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Paths of Recovery: Landscape Variability in Forest Structure, Function and Fuels After the 1988 Yellowstone Fires

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ABSTRACT

Understanding the rates, trajectories, and spatial variability in succession following severe wildfire is increasingly important for forest managers in western North America and critical for anticipating the resilience or vulnerability of forested landscapes to changing environmental conditions. However, few long-term studies have considered succession following severe, stand-replacing wildfires over large areas. This research focused on succession after the 1988 Yellowstone fires and tested hypotheses within three overarching questions: (1) Are stand structure and function beginning to converge twenty-five years after the Yellowstone Fires, and what mechanisms may contribute to convergence or divergence? (2) Are plant community composition and species richness converging or diverging across gradients in local fire severity, postfire lodgepole pine density, elevation and soil type a quarter-century after the 1988 fires? (3) How do canopy and surface fuels vary across the postfire landscape, and how will the variation in fuels influence potential fire behavior a quarter century postfire? Twenty-five years after the 1988 fires, we re-sampled permanent plots in lodgepole-pine (*Pinus contorta* var. *latifolia*) forests in Yellowstone National Park (Wyoming, USA) that burned in the 1988 fires and were distributed widely across the landscape.

Stand structure and function. A quarter century after the 1988 fires, postfire lodgepole pine density remained very high (mean = 21,738 stems ha^{-1}) but varied substantially across the landscape, ranging from zero to 344,000 stems ha^{-1}. Stem density increased in most study plots between postfire years 11 and 24, declining only in plots where 11-yr-postfire stem density was > 72,000 stems ha^{-1}. Existing allometric equations developed from older (mature) and younger (10-yr old) lodgepole pines did not predict biomass and aboveground net primary production (ANPP) well in 25-yr old trees. We developed new allometric equations based on 60 harvested trees, then used these new equations with stem density and measurement made on individual trees to predict stand-level ANPP. Mean ANPP was high (mean = 5 Mg ha^{-1} yr^{-1}, range 0 to 16.5). Stems were small in high-density stands, but stand-level lodgepole pine leaf area, foliage biomass and ANPP increased over time and with increasing stem density. Lodgepole pine ANPP and/or stem density were strongly correlated with many indicators of ecosystem function, but there was no evidence to indicate widespread nitrogen limitation of lodgepole pine in the 25-yr old stands. Rather, our data indicate that lodgepole pine stem density is continuing to act as a "master variable" that governs ecosystem process rates in these young stands.

Plant community composition. Postfire species richness increased rapidly during the first five years and had largely stabilized within 12 years postfire. Plant communities were dominated by native species, many of which resprouted from surviving roots and rhizomes following fire. Although species occurrence varied initially with burn severity, these early differences converged across burn-severity classes between 1991 and 2000. Patterns of species occurrence varied with substrate and local climate conditions; these effects of the abiotic template were detectable early after fire and persisted through the 25 years. We found no evidence for convergence in community composition across abiotic gradients. However, effects of the aggrading lodgepole pine canopies on the plant community became more pronounced, and by 2012, lodgepole pine density was the strongest predictor of postfire plant communities. Of 40 species showing a significant relationship with lodgepole pine in 2012, probability of occurrence declined with increasing pine density for 38 species. Re-measurement of permanent plots in which aspen (*Populus tremuloides*) had established from seed following the 1988 fires revealed that aspen were persisting, although declining in stem density, and elongating. The 1988 fires, in concert with warming temperatures, appear to have facilitated an expansion of aspen within the Yellowstone landscape.

Fuels and potential fire behavior. Although all stands in our study were the same age and had regenerated following the same fires, fuel complexes in the 24-yr old stands varied tremendously across the landscape. Regenerating lodgepole pine density was a strong positive predictor of canopy and fine fuel loads. Available canopy fuel loads and canopy bulk density met or exceeded levels reported for mature lodgepole pine forests, averaging 8.53 Mg ha^{-1} and 0.24 kg m^{-3} respectively. Fine surface fuels

were lower, but 1000-hr fuels were similar or higher than in mature lodgepole pine forests. Total surface-fuel loads averaged 123 Mg ha^{-1}, of which 90% was in the 1000-hr fuel class. Change in surface fuels between 1996 and 2012 were consistent with increasing fine-fuel deposition from growing young trees, and increasing 100- and 1000-hr fuels from the falling of fire-killed trees.

In conclusion, the subalpine forests of Yellowstone National Park were extremely resilient to the large, severe 1988 fires, recovering rapidly in the absence of any management intervention. After 25 years, these early seral stands are complex, rich in native plant species, highly productive, and tremendously variable, having created a heterogeneous mosaic of stand structure and function across the postfire landscape. Pre-fire species richness, species composition, and total vegetative cover were largely re-established by 12 years postfire throughout almost all of the burned area. Tree densities equal or (more typically) exceed pre-fire densities in almost every burned stand. Initial postfire lodgepole pine density, which varied enormously across the burned landscape due to differences in pre-fire serotiny among stands and variations in burn severity, now drives landscape patterns of stand structure and function and plant community dynamics. Postfire lodgepole pine density also drives the amount and landscape pattern of canopy fuels in these young stands, but prefire stand structure drives the coarse woody fuels. Our data provide benchmarks relevant for postfire succession following more recent fires in Yellowstone and throughout the region. We strongly recommend that datasets akin to those presented here be developed for future fires throughout the Northern Rockies so that differences can be readily detected.

BACKGROUND AND PURPOSE

Understanding the rates and spatial variability in succession following severe wildfire is increasingly important for forest managers in western North America and critical for anticipating the resilience (or vulnerability) of forested landscapes to changing environmental conditions. Fire regimes are shifting rapidly, climate change is altering the regeneration success of some species, and the tempo of change is accelerating. In the northern Rocky Mountains, the number of large fires has increased in association with warmer temperatures, earlier snowmelt, and longer fire seasons (Westerling et al. 2006), and this trend is likely to continue with projected climate change. Young forests are increasing throughout the West in response to greater fire activity, and understanding their dynamics is essential for good stewardship of these rapidly changing landscapes. Stand-replacing forest fires trigger significant shifts in stand structure and composition, and their footprints shape forested landscapes long into the future (Kashian et al. 2005a, b; 2013). Successional trajectories set the stage for future carbon storage, abundance of surface and canopy fuels, and habitat for many native (and possibly non-native) species—all issues of concern for today's forest managers. However, there is a paucity of long-term studies that have considered succession following severe, stand-replacing wildfires over large areas. This study focused on succession after the 1988 Yellowstone fires to directly address these critical needs.

The 1988 Yellowstone fires ushered in the new era of wildfire in the West (Running 2006). The size and heterogeneity of the fires created novel opportunities to study succession and ecosystem processes at an unprecedented scale following severe fire in a wilderness-like setting. The 1988 fires burned under conditions of extreme drought and high winds, and ultimately they affected ~600,000 ha in Greater Yellowstone. Despite their large extent, the 1988 fires produced a complex landscape mosaic of patches that varied in size, shape and burn severity. Our studies of the fires began in 1989, and field sampling in the burned area occurred through 2005. Our earlier data revealed that plant re-establishment was surprisingly rapid, but early succession varied across the landscape with patch size and burn severity (Turner et al. 1997, 1999). Perhaps the most striking feature of early postfire succession was the extremely high variability in tree regeneration: densities of lodgepole pine (*Pinus contorta* var. *latifolia)*, the dominant tree species, ranged from zero to over 500,000 stems ha^{-1}, primarily in response to differences in the proportion of lodgepole pine trees in the prefire stand that bore serotinous cones, and local fire severity (Turner et al. 1997, 1999). Postfire plant community composition also varied widely, largely in response to environmental gradients, prefire community composition, and fire size and severity. After nearly 25 years of succession, important questions remained. We re-sampled postfire vegetation and forest structure within the area burned by the 1988 Yellowstone fires, testing hypotheses within the context of three overarching questions.

Question 1: Are stand structure and function beginning to converge twenty-five years after the Yellowstone Fires, and what mechanisms may contribute to convergence or divergence? The ability of lodgepole pine to re-establish following fire is well known, but the range of postfire lodgepole pine densities measured after the 1988 fires (Turner et al. 1997, 1999, 2003, 2004) surprised scientists and managers. From 90 widely distributed 0.25-ha plots we sampled in 1999, mean and median postfire lodgepole pine densities were 29,380 ha^{-1} and 3,100 ha^{-1}, respectively. Twenty percent of the burned landscape had tree densities >20,000 ha^{-1}, but some areas had few or no trees ha^{-1}. This variability in postfire stand density also established a functional mosaic in which the pools and fluxes of carbon and nitrogen were strongly related to tree density, as well as elevation (Turner et al. 2004, 2009; Schoennagel et al. 2008). Chronosequence studies have shown that tree density and growth rates converge ca. 200 yrs following fire (Kashian et al. 2005a, 2005b), but stand dynamics in young postfire lodgepole pine cohorts that regenerated naturally after severe fire have received little study. We hypothesized that landscape variation in postfire lodgepole pine density would have declined since 1999, primarily in response to density-dependent mortality, suggesting that processes leading to convergence in stand structure are beginning to dominate the successional landscape. We further hypothesized that the fire-induced variability in stand structure would interact with environmental gradients to produce a landscape mosaic of process rates within the burned area. We predicted that postfire tree density would remain a "master variable" that largely determines stand-level ecosystem function. Specifically, we predicted that stand-level aboveground net primary productivity (ANPP), leaf area index (LAI), carbon stocks and foliar nitrogen pools would be declining in high-density stands but increasing in stands of low or moderate density. In addition to re-sampling our long-term plots in postfire lodgepole pine, we opportunistically also sampled forests near the lower limit of montane tree cover, which are expected to be vulnerable to warming climate, potentially converting to non-forest for prolonged periods if affected by stand-replacing fire. Such disturbance-catalyzed shifts are by nature stochastic, offering few opportunities to test these predictions. Thus, we also investigated long-term (24-year) regeneration dynamics in Douglas-fir (*Pseudotsuga menziesii* v.*glauca*) forests, which compose the lower treeline yet have received little study. We hypothesized that dry, lower-margin stands would be less likely to attain self-replacement than more mesic stands farther from lower treeline.

Question 2: Are plant community composition and species richness converging or diverging across gradients in local fire severity, postfire lodgepole pine density, elevation and soil type a quarter-century after the 1988 fires? A central objective in our Yellowstone research has been to understand the relative influence of stochastic vs. deterministic factors on postfire ecosystem development, and how these influences may change through time. We define stochastic variables as those that are typically related to the fire disturbance *per se*, e.g., local fire severity and patch size, whereas deterministic variables are constant and largely unchanged by the fire, e.g., local climate and soil conditions. Species richness varied inversely with local fire severity (a stochastic variable) during the first five years after the 1988 fires; however, after eight years richness was similar across all burn severity classes (Romme and Turner 2004), suggesting that stands burned at different severities were converging in community structure over time. In contrast, initially small differences in richness between very infertile low-elevation sites and less infertile high-elevation sites became greater over the same time period, indicating that elevation and soil type (deterministic variables) were producing divergence in postfire community structure over time. We hypothesized that the influence of stochastic variables, e.g., local fire severity and patch size, on community development would continue to diminish over time, and that postfire communities would diverge along deterministic abiotic gradients. Species richness initially was unaffected by postfire lodgepole pine density because the tree seedlings were so small (Anderson and Romme 1991). However, by a quarter century after the fires, we hypothesized that richness would be inversely related to lodgepole pine density because the trees have grown large enough to compete with the herbaceous plants. We also have followed trajectories of select individual plant species since the 1988 fires. One surprising "invader" of burned sites after 1988 was quaking aspen (*Populus tremuloides*), which produced abundant seedlings through a rare episode of sexual reproduction (Romme et al. 1997). Survival and growth of these new genetic individuals (genets) varied with elevation, soil type, and browsing pressure; their success generally has been greater at higher elevations and on less infertile soils (Romme et al. 2005). We hypothesized that abundance and size of post-1988 aspen would have increased on higher, more fertile sites, and have decreased on lower, less fertile sites.

Question 3: How do canopy and surface fuels vary across the postfire landscape, and how will the variation in fuels influence potential fire behavior a quarter century postfire? Successional dynamics ultimately generate the fuels available for future fires, and understanding the rate at which fuels re-accumulate and how they vary across the landscape will help managers anticipate and respond to future fire behavior. The 1988 fires consumed nearly all of the fine fuels but surprisingly little (~8%) of the large (> 7.5 cm diameter) surface fuels (Tinker and Knight 2000). Thus, the initial postfire landscape had minimal fine surface and canopy fuels but abundant large fuels (logs remaining on the forest floor plus standing fire-killed trees). When measured in 1996-97, surface fuels within 1988 burned forests averaged ~60 Mg ha^{-1}, of which nearly 75% was coarse wood (Tinker and Knight 2000). Postfire lodgepole pine trees contributed little to fuels in 1996-97, as the seedlings were still small. Furthermore, most of the downed coarse wood was “inherited,” i.e., already on the forest floor before the 1988 fires. As succession proceeds, large surface fuels increase as fire-killed trees fall to the forest floor, and canopy fuels increase with the growth of foliage biomass in the regenerating lodgepole pines. We predicted that the rate of increase in canopy and dead surface *fine fuels* would be positively related to postfire tree density, but the rate of increase in *large dead surface fuels* would be related instead to pre-fire stand density and basal area. Spatially, we expected postfire lodgepole pine density to again be a “master variable” influencing the abundance and profile of canopy and fine surface fuels. Specifically, we predicted that live canopy fuel load would increase but live herbaceous fuels would decrease with increasing postfire lodgepole pine density, and canopy base height would also increase with postfire tree density (because lower branches will be self-pruning). However, because large surface fuels result from prefire stand structure, we expected variation in large surface fuels to be unrelated postfire tree density. We further hypothesized that heterogeneity of successional forests in the post-1988 landscape, particularly postfire tree density, would produce heterogeneity in potential fire behavior. Specifically, we predicted the probability of active crown fire to increase with postfire tree density because canopy fuels would be abundant and contiguous, and such fire would likely be stand replacing. We predicted a low probability of any fire in low-density stands because surface and canopy fuels are sparse and discontinuous. We predict elevated probability of passive crown fire in stands of intermediate density because canopy fuels are relatively abundant and canopy base height is low. Spatial heterogeneity in fuels and fire behavior could enhance the resilience of the young successional forests by limiting the potential extent of severe fire.

LOCATION AND STUDY DESCRIPTION

Location. We re-measured plots within forests burned by the 1988 fires in Yellowstone National Park (YNP), which encompasses ca. 9,000 km^2 in northwestern Wyoming (Fig. 1.) Stand-replacing fires occur in YNP at 100-300 yr intervals (Schoennagel et al. 2003), but the 1988 fires were remarkable for their severity and size, affecting ~36% of YNP. About 80% of YNP is dominated by lodgepole pine forest, although subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) may be locally abundant. In these forests, severe fire kills all trees and consumes the shallow litter layer present in unburned forests. Postfire forests in YNP initially have nearly complete cover of mineral soil and essentially no duff.

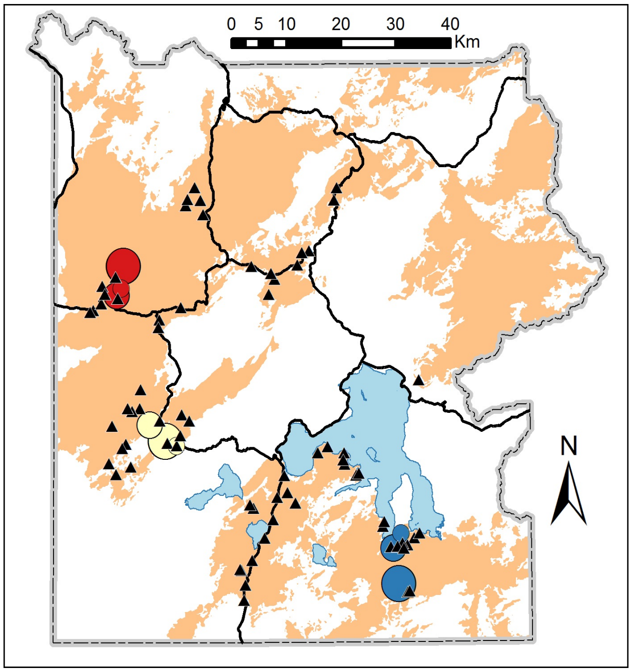

Fig. 1. *Map of Yellowstone National Park showing extent of the 1988 fires (orange) and the 72 plots (triangles) re-measured in this study and patches (circles) studied for plant community composition. Symbols are not to scale.*

Study overview. We re-measured multiple sets of vegetation plots. To evaluate change and variability in stand structure and function, how plant community composition and species richness vary with tree density, and how fuels and potential fire behavior vary across areas burned in 1988, we re-sampled 72 plots (50 m x 50 m, Fig. 1) in 2012 that were sampled initially in 1999 (Turner et al. 2004). These plots are widely distributed and represent the range of conditions found within the burned area. To identify potential mechanisms underpinning vegetation changes, additional variables (e.g., soil and foliar nitrogen, litter quantity and quality) were re-measured from

2012-13 in 14 of the 72 plots (Levitt 2006, Turner et al. 2009). To evaluate change in fuels since 1996-97, we re-sampled fuel plots in 2012 (Tinker and Knight 2000). To evaluate the relative importance of stochastic and deterministic factors on plant community composition, we resampled in 2013 vegetation plots within the centers of three patches of high-severity crown fire that we established in 1990 (Turner et al. 1997, 2003; Romme and Turner 2004). For each of the three overarching questions, we briefly describe the study and summarize key findings below.

Question 1: Are stand structure and function beginning to converge twenty-five years after the Yellowstone Fires, and what mechanisms may contribute to convergence or divergence?

Study description. We resampled permanent plots in lodgepole pine-dominated forests burned in the 1988 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, but also that initial postfire stem density would still determine trajectories of biomass accumulation. Vegetation was re-sampled during summer 2012 in 0.25-ha plots ($n = 72$) following our previous protocols (see Turner et al. 2004 for full description). Briefly, lodgepole pine density was recorded along three 50-m x 2-m belt transects in each plot, and the diameter at breast height (DBH), basal diameter, and height of postfire lodgepole pine ($n = 25$ stems/plot) were recorded. For understory vegetation, percent cover was recorded by species within 0.25-m^2 sampling frames along each transect ($n = 25$ frames/plot). Although we had planned to re-sample all 90 plots, the difficulty in reaching and sampling these young forests far exceeded our expectation; the abundance of downed wood and young trees made navigation to the plots and sampling very difficult. The 72 that we re-sampled spanned the full range of environmental conditions and lodgepole pine stem densities.

To answer our questions about stand development, we first had to assess the growth rates and biomass allocation patterns of the young lodgepole pine trees. Therefore, in 2012, we harvested 60 24-yr old lodgepole pines from 21 sites spanning a range of tree densities (500 to 75,667 stems ha^{-1}). Our goal was to understand the influence of postfire stand density and age on tree-level total aboveground biomass (AB), component biomass (bole, branch, foliage), partitioning to components, ANPP and leaf area (LA). Existing allometric equations for younger (Turner et al. 2004) and older trees (Pearson et al.1984; Kashian et al. 2013) fit the current cohort of postfire trees poorly, so we developed new allometric equations for lodgepole pine trees in this size and age class (Copenhaver and Tinker 2014).

The new allometric equations were used to estimate lodgepole pine biomass, ANPP and LAI among the 72 re-sampled plots. Briefly, basal diameter was used to predict each response on each of the 25 trees measured in each plot. We then averaged measurements for the eight or nine trees on each transect, multiplied by stem density on that transect, and averaged across the three transects to predict stand-level lodgepole pine LAI (m^2 m^{-2}), aboveground biomass (Mg ha^{-1}) and ANPP (Mg ha^{-1} 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. 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 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. 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.

To further elucidate ecological mechanisms underpinning stand development, additional re-measurements were made in a subset of 14 plots (see Levitt 2006, Turner et al. 2009). Briefly, during summer 2012, we collected soil samples from each plot to quantify soil texture, soil pH, soil nutrients (C, N, P, K, Ca, Mg), soil organic matter, and to assay extracellular enzymes as indicators of soil microbial community activity. For one year, we also deployed litter traps to estimate litterfall, and free resin bags to index plant-available soil inorganic N (as in in Turner et al. 2009). Traps and resin bags were collected in summer 2013 and returned to the laboratory for analysis. During summer 2013, foliar nitrogen was sampled following the protocols we used in 2003 (Turner et al. 2009). Foliar samples were analyzed for C, N and a set of macro- and micronutrients at the University of Wisconsin Soil and Plant Analysis Laboratory following standard procedures.

Key findings. At the tree level, all traits on harvested lodgepole pine trees increased nonlinearly with increasing tree basal diameter, which remained the strongest single predictor of biomass, ANPP, and LA (Copenhaver and Tinker 2014; see Table 1 for final allometric equations). All biomass compartments, as well as ANPP and LA, were highly variable (CV > 1), with branch biomass being the most variable biomass component. Similar to 11-yr old trees, bole wood was still the largest component of both biomass and ANPP, followed by foliage and branch biomass and ANPP. Tree-level total AB and component biomass, along with ANPP and LA, all decreased with increasing stand density. Biomass partitioning also showed strong, but variable density-driven patterns, with foliage and branch biomass decreasing in higher density stands, while bole biomass increased with stand density.

Not surprisingly, all AB components, ANPP and LA all were significantly higher in 24-yr old trees than measurements from 11-yr old trees, but the variation among these structural components changed very little (Copenhaver and Tinker 2014). Foliage biomass was slightly more variable in the older trees, and branch biomass became slightly less variable, but overall variation remained very similar in all other compartments, likely because of maintenance of early relative differences in tree size throughout stand development. Overall, our results indicate that stand density and age explain much of the variation in tree characteristics and that 24 years after fire, the initial postfire regeneration density is still exerting significant influence on the structure and function of individual trees (Copenhaver and Tinker 2014).

Table 1. Summary of tree-level allometric equations built from 24-year-old lodgepole pine trees harvested from a range of stand densities across the Yellowstone subalpine plateaus. All equations are of the form $Y=aX^b$ where X=basal diameter in cm. Biomass is predicted in grams, ANPP in grams·year^{-1} and LA in m^2. From Copenhaver and Tinker (2014).

Dependent variable	***n***	***a***	***b***	**MSE**	***F*-ratio**	***p***
Total aboveground biomass (g/tree)	60	98.85	1.99	3742767	6.7	<0.0001
Foliage biomass (g/tree)	60	22.90	2.00	270457	1.5	<0.0001
Branch biomass (g/tree)	60	14.44	2.14	854592	6.8	<0.0001
Bole biomass (g/tree)	60	65.26	1.99	1537053	6.3	<0.0001
ANPP (g/tree/yr)	53	38.90	1.66	360453	13.4	<0.0001
Leaf area (m^2/tree)	55	0.02	2.34	3	0.4	<0.0001
1 hr branchwood (<1/4" diam.)	60	4.74	2.16	49603	2.6	0.035

Among stands, postfire lodgepole pine density remained very high (mean = 21,738 stems ha^{-1}, range = 0 to 344,067 stems ha^{-1}) at postfire year 24 and was tightly correlated with stem density at postfire year 11 (Fig. 2a; Turner et al. 2016). Surprisingly, 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^{-1} (Fig. 2b). 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 ANPP was high (mean = 5 Mg ha^{-1} yr^{-1}, range = 0 to 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 (Turner et al. 2016). 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 (Turner et al. 2016).

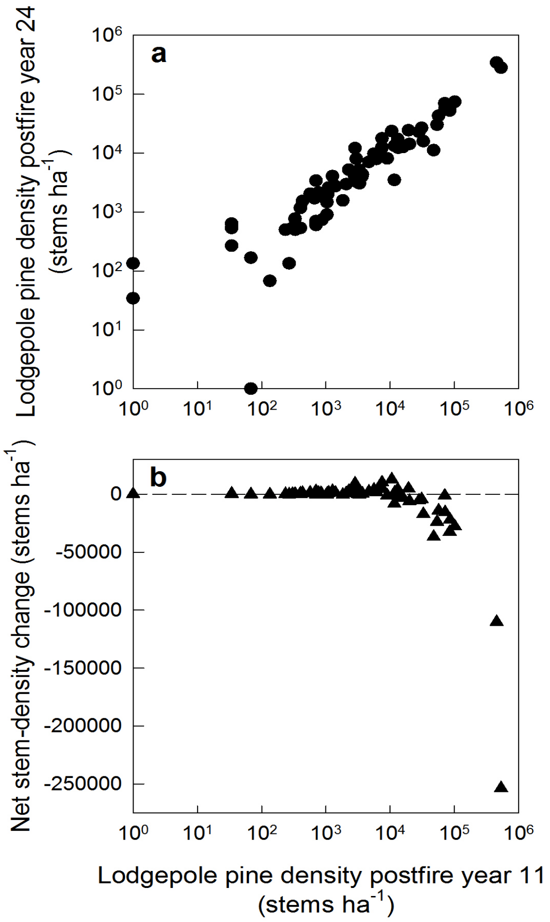

***Fig. 2**. (a) Lodgepole pine stem density at postfire year 24 and (b) net change in stem density versus stem density at postfire year 11. From Turner et al. (2016a).*

Indicators of ecosystem function varied substantially among the 14 stands re-sampled for the more intensive process measurements (Table 2) and changed over time. (These results are presented in greater detail here because the manuscript has not yet been submitted.) Litterfall has about doubled over the past decade, increasing from 35 g m^{-2} yr^{-1} in 2003 to 75 g m^{-2} yr^{-1} in 2013 (Table 2). In 2003, most litterfall (65%) was woody; by 2013, most litterfall (85%) was lodgepole pine foliage. The litter layer is re-developing, averaging nearly 500 g m^{-2} at postfire year 25 (Table 2). The litter layer is enriched in nitrogen relative to fresh litterfall (Table 2), consistent with litter in the immobilization phase of mineralization (Remsburg and Turner 2006). Soil pH, soil organic matter, and soil total N have not changed since 2003 (previously reported in Turner et al. 2009), nor have soil cations. When sampled previously in postfire year 15, the foliar N concentration of new lodgepole pine needles averaged 1.38%; only stands at very high density (> 80,000 trees ha^{-1}) were approaching moderate N limitation, indicated by N concentrations < 1.20%. When re-sampled in postfire year 25, foliar N concentration of new lodgepole pine needles averaged 1.33% (Table 2), and only the highest density stand (344,067 stems ha^{-1}) was notably low (1.04%). Composite needles (needles of all ages along a given branch) had average foliar N concentrations of 1.08% at postfire year 15 and again did not change by postfire year 25 (Table 2).

Table 2. Indicators of ecosystem function in 25-yr old lodgepole pine stands (n = 14) that regenerated following the 1988 Yellowstone Fires. Soils were sampled in 2012; process rates (litterfall, inorganic N availability) were quantified from 2012-2-13; and foliar chemistry was sampled in 2013.

Variable	Mean (SE)	Mininum	Maxinum
Litterfall and litter layer			
Total litter mass on forest floor (g/m^2)	498 (89)	107	1183
Litter N concentration (%)	0.82 (0.03)	0.65	1.06
Litter C:N ratio	62.5 (2.6)	48.9	81.0
Total fresh litterfall (g/m^2/yr)	75.2 (8.6)	12.8	122.6
Fresh litter N concentration	0.65 (0.02)	0.51	0.88
Fresh litter C:N ratio	84.2 (3.3)	58.0	104.9
Soil pH, organic matter and nutrient concentrations			
Soil pH	5.5 (0.06)	5.0	5.7
Soil organic matter (%)	3.0 (0.26)	1.5	4.6
Total N (%)	0.08 (0.007)	0.03	0.13
Phosphorus (ppm)	13.6 (0.90)	7.6	18.5
Potassium (ppm)	120 (5)	81	153
Calcium (ppm)	423 (46)	260	897
Magnesium (ppm)	69 (9)	42	177
Boron (ppm)	0.37 (0.02)	0.3	0.5
Annual inorganic N availability (resin-sorbed N)			
Nitrate (µg/g resin/day)	4.19 (1.08)	0.44	12.97
Ammonium (µg/g resin/day)	1.97 (0.47)	0.42	6.43
Extracellular enzyme activity (nmol/g soil organic matter/hr)			
Beta-glucosidase	2647 (275)	1381	4653
N-acetyl-glucosaminidase	3028 (394)	845	6039
Acid-phosphatase	8152 (589)	5856	13,352
Alpha-glucosidase	156 (13)	88	257
Celo-bio-hydrolase	201 (22)	99	420
Xylosidase	166 (11)	95	255
Peroxidase	116,028 (8097)	66,031	161,547
Phenol-oxidase	94,009 (8140)	43,176	154,237
Lodgepole pine foliar chemistry			
Composite-needle foliar [N]	1.11 (0.03)	0.98	1.28
Composite-needle C:N ratio	49.5 (1.22)	42.0	55.6
Needles-of-the-year foliar [N]	1.33 (0.04)	1.04	1.52
Needles-of-the-year foliar C:N ratio	39.4 (1.31)	34.2	50.0

Lodgepole pine ANPP and/or stem density was strongly correlated with many indicators or ecosystem function, and the directions of these relationships demonstrated that postfire stem density (and thus productivity) continued to control ecosystem process rates in these young stands. Stand-level lodgepole pine ANPP was strongly and positively correlated with annual litterfall (r = 0.83, p = 0.0002), and stongly and negatively correlated with fresh litter N concentration (r = –0.86 and p < 0.0001). However, lodgepole pine ANPP and stem density were not related to total soil N nor to total soil organic matter (all p > 0.4). At postfire year 15, lodgepole pine ANPP was not related to annual soil nitrate, ammonium or total inorganic N availability (Turner et al. 2009). However, by postfire year 25, lodgepole pine stem density was negatively associated with annual soil nitrate (r_s = -0.56, p = 0.0351), ammonium (r_s = -0.60, p = 0.0221) and total inorganic N availability(r_s = -0.70, p = 0.0052). If N was limiting lodgepole pine productivity, we would expect a positive relationship between soil N and inorganic N availability and stand-level ANPP. However, the relationship is negative. Furthermore, foliar N concentrations declined sharply with increasing lodgepole pine ANPP for composite needles (r = -0.85, p = 0.0001) and current year needles (r = -0.71, p = 0.0044). Thus, individual trees obtain less N as stand density increases. As was the case in 2003, we found no evidence that N limitation is yet widespread in the 25-yr old regenerating lodgepole pine stands, although the data indicate that lodgepole pine are depleting inorganic soil N. Understory productivity may be starting to experience some N limitation, as herbaceous ANPP was positively but more weakly associated in annual soil ammonium availability (r_s = 0.53, p = 0.0514).

Assays of extracellular enzyme activity suggest substantial competition between lodgepole pines and soil microbial communities for labile forms for both carbon and nitrogen substrates. Several of the extracellular enzyme activities were also positively correlated with lodgepole pine ANPP and stem density, indicating that the soil microbial community was expending more energy to obtain nitrogen and carbon substrates in high-density lodgepole pine stands. Especially strong relationships were observed between stand-level ANPP and beta-glucosidase (r = 0.70, p = 0.0055), N-acetyl-glucosaminidase (r = 0.78, p = 0.0010) and phenol-oxidase (r = 0.74, p = 0.0024), and moderately strong relationships between lodgepole pine stem density and alpha-glucosidase (r = 0.57, p = 0.03) and celo-bio-hydrolase (r = 0.67, p = 0.0089). There were no significant relationships with phosphatase, consistent with an absence of P limitation. Collectively, these data point toward postfire lodgepole pine stem density continuing to act as a "master variable" that controls ecosystem process rates in these young stands (Turner et al., in prep.).

For post-1988-fire Douglas-fir stands, our data revealed that mesic sites supporting dense forests pre-fire regenerated robustly regardless of burn severity, even in large high-severity patches, whereas dry sites did so only if nearby seed sources survived (i.e., small patch size or moderate burn severity) (Donato et al., in review). Regeneration continued over two decades, with higher levels of annual establishment associated with wetter conditions in preceding (not concurrent or subsequent) years. Self-replacement of stands by 24 years postfire was nearly universal in mesic sites, variable but common in dry sites not adjacent to the lower ecotone, and uncommon in dry sites near the ecotone – particularly if burned with high severity. Whether the lack of regeneration in ecotonal sites is categorically directional with warming climate or part of a long-term cycle is unresolved, but we estimate that the 1988 fires converted >4000 ha of lower-montane forest to grass/sage steppe for at least several decades, possibly indefinitely given current trends in climate. These data support the notion that climate-driven shifts in vegetation cover are likely to occur in punctuated fashion with disturbances, with relatively abrupt implications for montane forest cover, biogeography, and ecosystem function (Donato et al., in review).

Question 2: Are plant community composition and species richness converging or diverging across gradients in local fire severity, postfire lodgepole pine density, elevation and soil type a quarter-century after the 1988 fires?

Study description. We asked two questions about patterns and processes over the past 25 years: (1) Trends: Are plant species richness and community composition converging or diverging across gradients in elevation, soils, fire severity, and postfire lodgepole pine (*Pinus contorta* var. *latifolia*) density? (2) Processes: What are the major controls on postfire species composition, and has the relative importance of controls changed over time? We developed two time-series datasets: (i) 10-m^2 plots (*n* = 552) distributed among three geographic areas that differ in elevation and substrate; plots in each area represent the full spectrum of fire severities, and were sampled in 1991-2013. Although we had intended to re-sample species presence at all 552 of these smaller plots in 2013, this proved completely infeasible for several reasons. The sampling plots were largely in very remote locations, and navigation through these dense young forests was very difficult. The sample plots are small, and the rock cairns and/or stakes were often impossible to find because of dense and abundant downed fire-killed trees and regenerating lodgepole pine. Locational error would have swamped our ability to assess change over time, and the cost:benefit ratio for field effort was unfavorable. Therefore, we re-sampled the most severely burned centers of three (of nine) patches, one in each of three geographically distinct areas, which had been sampled from 1991 to 2000 (*n* = 42 plots). We were able to re-locate these plots successfully. Nonetheless, we fully analyzed our full dataset on plant community composition, none of which had been published previously. (ii) We also re-sampled species composition in the 0.25-ha plots (*n* = 72, as described above) that were established in 1999 and resampled in 2012. The long time-series data from the 10-m^2 plots were analyzed by tallying species richness and performing ordination analysis to examine community change over time. For the 72 plots, we used multi-level models to understand variables controlling plant community composition at two time periods.

In addition to our community-level analyses, we quantified effects of multiple ecological filters on a cohort of aspen that established from seed throughout burned lodgepole pine forests after the 1988 fires. We asked two specific questions (1) How have aspen presence, density, and size varied across the postfire landscape, and what filters explain these spatial and temporal patterns? (2) How do aspen above-and belowground biomass vary with lodgepole pine density? Here, we used data from the 72 plots described above for aspen presence and density, and re-sampled 22 permanent plots that had been established initially in 1996 (Romme et al. 2005) to assess change in aspen size.

Key findings. Species richness increased at all spatial scales of analysis, from individual 10-m^2 plots to the study area as a whole (Fig. 3); richness increased most rapidly during the first five years, and had largely stabilized by 2000 (12 years postfire). Most of the postfire species recorded in a given area had been present in that area before the fire; many plants survived the fire as roots or rhizomes and regenerated rapidly by sprouting. As a result, geographic areas having different local climate and soil characteristics (the “abiotic template”) had distinctive species assemblages soon after the fire, and they remained distinct throughout the first 25 years of postfire succession. In addition to the re-sprouting survivors, the most severely burned areas initially supported a suite of species that are uncommon in mature forests: annual and biennial forbs that establish preferentially on bare soil and species having heat-stimulated soil seed banks. However, composition converged across burn-severity classes from 1991 to 2000.

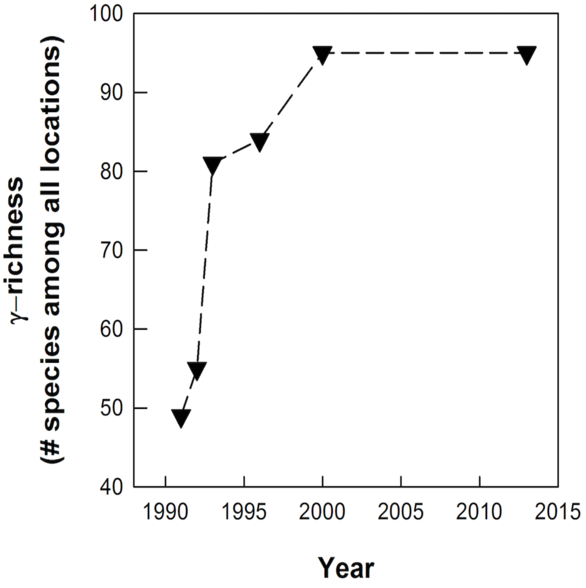

Fig. 3. *Species richness over time in the centers of three patches of high-severity crown fire (n = 42 plots) that burned in the 1988 Yellowstone Fires and were resampled through 20013. (From Romme et al. in review).*

Table 3. Plant species that increased or decreased substantially in abundance (i.e., that increased or decreased by >50% in percent of plots in which it was recorded) from 1999 to 2012 in 72 0.25-ha plots broadly distributed across the areas that burned in the 1988 Yellowstone fires.

Species characteristics	**Plots where present (%)** 1999	2012	**Species**
Species that decreased substantially from postfire years 11 to 24			
Annuals, biennials, or short-lived perennials	4	0	*Androsace septentrionalis*
	29	14	*Collomia lineata*
	17	7	*Gentiana amarella*
	31	14	*Epilobium ciliatum*
Long-lived perennial grasses typical of grasslands and other non-forest environments	13	1	*Agropyron* sp.
	4	0	*Phleum pratense*
Long-lived perennial forbs, relatively shade intolerant, typical of various environments	25	8	*Antennaria rosea*
	25	4	*Cirsium arvense*
Long-lived perennial grasses of unknown shade tolerance, typical of forest environments	72	29	*Agrostis scabra*
	14	1	*Bromus* sp.
	54	25	*Poa* sp.
	82	4	*Trisetum spicatum*
Long-lived perennial forbs of moderate shade tolerance, typical of forest environments	24	3	*Fragaria vesca*
Long-lived perennial forbs of unknown shade tolerance, typical of forest environments	15	3	*Arnica latifolia*
	14	1	*Spirea betulifolia*
	25	1	*Agoseris aurantiaca*
	6	0	*Claytonia lanceolata*
	8	0	*Eury integrifolia*
	15	4	*Hieracium triste* var. *gracile*
	8	0	*Machaeranthera canescens*
	19	1	*Pseudognaphalium macounii*
Species that increased from postfire years 11 to 24			
Long-lived perennial forb of moderate shade tolerance, typical of forest environments	4	7	*Thalictrum* sp.
Long-lived perennial forbs of unknown shade tolerance, typical of forest environments	10	21	*Astragalus miser*
	4	11	*Eriogonum umbellatum*

Among the 72 0.25-ha plots, we recorded 58 species that were present in at least 5% of the plots in 1999 and 52 species that met this criterion in 2012. The species that changed substantially from 1999-2012 were consistent with the increasing importance of the aggrading lodgepole pine canopies (Table 3). Only three species increased substantially, i.e., the proportion of plots in which they were recorded increased by $\geq$50%; all were perennials, and all were typical of mature forest environments. Twenty-one species became less abundant (decreased by $\geq$50%). Of these, four were short-lived forbs (annuals, biennials, or short-lived perennials), two were species typical of grasslands or other non-forest habitats, and two were relatively shade-intolerant forest species (Table 3). Five species were relatively rare in 1999 (present in <10% of the plots), and all five of these were absent in 2012; one was an annual and one was typical of non-forest environments, as would be expected in an increasingly shady environment. However, the other three that disappeared from the plots were species of mature forests.

Deterministic effects of the abiotic template on plant community composition were consistently strong in both years; species were more likely to be present (and therefore would yield greater species richness) in plots on less infertile substrates; where precipitation, which is dominated by snow, was lower; and where temperatures were warmer. Among the stochastic drivers, effects of fire severity were surprisingly ephemeral, having a modest influence in 1999 but no effect by 2012. Postfire lodgepole pine density – stochastic because it was generated by prefire stand condition and local burn severity – had no effect on plant community composition in 1999 but was the strongest predictor in 2012, with strong negative effects on annuals and shade-intolerant herbs (Romme et al., in review). Lodgepole pine density had a significant effect on 77% of the 52 species measured, with 38 species more likely to occur where pine density was lower and two species more likely to occur where pine density was greater. Distance to unburned forest was not significant in either time period, suggesting that the stochastic effects of burn patch size and shape also were of little importance for understory communities by postfire year 11.

For the postfire aspen cohort, our re-measurements revealed that aspen persisted to postfire year 25 in 58% of the 72 plots in which aspen were present in postfire year 11, and mean stem density declined from 522 to 310 stems ha^{-1} (Hansen et al., in review). Mean aspen height doubled (from 29 to 59 cm) during this time period; although aspen were generally small, the tallest aspen reached a height of 323 cm, which was considerably more than the tallest aspen recorded in 1996 (92 cm). Ecological filters related to climate, competition, herbivory, and soils differentially affected aspen presence, persistence, and size. Growing season temperature, inter-specific competition, and herbivory also changed through time, altering their effects on the colonizing cohort, and shifting where in the landscape aspen persistence and growth were ultimately favored (Hansen et al., in review). Eleven years postfire, aspen were favored at warmer, low elevations; ungulate browsing strongly constrained aspen heights; and competition was unimportant. By 25-years postfire, temperatures had warmed, and aspen were more likely to persist at cooler, high elevations. Browsing pressure declined with ungulate population size during this time, but aspen height and basal diameters were constrained by dense, rapidly growing postfire conifers. Aspen height also increased relative to root length in high-density lodgepole pine. Landscape mosaics of ecological filters shift over space and time and can facilitate or constrain the persistence and growth of colonizing species. Long-term study of post-disturbance colonizing cohorts can reveal how species distributions are responding to real-time environmental change.

Question 3: How do canopy and surface fuels vary across the postfire landscape, and how will the variation in fuels influence potential fire behavior a quarter century postfire?

Study description. We sampled fuels across the forests regenerating from the 1988 fires to answer three specific questions: (1) How do canopy and surface fuel loads vary within and among stands across the burned landscape? (2) How do canopy and surface fuels vary with pre- and postfire stand structure and environmental conditions? (3) How have surface fuels changed since 1988? During the summer of 2012, we measured canopy, surface, and herbaceous fuel characteristics in 24-year old postfire forests across YNP. Ten plots were originally established in 1996 (Tinker and Knight 2000) and the 72 plots were established in 1999 (Turner et al. 2004) and are the same plots in which we re-sampled postfire stand structure and plant community composition. Surface fuels had previously been measured in 1996 on 10 sites (Tinker and Knight 2000) but no fuel measurements were collected on the Turner et al. (2004) sites in 1999. All 82 plots were used to evaluate our first two questions, and the 10 sites sampled in 1996 were re-measured to address our third question. Spatial independence was confirmed using the Moran's I test (*P* = 0.192). To our knowledge, this study includes the most expansive fuels dataset collected within a single wildfire footprint. We measured canopy, surface, and understory vegetation fuels at all 82 sites. We used 12 20-m planar intercept fuels transects within a 0.25 ha (50 x 50 m) fixed-area plot at each site (Brown 1974, Brown et al. 1982) for surface fuel estimation. Litter and duff depth (cm) were measured at three locations spaced at 2- m intervals at the beginning of each transect. We assessed canopy fuel profiles from estimates of stem density and size in each plot and understory vegetation cover was estimated visually by species within 25 0.25-m^2 quadrats (Turner et al. 2016a. We also measured litter bulk density (kg m^{-3}) in 14 plots that spanned a representative range of postfire seedling densities.

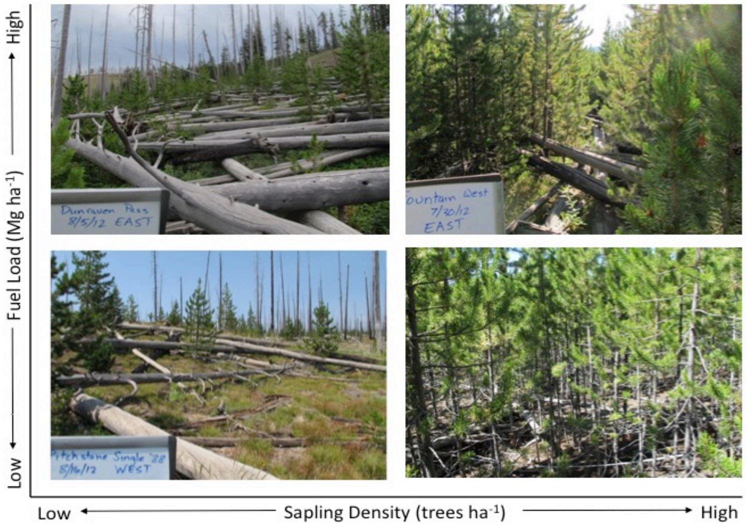

Fig. 4*. The great range of variability in 24-year-old lodgepole pine forest structure and fuel characteristics developing after the 1988 Yellowstone fires. Photos from 2012, postfire year 24 (from Nelson et al., in review)*

To investigate how fire behavior varies in 24-year-old forests in Yellowstone National Park, we first aggregated the 83 fuel profiles into groups of similar fuel loads using a cluster analysis. We are now developing custom fuel models using these clustered fuel groups and direct input from local land managers (Nelson et al. in prep.). Custom fuel models include a hybrid approach for separately estimating surface fire rate of spread (ROS) and fire intensity (as done by Schoennagel et al. 2012). Surface fire ROS is estimated using custom fuel models in the BehavePlus software program (Andrews et al. 2003) and results are calibrated with fire observations provided by land managers in the greater Yellowstone region. Fire intensity incorporates 1000-hr fuel loads using Byram's (1959) model. Model parameters—fuel consumption and rate of spread—were estimated by incorporating 1000-hr fuels with fine fuels in the First Order Fire Effects Model (Reinhardt and Dickinson 2010) and using the calibrated BehavePlus ROS results, respectively. The conditions under which passive, active, and independent crown fires may occur are being simulated using the van Wagner (1977) and Rothermel (1991) crown fire models. Fire weather was varied systematically between the 50th and 99th percentile weather conditions to elucidate differences in fire behavior for each fuel group as fire weather varies.

Key findings. Although all stands in our study were the same age and regenerated following the same fires, fuel complexes in these 24-yr old stands varied tremendously across the landscape (Fig. 4, Table 4). Regenerating lodgepole pine density was a strong positive predictor of canopy and fine fuel loads. Available canopy fuel loads and canopy bulk density met or exceeded levels reported for mature lodgepole pine forests averaging 8.53 Mg ha^{-1} [0.0-46.6] and 0.24 kg m^3 [0.0-4.6], respectively. Fine surface fuels were lower but 1000-hr fuels were similar or higher than in mature lodgepole pine forests. Total surface-fuel loads averaged 123 Mg ha^{-1} [43.3- 206.75] of which 90% was in the 1000-hr fuel class.

Table 4. Fuel load and fire behavior parameter estimates in low-, moderate- and high-density lodgepole pine stands that regenerated after the 1988 fires. Fuel loads are reported in Mg ha^{-1}, and bulk density is in km m^{-3}. Values are mean (1 SE), and letters indicate significant differences among density classes in the same row using Tukey's HSD, $\alpha = 0.05$.

	Lodgepole pine stem-density class			
	Low (< 1000 stem ha^{-1})	Moderate (1000–50,000 stem ha^{-1})	High (> 50,000 stem ha^{-1})	All
Sample size	$n = 18$	$n = 56$	$n = 9$	$n = 83$
Mean stand density (trees ha^{-1})	430 (67)	8,771 (1149)	124,474 (36482)	19508 (5645)
Crown				
Mean crown base height (m)	0.14 (0.02)^{a}	0.47 (0.03)^{b}	0.69 (0.07)^{c}	0.42 (0.03)
Available crown bulk density	0.60 (0.07)^{a}	0.75 (0.04)^{a}	1.51 (0.17)^{b}	0.80 (0.04)
Canopy				
Foliage biomass	0.84 (0.18)^{a}	8.27 (0.73)^{b}	15.12 (3.65)^{c}	7.49 (0.76)
1-hr branch biomass	0.26 (0.06)^{a}	2.43 (0.21)^{b}	3.81 (1.09)^{b}	2.14 (0.22)
Available canopy fuel load[†]	0.97 (0.20)^{a}	9.50 (0.84)^{b}	16.64 (4.25)^{c}	8.53 (0.87)
Total canopy biomass	3.52 (0.74)^{a}	34.94 (3.11)^{b}	63.73 (15.62)^{c}	31.63 (3.25)
Canopy length (m)	3.48 (0.34)^{a}	3.77 (0.12)^{a}	1.77 (0.32)^{b}	3.49 (0.13)
Canopy bulk density [§]	0.03 (0.00)^{a}	0.24 (0.02)^{b}	0.66 (0.12)^{c}	0.24 (0.03)
Live surface fuels				
Herb/Gram	1.71 (0.10)^{a}	0.98 (0.09)^{b}	0.81 (0.15)^{b}	1.11 (0.07)
Shrub	0.10 (0.03)^{a}	0.15 (0.02)^{a}	0.13 (0.05)^{a}	0.13 (0.02)
Dead surface fuels				
Litter depth	0.59 (0.16)^{a}	1.19 (0.10)^{b}	1.73 (0.36)^{b}	1.10 (0.09)
Litter	2.98 (0.78)^{a}	5.96 (0.51)^{b}	8.70 (1.80)^{b}	5.61 (0.46)
1-hr	0.10 (0.01)^{a}	0.18 (0.02)^{b}	0.29 (0.04)^{c}	0.17 (0.01)
10-hr	2.02 (0.19)^{a}	2.35 (0.11)^{a}	2.35 (0.33)^{a}	2.28 (0.09)
100-hr	4.45 (0.32)^{a}	4.95 (0.23)^{a}	7.18 (1.13)^{b}	5.08 (0.22)
Sound 1000-hr	78.48 (7.54)^{a}	82.52 (5.64)^{a}	53.96 (7.83)^{a}	78.55 (4.31)
Rotten 1000-hr	39.24 (4.84)^{a}	31.13 (2.68)^{a,b}	17.64 (5.33)^{b}	31.42 (2.23)
Total surface fuel load	127.27 (10.62)^{a}	127.09 (5.62)^{a}	90.12 (10.33)^{b}	123.12 (4.70)

[†] Available canopy fuel load = foliage + 0.5*(1-hr branch wood)

[§] Computed using the biomass-percentile method (Reinhardt et al. 2006)

Pre-fire successional stage (Despain 1990) influenced the size and proportion of sound and rotten logs and was the best predictor of 100-hr and 1000-hr fuel loads in postfire stands (Fig. 5). LP0 represents postfire stands (0–40 yrs) where lodgepole pine has recolonized the site but has not yet produced a closed canopy. LP1 (40–150 yrs) consists of a single cohort of dense, young lodgepole pine in the young pole stage. LP2 (150–300 yrs) consists of closed canopies dominated by lodgepole pine with tree seedlings in the understory. LP3/4 (> 300 yrs) are multi-cohort stands with ragged canopy characteristics dominated by old lodgepole pine but including Engelmann spruce and subalpine fir in the sub-canopy (LP3) or, on very infertile sites, supporting only lodgepole pine (LP4). The highest proportion of rotten logs was found in stands classified as early succession before the fires and the highest proportion of sound logs occurred in stands classified in later pre-fire successional stages.

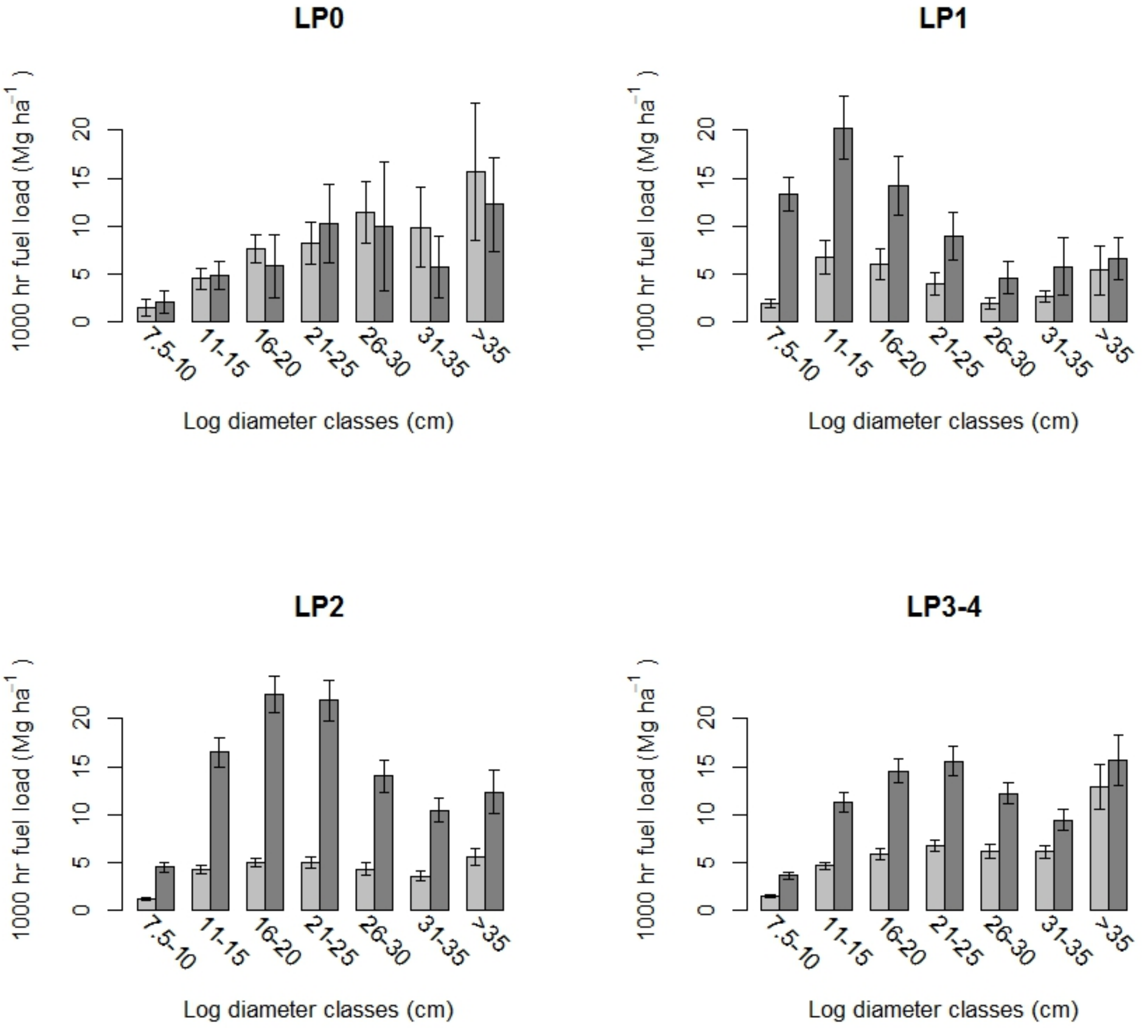

Fig. 5. *Coarse fuel loads by log size and decay status for each pre-fire successional stage. Rotten log fuel loads are depicted with light gray bars and sound log fuel loads are depicted with dark gray bars. From Nelson et al. (in review).*

Between eight and 24 years postfire, surface fuel loads increased by 2-3 times (except 1-hr fuels), but within-plot variability decreased, implying that the spatial continuity of fuels increases with time (Nelson et al. in review). Among-plot variation was greater in canopy fuels than surface fuels, and for nearly all fuel variables, within-plot variation was greater than among-plot variation. The wide range in canopy and surface fuel loads suggests that stand age is a poor surrogate for predicting fuels in young postfire lodgepole pine stands, and that fire potential will vary widely across the burned landscape.

Several fires already burned lodgepole pine forests that regenerated following the 1988 fires. Notably, these "reburns" included a full spectrum of fire behavior, including active crown fire, in stands ranging from 12 to 24 years postfire (Fig. 6). We have obtained fire-behavior observations in these reburns from fire monitoring programs in Yellowstone and Grand Teton National Parks, and Bridger-Teton National Forest. Post-1988 reburns occurred in areas of the 2000 Boundary Fire, 2002 Phlox Fire, 2006 Stinky Fire, 2010 Antelope Fire, 2012 North Buffalo Fire, and 2012 Cygnet Fire. Fire-behavior observations are being integrated into our analyses and used to calibrate and evaluate the models (Nelson et al. in prep). Final simulations are forthcoming.

***Fig. 6**. The 2012 Cygnet Fire burned as a crown fire through 24-yr old lodgepole pine that regenerated after the 1988 Yellowstone Fires. Photo by M. G. Turner, July 2013.*

MANAGEMENT IMPLICATIONS

The subalpine forests of Yellowstone National Park were extremely resilient to the large, severe 1988 Fires, recovering rapidly in the absence of any management intervention. After 25 years, these early seral stands are complex, rich in native plant species, highly productive, and tremendously variable, having created a heterogeneous mosaic of stand structure and function across the postfire landscape. Pre-fire species richness, species composition, and total vegetative cover were largely re-established by 12 years postfire throughout almost all of the burned area. Tree densities equal or (more typically) exceed pre-fire densities in almost every burned stand. Initial postfire lodgepole pine density, which varied enormously across the burned landscape due to differences in pre-fire serotiny among stands and variations in burn severity, now drives landscape patterns of stand structure and function and plant community dynamics. Postfire lodgepole pine density also drives the amount and landscape pattern of canopy fuels in these young stands, but prefire stand structure drives the coarse woody fuels.

Postfire stand structure and function

Managers needing to estimate tree- or stand-level biomass, productivity and/or carbon storage in lodgepole pine trees ca. 25-yrs of age should use the new equations developed in this study. We developed new allometric equations based on empirical measurements of 60 24-yr old lodgepole pine trees (Table 1), and these equations fit very well (Copenhaver and Tinker 2014). Allometric equations developed for older (mature) and younger (10-yr old) lodgepole pines both perform poorly for estimating biomass and productivity lodgepole pines in this size class.

Stand age is not an adequate surrogate for estimating stand structure and function in 25-yr old postfire lodgepole pine forests. Although forest age is indeed known to be a driver of forest structure and function, the landscape variation in post-disturbance regeneration among stands of the same age confounds simple age-based relationships, even at 25 years postfire. This is because the variation in postfire stem density remains very large (from zero to > 340,000 stems ha^{-1}), and this in turn produces tremendous variability in tree density, tree size, and tree- and stand-level productivity–even though all of these stands are of the same age. Our study highlights the importance of accounting for that variability when managers consider the mosaic of stand ages across the landscape.

There is a tradeoff in the effects of stem density on tree vs. stand productivity. Increased stem density was associated with smaller, less productive individuals. Specifically, ANPP of individual trees was reduced by 250 g stem^{-1} 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. High-density postfire regeneration contributes to very rapid recovery of biomass at the ecosystem level (Turner et al. 2016a). Thus, "doghair" stands play an important role in carbon sequestration, an important ecosystem service.

Twenty-five year old postfire lodgepole pine stands are remarkably productive. Lodgepole pine LAI, biomass and ANPP all increased over time, as expected for an aggrading forest, but mean ANPP at postfire year 24 (5 Mg ha^{-1} yr^{-1}) exceeded maximum values reported for developing stands in other studies. For example, three even-aged lodgepole pine stands in southeastern Wyoming reached maximum rates of 2.5–3.2 Mg ha^{-1} 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 et al. 2013). Topo-edaphic conditions had relatively small additional effects on ANPP in this landscape.

Early postfire lodgepole pine regeneration density affected net recruitment and mortality by postfire year 24 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 intra-specific competition. Together, these two opposing population processes will steadily reduce the range of variation in stem density.

There is no evidence of widespread nitrogen limitation of lodgepole pine productivity across the post-1988 fire landscape. Low foliar N concentrations in current-year needles suggest N limitation in stands of the highest densities (344,000 stems ha^{-1}), and perhaps the beginning of N limitation in stands moderately high densities (> 40,000 stems ha^{-1}). However, most of the landscape is below this level (median stem density = 2,900 stems ha^{-1} in 2012), and current-year needle foliar N is well above 1.2% in stands of low to moderate stem density. However, the developing lodgepole pine stands are now strongly influencing soil nutrient availability and competing effectively with the soil microbial community and understory vegetation.

Plant community composition and species richness

Even following high-severity fire, native postfire plant communities recovered rapidly without intervention. Species richness within our plots increased over the first 12 years following fire, then largely stabilized. Postfire vegetation has been dominated overwhelmingly by native species, except in localized places where non-natives had been present before the fires (e.g., along trails). Even where non-native species flourished briefly, densities declined over time as native cover and biomass increased. Thus, there in these subalpine forests that have a long history of infrequent, high-severity fire, there is no need for management intervention to assist or accelerate postfire succession. Indeed, intensive management can potentially introduce undesirable species.

Effects of burn severity on postfire community composition were short lived, and distance from unburned forest had little effect. Fire size and severity had little lasting impact on the patterns of postfire succession in Yellowstone's lodgepole pine forests because most forest floor species regenerated promptly by re-sprouting of surviving roots and rhizomes, and most lodgepole pine re-established from seed released by local canopy seed banks. The abiotic template – especially variables related to substrate and climate – had a much stronger influence on plant community composition. However, that natural re-forestation of larger patches of high burn severity could be impaired in other Rocky Mountain forests where the dominant tree species lack the serotinous cones that characterize logepole pine.

Triggered by the 1988 fires, and likely facilitated by warming temperatures, the postfire recruitment of seedling aspen allowed aspen to expand its range within YNP, relative to its prefire distribution. After 25 years, although aspen have declined somewhat in frequency and density, surviving stems are elongating and have developed ramet structure. Temperature has warmed in Yellowstone since the 1988 fires, and this warming appears to have already affected the geographic distribution of postfire aspen. Long-term study of post-disturbance colonizing cohorts can reveal how species distributions are responding to real-time environmental change.

Fuels and potential fire behavior

Stand age alone is inadequate for predicting fuels in young lodgepole pine stands that regenerated naturally from stand-replacing fire. Although all stands in our study were the same age and arose from fires that burned in the same year, fuel complexes in these 24-yr old stands varied tremendously across the landscape. Available canopy fuels varied ~50-fold (0.0 to 48.6 Mg ha^{-1}), and total surface fuel loads varied ~4-fold (43.3 to 206.7 Mg ha^{-1}). Fine surface fuels were generally less than those reported in mature lodgepole pine forests, yet canopy and 1000-hr fuels were similar or higher than those found in mature lodgepole pine forests.

Postfire stand structure, especially live lodgepole pine stem density, was a strong positive predictor of canopy and fine fuel loads. All canopy (e.g., crown base height, bulk density, and fuel loads) and fine-surface fuel (litter, 1-hr, 10-hr fuel loads) characteristics varied strongly with postfire stem density. This pattern highlights the over-riding influence of postfire stem density on stand-level estimates of canopy and fine fuel biomass, despite the fact that denser stands have smaller tree sizes and smaller tree-level ratios of crown fuel biomass to total tree biomass.

Pre-fire successional stage was the most important driver of large woody surface fuels—influencing the size and proportion of sound and rotten logs, and predicting 100-hr and 1000-hr fuel loads. The highest proportion of rotten logs was found in stands classified as early successional before the fires, and the highest proportion of sound logs occurred in stands classified in later successional stages before the fires.

After twenty-four years of postfire forest development, available canopy fuel loads and canopy bulk density in many stands met or exceeded values reported for mature lodgepole pine forests. Approximately 45% of stands in this study have available canopy fuel loads greater than 10 Mg ha^{-1}, and the highest available canopy fuel load (48 Mg ha^{-1}) in our study was greater than the maximum value found in mature lodgepole pine forests. Given extreme fire weather conditions, many stands have adequate fuel loads and fuel continuity to support crown fire. Available canopy fuel loads averaged 8.53 Mg ha-1 [range 0.0-46.6] and canopy bulk density averaged 0.24 kg m-3 [range 0.0-4.6].

Surface fuel loads increased for 10-hr, 100-hr, and 1000-hr fuel classes but not 1-hr fuels between postfire years 8 and 24 (i.e., between 1996 and 2012). Increases in 10-hr, 100-hr and 1000-hr fuels were consistent with fire-killed trees falling, and the lack of increase in 1-hr fuels suggests a balance between 1-hr fuel deposition from young trees and decomposition rates. Changes in surface fuels between 1996 and 2012 imply that fuel deposition from growing young trees and the falling of fire-killed trees are the dominant factors shaping surface woody fuels during the first 24 years of forest development (Table 4).

Fire observations collected from land managers indicate that crown fires can occur in young, postfire lodgepole pine forests during periods of extreme fire weather. During moderate fire weather, rates of spread and fire intensity are lower in young lodgepole pine than in mature lodgepole pine forests. On sites with abundant coarse fuels, smoldering combustion can allow fires to "hold over" until fire weather conditions (e.g., high winds and low relative humidity) are appropriate for rapid fire spread.

RELATIONSHIP TO OTHER RECENT FINDINGS AND ONGOING WORK

Relationship to other recent findings

Our results contribute substantially to the recent and growing body of research focused on early seral forests in the western US. The complexity and landscape variation of young forests had not been well studied, but their importance is increasingly appreciated (Swanson et al. 2011, Donato et al. 2012). The steady increase in fire frequency and area burned throughout the western US means that the extent of young forests will continue to grow as fire frequency and annual area burned increase throughout the West ((Westerling et al. 2011, Barbero et al. 2015), so it is important to understand these younger forests and their dynamics.

Rapid postfire recovery of plant communities has also been documented in severity other ecosystems, suggesting that this is the typical pattern in temperate coniferous forests. Examples include ponderosa pine-Douglas-fir (*Pinus ponderosa*-*Pseudotsuga menziesii*) forests in Colorado (Fornwalt and Kaufmann 2014, Abella and Fornwalt 2015), Douglas-fir dominated forests in Oregon (Donato et al. 2009), spruce-fir (*Picea engelmannii*-*Abies lasiocarpa*) forests in the Teton Range just south of Yellowstone Park (Doyle et al. 1998), western red cedar-western hemlock (*Thuja plicata*-*Tsuga heterophylla*) forests in Idaho (Stickney 1986), and coastal serotinous pine forests in California (Harvey and Holzman 2014).

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 to 200 years (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, 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 are of high interest in carbon cycle science (Goetz et al. 2012) and important given expected increases in wildfire activity. Carbon stocks in subalpine forests recover to prefire levels within ca. 100 years following high-severity fire (Bradford et al. 2008, Smithwick et al. 2009, Kashian et al. 2013), but landscape variation in postfire stand development determines whether and when prefire levels are reached.

Relationship to ongoing work

Our study of spatial variation in post-1988 fuels and potential forest behavior provided the foundation for several additional grants and awards received by PhD student Kellen Nelson. In 2014, Nelson received the Boyd Evison Graduate Fellowship, a University of Wyoming—National Park Service Research Center Grant, and an American Alpine Club Research Award. With this funding, Nelson established 51 plots aimed at comparing spatial and temporal patterns in fuel loads, fuel moisture, micro-climate and forest structure contrasting young (post-1988), mature and mountain pine beetle-affected lodgepole pine stands. Two mechanistic fuel-moisture models—one established surface-fuel moisture model and one novel canopy-fuel moisture model developed by Nelson—will be evaluated using these data. Additionally, Nelson developed and constructed a low-cost, open-source weather monitoring system capable of incorporating a large selection of high-accuracy sensors at a fraction of the cost of commercial systems (10-100 times less). In 2015, Nelson also received a JFSP—Graduate Research Innovation Grant

(GRIN, #15-2-01-63) to investigate climate-fire-vegetation interactions across the Greater Yellowstone Ecosystem. This project addresses vegetation feedbacks on fire-regime regulation under future climate scenarios in Yellowstone National Park and will integrate findings from this and other studies mentioned above into a landscape-fire-succession model—FireBGC.

This project inspired four additional studies that are ongoing in the Turner Lab. First, with funding from a National Science Foundation Graduate Research Fellowship, PhD student Winslow Hansen began an experiment in YNP to assess the interactions of stand-replacing fire and postfire climate conditions on tree regeneration. Here, we documented rapid and robust postfire tree regeneration after the 1988 fires, but as climate continues to warm, questions arise about whether regeneration following future fires will be as reliable. Hansen has an ongoing experiment underway to address this question, and this will be part of his PhD dissertation. Second, also with funding from a National Science Foundation Graduate Research Fellowship, MS student Catherine Frock conducted an experiment during summer 2013 to assess rates of seed removal (an index of seed predation) by small mammals in recently burned and unburned forests in Greater Yellowstone. We have never previously assessed a potential role of seed predation on postfire tree establishment, but if seed removal rates are high, they could affect postfire succession, especially if seed supply was low. Initial results indicate high rates of seed removal (85% of seeds placed in field settings for 28 days) and no significant differences in seed removal rates between burned and unburned forests (Frock, in prep.). Third, to follow up on our ecosystem process work, BS student Aisha Ba received funding from a UW-Madison Hilldale Award for Undergraduate Research. Ba's study was designed to quantify the soil microbial community in the post-1988 lodgepole pine stands and disentangle the effect of lodgepole pine density or productivity from climate variation on soil microbes. Sampling was conducted in 2014, and laboratory work is in progress. Fourth, in conjunction with a sabbatical by Dr. Rupert Seidl in the Turner Lab at UW-Madison, we are using the data on post-1988 lodgepole pine stand structure to model the development of the 72 0.25-ha stands across the landscape for the next 100 years. This work is in progress and an initial manuscript will be completed in 2016. Thus, our group has successfully amplified the research funded by this JFSP award.

FUTURE WORK NEEDED

As we look ahead, Yellowstone's postfire forests may be effective sentinels of change. As climate continues to warm and fire activity increases, whether the ecological resilience observed after the 1988 Yellowstone Fires will be observed following future fires is not known (Romme and Turner 2015, Turner et al 2016b). Our data provide benchmarks relevant for postfire succession following more recent fires in Yellowstone and throughout the region (Romme et al. 2011). We strongly recommend that datasets akin to those presented here be developed for additional fires throughout the region so that differences can be readily detected.

With projected increases in fire frequency and severity, there will be increased opportunities for short fire return intervals that re-burn immature forests. Some conventional wisdom considers these young forests to be less likely to burn relative to mature forests, but our data suggest that fuels are no longer limiting in many areas that regenerated after the 1988 fires. Future studies should assess fire behavior and burn severity in any fires that re-burn post-1988 forests in the future and quantify postfire vegetation dynamics, as well. Such studies will allow models of potential behavior to be evaluated and detect potential shifts in postfire succession in response to climate-fire interactions.

DELIVERABLES

(A) Deliverables crosswalk table from original research proposal with current status.

Deliverable Type	Description	Current status
Refereed publication	Landscape variation and trends in postfire stand structure and function (Question 1, 1st season field data; Turner)*	**Completed** (Turner et al. 2016a)
Refereed publication	Landscape variation and trends in postfire community composition** (Question 2, 1st season field data; Romme)	**Completed** (Romme et al. in review)
Refereed publication	Landscape variation and trends in postfire fuels and fire behavior (Question 3, 1st season field data+modeling; WY student-Nelson/Tinker)***	**Completed** (Nelson et al. in review)
Refereed publication	Mechanisms of convergence/divergence in postfire structure and function (Question 1, 2nd season field data; Turner)	**In preparation** (Turner et al. in prep)
Refereed publication	Long-term trajectories of postfire succession** (Question 2, 2nd season field data; Romme)	**Completed** (Romme et al. in review)
PhD Dissertation	Graduate student thesis on fuels and fire behavior (Question 3, Univ. Wyoming student)	**In progress** (Nelson, in prep)
Conference presentations	We anticipate 4-6 presentations at national meetings (e.g., Ecol. Soc. America, IAWF, US-IALE) (All)	**Completed** See full listing below
Access to data via website	Online data (to be made public once published); most data will accompany manuscript publication and be available in Dryad	**Data are ready**, posting is awaiting publication
Presentations, briefings for regional managers	Presentations at Yellowstone biennial science conference and regional manager meetings; 1-4 page manager briefings	**Completed** See full listing below
Article in YELLOWSTONE SCIENCE	Article for a general audience about what has been learned about 25 yrs of postfire succession (Turner, Romme, Tinker)	**Completed** (Romme & Turner 2015)

**Completed, and also generated an additional paper on the lodgepole pine tree-level allometry (See Table B).*

***These were completed, but we decided to include the data in a single, more synthetic manuscript, rather than separate papers.*

****This was completed, but we decided to split this task into two manuscripts—one on fuels and a second forthcoming manuscript on fire behavior—to better represent the depth of findings and streamline the review process (See Table B).*

(B) Additional deliverables, beyond those listed in the original proposal, resulting from this project.

Deliverable Type	**Description**	**Status**
Refereed publication	Policy forum article in Science, coauthored by Romme, Turner and other fire scientists, and featuring 1988 fires	**Completed** (Stephens et al. 2013)
Refereed publication	Peer-reviewed paper on tree-level allometric equations and biomass partitioning in young postfire lodgepole pines	**Completed** (Copenhaver and Tinker 2014)
Refereed publication	Peer-reviewed invited book chapter from National Park Service Centennial Summit	**Completed** (Turner et al. 2016b)
Refereed publication	Synthesis paper on mechanisms of post-disturbance forest resilience in temperate forests (co-led by Johnstone and Turner)	**Completed** (Johnstone et al., in review)
Refereed publication	Analysis of persistence and growth of the post-1988 fire cohort of seedling aspen that established throughout burned lodgepole pine forest	**Completed** (Hansen et al., in review)
Refereed publication	Analysis of post-1988 fire Douglas-fir regeneration	**Completed** (Donato et al., in review)
Refereed publication	Effects of climate and tree productivity on soil microbial communities in post-1988 fire lodgepole pine forests (from Aisha Ba's undergraduate research project)	**In preparation** (Ba and Hansen, in prep)
Refereed publication	Manuscript using Forest Vegetation Simulator (FVS) to project stand-development trajectories for post-1988 fire lodgepole pine and Douglas-fir for 100 yrs	**In preparation** (Seidl, Donato, Turner, in prep)
Refereed publication	Landscape variation and potential fire behavior – additional paper focused on the modeling aspects of Question 3; led by PhD student Kellen Nelson)	**In preparation** (Nelson et al. in prep)
MS Thesis	Effects of fire on lodgepole pine seed removal by small mammals, Cat Frock's MS thesis, University of Wisconsin-Madison	**In preparation** (Frock 2015)
PhD Dissertation	Chapter on post-1988 fire aspen cohort in Winslow Hansen's PhD dissertation, University of Wisconsin-Madison	**In preparation** (Hansen, in prep)
PhD Dissertation	Chapter on biomass and ANPP allometric equations for 24-yr old lodgepole pine in Paige Copenhaver-Parry's PhD dissertation, University of Wyoming	**In preparation** (Copenhaver-Parry, in prep)

DELIVERABLES

Refereed publications (10 published or in review)

Copenhaver, P. E. and D. B. Tinker. 2014. Stand density and age affect tree-level structural and functional characteristics of young, postfire lodgepole pine in Yellowstone National Park. Forest Ecology and Management 320:138-148.

Donato, D. C., B. J. Harvey, and M. G. Turner. Regeneration of lower-montane forests a quarter-century after the 1988 Yellowstone Fires: a fire-catalyzed shift in lower treelines? Ecology (In review).

Hansen, W. D., W. H. Romme, A. Ba, and M. G. Turner. Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone. Forest Ecology and Management (In review).

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, T. Schoennagel, and M. G. Turner. Changing disturbance regimes, climate warming and forest resilience. (*Johnstone and Turner co-led this manuscript). Frontiers in Ecology and the Environment (In review).

Nelson, K. N., M. G. Turner, W. H. Romme, and D. B. Tinker. Pre- and postfire forest structure influence fuel loads in 24-yr old postfire lodgepole pine forests. Ecological Applications (In review).

Romme, W. H. and M. G. Turner. 2015. Ecological implications of climate change in Yellowstone: moving into uncharted territory? Yellowstone Science 23(1):6-13.

Romme, W. H., T. G. Whitby, D. B. Tinker and M. G. Turner. Deterministic and stochastic processes lead to divergence in plant communities during the first 25 years after the 1988 Yellowstone Fires. Ecological Monographs (In review).

Stephens, S. L., J. K. Agee, P. Z. Fulé, M. P. North, W. H. Romme, T. W. Swetnam, and M. G. Turner. 2013. Managing forests and fire in changing climates. Science 342:41-42.

Turner, M. G., D. C. Donato, W. D. Hansen, B. J. Harvey, W. H. Romme, and A. L. Westerling. 2016b. Climate change and novel disturbance regimes in national park landscape. In: S. R. Beissinger, D. D. Ackerly, H. Doremus, and G. Machlis, editors. Science for parks, parks for science. University of Chicago Press, Chicago, IL. (In press).

Turner, M. G., T. G. Whitby, D. B. Tinker, and W. H. Romme. 2016a. Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function? Ecology (In press).

Theses and Dissertations

Copenhaver-Parry, P. E. 2016. (expected). Scale-dependent contributions of abiotic and biotic factors to tree species composition patterns in the U.S. Rocky Mountains. PhD dissertation, University of Wyoming, Laramie, WY.

Frock, C. F. 2015 (expected). Local habitat structure affects post-dispersal seed removal in burned and unburned lodgepole pine forests. MS Thesis, Department of Zoology, University of Wisconsin-Madison. (Defense date is 17 December 2015)

Hansen, W. D. 2018 (expected). Subalpine-conifer forest response to climate warming and novel fire regimes in Yellowstone. PhD Dissertation, University of Wisconsin-Madison. (Chapter on aspen, related to this JFSP award, is completed.)

Nelson, K. N. 2016 (expected). Forest dynamics, fire, and climate change in Yellowstone National Park. PhD Dissertation, University of Wyoming, Laramie, WY.

Conference Presentations and Invited Academic Lectures (chronological)

2013

Nelson, K. N., D. B. Tinker, C. M. Hoffman, P. E. Copenhaver, M. G. Turner, and Bill H. Romme. 2013. The variability of forest fuels and patterns of trees influence the heterogeneity of fire behavior and effects in young lodgepole pine forests. US International Association of Landscape Ecology, Austin, TX.

Nelson, K. N., W. H. Romme, M. G. Turner and D. B. Tinker. 2013. Surface and canopy fuels vary widely in 24-yr old postfire lodgepole pine forests. American Geophysical Union, San Francisco, CA.

Turner, M. G. 2013. Natural disturbances: Lessons from Yellowstone. Natural Disturbance Conference, Bavarian Forest National Park, Germany, 29 April – 3 May. (Invited keynote speaker).

Turner, M. G. 2013. Landscape patterns of early postfire lodgepole pine regeneration dominate stand structure and function 24 years after the 1988 Yellowstone Fires. (Poster) Annual Meeting of the Ecological Society of America, Minneapolis, MN, August 4-9.

Turner, M. G. 2013. Landscape in transition? Climate change, fire, and vegetation in Greater Yellowstone. Departmental Colloquium, Forest and Wildlife Ecology, UW-Madison, September 20.

2014

Hansen, W. D., W. H. Romme and M. G. Turner. 2014. Fire and climate interact to foster an expansion of seedling aspen after the 1988 Yellowstone Fires. Annual Meeting of the Ecological Society of America, Sacramento, CA, August 10-15.

Hansen, W. D., W. H. Romme and M. G. Turner. 2014. How have changing environmental conditions affect a postfire cohort of aspen seedlings 25 years after the 1988 Yellowstone Fires? 12th Biennial Scientific Conferences on the Greater Yellowstone Ecosystem. Yellowstone National Park, WY, 6-8 October 2014.

Romme, W. H., M. G. Turner, D. B. Tinker and T. G. Whitby. 2014. Postfire plant community dynamics in subalpine forests: the first 25 years after the 1988 Yellowstone fires. 12th Biennial Scientific Conferences on the Greater Yellowstone Ecosystem. Yellowstone National Park, WY, 6-8 October 2014.

Turner, M. G. and J. F. Johnstone. 2014. Changing climate and novel fire regimes alter tree recruitment and postfire succession in northern conifer forests. Invited for Organized Oral Session, Annual Meeting of the Ecological Society of America, Sacramento, CA, August 10-15.

Turner, M. G. 2014. Fires and insects and warming, oh my! The importance of science-based management in Greater Yellowstone. A. Starker Leopold Lecture (Invited), 12th Biennial Scientific Conferences on the Greater Yellowstone Ecosystem, Yellowstone National Park, WY, 6-8 October 2014.

*PI Turner also co-organized a special session on forest resilience at the Ecological Society of American annual meeting in 2014 with Jill Johnstone.

2015

Turner, M. G. 2015. Landscape in transition? Climate change and disturbance regimes in Yellowstone. Storer Life Sciences Endowment Speaker in "Major Issues in Modern Biology." University of California-Davis. 25 February. (Invited)

Turner, M. G. 2015. Climate change and novel disturbance regimes in national park landscapes. Plenary speaker, National Park Service Centennial Summit: Science for Parks, Parks for Science. University of California-Berkeley, 25-27 March. (Invited).

Turner, M. G. 2015. Climate change, disturbance, and the future of Yellowstone. Wisconsin Ecology Fall Symposium, University of Wisconsin-Madison, 14 October. (Invited).

Outreach to Managers and the Public

We have been very active in presenting the results of our research at meetings that are well attended by forest managers throughout the West:

- Turner presented a webinar, "Climate, fire and vegetation in Yellowstone National Park," as part of the US National Park Service monthly webinar series (Fire Series II: Changing fire regimes, management, and people in the Sierras and Yellowstone National Park.) Delivered service-wide from Grand Teton National Park, July 11, 2013.
- Turner was a Scientific Co-leader, and Harvey was a participant, in a COMPASS workshop on Communicating Fire Science that was held in Seattle, WA, April 23-26, 2014. This workshop was held for ~20 US fire scientists and was led by Nancy Baron, the lead trainer for COMPASS, and four top-level science journalists. The main focus was training scientists to communicate results of fire-related research more effectively to diverse audiences.
- Turner gave the A. Starker Leopold Lecture at the Yellowstone Biennial Science Conference (October 2014) and Romme, Hansen and Nelson all gave presentations
- Turner delivered a keynote presentation at the National Park Service Centennial Summit at UC-Berkeley (March 2015)
- Turner delivered a public lecture, "Climate change, fire and the future of Greater Yellowstone," attended by many residents and agency scientists, at the Teton County Library at the invitation of the Jackson Hole Conservation Alliance (September 30, 2015).
- Romme and Turner wrote an article for YELLOWSTONE SCIENCE that is strongly based on understanding of the 1988 fires, but considers the implications of climate change on the future of Yellowstone's forest ecosystems
- Turner and former PhD student Brian J. Harvey presented in a field trip for managers that focused on the 1988 Yellowstone Fires and was organized by the Northern Rockies Fire Science Network (October 2015)
- Nelson delivered a lecture—Forest Ecology Basics—to the Wyoming Governor's Forest Health Task Force. This lecture was attended by statewide forest health stakeholders including county commissioners, USFS and BLM representatives, forest industry representatives, ranchers, conservation groups, and governor staff members.

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