Project Title: Interactions among climate, wildfire, and forest regeneration at lower treeline the U.S. Northern Rockies

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Principle Investigator:

Dr. Philip E. Higuera
Department of Forest, Rangeland, and Fire Sciences
University of Idaho
875 Perimeter Drive MS 1133
Moscow, ID 83843-1133
Phone: (208) 885-6024
E-mail: phiguera@uidaho.edu

Student Investigator:

Kerry B. Kemp
Department of Forest, Rangeland, and Fire Sciences
University of Idaho
875 Perimeter Drive MS 1133
Moscow, ID 83843-1133
Phone: (303) 507-4603
E-mail: kkemp@uidaho.edu

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1. Abstract

Recent increases in area burned in the western U.S. have raised concerns about the resilience of forests to large wildfires, particularly in dry mixed-conifer forests, where climate change and 20th-century land management have altered species composition, fuel loads, and fire regimes. To study forest resilience to recent wildfires, we examined patterns of post-fire conifer regeneration across 182 sites in 21 recent large fires in dry-mixed conifer forests of the U.S. northern Rocky Mountains. We used logistic and negative binomial regression to predict the probability of establishment and abundance of conifers 5 to 13 years post-fire, as a function of fire legacies (burn severity, distance to nearest live trees, and time since fire), landscape features (elevation, aspect, and slope), and ecological conditions (vegetation and canopy cover, tree density). Seedling densities varied widely across all sites (0 – 127,500 seedlings ha^{-1}) and were best explained by variability in distance to live seed sources ($\beta = -0.014$, $p = 0.002$) and pre-fire tree basal area ($\beta = 0.072$, $p = 0.008$). The probability of seedling establishment decreased greatly beyond a threshold of 95 m from the nearest live seed source. Across all areas within the fires we studied, 75% of the burned area with high tree mortality was within this 95-m threshold, suggesting the presence of live seed trees to facilitate natural regeneration. Combined with the mix of species present within the burn mosaic, dry mixed-conifer forests appear resilient to recent large fires across our study region. This resilience would be undermined if in the future, shorter fire-return intervals prevented stands from reaching reproductive maturity, if fires were characterized by significantly larger high-severity patches, or if post-fire climate conditions were unsuitable for seedling establishment and survival.

Key findings:

- Dispersal distance is a primary filter on post-fire conifer regeneration. Therefore, the size and spatial configuration of stand-replacing burned patches are likely to drive patterns of post-fire succession in dry mixed-conifer forests of the Northern Rockies.

- We identified a threshold distance to live trees of 95 m, beyond which the probability of seedling establishment was unlikely. Within the large wildfires we sampled, more than 75% of the area within patches burned by stand-replacing fire were less than 95 m from an edge, implying that the majority of burned area was close to live seed sources and thus had a high probability of successful natural regeneration.

- In addition to the importance of nearby live seed sources, Douglas-fir regeneration was more abundant on sites higher in elevation and with a lower heat load, which represent cooler, wetter locations. In the future, we may expect to see more successful post-fire regeneration of Douglas-fir in climatically favorable microsites.

- The mix of different species present within the burn mosaic ensures that some species will successfully regenerate post-fire, regardless of burn severity, seed dispersal distances, or environmental conditions. We suggest that dry mixed-conifer forests are largely resilient to recent large fires across our study region.

2. Background and Purpose

Large wildfires have been increasing worldwide over the past several decades (Kasischke and Turetsky 2006; Westerling et al. 2006; Pausas and Fernández-Muñoz 2012), a pattern predicted to continue in many forested regions with even moderate climate warming (Flannigan et al. 2009; Pechony and Shindell 2010; Littell 2011; Rogers et al. 2011). Large disturbances, including wildfires, shape ecosystem structure and function for decades to centuries, and shifts in their frequency, size, or intensity can have unknown implications for forest resilience (Turner 2010). We use the term "resilience" to describe the capacity of a system to absorb disturbance without transitioning into a qualitatively different state, emphasizing the maintenance of system structure and function (Holling 1973; Groffman et al. 2006; Moritz et al. 2011). Large, intense wildfires can reduce forest resilience by shifting post-fire species assemblages (Johnstone et al. 2010a,b) or initiating type conversions to non-forest vegetation (Savage and Mast 2005; Odion et al. 2010). Thus, understanding forest resilience to future wildfires, particularly in the context of climate change, depends upon identifying the mechanisms through which large fires influence tree regeneration and composition.

Dry mix-conifer forests of the western U.S. may be particularly vulnerable to ongoing and future shifts in wildfire activity (e.g., Williams et al. 2010), given the combined effects of 20th-century land use and land management practices on species composition, fuel loads, and fire regimes (e.g., Hessburg et al. 2000; Keeling et al. 2006; Naficy et al. 2010). Of particular concern in these ecosystems is the possibility that large, stand-replacing wildfires will remove viable seed sources over large areas, significantly delaying or preventing post-fire forest recovery (Stephens et al. 2013) and converting forested areas into a qualitatively different vegetation type. However, given that nearly all wildfires include patches of stand-replacing fire interspersed with low- to-moderate severity patches (Turner and Romme 1994; Baker et al. 2007; Odion et al. 2014), an alternative scenario is that spatial heterogeneity in fire effects will allow for forest recovery and resilience to fire (Halofsky et al. 2011).

Forest recovery, or conversely, type-conversion, after large mixed-severity wildfires depends upon a combination of factors, including spatial variability in fire effects, pre-fire species composition, species-specific persistence mechanisms, and post-fire abiotic (e.g., topography, climate) and biotic (e.g., canopy opening, competition) conditions (Stephens et al. 2013). In forests where fire-resilient and fire-resistant (Baker 2009; Keeley et al. 2011) species co-occur, like dry mixed-conifer forests in the U.S. northern Rocky Mountains, the diversity in species and stand structure may increase forest resilience to variable fire effects (Halofsky et al. 2011). Fire-resistant species, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), have thick bark and high crown base heights that facilitate survival of low-intensity surface fires and successful regeneration into low- and moderate-severity patches. Resprouting species, such as aspen (*Populus tremuloides* Michx), or serotinous species, such as lodgepole pine (*Pinus contorta* Douglas ex Loudon), however, are more likely to regenerate after stand-replacing fire (Turner et al. 1997; Franklin and Bergman 2011; McKenzie and Tinker 2012). Understanding how different landscape patterns of mixed-severity fires impact forest structure and regeneration can be particularly challenging, however, in part because of high variability in pre- and post-fire conditions and variability within and among fire events.

Studies of conifer regeneration from single mixed-severity fire events (e.g., Lentile et al. 2005; Donato et al. 2009; Crotteau et al. 2013) or small geographic regions (e.g., Shatford et al. 2007; Collins and Roller 2013), have helped highlight the singular importance of burn severity, patch size, or abiotic conditions on post-fire regeneration. It remains unclear, however, how these results scale up to multiple fire events across broad regions. Here, we quantified natural post-fire seedling regeneration in 21 large (> 400 ha), individual mixed-severity fire events across a 21,000 km^2 region, spanning most of the range of dry mixed-conifer forests in the U.S. northern Rockies. We combined field data with statistical modeling to quantify the relationships among post-fire seedling abundance and composition, wildfire patch metrics, and abiotic and biotic variables. The broad extent of our study gives us the unique opportunity to identify important mechanisms that drive patterns of forest recovery at large-scales and infer the resilience of dry mixed-conifer forests to future large fires and climate change.

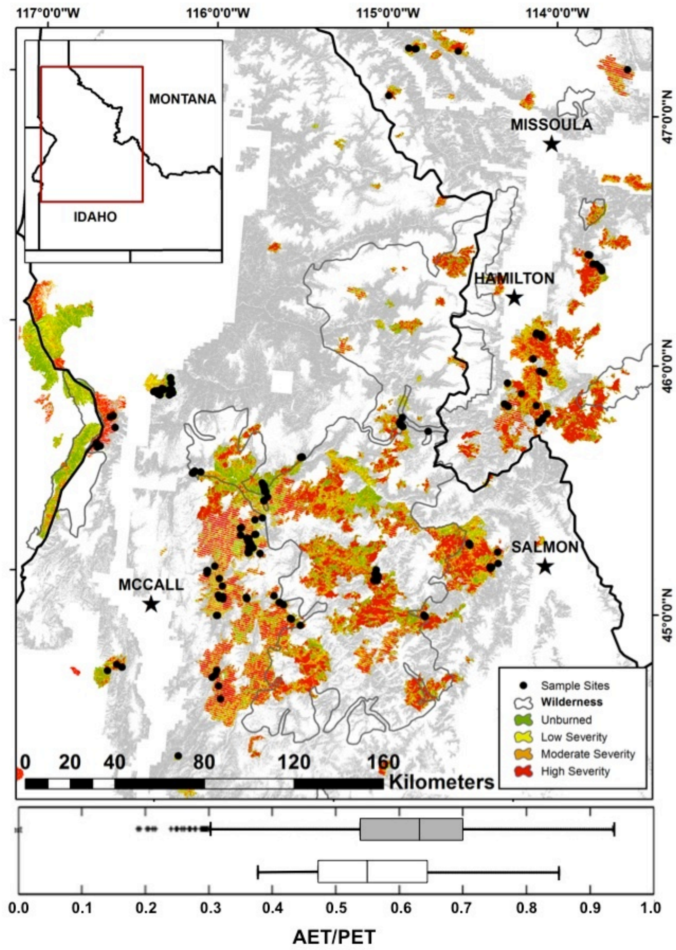

Figure 1. We sampled 182 sites in 21 individual fire events that burned in either 2000 or 2007 across central Idaho and western Montana. We stratified sites across gradients in elevation, aspect, and burn severity to represent the full range of climates in dry-mixed conifer forests (grey shading). Climate is defined here by the ratio of actual to potential evapotranspiration, shown below the map with boxplots for dry-mixed conifer forests (grey) and our sample sites (white). Boxplots delineate the 25th, 50th, and 75th percentiles and whiskers correspond to the 10th and 90th percentiles.

3. Study Description and Location

3.1 Study region

Our study region encompasses the range of dry mixed-conifer forests in the U.S. northern Rockies, spanning a four-degree south to north latitudinal gradient (Fig. 1). Dry-mixed conifer forests in this region are dominated by Douglas-fir and varying proportions of ponderosa pine, grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), and lodgepole pine. Across the study region, average temperatures range from 13.8°C to 21.1°C in July and -6.8°C to -0.6°C in January, and total precipitation ranges from 398 mm to 886 mm (PRISM 2014). The study region experiences warm, dry summers and wet winters. Soils are dominantly inceptisols and entisols derived from granitic Idaho batholith parent material (USDA 2014).

Terrain is characterized by steep topography, with dramatic ecotone boundaries and steep elevation gradients that encompass multiple biomes from river valleys to ridgetops. South-facing hillslopes at low elevations are dominated by ponderosa pine with some mixed Douglas-fir, while north-facing slopes at the same elevation can maintain a mix of Douglas-fir, grand fir, and lodgepole pine. Low elevation dry-mixed conifer forests dominated by ponderosa pine historically experienced surface fires with return intervals of years to decades (Heyerdahl et al. 2008a,b), while higher elevations and more mesic sites experienced less frequent, mixed- or even high-severity fires (Arno et al. 2000; Baker et al. 2007; Odion et al. 2014).

3.2 Sampling design

In the summer of 2012 and 2013, we sampled a total of 182 sites, stratified across the range of biotic and abiotic gradients characterizing dry mixed-conifer forests of the region. To identify potential sampling sites, we used a geographic information system (ArcGIS 10.0) to randomly select points within defined elevation, aspect, and fire severity classifications, in large (> 400 ha) fires that burned in 2000 and 2007 (Gibson 2006; Morgan et al. 2008; Gibson et al. 2014). Vegetation and topography were characterized using the LANDFIRE (2010) database and digital elevations models (DEMs) for forested regions within Idaho and western Montana. We used Relative differenced Normalized Burn Ratios (RdNBR; Miller and Thode 2007) derived from Landsat TM+ satellite imagery from the Monitoring Trends in Burn Severity (MTBS 2011) project to initially classify burn severity into four categories: (1) unburned-unchanged, (2) low severity, (3) moderate severity, and (4) high severity. Sites were classified as "unburned" if they did not burn in either 2000, 2007, or in the 28- or 29- years covered by the MTBS data (e.g., since 1984). Within all four burn severity classes, we selected potential sites across three equally distributed elevation bands, with northeast- or southwest-facing aspects. Additional criteria for potential sites included a minimum polygon size of 0.81 ha (3 x 3 30-m pixels) to account for imprecision in satellite-derived data, separation of at least 120 m from other sites to minimize spatial autocorrelation, and proximity (within 2.5 km) to roads or wilderness research stations to maintain accessibility. Fifteen percent of sites were within federally designated wilderness areas; in all cases, sites that had been salvage logged or planted post-fire were excluded from sampling (USDA Forest Service personnel, pers. comm.). Our stratification resulted in sample sites which spanned the full range of climates characterizing dry mixed-conifer forests in the region (Fig. 1).

At each site, burn severity was field verified using environmental evidence including estimates of percent tree mortality, bole scorch, and shrub stem mortality. If a site did not fall within the desired burn severity classification, or was inaccessible, the location was offset by 30 m in cardinal directions until the desired stratification was attained. Live tree seedlings were counted within a variable width 1 to 10 m wide, 60 m long belt transect, with transect width determined prior to sampling based on visual estimates of seedling density. Vegetation cover, overstory tree basal area, and tree canopy cover were measured at 0, 30, and 60 m along each transect and averaged for a site. Vegetation cover was classified by lifeform (shrub, forb, graminoid, tree) within 1 m^2 sub-quadrats. Overstory tree basal area was quantified using a 2 or 4 m^2 ha^{-1} basal area factor prism, and canopy cover was recorded using a densitometer. Overstory tree species, diameter at 1.37 m height, and mortality were also recorded and used to calculate the density of live and dead trees for each species. We quantified the distance to a live seed source by measuring the ten nearest live seed trees of all species from the transect center using a laser range finder (Truepulse® 360 B/Laser Technology) and averaging these distances for a site. Seed trees were confirmed to either have cones or be large enough to be reproductively mature. Distances greater than 500 m could not be measured. Additional site level data included slope, aspect, latitude, longitude, and elevation. Slope, aspect, and latitude were used to estimate potential heat load from direct solar radiation by calculating a heat load index (following McCune and Keon 2002).

3.3. Statistical analysis

We used a two stage modeling approach to examine patterns of natural seedling regeneration as a function of three categories of response variables: legacies of the fire (e.g., burn severity, distance to live seed source), abiotic environmental variables (e.g., elevation, heat load), and biotic environmental variables (e.g., vegetation cover, tree basal area, and tree canopy cover; Table 1). We first used a logistic regression model to predict tree seedling presence or absence and then used a negative binomial or zero-inflated negative binomial model to predict tree seedling abundance (count). Logistic and count models were compared to evaluate whether the processes influencing seedling presence and abundance differed. All analysis were completed in R version 3.0.2 (R Core Team 2013) using the "MASS" package (Venables and Ripley 2002) for the negative binomial models and the "pscl" package (Zeileis et al. 2008; Jackman 2012) for the zero-inflated models. The logistic regression models are part of the standard statistical package in R.

3.3.1 Logistic regression models for seedling presence-absence

Five logistic regression models were developed using a binomial distribution to predict the presence or absence of tree seedlings. These models included a model for all species present on the site, and four species-specific models for species present on > 15% of the sites: Douglas-fir, ponderosa pine, lodgepole pine, and grand fir. All predictor variables were tested for collinearity using Spearman's rank correlation. Tree canopy cover was dropped from each model because it was well correlated ($\rho > 0.5$) with overstory tree basal area and the average distance to a live seed source. Models were then constructed using the remaining predictor variables and a censor variable indicating whether seed sources were present and measured on a site (Table 1). We examined the sensitivity of the parameter estimates (β) using forward-backward stepwise selection with AIC selection criteria and determined there was little change in these estimates due to model reduction. Therefore, we kept the fully specified models with all variables for comparative purposes.

Table 1. Predictor variables included in all statistical models and their methods of measurement. For comparative purposes, all variables deemed independent were used in both analyses.

Category	Variable	Method of measurement	Units	Type	Range
Fire	Distance to the nearest live seed source	Field measured (10 closest trees; averaged)	m	Continuous	Bounded [0 500]
	Burn Severity	RdNBR and field verified	Unitless	Categorical	Unburned [0], Low [1], Moderate [2], High [3]
	Time Since Fire	Derived from year of sampling minus year of burn; if unburned during year of sampling, MTBS data from 1984 - present were used to determine prior burn severity and TSF	Yrs	Continuous	Discrete values [5,6,12,13, 19, 26, 29]
	Distances > 500 m	Indicator variable for censored values where a value of [1] indicates the observation was censored (i.e., undetectable) and a value of [0] indicates the variable was not censored (i.e., measured)	Unitless	Indicator Variable; Constant	Discrete [0 or 1]
Abiotic Environment	Elevation	Field measured	m	Continuous	Bounded [675 2203]
	Heat Load Index	Derived from slope, aspect, latitude (McCune and Keon 2002)	Unitless	Continuous	Not bounded [0 1.006]
Biotic Environment	Tree Basal Area	Field measured (3 plots at 0, 30, 60 m; averaged)	m^2/ha	Continuous	Not bounded [0 49.3]
	Understory Vegetation Cover	Field measured (3 plots at 0, 30, 60 m; averaged)	%	Continuous	Not bounded [18.67 148.33]
	Canopy Cover*	Field measured (3 plots at 0, 30, 60 m; averaged)	%	Continuous	Bounded [0 100]

* Canopy cover was not included in any analysis because it was significantly correlated ($\rho > 0.5$) with distance to seed source and stand density.

We assessed logistic model fit using the three summary measures: the deviance residual, a Hosmer-Lemeshow test, and the area under the curve (AUC) of a receiver operating characteristic (ROC) curve. The AUC for each model (Fawcett 2006) can vary from 0.5 (random) to 1.0 (perfect prediction), where 0.7-0.8 is "acceptable", 0.8-0.9 is "excellent", and 0.9-1 is "outstanding" discrimination between the model predictions and the observed data (Hosmer et al. 2013). Additionally, to discriminate between presences and absences based on the modeled probabilities, we used a classifier value calculated from the ROC curve that maximized the rate of true positives while minimizing false positives for each model (Fawcett 2006). Using this classifier value, we calculated the positive predictive rate (PPR; i.e., the ratio of true positives to the sum of true and false positives) and the negative predictive rate (NPR; i.e., the ratio of true negatives to total negatives) to evaluate how well models predicted the actual presence or absence of tree seedlings across our study sites. To avoid model overfitting, we subsequently used cross-validation techniques to evaluate the Hosmer-Lemeshow statistic and AUC for each model (Hosmer et al. 2013).

3.3.2 Count models for regeneration abundance

Our tree seedling count data had a high proportion of zeros (26% for all species combined; 35, 68, 74, and 86% for Douglas-fir, ponderosa pine, lodgepole pine, and grand fir, respectively) and the distribution of seedling counts was strongly left-skewed. Therefore, we considered a number of alternative generalized linear models for discrete skewed data, following the procedures outlined by Zeileis et al. (2008). Because our data displayed significant overdispersion (e.g., the variance was larger than the mean), we modeled the abundance of all species and the abundance of Douglas-fir using a generalized linear model with a negative binomial distribution. We developed zero-inflated negative binomial models for the abundance of ponderosa pine, lodgepole pine, and grand fir (Martin et al. 2005; Zuur et al. 2009; Hilbe 2011).

To compare the variables influencing presence and abundance of tree seedling regeneration, we kept all of the predictor variables used in the logistic regression model in the count models. Zero-inflated models were parameterized with an intercept-only predictor function for the zero portion of the model (Zuur et al. 2012). In addition, an offset variable was included in each count model to correct for the variable sampling area. Five sites were removed from this analysis because we failed to record the transect area ($n = 177$).

We compared predicted and observed values from each of the count models were using Spearman's rank correlation. Model fit was assessed visually by plotting the Pearson's residuals against the fitted values (Zuur et al. 2009). Furthermore, we performed a goodness-of-fit test using Monte Carlo simulations ($n = 1000$) to calculate the Pearson's chi-squared statistic, where the expected probabilities from the parameterized model are used to generate new observations set as the "observed" counts. These observed counts are then compared to the "expected" counts drawn from a random negative binomial distribution. A significant lack of fit is indicated by a p-value ≤ 0.05. We also calculated the Pearson's chi-squared test statistic and p-value using cross-validation for each model (n = 1000).

3.4 Patch size analysis

To determine the proportion of the landscape burned in stand-replacing wildfire, we used the classified MTBS data for the 21 sampled fire events and calculated the mean distance from each pixel classified as high severity to the nearest pixel of lower severity (i.e., classified as moderate, low, or unburned). Distance calculations were made from the raster images of the individual fires within R using the "gdistance" (Etten 2014) and "rgal" (Bivand et al. 2014) packages. Because pixel size in the MTBS dataset is 30 m, the minimum distance from a high severity pixel to an edge was 30 m if the two pixels were adjacent. We merged all fires for a single year (2000 or 2007) into a single raster and calculated the cumulative proportion of high burn severity pixels that were various distances from a pixel of lower burn severity. These distributions were compared to the average distance from live seed source trees measured on the ground at each of our high burn severity sites (n = 61).

4. Key Findings

We counted over 10,000 seedlings of eight different species on 182 sites across our study region. Douglas-fir was the most abundant species, present on 120 sites (66%). Total seedling densities ranged from 0 to 1.3×10^6 seedlings ha^{-1} and ranged four orders of magnitude for the most abundant individual tree species, from 0 to 3763 seedlings ha^{-1} (Fig. 2). Seedling densities did not vary significantly between the two fire years (Mann-Whitney U test: W = 4378, p = 0.456). Nine sites had no seed sources within 500 m (the maximum detectable distance), and of these nine sites, only one had seedlings present, all of which were lodgepole pine (Fig. 2).

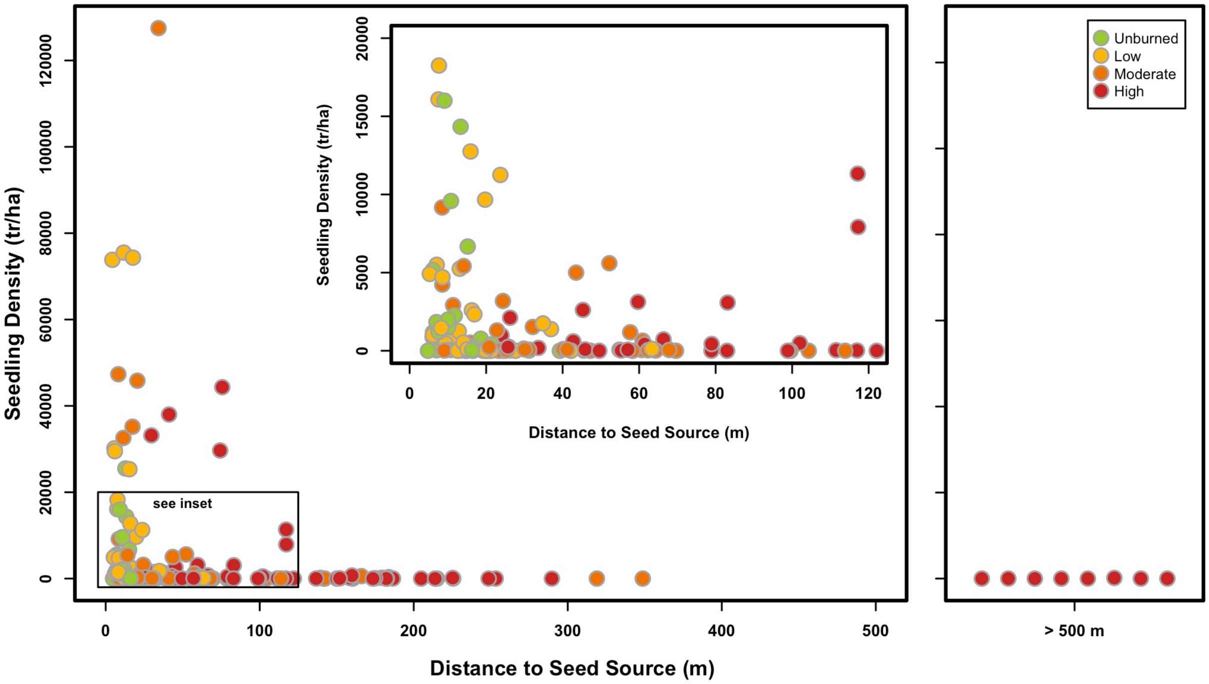

Figure 2. Seedling density as a function of the distance to a live seed source. Each site is additionally colored by burn severity. The maximum distance that could be measured was 500 m from the transect center. Sites with no live seed sources within 500 m are presented in the right panel.

4.1 Dispersal distance is a primary control on post-fire regeneration

In dry-mixed conifer forests of the U.S. northern Rockies, post-fire regeneration is strongly controlled by landscape structural characteristics resulting from burn patterns. Distance to a live seed source was the most important variable predicting seedling presence ($\beta = -0.014$, $p = 0.002$; Table 2) and seedling abundance ($\beta = -0.007$; $p << 0.001$), with a lower probability of regeneration with increasing distance for all the examined species in our study, except lodgepole pine. (Fig. 3; Table 2). Burned areas without nearby residual live seed trees had few or no conifer seedlings five to 13 years after fire, regardless of the severity with which the patch burned (Fig. 2). Observed post-fire seedling regeneration of Douglas-fir, ponderosa pine, and grand fir mimicked the expected dispersal curves of wind-dispersed species, where the number of viable seeds deposited decreases exponentially with distance from the patch edge (Greene and Johnson 1996; Fig. 3). This observed pattern suggests that dispersal limitation is more significant than density-dependent mortality in determining post-fire recruitment across our broad study region (Greene and Johnson 2000).

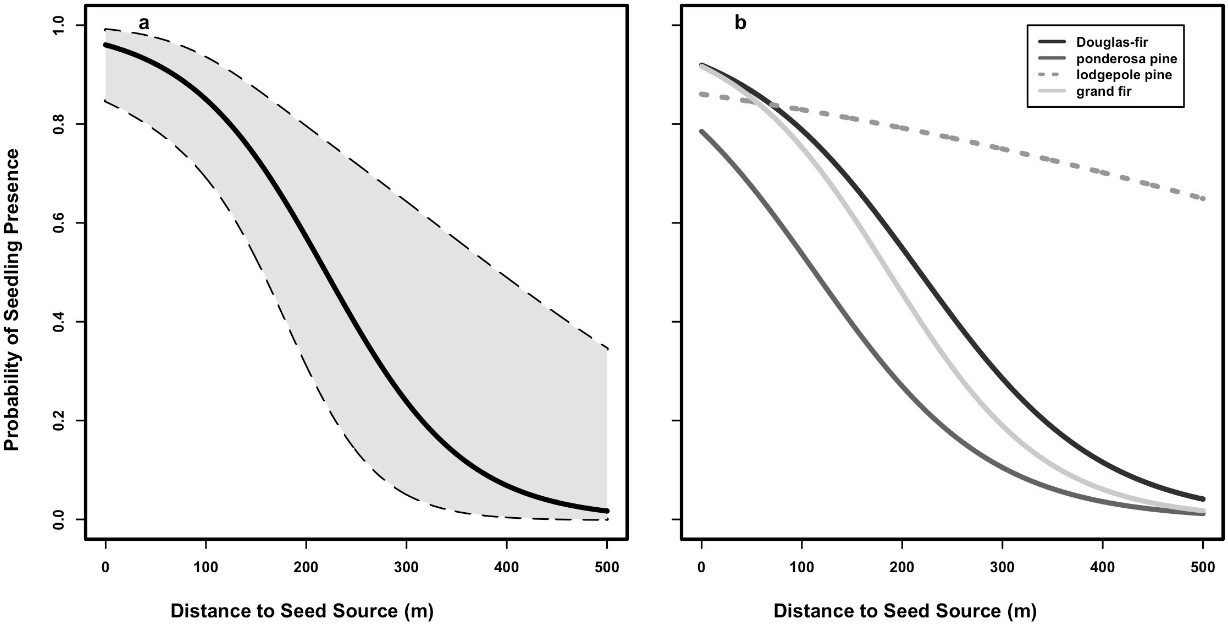

Figure 3. Relationship between the probability of seedling presence and distance to a live seed source for (a) all species and (b) the four most abundant species, when all other variables in the model are held at their median values. The shaded region between the dotted lines represents the 95% confidence intervals on the predicted values for the all species model. In panel (b), a dashed line indicates that the relationship between distance and seedling presence was not significant for that species ($p > 0.05$). Confidence intervals are not shown in panel (b) because they overlap for all species.

Table 2. Parameter estimates from the logistic and negative binomial models for each predictor variable. Estimates are only listed if they were significant for that model. Asterisks indicate levels of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. For each species-specific model, a censored variable was included for distance to a live seed source, where 1 indicates that the distance was accurately measured, and a 0 indicates that the distance was > 500 m or not detected visually from the transect center. If significant, the censor variable indicates that the odds of seedling abundance were lower without a live seed tree present.

	All seedlings		Douglas-fir		ponderosa pine		lodgepole pine		grand fir	
	binary	count	binary	count	binary	count	binary	count	binary	count
Distance to Seed Source (m)	-0.014**	-0.007***	-0.011**	-0.006**	-0.011*	-0.009*	-	-	-0.013*	-
Low Burn Severity	-	-	-	2.051*	-	-	-	-	-	-
Moderate Burn Severity	-	-	-	2.578**	-	-	-	-	-	-
High Burn Severity	-	-	-	-	-	-	-	-	-	-
Time Since Fire (yrs)	-	-	-	0.146***	-	-	-	-	-	-
Censor Variable (Dist. to Seed Source)	NA	NA	-	-1.204*	-2.630***	-3.085***	-3.134***	-2.252**	-2.701***	-2.049**
Elevation (m)	-	-	0.001*	0.001*	-	-	0.002*	-	-	-
Heat Load Index	-	-	-2.452*	-2.997***	-	-	-2.271*	-	-	-
Tree Basal Area (m^2/ha)	0.072**	0.032*	0.072**	0.042**	-	-	-	-	-	-0.070*
Understory Vegetation Cover (%)	-	-	-	-	-	-	-	-	-	-0.043***
Log(Area)	NA	-1.147***	NA	-1.020***	NA	-	NA	-1.505*	NA	-0.895*

We identified an optimal classifier probability for the all species model of 0.87 with the ROC analysis (Table 3), above which seedlings were predicted to be present. This optimal probability threshold corresponded to a maximum distance of 95 m from a live seed source (Fig. 3a) and integrates differences in climate, burn severity, and biotic environmental conditions across our study region. The optimal probably threshold for ponderosa pine seedling presence was within 60 m of a live seed tree, roughly 75 m from a live seed source for Douglas-fir, and as far as 165 m from a live seed tree for grand fir (Table 3, Fig. 3b). These threshold values falls within the range of dispersal distances documented for species found on our sites, which can range from 20 m to 180 m for ponderosa pine and Douglas-fir seeds and between 40 and 120 m for grand fir seeds (McCaughey et al. 1986, Vander Wall 2003). Our study adds to a growing body of literature emphasizing the importance of nearby live seed sources for post-fire regeneration (e.g., Keyser et al. 2008; Donato et al. 2009; Haire and McGarigal 2010).

Our all-species logistic model correctly predicted the proportion of sites with at least one seedling species present 93% of the time (PPR) and all species absent (NPR) 39% of the time. The model distribution fit the data well ($p > 0.08$; Table 3). An AUC value of 0.826 indicated an excellent ability to discriminate between sites with and without seedlings across our extensive sample region (Table 4), which was robust to cross-validation. Furthermore, each of the cross-validated species-specific logistic regression models predicting tree seedling presence performed better than random, as indicated by median AUC values greater than 0.5 (Table 3). Logistic models correctly predicted the proportion of sites with seedling presence between 69 – 91% of the time (PPR), and correctly predicted the proportion of sites with seedlings absent (NPR) between 47 and 91% of the time (Table 3). Deviance chi-squared and Hosmer-Lemeshow statistics validated the fit of our data to a binomial distribution ($p > 0.05$), and were confirmed by cross-validation for most models (Table 3). Negative binomial models for seedling abundance performed less well. Some variability between the predicted estimates and the observed seedling counts were present in these models. Correlation between the predicted and observed counts ranged from 0.4 to 0.7 (Table 3). For example, the all-species model tended to overpredict the abundance of seedlings on sites. However, 45% of the observed seedling counts fell within the range of predicted counts, +/- two standard errors (Fig. 4). The species-specific models correctly predicted 41 to 50% and overpredicted between 31 and 60% of observations.

4.2 Secondary controls on seedling regeneration

Where seed sources were available, seedling regeneration was highly variable, suggesting that seed source is a necessary but insufficient explanation of seedling abundance. Abundant regeneration depends upon successful germination, survival, and growth, all of which are influenced by stochastic processes and environmental conditions that vary at fine scales (e.g., Bonnet et al. 2005). Tree basal area was the primary biotic environmental variable influencing seedling abundance in our study. Basal area is often used as an indicator of site productivity as it measures both size and density of trees in a stand. Sites with a higher pre-fire tree basal area (and, subsequently, higher productivity) had a significantly higher probability of seedling presence ($\beta = 0.072$, $p = 0.008$; Table 3), though this pattern was most apparent at sites with low basal areas. Thus, gradients in resource availability that make pre-fire stands productive, such as soil fertility and moisture availability, likely also influence post-fire germination and tree seedling survival (e.g., Clarke et al. 2005; Röder et al. 2008; Casady et al. 2010). Relative to distance to seed source, however, our results suggest only a minor influence of site productivity (tree basal area) on tree seedling regeneration, as all sites with a basal area > 5 m^2 ha^{-1} had > 95% probability of tree seedling establishment.

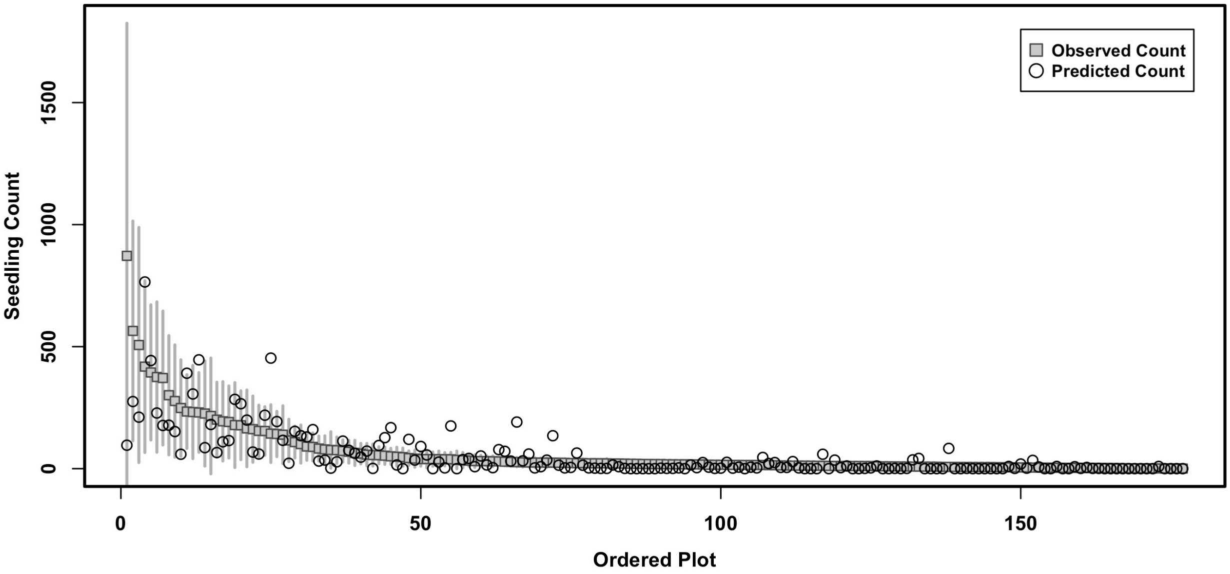

Figure 4. Negative binomial model results. Observed (filled squares) and predicted (open circles) counts with two standard errors (bars) around the predicted count estimates from the negative binomial all-species model. Observations are ordered on the x-axis from lowest to highest predicted count.

The importance of environmental gradients was most pronounced for Douglas-fir regeneration. Moderate- and low-severity burns had 8 and 13 times higher expected counts of Douglas-fir seedlings, respectively, than unburned sites (Table 3), suggesting that moderate increases in resource availability, such as increased light, nutrients, or mineral soil, favored seedling establishment and survival (e.g., Palik et al. 1997). Recruitment also increased on higher elevation sites and sites with a lower heat load (Table 3), representing cooler, wetter locations on the landscape. High summer temperatures and water availability limit Douglas-fir growth across its range in the northern Rockies (Littell et al. 2008), and our data suggest that these factors also limit seedling establishment and survival. Douglas-fir abundance was also higher on sites with a longer time since fire (Table 3). For a sporadic seed producing species like Douglas-fir, this is expected, as the probability of successful establishment accumulates over time. However, we caution the extrapolation of these results to sites outside of our study region given that this model did not cross-validate well, nor was this relationship significant for the other species examined. Further, this result suggests that regeneration for the other species we examined may have been pulsed in a single event post-fire, a result of seedling mortality over time, or due to our sample period not being long enough to pick up multiple pulses of successful post-fire establishment.

Additional environmental variables also helped predict the presence or abundance of lodgepole pine and grand fir across the study region (Table 3). Lodgepole pine tree seedlings were more likely to be present at higher elevations and on sites with a low heat load index (Table 3).

Table 3. Performance among the full logistic and negative binomial models for all species and the four most abundant species. Model fit statistics indicate a significant lack of fit of the distribution to the data if the p-values are < 0.05. PPR is the positive predictive rate, defined as the proportion of times presences were correctly predicted as such. NPR is the negative predictive rate, defined as the proportion of times absences were correctly predicted as such.

	Logistic Regression								Negative Binomial GLM		
	Deviance residual		Hosmer-Lemeshow statistic		Reciever Operating Curve (ROC)				Spearman's rank	Pearson's statistic	
Models	χ^2	p	χ^2	p	AUC [95% CI]	Classifier	PPR	NPR	ρ	χ^2	p
All species	156.4	0.781	4.7	0.789	0.826 [0.758 - 0.894]	0.87	93.2	39.4	0.70	1066.5	0.144
Douglas-fir	165.6	0.601	13.7	0.091	0.850 [0.790 - 0.909]	0.84	91.4	46.8	0.71	455.2	0.337
ponderosa pine	166.1	0.591	18.5	0.018	0.841 [0.782 - 0.900]	0.66	83.3	75.9	0.49	122.3	0.007
lodgepole pine	150.3	0.871	7.3	0.503	0.857 [0.795 - 0.919]	0.65	80.0	80.2	0.60	1287.8	0.132
grand fir	108.3	0.999	10.0	0.263	0.847 [0.765 - 0.929]	0.58	68.8	91.0	0.36	329.8	0.127

However, these variables were not important for determining lodgepole pine abundance (Table 3). Grand fir abundance was negatively related to both vegetation cover and tree basal area and distance to a live seed source was not important for its abundance on a site (Table 3).

Stochastic processes that we did not quantify, such as variability in seed crops, microsite conditions, or favorable post-fire climate conditions (Brown and Wu 2005; League and Veblen 2006), could also account for some of the unexplained variability in seedling abundance across our study region. Seed masting events occur on average every 3 to 12 years in Douglas-fir and ponderosa pine stands in the U.S. northern Rockies (USFS 2012), for example, strongly limiting seed availability in intervening years. Likewise, seed predation likely limits successful germination and subsequent tree seedling regeneration (Vander Wall 1994; Zwolak et al. 2010; Lobo 2014). Given that the post-fire seedling recruitment period can be an important stage within long-term forest succession, further research examining the influence of stochastic variables, especially weather and climate, on post-fire regeneration, will be important for understanding the potential implications of shifts in climate on longer-term forest dynamics.

4.3 Post-fire tree seedling composition reflects pre-fire stand composition

Our conifer species composition data show relatively little difference between regenerating seedlings and the pre-fire mature tree composition, with the exception of a slight increase in lodgepole pine present in sites that burned in 2007, and a decrease in subalpine fir on sites where it was present and burned in 2007 (Table 4). This suggests that the mix of burn severities, patch sizes, and environmental conditions across the landscape perpetuated the stand conditions that were present prior to fire. At the site scale, post-fire seedling composition may still vary as a function of pre-fire species composition of the live tree edge and species-specific tree regeneration mechanisms. For example, the abundance of seeds reaching the interior of patches depends upon a tree species' dominance on the intact forest edge (Greene and Johnson 2004), where edge dominance increases the seed rain of that particular species (e.g., Greene and Johnson 1996). Infilling by shade tolerant species in the absence of fire could therefore alter the seed rain available to recolonize a patch post-disturbance (Perry et al. 2011), especially if those species are prolific seed producers. These factors, in combination with our model predictions of further dispersal distances for grand fir (i.e., 2-3 times the distance of Douglas-fir and ponderosa pine) and additional empirical evidence (McCaughey et al. 1986), suggest that grand fir has the potential to recolonize larger burned patches and increase in dominance post-fire (e.g., Crotteau et al. 2013). This effect may be especially pronounced in areas that have reduced tree cover of Douglas-fir and ponderosa pine from prior logging.

Species-specific regeneration mechanisms may also determine which dry-mixed conifer tree species recolonize different patches post-fire. Lodgepole pine, for example, can regenerate in the absence of a live seed source where it has serotinous cones stored in an aerial seed bank. Though serotiny can vary considerably across a landscape (Schoennagel et al. 2003), stands with high pre-fire serotiny can have prolific regeneration in stand-replacing patches (Turner et al. 1997; Schoennagel et al. 2003). Large, stand-replacing patches may therefore favor the recruitment of lodgepole pine.

Table 4. Density, richness, and species composition of pre-fire trees and post-fire seedlings. Conifer species composition is calculated as the percent of total tree density pre-fire and seedling density post-fire for on each site, averaged across all sites. Listed under each species in parentheses is the number of sites on which each species was found (n = 182). Western white pine was found on one site but is not included in the table because of its low abundance. Data are means +/- 2 SE.

Time	Conifer Density (trees ha^{-1})	Average Conifer Species Richness (by plot)	Conifer Species Composition* (Mean % of plot density ± 2 SE)						
			Douglas-fir (120)	ponderosa pine (58)	lodgepole pine (48)	grand fir (27)	Englemann spruce (22)	western larch (13)	subalpine fir (11)
pre - 2000 fire (n = 84)	361 ± 61	1.8 ± 0.1	38.9 ± 3.4	12.3 ± 4.2	29.1 ± 12.9	20.3 ± 9.4	NP	19.8 ± 19.5	NP
post - 2000 fire (n = 84)	7047 ± 1714	2.1 ± 0.1	35.3 ± 4.3	16.2 ± 7.1	19.2 ± 7.9	24.1 ± 10.6	2.5 ± 2.3	16.9 ± 13.1	13.1 ± 12.0
pre- 2007 fire (n = 98)	421 ± 48	2.2 ± 0.1	32.7 ± 3.9	18.9 ± 5.0	15.8 ± 5.6	22.3 ± 9.7	6.8 ± 7.3	7.1 ± 6.6	18.5 ± 6.2
post- 2007 fire (n = 98)	8153 ± 2006	2.2 ± 0.1	24.1 ± 4.4	23.1 ± 5.6	24.0 ± 5.7	19.0 ± 7.5	5.1 ± 4.6	9.3 ± 11.8	1.7 ± 1.7

* Western white pine was found on one site but its density was so low that it did not contribute to the overall species composition. NP indicates that species was not present on any of the sampled sites.

4.4 Variability in the burn mosaic and size of patches ensures forest resilience

Because dispersal distance acts as a primary filter on post-fire conifer regeneration, the size and spatial configuration of stand-replacing patches across the landscape become key drivers of post-fire successional trajectories (e.g., Haire and McGarigal 2010). High severity (stand-replacing) burn patches were characterized by high tree mortality, but they tended to be adjacent to patches with only partial tree mortality. The mean distance from an area within a high severity patch to an edge ranged from 33 to 118 m for fires that burned in 2000 and from 31 to 122 m in fires that burned in 2007. Over 85% of the area burned in 2000 in high severity patches was less than 95 m from the nearest edge of a lower severity patch and 98% of the area was within 200 m from an edge. Likewise, in the 2007 fire events, 75% of the area burned by high severity fire was within 95 m of an edge and 94% of the area was within 200 m of a lower severity edge. Even though the wildfires we sampled within were large (>400 ha), the majority of burned area was close to live seed sources and thus had a high probability of successful natural regeneration. This finding is corroborated by several prior studies from diverse forest types; for example, 75% of stand-replacement patches in subalpine forests in Yellowstone National Park were less than 200 m from a live forest edge (Turner et al. 1994), and 58% of stand-replacement patches in a mixed-conifer forest in southern Oregon were within 200 m of a live forest edge (Donato et al. 2009). Thus, even within large fires, only a small proportion of high-severity patches will exceed a size where successful natural regeneration is unlikely. This diversity in burned patch sizes creates landscapes that are largely resilient to mixed-severity fires, regardless of burning conditions or forest type.

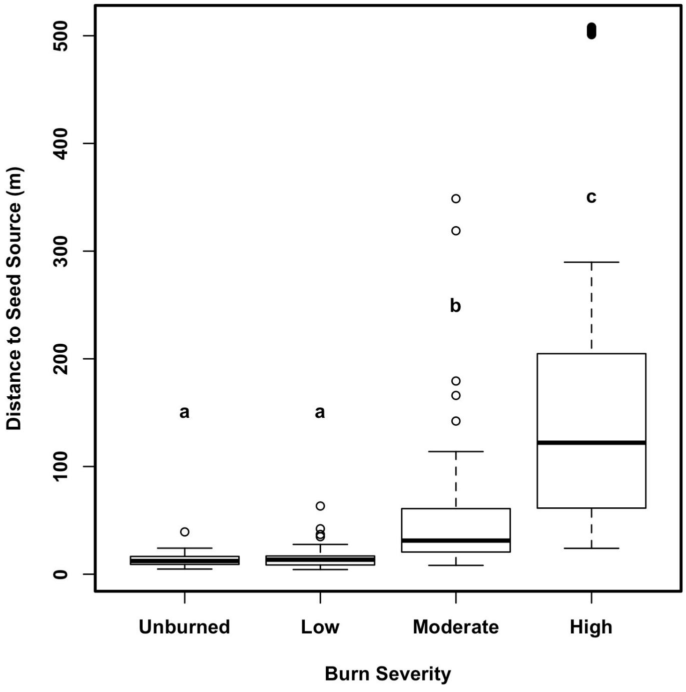

Figure 5. Relationship between burn severity and the average distance to a live seed source. Burn severity was initially categorized using satellite RdNBR data and subsequently field verified. Letters denote to statistical differences between the treatments. High severity patches are significantly further on average to live seed trees than moderate, low, or unburned patches. Low severity and unburned patches did not differ in the average distance to a live seed source.

Even though stand-replacing patches were characterized by being further from live seed sources, burn severity was not a significant factor influencing seedling presence or abundance for any of the species except Douglas-fir. Rather, distance to a live seed source overrode burn severity in the models. Specifically, sites within patches burned at high and moderate severity were further from live seed source trees than sites in either low or unburned patches (Fig. 5; Kruskal-Wallis Test: $\chi^2 = 117.809$, d.f. = 3, $p << 0.001$). Sites that burned at moderate severity were a median distance of 31 m from a live seed source, while sites that burned at high severity were a median distance of 122 m from a live seed source, compared to 12 and 13 m for unburned and low severity sites, respectively (Fig. 5).

5. Management Implications

Resilience of forests to large, severe wildfires is of ecological and management significance, particularly given ongoing climate change and the potential implications of increased forest density from prior forest and fire management (Keeling et al. 2006; Naficy et al. 2010). Our results highlight important interactions between the spatial distribution of high-severity patches and seed dispersal mechanism as the primary controls of post-fire regeneration. Patterns of high-severity fire in combination with seedling abundance data from across our large study region suggest that dry-mixed conifer forests have been resilient to recent large fires. Our results improve our understanding of forest resilience to wildfires and have important implications for addressing the impacts of shifting fire regimes and climate change on forest persistence.

The spatial characteristics of mixed-severity fires and pre-fire species composition interact to promote resilience of dry mixed-conifer forests to large wildfires, even when those fires burn under a variety of weather conditions. Most patches burned by stand-replacing fire in the large regional fire events we studied were close to live trees which likely included seed sources for conifer regeneration. Over 80% of low severity patches and approximately 40% of moderate severity patches we sampled exceeded the desired seedling densities considered sufficient to regenerate a stand to its pre-fire density, which can range from 180 trees ha^{-1} to 370 trees ha^{-1} in dry mixed-conifer forests across the northern Rockies region (S. Fox, USFS; pers. comm.). Sparse natural regeneration was primarily observed in large, high severity patches (i.e., patch interiors > 95 m from an edge). Although burn severity was a poor predictor of ecological response in our study, it is directly related to dispersal distance, as by definition high severity patches have fewer residual live trees and are further from live seed sources. Therefore, the residual landscape pattern of the fire (e.g., the burn mosaic) is key to maintaining current forest diversity and structure after future wildfires.

Although there is considerable concern surrounding large fire events, patch scale heterogeneity present across the burned landscape in the U.S. northern Rockies suggests that these forests will recover to pre-disturbance species composition and diversity. Our conclusion is predicated upon the fact that forests remain unburned long enough for live trees to reach reproductive maturity, the proportion of high-severity patches far from seed sources does not increase significantly in the future, and climate change does not shift post-fire environmental conditions so as to limit successful tree seedling establishment and growth. The range of suitable climate conditions for mature tree species in the U.S. northern Rockies may shift considerably in the coming decades (Rehfeldt et al. 2006; Rehfeldt et al. 2008), and it is likely that the regeneration niche of seedlings is even narrower (Grubb 1977; Jackson et al. 2009: Dobrowski et al. 2015). Additionally, extrapolations of statistical fire-climate relationships suggest a potential two- to five-fold increase in the median area burned in the U.S. northern Rockies by mid-century (Littell 2011), implying an increase not only in frequency, but also fire size. Short fire-return intervals may limit the potential for regeneration success and remove future seed sources (Keeley et al. 1999; Johnstone and Chapin 2006; Brown and Johnstone 2012). More intense and severe fire may also favor species that are well adapted to regenerate in the absence of live seed sources nearby (e.g., lodgepole pine and grand fir).

Understanding how large, mixed-severity fires impact the regeneration and resilience of forests will become increasingly important for making sound forest and fire management decisions in a warmer, more fire prone future. Conifer regeneration and habitat restoration are important management priorities following fire, and abundant natural post-fire tree regeneration may limit the area managers need to treat these objectives. In large, high severity patches, sparse natural regeneration may result in delayed successional trajectories or altered vegetation states. Managers aiming to insure post-fire recovery should therefore focus regeneration efforts on high-severity patches with large distances (> 100 m) to live seed sources. As area burned continues to increase, the amount of area burned severely will also increase (Dillon et al. 2011). If the size of high severity patches and the relative proportions they occupy on the burned landscape increases with future climate change, or if the post-fire environmental conditions shift significantly relative to the past several decades (Rehfeldt et al. 2006), the resilience of dry mixed-conifer forests to large wildfires that we documented will be increasingly compromised.

6. Relationship to Ongoing Work

The research and results detailed in this work are based on stand level attributes collected on specific sites. These data and results emphasize the importance of site-specific factors related to the burn mosaic in determining post-fire seedling establishment. However, the distribution of seedlings is likely to be characterized by a number of different factors and their intersection, including the adult niche, which is where a seed source exists, the dispersal niche, or where seeds can disperse to, and the establishment niche, which defines safe sites for germination and establishment of seedlings (Young et al. 2005). Although this work has established how fire can modify the adult niche through overstory mortality and the dispersal niche by making live seed sources more distant from some sites, it is probable that broad scale climate factors will modify the establishment niche. Therefore, we are furthering this analysis by utilizing downscaled climate data (800 m resolution) as predictors of forest recovery across space to understand how climate mediates the role of fire in determining suitable habitat for seedling regeneration.

We are using generalized additive models (GAMs) to model the relationships between temperature, precipitation, and energy (e.g., AET, PET) variables and seedling regeneration. All models will also include measured distances to live seed sources (to approximate the dispersal niche), live tree basal area (to approximate the adult niche), and satellite burn severity data (RdNBR) along with the most significant climate variables for the most abundant species on our sites. A full model will be established for all 182 sites in the study and then the data will be partitioned to explore whether these relationships vary for establishment versus survival (seedlings > 3 yrs old), in sites with higher burn severity, or near the range margins for particular species. Additionally, this analysis will allow us to evaluate whether seedling regeneration is more sensitive to a change in climate (e.g., increase in mean annual temperature of several degrees) or an increase in mean distances to nearby seed sources.

7. Future Research Needs

Climate change predictions suggest that more area will burn in the future which is likely to result in proportionately more area burning severely. Several studies have attempted to quantify whether changes have occurred in the proportion of area burned severely through time (e.g., Millar et al. 2009, Dillon et al. 2011, Cansler and McKenzie 2014) though there is currently no consensus on the subject, with some regions exhibiting changes in the proportion of area burned severely and other regions not exhibiting this change. As more satellite burn severity data become available, these types of studies, especially within ecoregions, will help determine the potential consequences of changing climate on post-fire regeneration and forest resilience. Additionally, there is a need to understand how fire patterns and patch dynamics differ in forests with a history of land management and fire suppression vs. areas where the natural role of fire has been maintained. Whether or not the patterns of burn severity and patch size differ as a result of management history would provide important information for forest restoration efforts.

Furthermore, few studies have examined the relationships between interannual climate and seedling regeneration at the grassland-forest boundary. Species at this ecotone are likely to be more susceptible to range contractions with future climate change (e.g., Bell et al. 2014), and, thus, it will be important to understand the physiological and climatic mechanisms responsible for seedling establishment and failure along this boundary.

8. Deliverables, description, and delivery dates.

Deliverable Type	Description & details	Delivery Date
Field visits with local managers	Lead and organized field trip with local land managers from the Payette National Forest for the University of Idaho NSF-IGERT Social Ecological Resilience Program. Council, ID. Interacted with silviculturists on the Payette, Nez Perce and Boise National Forests to coordinate locations of field sites Interacted with silviculturists on the Lolo, Bitterroot, and Salmon-Challis National Forests to coordinate locations of field sites	September 2014 July-August 2013 July-August 2012
Informative flyers	Two-page description of results for dissemination to managers. Sent to Nez Perce, Salmon-Challis, Payette, Boise, Lolo, and Bitterroot National Forests and Region 1 Silviculturist. Available at: http://dx.doi.org/10.6084/m9.figshare.1336075	March 2015
Webinar & Conference Presentations	**Kemp, K.B.,** P.E. Higuera, and P. Morgan (2015) Resilience and regeneration after wildfire in dry mixed-conifer forests of the US northern Rockies. Webinar: Northern Rockies Fire Science Network. DOI: http://dx.doi.org/10.6084/m9.figshare.1333592. **Kemp, K.B**., P.E. Higuera, and P. Morgan. (2014). Post-fire tree recruitment in the U.S. Northern Rockies: The influence of seed source proximity and environmental conditions. Contributed talk: Ecological Society of America Annual Meeting; Sacramento, CA. **Kemp, K.B.**, P.E. Higuera, and P. Morgan. (2014). Post-fire tree recruitment in the U.S. Northern Rockies: The influence of seed source proximity and patch size. Invited talk: International Association of Wildland Fire and Association for Fire Ecology Large Wildfires Conference; Missoula, MT.	February 2015 August 2014 May 2014
Curriculum development and guest lectures	Guest Instructor. NATR 108: Introduction to Natural Resources. Fire Ecology Section. Wenatchee Valley Technical Preparation Program. Wenatchee, WA. Developed curriculum including labs, field trips, and lectures. 12 contact hours. Guest Instructor. Wenatchee River Institute. Fire Ecology Field Day. Taught and planned activities for 9th Grade Wenatchee High School Agricultural Science Students. Leavenworth, WA.	April 2015 November 2014

	Guest Lecture. FOR 326: Fire Ecology and Management. Fire and Disturbance Interactions in Subalpine Forests. University of Idaho. Primary Instructor: Dr. Philip Higuera. Guest Lecture. FOR 326/426: Fire Ecology and Management. Fire and Disturbance Interactions in Subalpine Forests. University of Idaho. Primary Instructors: Dr. Philip Higuera / Camille Stevens-Rumann. Guest Lecture & Invited Speaker. Climate Change Deliberation with Forest Managers of the Northern Rockies: Our Experience with a New Paradigm of Graduate Education. Northwest Climate Science Center Climate Change Bootcamp, McCall Outdoor Science School. McCall, ID. Guest lecture. FOR 426: Fire Ecology and Management. Disturbance Interactions. University of Idaho. Primary Instructor: Dr. Philip Higuera.	October 2014 September 2013 July 2013 September 2012
Referred publication	**Kemp, K.B.,** P.E. Higuera, and P. Morgan. (in review) Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. In review since 3/2015: *Landscape Ecology.*	March 2015
Dissertation	Kemp will defend her dissertation in October 2015 and graduate in December 2015	October 2015

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