. 1. Map of Yellowstone National Park, Wyoming, USA, showing locations of all 72 study plots and the pattern of the 1988 fires (orange shading).

Holocene (Romme and Despain 1989, Meyer and Pierce 2003, Millsbaugh et al. 2004, Whitlock et al. 2008, Higuera et al. 2011). However, the 1988 fires were remarkable for their severity and size. They resulted from synoptic climate patterns, not from past fire suppression, and were only minimally affected by variation in stand age or structure (Johnson and Wowchuck 1993, Turner and Romme 1994, Turner et al. 1994, Bessie and Johnson 1995, Flannigan and Wottan 2001). In Yellowstone's forests, severe, stand-replacing fire kills all trees, consumes the shallow litter layer, and exposes mineral soil; postfire forests have essentially no duff. Tree regeneration was rapid (Turner et al. 1999), and stem density patterns established in the first 2 yr following fire had not changed through 2000, the twelfth year after the fire (Turner et al. 2003, Turner 2010).

Data collection

Ninety widely distributed 0.25-ha plots were established in 1999 (11 yr postfire) in areas that had burned in 1988 as stand-replacing fire in mature forests (Turner et al. 2004). During summer 2012 (24 yr postfire),

vegetation was resampled in 72 of these plots that spanned the full range of postfire stand densities recorded in 1999. Plots were relocated by navigating to a rock cairn that marked each center point (coordinates in UTM NAD83 Zone 12N) with a global positioning system unit, and field sampling followed methods used previously (see Turner et al. [2004] for full description). Briefly, postfire live stem density was recorded by species in each plot along three parallel 50×2 m belt transects oriented to the north and separated by 25 m. Additionally, current-year lodgepole pine seedlings and dead postfire lodgepole pine stems were tallied. Percent cover of understory plants was recorded by species within eight 0.25-m^2 quadrats positioned at 5-m intervals along the two outer transects, and nine quadrats positioned similarly along the center transect ($n = 25$ quadrats per plot). For the lodgepole pine nearest to each 5-m interval ($n = 25$ trees per plot), we recorded basal diameter and height; for stems >1.4 m tall, diameter at breast height (DBH) was measured. In addition, we recorded the presence and abundance of cones and whether any serotinous cones were present on each tree. Serotinous cones were identified by their age (>3 yr) and morphology

(assymetrical shape, acute angle of branch attachment, tightly closed, and weathered gray color), as in prior studies (Tinker et al. 1994, Turner et al. 1997, 2007, Schoennagel et al. 2003). We computed the percentage of trees with cones, the percentage of trees bearing serotinous cones, and stand-level cone abundance (mean cones per stem \times stem density).

Foliage biomass, total aboveground live biomass, LAI, and ANPP were estimated for each measured lodgepole pine by using new allometric equations developed from destructive sampling of 60 24-yr-old lodgepole pines within our study area (Copenhaver and Tinker 2014). Basal diameter was used to predict each response, and the models performed well (Copenhaver and Tinker 2014). We averaged measurements for the eight or nine trees on each transect, multiplied by stem density on that transect, then averaged across the three transects to predict stand-level lodgepole pine LAI (m^2/m^2), aboveground biomass (Mg/ha), and ANPP ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$). Understory ANPP was estimated from species-specific allometric equations based on aboveground percent cover, which we developed previously (Turner et al. 2004). These equations were applied to the percent cover of each species recorded in the 25 quadrats in each plot. Total herbaceous ANPP was computed by summing across all graminoid and forb species.

Environmental covariates

Topoedaphic covariates included elevation (meters above sea level) and substrate, which was grouped into four categories, according to physical characteristics of the soil and their expected effect on vegetation (Turner et al. 2004). Ranked numerically from least to most fertile based on nutrient status and water-holding capacity (Turner et al. 2004), substrate categories included (1) rhyolite till, which occurs on uplands and is derived from rhyolite-based glacial till; (2) rhyolite glacial, located on glacial outwash plains; (3) rhyolite low-base saturation, occurring on lake plains and derived from rhyolite-based glacial rubble; and (4) andesite, including soils derived from andesite, as well as alluvial deposits. All plots were in stand-replacing fire, but in case there were effects of variation in fire severity, satellite-derived measures of 1988 burn severity were acquired from the Monitoring Trends in Burn Severity database (MTBS; Eidenshink et al. 2007; data *available online*).⁵ We used the differenced Normalized Burn Ratio (dNBR), which is an appropriate index of fire severity when all study sites had similar pre-fire vegetation. To avoid interpolation errors when projecting dNBR to the UTM for plot center, we used a 3×3 window smoothing algorithm on the dNBR layer. Because unburned forest could potentially influence post-fire stem density, we calculated distance from each plot to the nearest unburned forest (defined as dNBR < 100 on the 30-m resolution dNBR map) in ArcMap (ESRI, Redlands, California, USA). Gridded precipitation

PRISM data (4-km resolution) were used to calculate mean annual precipitation for the prior decade (2003–2012) for each plot (PRISM Climate Group 2014). Slope and aspect were not included because plots were on flat terrain to eliminate these potentially confounding effects. See Appendix S1: Table S1 for mean values.

Data analysis

Data on variables related to stand structure and function were summarized across plots, and mean, median, range, and coefficient of variation (CV) were calculated and compared with the 1999 data. Data were tested for normality, and lodgepole pine density, LAI, total aboveground live biomass, foliage biomass, and ANPP were transformed using $\log_{10}(x + 1)$ prior to subsequent analysis. Three plots were removed from all analyses that directly compared 1999 and 2012 plot-level data because error in the 1999 GPS coordinates prevented their precise relocation. All statistical analyses were performed in SAS version 9.4 (SAS Institute 2015).

Multiple linear regression was used to relate postfire year 24 stem density and new seedling density to postfire year 11 stem density and the environmental covariates. We computed the net difference in stem density between the two years for each plot ($n = 69$) and the frequency of plots with a net increase or decrease, then modeled net stem-density change as a function of stem density at postfire-year 11. Scatter plots indicated nonlinear relationships of both net stem-density change and density of postfire standing dead lodgepole pines with postfire year 11 stem density. Therefore, we used segmented regression to test for the significance and position of breakpoints in the relationship between these two response variables and postfire year 11 stem density. Segmented regression minimizes the sum of squares of the differences between the dependent and independent variables by incorporating the possibility of a breakpoint in the data and producing separate linear relationships for data on either side of value of the independent variable identified as the breakpoint. Finally, because explanatory variables associated with a net increase or decrease in stem density could differ, effects on net stem-density change were modeled separately for stands that gained or lost stems.

For stand structure variables (mean tree height, basal diameter, DBH, and cone prevalence), we assessed relationships with stem density by correlation analysis. For stand function variables (lodgepole pine LAI, aboveground biomass and ANPP, and herbaceous ANPP), we evaluated effects of stem density as well as environmental covariates using general linear models. We used Adaptive Lasso Selection with the Schwarz Bayesian Criteria (SBC) to identify the most parsimonious model, then determined the explanatory power (partial r^2) for each covariate included in the selected model. The SBC method applies weights to each of the parameters in forming the lasso constraint (Zou 2006) and performs exceptionally well among alternative model selection methods (Beal 2007).

⁵ www.mtbs.gov

To evaluate landscape variation in stand structure and function across years, we compared coefficients of variation (CV) for each response variable in 1999 and 2012. We also computed the nonparametric equivalent, the quartile coefficient of dispersion (QCD), and results were consistent. We report only the CV here for comparison with prior studies. The nonparametric Brown-Forsyth's test was used to test homogeneity of variance between time periods.

RESULTS

Postfire stand structure

Stem density.—Twenty-four years after the 1988 fires, postfire lodgepole pine density remained very high, averaging >21,000 stems/ha and ranging from 0 to >340,000 stems/ha (Table 1; see Appendix S2: Fig. S1 for photos). Although the density of other conifers increased slightly, lodgepole pine remained dominant (Table 1). Lodgepole pine density (hereafter stem density) at postfire year 24 was strongly positively correlated with density at postfire year 11 (Fig. 2a; $r = 0.89$, $P < 0.0001$). Stem density also was negatively correlated with elevation ($r = -0.62$, $P < 0.0001$) and unrelated to distance from unburned forest. Density of first-year lodgepole pine seedlings was low (Table 1) and unrelated to stem density, distance from unburned forest, cone presence/abundance, or any other environmental variable measured in this study (all $P > 0.30$).

Between postfire years 11 and 24, stem density increased by ≥ 100 stems/ha in 58% of the sampled stands and decreased by ≥ 100 stems/ha in 34% of the plots (Fig. 3). Maximum net stem loss (253,533 stems/ha) was an order of magnitude greater than maximum net stem gain (12,834 stems/ha). Net change in stem density was not linearly related to postfire year 11 stem density (Fig. 2b). Segmented regression explained 85% of the variation in net stem-density change and identified a

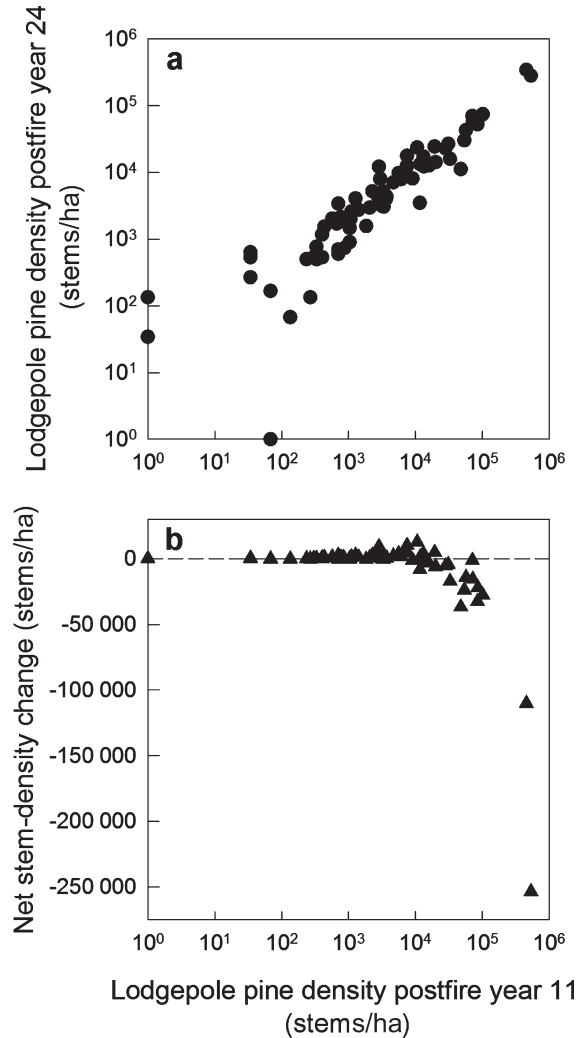


FIG. 2. (a) Lodgepole pine stem density in postfire year 24 and (b) net change in stem density between postfire years 11 and 24 plotted by stem density in postfire year 11.

TABLE 1. Postfire stem density in forest stands ($n = 72$) regenerating after the 1988 Yellowstone Fires. Stands were sampled in 1999 (Turner et al. 2004) and in 2012.

Tree species	Stem density (stems/ha)					
	Postfire year 11			Postfire year 24		
	Mean	Median	Min–Max	Mean	Median	Min–Max
<i>Pinus contorta</i> var. <i>latifolia</i>						
Live stems	33,054 ± 10 949	2900	0–535,000	21,738 ± 6397	4050	0–344,067
First-year seedlings (2012 only)	n/a			68 ± 19	0	0–900
Dead postfire stems (2012 only)	n/a			1284 ± 689	33	0–43,067
<i>Abies lasiocarpa</i>	9 ± 3	0	0–133	57 ± 24	0	0–1600
<i>Picea engelmannii</i>	5 ± 2	0	0–167	74 ± 29	0	0–1733
<i>Pinus albicaulis</i>	5 ± 2	0	0–100	44 ± 16	0	0–967
<i>Populus tremuloides</i>	329 ± 92	50	0–4367	117 ± 55	0	0–3933
Total of all species	33,184 ± 10,999	2983	0–538,900	22,030 ± 6389	4917	0–344,067

Notes: Error measure is SE. The range shows minimum (Min) to maximum (Max) values.

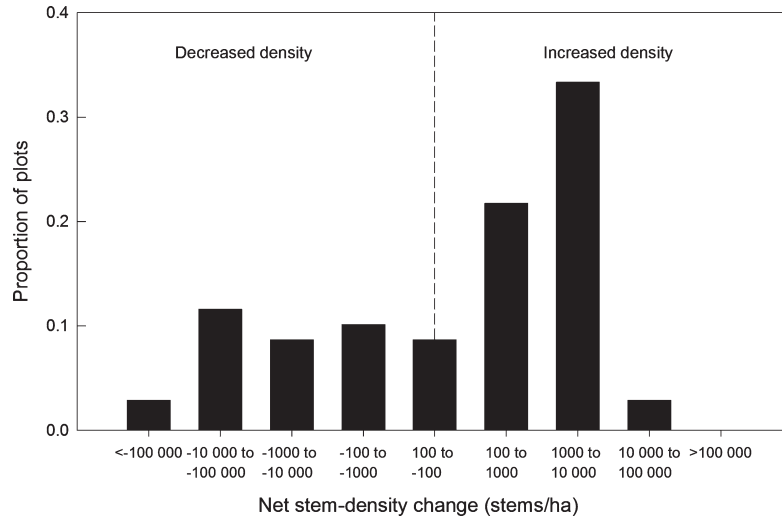


FIG. 3. Proportion of plots ($n = 69$) with different levels of net change in lodgepole pine stem density between postfire years 11 and 24 in areas burned in the 1988 fires. Dashed line indicates no change.

TABLE 2. Segmented regression model for net change in lodgepole pine stem density between postfire year 11 and 24 and for dead lodgepole pine stem density at postfire year 24 as a function of stem density at postfire year 11 ($n = 69$ plots).

Parameter	Parameter estimate β (SE)	95% confidence limits
Net change in live stem density from 1999 to 2012 (postfire year 11 to 24)		
Breakpoint in 1999 $\log(x + 1)$ stems/ha	$4.8584 \pm 0.0435\ddagger$	4.7715 to 4.9453
β for 1999 stem density < breakpoint	-2314 ± 1621	-5554 to 924
β for 1999 stem density > breakpoint	$-213,340 \pm 16,440$	-246,173 to -180,507
Model adj. $r^2 = 0.85$		
Density of dead stem density in 2012 (postfire year 24)		
Breakpoint in 1999 $\log(x + 1)$ stems/ha	$4.7618 \pm 0.3428\ddagger$	4.0771 to 5.4464
β for 1999 stem density < breakpoint	0.6656 ± 0.1093	0.4473 to 0.8839
β for 1999 stem density > breakpoint	1.49 ± 0.9182	-0.3356 to 3.3321
Model-adjusted $r^2 = 0.51$		

Note: Error measurement is SE.
 \ddagger Untransformed 1999 stem density = 72,177 stems/ha.
 \ddagger Untransformed 1999 stem density = 57,783 stems/ha.

breakpoint; stem density declined sharply where 11-yr-postfire stem density was >72,000 stems/ha but changed little in stands below the breakpoint (Table 2, Fig. 2b). Segmented regression explained 51% of the variation in density of standing dead lodgepole pines and also identified a breakpoint; standing dead stems increased substantially where 11-yr-postfire stem density was >57,700 stems/ha but changed little in stands below that threshold density (Table 2). Overlap of the 95% confidence intervals for the two thresholds suggests that net decline in live stems and increase in dead stems occurred at similar densities.

Net changes in stem density were explained differently in plots that gained or lost stems. Stands that gained stems ($n = 40$) had a median of 1175 stems/ha at postfire year 11; net gains increased with postfire year 11 stem density ($r_s = 0.75, P < 0.0001$) and declined with distance to unburned forest ($r_s = -0.44, P = 0.0042$; Fig. 4).

Stands that lost stems ($n = 23$) had a median of 15,850 stems/ha at postfire year 11; net losses increased with postfire-year-11 stem density ($r_s = -0.89, P < 0.0001$).

Stem size.—Mean stem height roughly tripled to about 3 m from postfire years 11 to 24, and mean basal diameter about doubled (Table 3). Mean stem height ranged from 0.4 to >5 m among stands (Table 3) and did not vary with stem density ($P = 0.3397$). Mean basal diameter and DBH also varied substantially among stands (Table 3) and declined with stem density (both $r = -0.69, P < 0.0001$). Mean per-stem foliage biomass, total aboveground biomass, and leaf area (Table 3) also declined with stem density (all $r = -0.62, P < 0.0001$).

Cone prevalence.—On average, 42% of lodgepole pines within a stand bore cones by postfire year 24, and cones per tree had tripled since postfire year 15 (Turner et al.

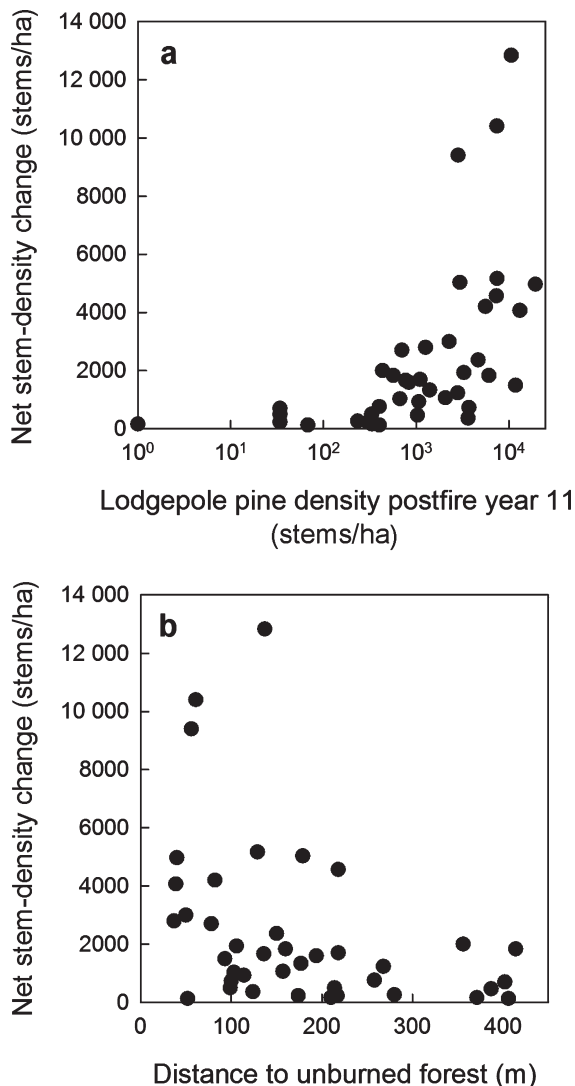


FIG. 4. In plots that gained stems between postfire years 11 and 24, net stem-density change (a) increased with postfire year 11 stem density and (b) declined with increasing distance to unburned forest.

2007); again, variation among stands was substantial (Table 3). The percentage of stems bearing cones was not related to stem density ($P = 0.72$), but the mean number of cones per stem declined with stem density ($r = -0.41$, $P = 0.0003$). However, total cone density within a stand increased with stem density ($r = 0.34$, $P = 0.0038$). No measures of cone abundance were related to density of first-year lodgepole pine seedlings.

Postfire stand function

Stand-level lodgepole pine LAI, foliage biomass, and live aboveground biomass all increased substantially from postfire years 11 to 24 (Table 3). LAI increased by about 56%, foliage biomass more than tripled, and total live aboveground biomass increased over seven-fold (Table 3).

Live aboveground biomass averaged 25.4 Mg/ha and exceeded 80 Mg/ha in some stands (Table 3). These measures also varied widely among stands (Table 3). The most parsimonious models explained 52–57% of the variance in LAI, foliage biomass, and total live aboveground biomass, with lodgepole pine stem density the strongest predictor (Table 4). Although individual trees in high-density stands were smaller, stand-level LAI and biomass in postfire year 24 were driven strongly by stem density (Fig. 5a). Substrate class was also significant, with each of these functional variables declining on the andestic substrate.

Mean annual lodgepole pine ANPP tripled from 11–24 yr postfire, increasing from 1.69–4.99 Mg·ha⁻¹·yr⁻¹, and variation across the landscape remained wide (Table 3). Lodgepole pine ANPP was tightly correlated with LAI ($r = 0.98$, $P < 0.0001$). The most parsimonious model for lodgepole pine ANPP explained 77% of the variation. Lodgepole pine ANPP increased with stem density (Fig. 5b), which explained most (69%) of the variance (Table 4). Environmental variables collectively explained another 8%; lodgepole pine ANPP declined with increasing distance from unburned forest, with increasing mean annual precipitation, and on andestic substrates (Table 4).

Mean annual herbaceous ANPP increased by about 40% from 11 to 24 yr postfire and was substantially lower than mean annual lodgepole pine ANPP (Table 4). The most parsimonious model of herbaceous ANPP at postfire year 24 only included stem density and explained relatively little (12%) of the variance (Table 4). Herbaceous ANPP declined with increasing stem density (Fig. 5c). Shrub ANPP increased but remained low (Table 3) and was not correlated with stem density or ANPP, nor any other variable measured in this study.

Change in landscape variability in stand structure and function

Among-stand variation in postfire lodgepole pine density changed little between postfire years 11 and 24 (CV = 285% and 250%, respectively; Fig. 6). Brown-Forsythe's test indicated no significant difference in variance between the 2 yr ($P = 0.3423$). Among-stand variation in measures of stem size was substantially less than among-stand variation in stem density (Fig. 6). Among-stand variation in measures of tree size (mean tree height and mean tree basal diameter) increased from postfire year 11–24 (CV = 32–37% and 33–43%, respectively). However, among-stand variation in mean tree biomass (mean foliage and total biomass per tree) decreased during that interval (CV = 88–83% and 93–79%, respectively). Brown and Forsythe's test indicated significant differences in among-plot variance between the two years for each of these variables (all $P < 0.0001$).

Among-stand variation in stand-level lodgepole pine LAI, foliage biomass, total aboveground live biomass,

TABLE 3. Variables associated with stand structure (tree morphology, cone prevalence) and stand function (basal area, leaf area index [LAI], aboveground biomass, and aboveground net productivity [ANPP]) for postfire lodgepole pine stands regenerating after the 1988 Yellowstone fires.

Variable	Postfire year 11†			Postfire year 24‡		
	Mean	Median	Min–Max	Mean	Median	Min–Max
Stand structure						
Mean stem morphology						
Height (m)	0.8 ± 0.03	0.8	0.4–1.8	2.9 ± 0.13	2.8	0.40–5.7
Basal diameter (cm)	2.6 ± 0.10	2.5	0.8–5.3	5.9 ± 0.3	6.0	1.1–12.6
DBH for trees >1.7 m tall (cm)	n/a			5.3 ± 0.3	5.3	0.9–10.1
Foliage biomass (g/stem)	168 ± 17	119	5–835	1375 ± 135	1033	18–5131
Total aboveground biomass (g/stem)	387 ± 43	262	9–2046	5522 ± 517	4373	99–19,667
Leaf area (m ² /stem)	0.82 ± 0.08	0.58	0.025–4.1	2.67 ± 0.26	2.02	0.04–9.87
Cone prevalence						
Proportion of trees with cones	–			0.42 ± 0.03	0.40	0–0.88
If cones present, proportion serotinous	–			0.11 ± 0.02	0	0–0.84
Cones per tree (number)	–			9.9 ± 1.34	4.5	0.0–56.2
Cones per stand (number/ha)	–			32,878 ± 9279	8648	0–542,564
Stand function						
Lodgepole pine (LAI) and biomass						
LAI (m ² /m ²)	0.74 ± 0.14	0.21	0–6.7	1.16 ± 0.11	1.03	0–4.0
Foliage biomass (Mg/ha)	1.53 ± 0.29	0.47	0–13.6	5.92 ± 0.58	5.26	0–20.41
Total live aboveground biomass (Mg/ha)	3.38 ± 0.65	1.07	0–31.4	25.4 ± 2.5	22.4	0–85.9
Stand ANPP						
Lodgepole pine (Mg·ha ⁻¹ ·yr ⁻¹)	1.69 ± 0.31	0.46	0–14.5	4.99 ± 0.49	4.23	0–16.5
Herbaceous (graminoid + forb) (Mg·ha ⁻¹ ·yr ⁻¹)	1.05 ± 0.05	1.01	0.02–2.10	1.44 ± 0.07	1.54	0.14–2.78
Shrubs (Mg·ha ⁻¹ ·yr ⁻¹)	0.06 ± 0.01	0.04	0–0.36	0.15 ± 0.02	0.09	0–0.74

Notes: Tree measurements were averaged for 25 trees in each stand, then averaged across plots ($n = 71$ because one plot had no postfire trees). Error measurement is SE.

†Allometric equations for postfire year 11 from Turner et al. (2004). Diameter at breast height and cone prevalence not measured because trees were too small at that time.

‡Allometric equations for postfire year 24 from Copenhagen and Tinker (2014).

and ANPP declined substantially from postfire year 11 to 24 (CVs declined from ~150% to 75%; Fig. 6). Brown and Forsythe's test indicated significant differences in variance between the two years for each of these variables (all $P < 0.0001$). Among-stand variation in herbaceous ANPP was lower (CV = 42%) and did not change between postfire year 11 and 24 (Fig. 6). Brown and Forsythe's test indicated no difference in variance ($P = 0.0623$).

DISCUSSION

Twenty-four years after the 1988 Yellowstone Fires, the landscape pattern of early postfire lodgepole pine establishment (Turner et al. 1997, 2004) continued to dominate the structure and function of these young forests. Increasing tree size and productivity are the norm in young aggrading forests, but the magnitude of the spatial heterogeneity in structure and function in these even-aged postfire stands was notable. Such variability in young forests has been underappreciated, in part because of relatively few opportunities for long-term study of natural postfire regeneration in the absence of

forest management. Our data also provide evidence that stand functional properties (e.g., LAI, biomass, ANPP) may converge earlier than stand structural properties (e.g., stem density and diameter). Although they have smaller trees, high-density stands are highly productive and accumulate biomass rapidly. At this stage of stand development, postfire lodgepole pine density appears to remain a "master variable"; effects of stem density trump effects of tree size on stand-level productivity.

Postfire stand structure

Initial patterns of tree regeneration interacted with biotic processes (competition, seed dispersal, cone production) to shape stand dynamics. Although mean stem density decreased, this was driven by large declines in relatively few stands of very high stem density (~50,000–70,000 stems/ha). Additional stands should self-thin in the future (Peet and Christensen 1980, Kashian et al. 2005a), and our data suggest that the age at which postfire lodgepole pine stands self-thin will vary with stem density. Reconstructions of stands across a chronosequence found that stands with initial density

TABLE 4. Model results for stand-function variables (lodgepole pine LAI, biomass, and ANPP, and herbaceous ANPP) at postfire year 24.

Explanatory variable	Parameter estimate	Partial r^2
LAI (SBC = -49 and adjusted $r^2 = 0.53$)		
Intercept	0.53	
Lodgepole pine density	0.54	0.53
Substrate class	-0.40	0.10
Foliage biomass (SBC = 186 and adjusted $r^2 = 0.52$)		
Intercept	29.3	
Lodgepole pine density	0.26	0.60
Substrate class	-2.08	0.07
Live aboveground biomass (SBC = 389 and adjusted $r^2 = 0.57$)		
Intercept	2.32	
Lodgepole pine density	12.9	0.70
Substrate class	-8.1	0.04
Lodgepole pine ANPP (SBC = -2449 and adj. $r^2 = 0.77$)		
Intercept	0.21	
Lodgepole pine density	0.26	0.69
Substrate class	-0.11	0.06
Distance to unburned forest	-0.0005	0.02
Mean annual precipitation	-0.002	0.01
Herbaceous ANPP (SBC = -76.3 and adjusted $r^2 = 0.12$)		
Intercept	1.93	
Lodgepole pine density	-0.135	0.17

Note: Models selection used Schwartz Bayesian Criteria (SBC) and results are presented for the final model.

>50,000 stems/ha self-thinned at rates much higher than stands with <20,000 stems/ha, and stands with initial density near 5000 stems/ha self-thinned very slowly (Kashian et al. 2005a). Our data suggest that these rate differences will likely manifest as differences in the onset of self-thinning, with high-density stands self-thinning earlier than stands at lower density. Longer-term study will be required to resolve these dynamics.

Counter to our expectations, stem density increased in most stands. Although Kashian et al. (2005a) found evidence for infilling, net recruitment in stands of relatively high density (30,000 stems/ha) was surprising. Relationships between net infilling and postfire stem density (positive) and distance to unburned forest (negative) indicate that both in situ (local cone production) and off-site seed sources (seed dispersal) contribute to these gains. Thus, our data support the notion that episodic tree recruitment can continue for decades, even in young stands characterized by closed canopies and self-thinning (Kashian et al. 2005a).

Early postfire regeneration density affected net recruitment and mortality in different ways. If early lodgepole pine density was moderate to sparse, *net recruitment* increased with stem density, suggesting the importance of cone production in the initial postfire cohort. If early lodgepole pine density was high, *net mortality* increased with stem density, suggesting the importance of

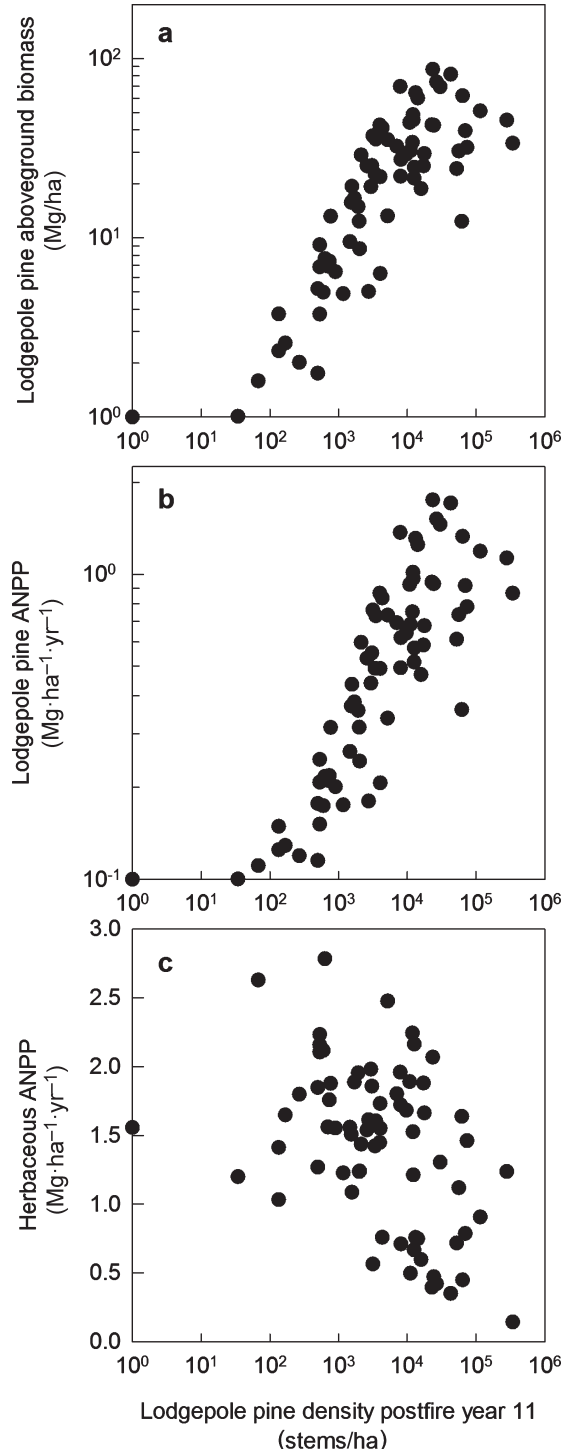


FIG. 5. Lodgepole pine (a) aboveground biomass and (b) aboveground net primary production (ANPP) increased with stem density at postfire year 24, whereas (c) herbaceous ANPP declined with stem density in stands ($n = 72$) regenerating from the 1988 fires.

intra-specific competition. Together, these two opposing population processes will steadily reduce the range of variation in stem density (Kashian et al. 2005a). Thus,

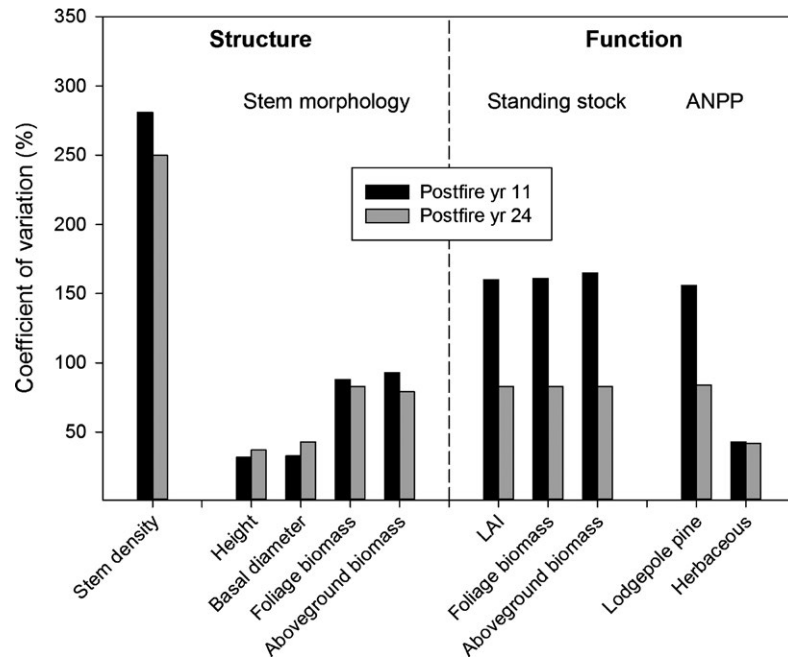


FIG. 6. Among-stand coefficients of variation for lodgepole pine stem density and variables associated with stand structure and function at 11 and 24 yr after the 1988 Yellowstone Fires ($n = 72$). LAI, leaf area index.

by influencing subsequent recruitment and mortality, effects of early stem density feed back over time to dampen the disturbance-generated differences among stands.

We identified important roles for both serotinous and non-serotinous cones during postfire stand development. The level of serotiny (proportion of trees bearing serotinous cones) varies within and among mature lodgepole pine stands (Tinker et al. 1994, Schoennagel et al. 2003, Pausas 2015). Initial postfire regeneration is dominated by seed release from serotinous lodgepole pines, and stem density is tightly correlated with the prefire prevalence of serotiny (Anderson and Romme 1991, Turner et al. 1997, 1999). However, recruitment between fires depends on seed release from non-serotinous cones. After 24 yr, abundant cone production and dominance of non-serotinous cones provides evidence for an in situ seed source that contributes to infilling. The prevalence of non-serotinous cones also suggests that regeneration after a short-interval re-burn could be low in many places (e.g., Brown and Johnstone 2012). Serotinous cones were observed only at lower elevations where prefire serotiny was high, a geographic pattern consistent with increased serotiny where fire-return intervals are <200 yr (Schoennagel et al. 2003, Talluto and Benkman 2014) and strong genetic control of this fire-adapted trait (Pausas 2015). However, lodgepole pine serotiny is under competing selection pressure from fire and pre-dispersal seed predation (e.g., by red squirrels, *Tamiasciurus hudsonicus*) on serotinous cones (Talluto and Benkman 2013). High seed predation rates shift the selective advantage to nonserotinous individuals, even at high fire

frequencies (Talluto and Benkman 2013, 2014). Our postfire regeneration data suggest an adaptive value to maintaining both serotinous and nonserotinous individuals within the population (Pausas 2015).

Postfire stand function

Lodgepole pine LAI, biomass, and ANPP all increased over time, as expected for an aggrading forest, but mean ANPP at postfire year 24 ($5 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) was greater than maximum values reported for developing stands in other studies. For example, three even-aged lodgepole pine stands in southeastern Wyoming reached maximum rates of $2.5\text{--}3.2 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ between ages 40 and 60 yr (Pearson et al. 1987). The high ANPP rates we observed may be due to several factors. The most important driver of stand-level ANPP was postfire stem density, with dense regeneration in these unmanaged young forests associated with very high rates of biomass accumulation. We found no previous studies that spanned the range of stem densities reported here, perhaps because such high densities are undesirable for timber production (e.g., Lindgren and Sullivan 2013). Topoedaphic conditions had relatively small additional effects on ANPP in this landscape, but a gradually warming climate could be enhancing ANPP. Temperature and length of growing season can limit lodgepole pine productivity (Kueppers and Harte 2005), and 10-yr mean growing season temperatures increased from 7.7°C to 8.5°C between the decades preceding our sampling years (Hansen et al., 2016). Finally, development of new allometric equations that predict biomass and ANPP

accurately for this age class may have contributed to higher rate estimates, as allometrics for younger or older stands do not perform well (Copenhaver and Tinker 2014). How ANPP will continue to change in these stands remains to be determined.

Our results highlight the trade-off in effects of stem density on tree vs. stand productivity. Increased stem density was associated with smaller, less productive individuals. In response to competition, lodgepole pines allocate biomass preferentially to terminal shoot elongation at the expense of branch and needle growth (Claveau et al. 2002). Height growth has priority over diameter growth, and competition influences diameter increment more than height increment (Coates 2000). Consistent with these effects of competition, our data showed that mean tree height did not vary with stem density, but mean stem diameter declined with increasing stem density (Table 3). Further, ANPP of individual trees was reduced by $250 \text{ g-stem}^{-1}\text{-yr}^{-1}$ for each doubling of stem density (Copenhaver and Tinker 2014). However, increased stem density was associated with an exponential increase in stand-level ANPP (log-log plot, Fig. 5b). High-density postfire regeneration contributes to rapid recovery of biomass at the ecosystem level.

In contrast to our expectation, herbaceous ANPP increased substantially over time (~40%) even as lodgepole pine biomass and productivity increased. Most herbs are perennials that have grown larger over time (M. G. Turner and W. H. Romme, *personal observations*). Increased herbaceous ANPP also could reflect species gains, as plot-level understory species richness has increased (Romme et al., *in press*); gradual climate warming (see above); or inter-annual variation in climate. Among stands, herbaceous ANPP declined with increasing stem density (Fig. 5c), suggesting within-stand competition between herbs and trees. However, explained variance in herbaceous ANPP was low, as in the past (Turner et al. 2004), and similar to observations made over 30 years of succession in conifer forests of the western Cascade Range (Oregon, USA) (Halpern and Lutz 2013). Shrub ANPP was minimal, in contrast to some western conifer forests in which shrubs are very abundant following fire (e.g., Lentile et al. 2007, Harvey and Holzman 2014). The only shrub routinely encountered in Yellowstone's forests is the slow-growing and small-statured *Vaccinium scoparium*.

Landscape variability in stand structure and function

We found evidence of mechanisms that would lead to convergence in stem density over time, but it was landscape variation in biomass and ANPP that declined most (Fig. 6). Differential changes in variance among response variables suggest considerable functional compensation among stands of different structure. Mediation of trade-offs between tree size and density at the stand level indicates substantial plasticity in how stands achieve similar functions. Nevertheless, among-stand variation in biomass and ANPP spanned two orders of magnitude and was

driven mostly by stem density. Understanding how other ecosystem processes (e.g., nutrient mineralization and uptake; Turner et al. 2009) vary among these young even-aged stands could yield additional insights into mechanisms underpinning stand development trajectories.

Our study illustrates that quantifying variability in functional rates within the same stand-age class could help to resolve uncertainty in landscape carbon budgets (Ryan et al. 1997, Kashian et al. 2006, Smithwick et al. 2009). Among-stand variation in productivity declines with time since fire, with rates converging in 100–200 yr (Kashian et al. 2005b, Bradford et al. 2008). However, relying solely on stand age to estimate C stocks and fluxes in young forests may lead to substantial error (i.e., one to two orders of magnitude). Estimates of regional carbon storage and fluxes should account not only for the entire mosaic of different stand ages and ecosystem types within a region (Buffam et al. 2011), but also for the spatial variation in process rates within a stand-age class. Understanding how disturbance interacts with forest age structure to affect stand-development pathways and carbon fluxes is of high interest in carbon cycle science (Goetz et al. 2012) and important given expected increases in wildfire activity (Westerling et al. 2011, Barbero et al. 2015). Carbon stocks in subalpine forests recover to prefire levels within 100 yr following high-severity fire (Bradford et al. 2008, Smithwick et al. 2009, Kashian et al. 2013), and repeated high-severity fires over millennia do not deplete C or N pools (Smithwick et al. 2009, Dunnette et al. 2014). However, fires that recur in stands that have not yet recovered their biomass may shift from C sinks to C sources (Smithwick et al. 2009), and landscape heterogeneity of postfire regeneration will contribute to this delicate balance. Landscape variation in disturbance and recovery must both be considered in regional carbon studies (Bradford et al. 2008, Balshi et al. 2009, Flannigan et al. 2009).

In conclusion, the 1988 fires left a lasting imprint on the Yellowstone landscape. After 24 yr, the early patterns of postfire lodgepole pine regeneration, which were contingent on prefire serotiny and fire severity, remained the dominant driver of stand structure and function. Trajectories of stand development vary substantially; some stands produce large trees relatively quickly, while others do not, and trade-offs between tree and stand productivity are apparent. Stand structure and function have not yet converged across the burned landscape, but our evidence suggests that function will converge sooner than structure.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/15-1585.1/supinfo>

DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.1pr7k>