

# Disturbance and productivity interactions mediate stability of forest composition and structure

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**Abstract.** Fire is returning to many conifer-dominated forests where species composition and structure have been altered by fire exclusion. Ecological effects of these fires are influenced strongly by the degree of forest change during the fire-free period. Response of fire-adapted species assemblages to extended fire-free intervals is highly variable, even in communities with similar historical fire regimes. This variability in plant community response to fire exclusion is not well understood; however, ecological mechanisms such as individual species' adaptations to disturbance or competition and underlying site characteristics that facilitate or impede establishment and growth have been proposed as potential drivers of assemblage response. We used spatially explicit dendrochronological reconstruction of tree population dynamics and fire regimes to examine the influence of historical disturbance frequency (a proxy for adaptation to disturbance or competition), and potential site productivity (a proxy for underlying site characteristics) on the stability of forest composition and structure along a continuous ecological gradient of pine, dry mixed-conifer, mesic mixed-conifer, and spruce–fir forests following fire exclusion. While average structural density increased in all forests, species composition was relatively stable in the lowest productivity pine-dominated and highest productivity spruce–fir-dominated sites immediately following fire exclusion and for the next 100 years, suggesting site productivity as a primary control on species composition and structure in forests with very different historical fire regimes. Species composition was least stable on intermediate productivity sites dominated by mixed-conifer forests, shifting from primarily fire-adapted species to competition-adapted, fire-sensitive species within 20 years of fire exclusion. Rapid changes to species composition and stand densities have been interpreted by some as evidence of high-severity fire. We demonstrate that the very different ecological process of fire exclusion can produce similar changes by shifting selective pressures from disturbance-mediated to productivity-mediated controls. Restoring disturbance-adapted species composition and structure to intermediate productivity forests may help to buffer them against projected increasing temperatures, lengthening fire seasons, and more frequent and prolonged moisture stress. Fewer management options are available to promote adaptation in forest assemblages historically constrained by underlying site productivity.

**Key words:** *climate change; ecological gradient; effective energy and mass transfer; fire exclusion; forest resilience; mixed-conifer forest; population dynamics; restoration; type conversion.*

## INTRODUCTION

In conifer-dominated forests of western North America and other regions where disturbance regimes have been modified by a century or more of fire exclusion by humans, fundamental ecological changes are occurring as a result of increased stand densities and changes to species composition (Allen et al. 2002, Taylor and Skinner 2003, Kitzberger et al. 2012, Fernandes et al. 2013,

Stephens et al. 2015). Transitions from historically disturbance-adapted species to assemblages adapted to more competition-oriented environments raise concerns about the stability and persistence of future forests, especially as long-term trends of warming temperatures and increasing variability of seasonal precipitation portend longer fire seasons coinciding with fuel structures that promote larger, higher severity fires (Westerling et al. 2003, Crimmins 2011, Cook et al. 2015). While changes to forest structure (Minnich et al. 1995, Sisk et al. 2005, Chavardès and Daniels 2016) and species composition (Cocke et al. 2005, Collins et al. 2011, O'Connor et al. 2015) have been recorded in many historically fire-adapted forests, the rate and degree of transition from fire-adapted to competition-adapted species assemblages appears to be highly variable. Differences in these

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transition rates provide an opportunity to identify the mechanisms behind assemblage formation and maintenance, and may provide insights into the resilience of species functional groups in response to the projected return of widespread and frequent fire to these systems.

Cessation of normal disturbance processes such as fire can result in a shift toward density-dependent interspecific and intraspecific competition as the primary driver of assemblage dynamics (Huston 1979, Grime 2006). Outcomes of density-dependent competition are governed by site quality and life history traits that favor competitive ability (Wilson and Keddy 1986, Kondoh 2001, Zhu et al. 2015). The mortality-driven transition of species assemblages from fire-adapted to competition-adapted life strategies can be delayed in systems dominated by long-lived individuals such as trees (Chesson and Warner 1981, Suding and Hobbs 2009, McDowell et al. 2011). A more sensitive measure of forest assemblage transition may be the deviation of species composition and abundance of early life stages of trees and shrubs that must cope with proximate environmental constraints (van Mantgem et al. 2006, Falk 2013, Bansal et al. 2014).

In conifer-dominated systems, traits of highly competitive species often include enhanced shade tolerance, slow growth, and retention of lower branches that increase photosynthetic capacity along the length of the tree bole (Burns and Honkala 1990, Messier et al. 1999, Franklin et al. 2002). Conversely, traits that allow a species to persist under conditions of frequent disturbance include rapid juvenile growth, self-pruning, thick bark, and longevity of mature individuals (Clark 1996, Bond and Keeley 2005, Keeley et al. 2011). Under conditions of frequent, low-severity disturbance such as surface fires, underlying relationships between site quality and competitive ability that would otherwise favor competition-adapted species can be masked by strong selection for species with disturbance-adapted traits (Kondoh 2001).

The interplay between fire frequency and site quality, measured as potential productivity, provides a dynamic selection mechanism for composition and structure of seedling functional groups. Persistence of disturbance-adapted species on productive sites requires a short interval to reproductive age relative to competition-adapted species, and frequent enough disturbance to limit competition among individuals (Kondoh 2001). Interruption of frequent disturbance results in resource limitation as available niche space is occupied by less disturbance-tolerant species, suppressing recruitment of disturbance-adapted species, and enabling establishment of competition-adapted species (Huston 2004, Comita and Hubbell 2009, Zhu et al. 2015).

We use a spatially explicit time series of forest regeneration composition following the exclusion of fire to test the effect of site productivity on the stability of species assemblages. Initial forest types are stratified by pre-fire exclusion species assemblage and disturbance regime. Throughout this paper, we refer to species existing in a stand prior to the period of fire exclusion as primary

species, and species that successfully establish and persist in a stand only after fire exclusion as secondary species. We test forest assemblage stability by comparing the proportion of primary to secondary species approximately 50 and 100 years into the period of fire exclusion.

We propose a model for the transition from primary to secondary species following fire exclusion that proceeds through three phases. The first phase is characterized by initial recruitment of primary and some secondary species during the assemblage-adapted disturbance interval. Once a typical fire-return interval is surpassed, recruitment of primary species tapers off and is replaced by robust recruitment of secondary species. Finally, continued exclusion of fire results in dominance of the understory by secondary species with little or no new recruitment of primary species without fire or additional disturbance (Fig. 1). Periods before and after the onset of fire exclusion provide an opportunity to compare time to peak recruitment of primary species, time to secondary species establishment, and subsequent changes to species assemblages following fire exclusion. We hypothesize that stability of forest assemblages following fire exclusion is a function of the relative roles of disturbance or site productivity in mediating forest species and structure. While we acknowledge that these roles are dynamic and interplay exists between them, historically disturbance-mediated species assemblages should be the least stable and historically productivity-mediated forest assemblages should be the most stable during the period of fire exclusion.

### Study area

We tested interactions between site productivity, forest assemblage stability, and historical disturbance regime by examining a series of adjacent forest types distributed along a gradient of potential productivity with distinct historical disturbance regimes that were homogenized following the onset of fire exclusion in the late 1800s (Grissino-Mayer et al. 1995, O'Connor et al. 2014). The study location in the Pinaleno Mountains of southeastern Arizona, USA, is one of several "Sky Island" ranges central to the development of early theories about elevational gradients and local constraints on species distributions (Shreve 1922). The study area above 2135 m is comprised of montane conifer forests distributed along an elevational gradient from low to high productivity (Pelletier et al. 2013) and frequent to infrequent historical fire regime (Grissino-Mayer et al. 1995, Swetnam et al. 2009, O'Connor et al. 2014). Lower elevation pine-oak communities consisting of ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelmann) and several oak species (*Quercus* spp.) transition to dry mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirbel) Franco), southwestern white pine (*Pinus strobiformis* Engelmann), and ponderosa pine, with a minor component of white fir (*Abies concolor* (Gor. and Glend.) Lindl. ex Hildebr.) (Johnson 1988). Above 2750 m, precipitation and temperature regimes

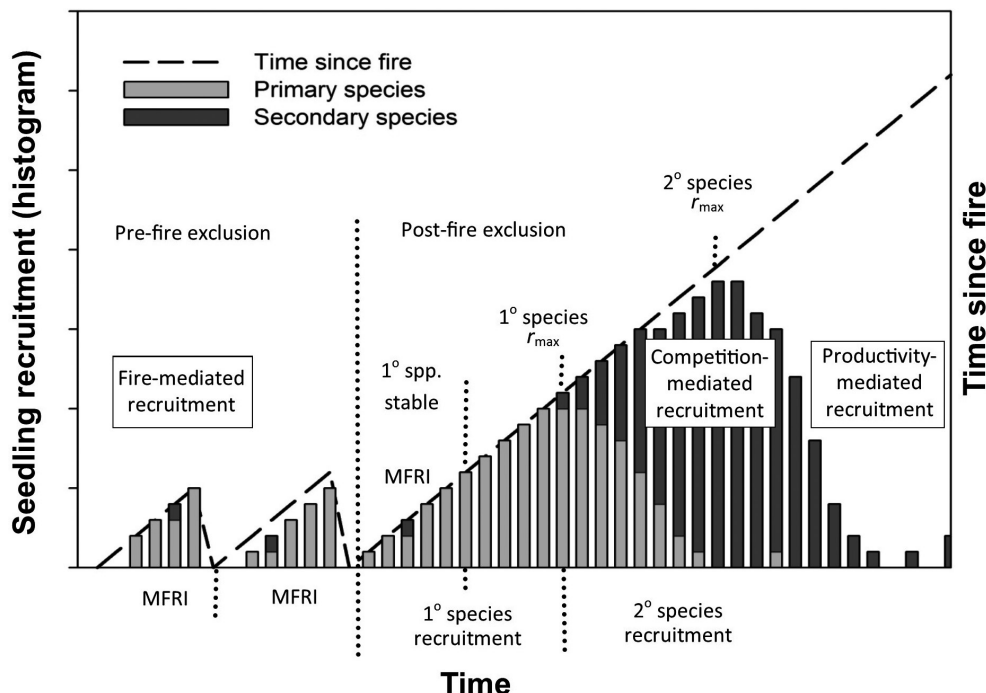


FIG. 1. Graphical model of transition from fire-mediated to competition-mediated to productivity-mediated seedling recruitment as a result of fire exclusion. Median fire return interval (MFRI) is the Weibull median probability interval (Grissino-Mayer 1999). Maximum recruitment of primary species ( $1^{\circ}$  species  $r_{\max}$ ) and secondary species ( $2^{\circ}$  species  $r_{\max}$ ) are measured from the onset of fire exclusion. Productivity-mediated recruitment reflects resource limitations of gap-dynamics recruitment patterns.

favoremicmixed-conifer forest dominated by Douglas-fir and white fir with minor components of southwestern white pine, corkbark fir (*Abies lasiocarpa* var. *arizonica* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and aspen (*Populus tremuloides* Michx.) (Johnson 1988). Above 3000 m and along north-facing slopes, spruce–fir forest becomes the dominant forest type, comprised of Engelmann spruce and corkbark fir interspersed with occasional Douglas-fir (Fig. 2). Prior to Euro-American settlement of the area in the 1870s (Bahre 1991), median fire return intervals in pine and dry mixed-conifer forests ranged from 3 to 10 years (Grissino-Mayer et al. 1995, O'Connor et al. 2014). Adaptation to frequent, low-severity, and primarily seedling-killing surface fires was inferred from the fire scar record, scorch marks found on oak, pine, and Douglas-fir species, and demographic evidence of seedling establishment only during short fire-free periods (O'Connor 2013). The mesic mixed-conifer forest was subject to less frequent (4–24 year interval) low- and mixed-severity fires that occasionally also killed some mature trees (O'Connor et al. 2014). These stands were composed of a mix of fire-adapted species also present in dry mixed-conifer forest, as well as a competition-adapted white fir component. Extant spruce–fir stands established after a high-severity (stand-replacing) fire in 1685 (Grissino-Mayer et al. 1995, Margolis et al. 2011, O'Connor et al. 2014). Engelmann spruce and corkbark fir developed a competition-adapted

species assemblage where gap dynamics driven by localized insect outbreaks and blow-down events were the primary disturbances during multi-century fire-free intervals (O'Connor et al. 2014, 2015).

Initial interruption of historical fire regimes coincided with completion of the Southern Pacific Railroad and an influx of livestock in the 1880s; however at local scales fire exclusion was a temporally variable process affected by livestock grazing, logging, and recreational use (Bahre 1998). The 1956 Nuttall Burn that affected approximately 1700 ha of dry mixed-conifer forest on the northwestern edge of the study area and 1984 Lindsey Fire that affected 1200 ha of pine forest on the western edge of the study area are the only recorded fires greater than 100 ha during the period of fire exclusion. After nearly a century without widespread fire in the majority of mixed-conifer and pine forests, a series of extensive insect outbreaks in the spruce–fir and mesic mixed-conifer forests began in the mid-1990s, followed shortly thereafter by fires in 1996 and 2004 that burned 14367 ha of mixed-conifer and spruce–fir forest at moderate to high severity (O'Connor et al. 2014), including more than two-thirds of the former spruce–fir extent (Koprowski et al. 2005, O'Connor et al. 2015).

#### METHODS

We established a systematic grid of 54, 0.05-ha circular plots spaced 1 km apart to collect tree demographic and

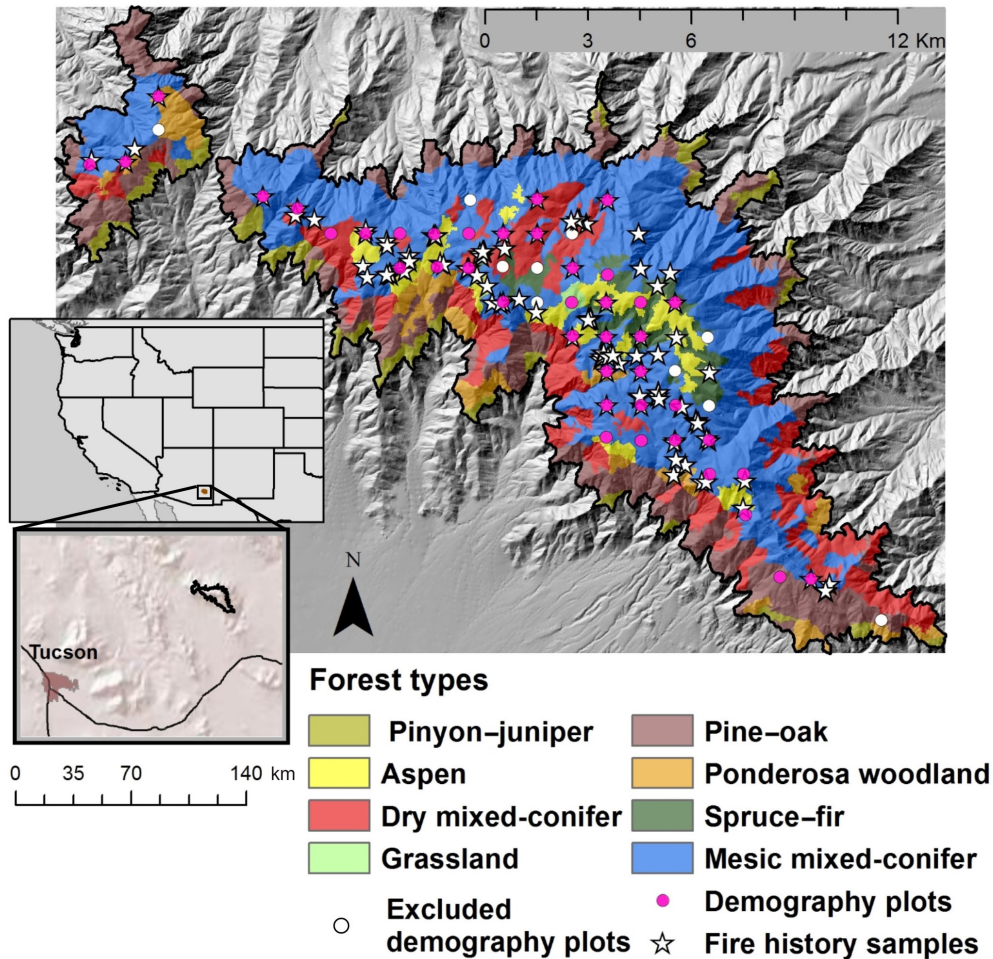


FIG. 2. Sampling locations and vegetation of the Pinaleno Mountains above 2135 m. Distribution of vegetation varies by elevation and aspect. Pine-oak woodlands near the lower elevation limit about dry and mesic mixed-conifer forests along the elevation gradient leading to the central high-elevation spruce-fir forest, much of which is currently dominated by aspen and post-fire herbaceous vegetation. Data are reprocessed from LANDFIRE biophysical setting rapid refresh 2008 (LANDFIRE 2012) with a minimum patch size of 6.75 ha.

fire history information across the landscape (O'Connor et al. 2014) (Fig. 2). Trees  $\geq 19.5$  cm diameter at breast height (DBH, 1.37 m) were sampled over the entire plot area; trees and saplings between one and 19.4 cm DBH were sampled on a nested sub-plot equal to one-third of the area of the full plot (0.017 ha). Increment cores were taken from live trees within 20 cm of the soil surface whenever possible to minimize the offset between true establishment date and tree pith date. Cross sections were taken from snags and stumps. Seedlings and saplings less than one cm DBH were sampled at ground level in the subplot and were tallied by species over the full plot area. Thirteen plots determined to have a history of logging were eliminated from analysis, identified by maps provided by the Coronado National Forest (Swetnam et al. 2015) and confirmed by stand ages. Over decadal to centennial timescales logging can significantly increase forest densities and alter natural species composition (Naficy et al. 2010).

Fire-scarred material was collected from live trees, snags, and stumps within demography plots and while traveling among plots. Fire history information from an earlier collection (Grissino-Mayer et al. 1995) coincided with four of the 54 demography sampling locations and was included as part of a mountain-wide fire history reconstruction (O'Connor et al. 2014).

Increment cores and cross-sections were mounted and surfaced following standard procedures to ensure annual accuracy of ring dates (Stokes and Smiley 1968, Speer 2010). Samples were crossdated using a combination of visual pattern matching (Yamaguchi 1991), skeleton plots (Douglass 1947), and statistical verification using the program COFECHA on measured ring widths (Holmes 1983, Grissino-Mayer 2001). Pith dates were estimated on samples that did not include pith but with enough ring curvature to use concentric ring pith locators (Applequist 1958). Samples in which estimated pith was



more than 10 years from the innermost ring were excluded from analyses.

#### *Data treatment and analysis*

To prepare field-collected tree measurements and counts for statistical analysis, we converted individual records to standardized indices of relative species importance (based on abundance and basal area) at each plot location. Relative species importance indices were used to differentiate between historical forest types, within which tree establishment dates and point fire history reconstructions were used to test relationships between tree establishment, time since fire, and regional climate. We used time series of plot-level relative species importance along a gradient of productivity to test the relationship between post-fire assemblage stability and site potential productivity (Chorover et al. 2011, Rasmussen et al. 2011). Similarity of species assemblages and stand densities, computed at three time steps in 1870, 1955, and 1995 was used to test the influence of site potential productivity on forest assemblage stability following fire exclusion. Time steps used to track species changes precede known events that influenced forest dynamics: 1870 being the last date of reliable species composition reconstruction prior to widespread fire exclusion, 1955 is the year prior to a fire that affected two demography plots, and 1995 is the last year of landscape-scale fire exclusion, prior to a series of high-severity fires and insect outbreaks affecting much of the spruce–fir and parts of the mesic mixed-conifer forest.

Recruitment dates from trees with DBH smaller than 19.5 cm, sampled on a subplot, were normalized to densities equivalent to the larger plot area (Appendix S1: Table S1). Stem density calculations used all tree size classes including seedlings. Recruitment dates were binned by 5-yr intervals to account for variability in age at sampling height and uncertainties in pith date estimations. Species importance values (IV) were calculated for each plot as a function of the relative frequency and basal area of the six dominant conifer species (Taylor 2001). We used Wards method of agglomerative hierarchical clustering to group plots into forest types based on IV rankings (hclust package; R Core Team 2013). Prior to clustering, IVs were transformed to Jaccard distance to minimize the effect of zeros in the data set (McCune et al. 2002). Clusters computed for trees living in plots in the year 1870 were used to determine pre-fire exclusion forest types, which were then tracked for seedling recruitment and stem densities through time.

Plot-scale fire histories were reconstructed from fire-scarred material within 500 m of plot center, creating a continuous spatial fire history reconstruction within and around the gridded plot network (O'Connor et al. 2014) (Fig. 2). To analyze seedling establishment response to time-since-fire at the landscape scale (both before and after fire-exclusion), tree establishment dates were normalized to the last recorded fire date associated with each

individual plot before being pooled by pre-fire exclusion forest type. Onset of fire exclusion was defined as the year after the last recorded fire date within each plot. Intervals from the start of fire exclusion to peak seedling recruitment, and from fire exclusion to establishment of secondary species, were calculated at the plot scale. A peak in primary species establishment was defined as the 5-yr bin prior to the first decline in seedling recruitment following fire exclusion. Establishment of secondary species was defined as the first of two or more consecutive 5-yr bins in which species not present during the pre-fire exclusion period established and persisted.

Interannual climate variability is known to influence both the success of seedling recruitment and the likelihood of fire occurrence and spread (Brown and Wu 2005). In addition to time-since-fire, we tested seasonal precipitation and drought indices for their relationship to landscape-scale seedling establishment before and after the period of fire exclusion. We used the 5-yr means of a reconstructed annual precipitation index for southeast Arizona (Griffin et al. 2013) and summer Palmer Drought Severity Index (PDSI; Cook and Krusic 2004, grid point 105) to test the effects of inter-annual precipitation and drought on seedling establishment from 1800 to 2005. Tree-ring data used by Griffin et al. (2013) and Cook and Krusic (2004) are independent of ours.

The frequency of fire occurrence at each plot location was estimated by O'Connor et al. (2014) using the Weibull median probability interval (WMPI) (Grissino-Mayer 1999, Sutherland et al. 2013) calculated from the composite record for fires recorded on two or more trees (Falk et al. 2011). The WMPI is a robust measure of central tendency in distributions of fire intervals, which are often right-skewed (Grissino-Mayer 1999, Falk 2004), and provides an index of fire interval as an independent variable in analyzing changes to species selection and seedling recruitment. If no fire-scarred material was recovered within 500 m of a demography plot but information was available from two or more adjacent plots, WMPI was interpolated from adjacent plot locations with inverse distance weighting of the four nearest plot locations using a power function of two (Swetnam et al. 2011, O'Connor et al. 2014).

#### *Site productivity*

Effective energy and mass transfer (EEMT), expressed in  $\text{MJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ , is a pedogenic measure derived from precipitation, temperature, and vapor pressure deficit that correlates strongly with soil thickness and terrestrial biomass (Rasmussen et al. 2011, Pelletier et al. 2013). We used EEMT as an independent proxy of potential site productivity. Values for each plot were extracted from a 30 m downscaled EEMT projection generated from normalized precipitation, temperature, and dew point over the period 2000–2009 (Pelletier et al. 2013).

To assess the relationship between potential site productivity and species composition prior to fire exclusion

we used a multivariate regression tree in which EEMT was used to partition the variance in a Hellinger-transformed IV matrix for trees present in the year 1870 (De'Ath 2002) (Appendix S1: Fig. S1). The regression tree was pruned to the best fit to minimize cross-validated error based on 1000 iterations (mvpert package; R Core Team 2013). The Hellinger transformation is robust to zero-inflated data and is back-transformable to retain individual species' contributions to tree splits (Legendre and Gallagher 2001). To quantify changes within forest types over time, we used a nonparametric multivariate test of dispersion (Anderson 2004). While Hellinger distance can be used for distance-based nonparametric tests of dispersion (Anderson 2006), retention of individual species traits was not necessary, so we opted instead to use the more conventional Jaccard distance transformation to characterize the ecological gradient of the IV matrix. The transformed matrix was tested for changes in dispersion at three time steps in the program PermDisp2 (Anderson 2004, 2006). We used pairwise *t* tests to determine the significance of changes to the dispersion of IVs (centroids and median values) in low, intermediate, high, and very high potential site productivity as defined by the four nodes of the regression tree classification of plots by EEMT (Appendix S1: Fig. S1) for trees present in 1870, 1955, and 1995 (Table 1). Paired *t* test statistics and *P* values were based on 4999 permutations of point dispersion values at each time step. To account for the increased possibility of Type 1 error resulting from multiple pairwise tests, a conservative Bonferroni correction was used to determine significance of *P* values (Gotelli and Ellison 2004).

TABLE 1. Changes in the dispersion of importance value centroids over time for each effective energy and mass transfer (EEMT) productivity class.

Groups	Centroid <i>t</i>	<i>P</i> (perm)	Median <i>t</i>	<i>P</i> (perm)
Low EEMT sites ( <i>n</i> = 10)				
1870 × 1955	2.527	0.105	2.030	0.064
1870 × 1995	2.182	0.089	2.043	0.062
1955 × 1995	0.517	0.694	0.275	0.787
Intermediate EEMT sites ( <i>n</i> = 19)				
1870 × 1955	3.371	<b>0.003†</b>	2.943	<b>0.006†</b>
1870 × 1995	4.785	<b>0.001†</b>	4.173	<b>0.001†</b>
1955 × 1995	0.875	0.583	0.707	0.482
High EEMT sites ( <i>n</i> = 8)				
1870 × 1955	0.821	0.546	0.971	0.366
1870 × 1995	0.828	0.509	0.891	0.379
1955 × 1995	0.050	0.968	0.049	0.960
Very high EEMT sites ( <i>n</i> = 4)				
1870 × 1955	0.765	0.508	0.214	0.802
1870 × 1995	0.771	0.499	0.157	0.894
1955 × 1995	0.045	0.971	0.125	0.867

Notes: Groups are pairwise comparisons between time intervals (1870, 1955, 1995). Centroid and median *t* are measures of dispersion from a centroid for each productivity class. *P* values are computed from permutation of residuals (perm).

†Bonferroni correction for multiple pairwise comparisons; value to reject null hypothesis  $\alpha < 0.017$ . Significant differences ( $P < 0.017$ ) are highlighted in boldface text.

The distribution of species assemblages in projected species space in the year 1870 was compared to that of assemblages in 1955 and 1995 with nonmetric multidimensional scaling (NMDS; labdsv package; R Core Team 2013) constrained to two dimensions and using 299 iterations. To compare results to the nonparametric test of dispersion, the IV matrix at each time step was transformed to Jaccard distance with a gradient of EEMT fit to the solution for reference to site potential productivity.

## RESULTS

Demographic reconstruction of species dynamics was based on establishment (pith) dates from 834 individual trees determined from 2205 crossdated samples at 41 plot locations. Fire history was reconstructed from 1201 crossdated fire scars collected from 241 trees at 130 fire recording locations.

The onset of fire exclusion varied temporally over approximately 30 years, starting in the mid-1860s in mesic high-productivity sites before proceeding across most of the landscape in the 1880s and 1890s, and in a few drier and lower productivity sites as late as the early 1900s. Small isolated fires continued in dry sites into the 1920s but seedling recruitment appears to have been constant across the productivity gradient by the 1890s (Appendix S1: Table S2). Pooled seedling establishment dates indicate that the pulse of seedling recruitment associated with the initial period of fire exclusion in the late 1800s coincided with a 30-yr period of below-average precipitation (Fig. 3). The rate of seedling recruitment continued to accelerate until the late 1920s during a prolonged pluvial (wet) period and then began to slow, even as precipitation remained above average through the late 1930s. Following the pluvial period, the rate of seedling establishment continued to decline for the majority of the 1940s–1990s except for a minor pulse of recruitment following the 1956 fire. The rate of seeding establishment was not significantly associated with the 5-yr change in average seasonal precipitation or drought indices over the entire period 1800–2005 (multivariate regression of recruitment on change in 5-yr average precipitation index and PDSI,  $R^2 = -0.04$ ,  $P = 0.733$ ), or the major period of seedling recruitment from 1870 to 1940 ( $R^2 = -0.162$ ,  $P = 0.856$ ), indicating that a shift in climate conditions was not responsible for at least the first three decades of increased seedling recruitment.

Five sites in the mixed-conifer forest had historical fire intervals (WMPI values) much longer than surrounding forests with similar potential site productivity and species assemblages. For demographic analysis, these forests were grouped post hoc as an independent “fire-sheltered mixed-conifer” class based on pre-1870 differences in species composition and fire frequency in comparison to other mixed-conifer forests.

Effective energy and mass transfer alone explained 39% of species assemblage variability (measured as multivariate species IV values), by partitioning IV variance of the five

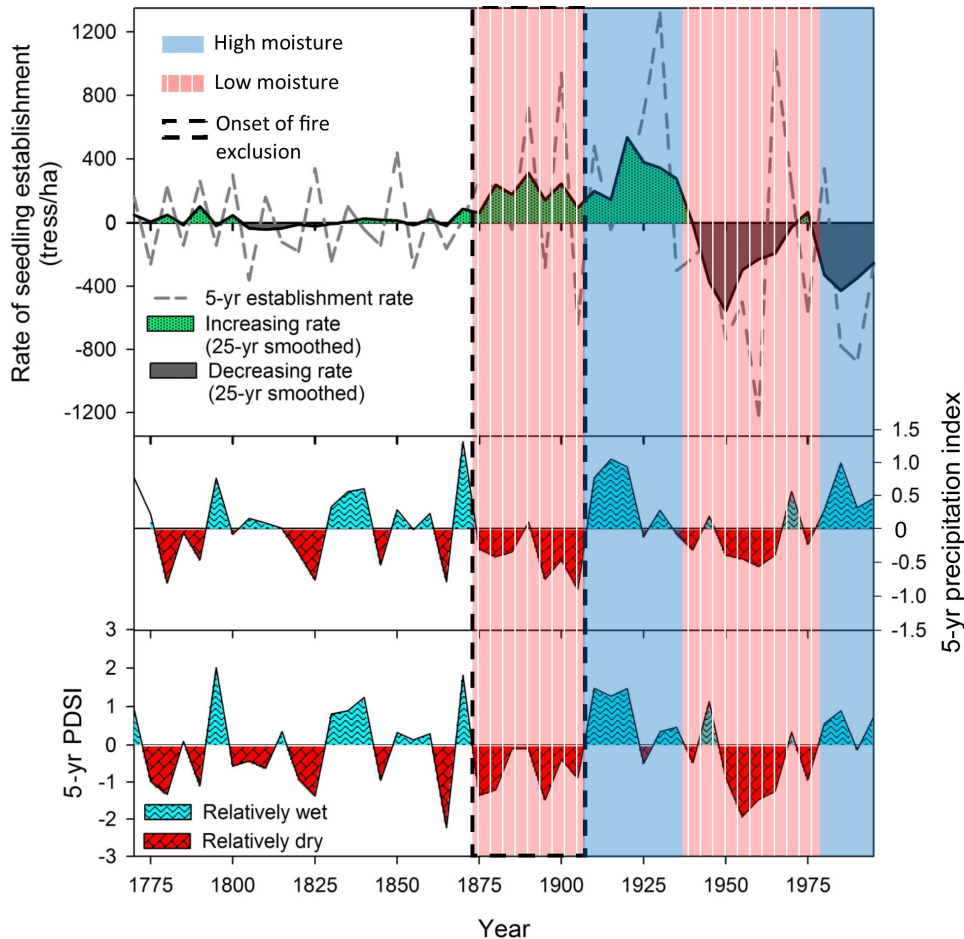


FIG. 3. Association between rate of seedling establishment, annual precipitation, and drought. Seedling establishment rate is calculated for each 5-yr interval and as a 25-yr smoothed moving average. Precipitation index is adapted from Griffin et al. (2013). Palmer drought severity index (PDSI) is adapted from Cook and Krusic (2004) grid point 105 for southeast Arizona. Dashed polygon denotes start of fire exclusion across the landscape. Red striped pattern polygons indicate period of lower than average annual precipitation. Blue solid polygons indicate periods of higher than average annual precipitation. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

forest types into four distinct site productivity classes. The gradient of EEMT values aligned with the general descriptions of forest types in Sky Island systems (Warshall 1995). Low productivity sites ( $EEMT < 37.2 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) were primarily pine dominated ( $n = 7$ ) but included some dry mixed-conifer sites ( $n = 3$ ) near the upper productivity threshold. Intermediate productivity sites ( $37.2 \leq EEMT < 43.7 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) included the majority of dry and mesic mixed-conifer forest ( $n = 19$ ) with drier forests at the lower end of the productivity gradient and wetter forests at the higher end of the distribution. High productivity sites ( $43.7 < EEMT < 45.2 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ,  $n = 8$ ) were composed of fire-sheltered mixed-conifer and some spruce–fir forest, and very high productivity sites ( $EEMT > 45.2 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ,  $n = 4$ ) were spruce–fir forest.

In the century following fire exclusion, stability of forest assemblages varied considerably among forest types and along the gradient of forest productivity. On the lowest productivity sites, forests with regeneration

dominated by ponderosa pine in 1870 were still pine dominated in 1996, and fewer than one-half of plots contained secondary species after a century of fire exclusion (Fig. 4a). The rate of seedling recruitment in these stands peaked within 15 years of fire exclusion, with the majority of successful recruitment occurring within the first 25 years, resulting in an eight-fold increase in stem densities from 60 to 500 trees/ha. Additional recruitment occurred only after additional fires, allowing the pine-dominated species assemblage to remain intact over the study period.

Mixed-conifer forests on intermediate productivity sites were the least stable species assemblages following fire exclusion. In dry mixed-conifer stands successful recruitment of secondary species began shortly after the median fire return interval of 9.2 yr was surpassed, and continued for approximately 60 yr (Fig. 4b). Over this period, rates of seedling establishment and increasing stem density remained relatively constant. Time to peak

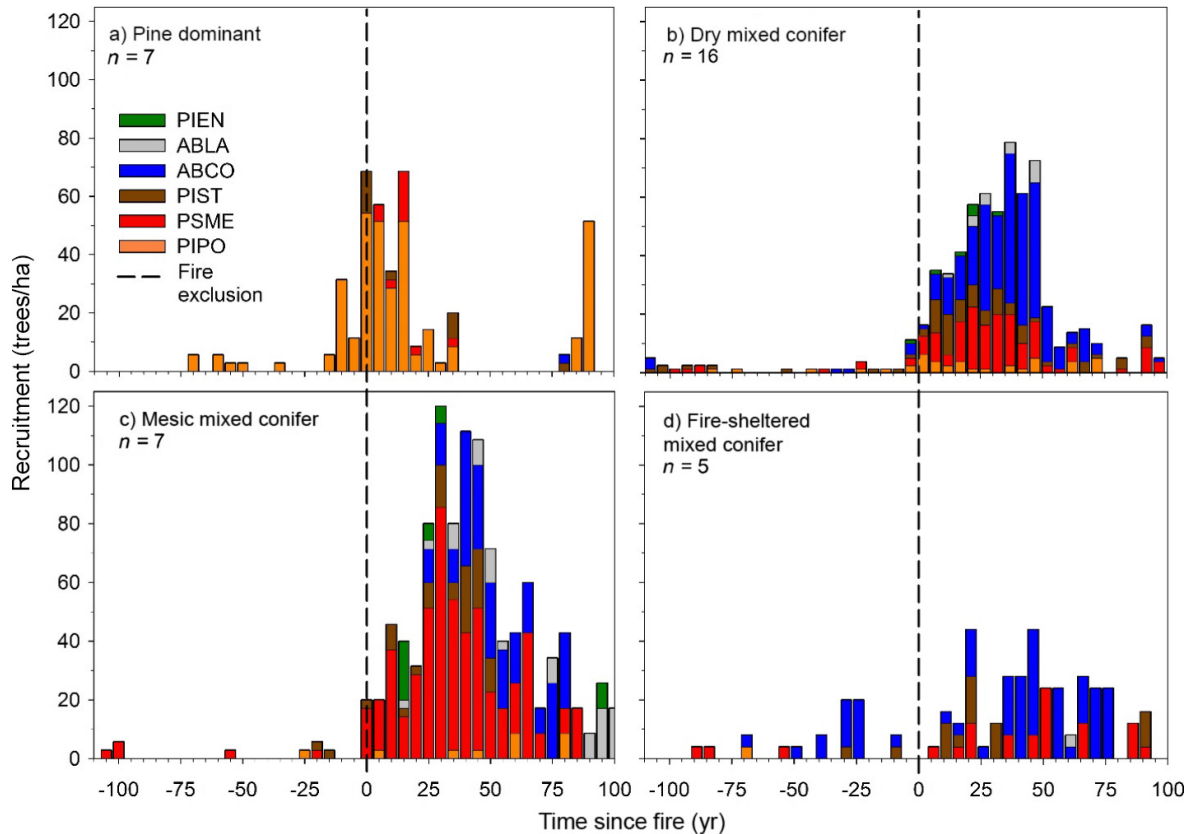


FIG. 4. Mean seedling recruitment by pre-fire exclusion forest type. Seedling recruitment dates are normalized to site-specific time since fire. Species codes are PIEN, Engelmann spruce; ABLA, corkbark fir; ABCO, white fir; PIST, southwestern white pine; PSME, Douglas-fir; and PIPO, ponderosa pine.

recruitment was considerably longer (50 yr) and total stems per hectare was higher than in lower productivity pine-dominated sites (Appendix S1: Table S2). Median tree densities increased 14-fold in intermediate productivity sites from 60 to 860 trees/ha in the century following fire exclusion (Fig. 4b; Appendix S1: Table S2).

Higher productivity sites dominated by mesic mixed-conifer (Fig. 4c) and fire-sheltered mixed-conifer (Fig. 4d) forest types were susceptible to recruitment of secondary species when historical fire intervals were relatively short (Fig. 4c) and more stable when historical fire intervals were relatively long (Fig. 4d), although stem densities increased regardless of historical fire interval. Median stem densities increased 18-fold in mesic mixed-conifer forests and 11-fold in fire-sheltered forests during the century of fire exclusion (from 80 to 1460 and from 100 to 1080 trees/ha, respectively, Appendix S1: Table S2).

In the highest productivity mesic spruce–fir forest, where the fire return interval exceeded 300 yr (O'Connor et al. 2014), there was no evidence of a post-fire exclusion shift in recruitment or composition (Fig. 5; test of 5-yr binned recruitment for the 50-yr period 1837–1882 vs. the 50-yr period 1887–1932, one-tailed  $t$  test,  $P = 0.483$ ). Species dynamics in these sites correspond to establishment after a stand-replacing fire in 1685 followed by

more than 250 yr of low-level periodic disturbance and seedling recruitment unrelated to fire (O'Connor et al. 2014, 2015). Minor changes to species composition and tree densities in high productivity sites do not appear to be related to the onset of fire exclusion in surrounding forests and are more likely attributable to bark beetle outbreaks, other smaller scale disturbances, and failure of Douglas-fir seedling recruitment after canopy closure in the mid-1700s (Schmid and Hinds 1974, Veblen et al. 1991, O'Connor et al. 2015). From 1870 to 1995, median stem densities in spruce–fir forests increased by approximately 50%, from 460 to 700 trees/ha (Fig. 5), although the change in stem densities was variable among plot locations.

Time to secondary species establishment, a proxy for the stability of species assemblages following fire exclusion, was greatest in low and high productivity forests where successful establishment of secondary species occurred in fewer than half of sites in the century following fire exclusion (Appendix S1: Table S2). Average time to secondary species establishment was shortest (15 yr) in intermediate productivity dry mixed-conifer forests, followed by higher productivity mesic mixed-conifer (40 yr) and fire-sheltered mixed-conifer (60 yr) sites (Appendix S1: Table S2).



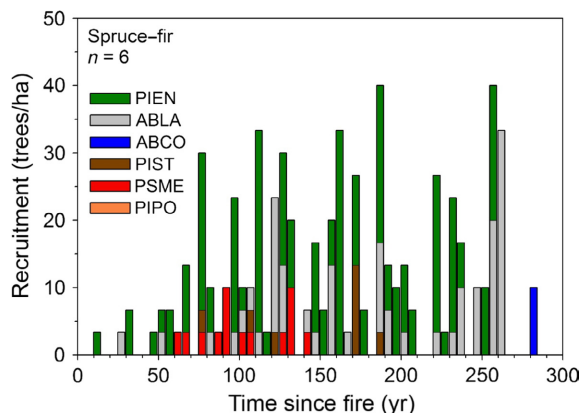


FIG. 5. Mean seedling recruitment in spruce-fir forest. Year zero represents a stand-replacing fire in 1685; fire exclusion in surrounding forest begins around year 1955. Species codes are as in Fig. 4.

Compositional stability of species assemblages did not change significantly over the study period in low (pine-dominated), high (fire-sheltered and some mesic mixed-conifer), and very high (spruce-fir-dominated) site productivity classes (Table 1, Fig. 6). In contrast, intermediate productivity (dry mixed-conifer and some mesic mixed-conifer) sites underwent a significant change in species assemblages during the first 85 years of the fire exclusion period from 1870 to 1955 ( $P < 0.003$ ) and over the whole study period from 1870 to 1995 ( $P < 0.001$ , Table 1, Fig. 6). The NMDS ordination with final stress of 18.9 revealed that compositional stability in pine-dominated forests decreased with increasing site productivity, such that the difference between past and present forest composition was greatest near the threshold of intermediate site productivity. The majority of intermediate productivity mixed-conifer sites had species composition similar to that of lower productivity sites in 1870 but shifted toward species composition characteristic of higher productivity sites by 1955 and continued to diverge from historical species composition for at least the next 40 yr. Similarity of species composition in 1870 and 1995 was lowest in these intermediate productivity sites with EEMT values ranging from 37.2 to 43.7  $\text{MJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ . Higher productivity mesic mixed-conifer, fire-sheltered mixed-conifer, and spruce-fir sites had the least change in species composition through time, although there was a trend of increasing species divergence with decreasing EEMT toward intermediate productivity values.

#### DISCUSSION

Twentieth-century fire exclusion in western North America and other forested regions began one of the largest unintended landscape ecology experiments in human history. Resulting changes to forest structure, species composition, and fire behavior continue to influence forest resilience, stability, and adaptability to projected future climate conditions (Fulé et al. 2009,

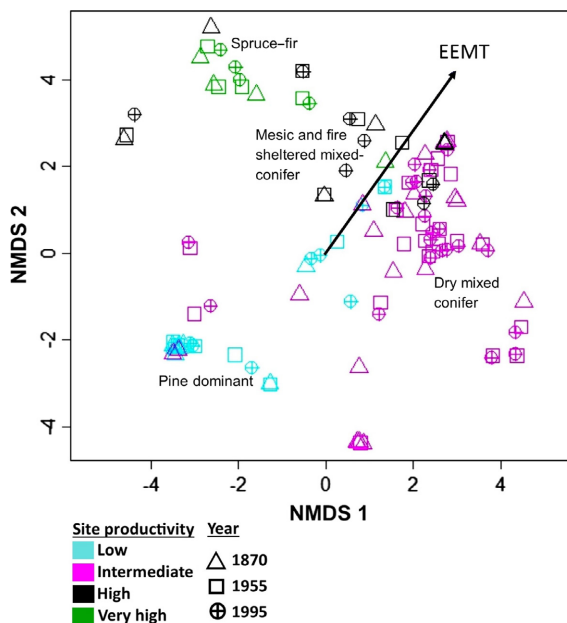


FIG. 6. Stability of species assemblages through time represented as nonmetric multidimensional scaling (NMDS) of Jaccard-distance-transformed importance value scores. Shapes correspond to different time steps. Colors correspond to different levels of potential site productivity. Close proximity or overlap between different shapes of the same color indicates species assemblage stability through time. Forest type labels are relative locations along the site productivity gradient measured as effective energy and mass transfer (EEMT).

Allen et al. 2010, Kitzberger et al. 2012, Williams et al. 2013). In forest systems studied here, a pulse in seedling recruitment and orders-of-magnitude increases in stand densities in all but the most productive, competition-adapted forests with the longest natural fire return intervals, coincided with the interruption of historical fire intervals by Euro-American settlement. The pulse of seedling recruitment was not associated with changes to patterns of precipitation or drought, providing strong evidence for fire exclusion as the starting point for a cascade of ecological changes that were then reinforced by plant competitive interactions over the next century.

Differences in the stability of species assemblages following the exclusion of fire were strongly associated with site productivity. In sites where frequent fire was the primary driver of species composition and stand structure, the lowest productivity, pine-dominated sites remained compositionally stable while, in adjacent intermediate productivity mixed-conifer sites, seedling recruitment shifted from fire-adapted to competition-adapted species within the first two decades of fire exclusion. Spruce-fir and fire-sheltered mixed-conifer sites with the longest historical fire return intervals and highest potential productivity also remained compositionally stable following fire exclusion. Stability of species composition in these more competition-adapted forests declined with a reduction in site productivity, eventually approaching that of intermediate productivity mixed-conifer forests.

The several-fold increase in stem densities in pine-dominated and mixed-conifer forests suggests that prior to fire exclusion, disturbance was a primary limiting factor of forest structure in both forest types. However, the compositional stability of pine-dominated forests also suggests that species assemblages mediated by low site productivity are subject to additional constraints beyond those characterized by a disturbance-mediated or competition mediated system. These relatively stable, lower-productivity assemblages may overlap spatially and ecologically with more disturbance-mediated species assemblages as long as disturbance regimes remain constant.

The lowest productivity pine-dominated and highest productivity spruce–fir-dominated sites tended to reach peak seedling recruitment within their respective median fire return intervals. Time to peak recruitment is a proxy for assemblage recovery time (Pimm 1984) or “engineered resilience” (Folke 2006), suggesting that both of these forest types are dynamically stable for their respective disturbance return intervals. Site conditions in lower productivity sites, characterized by shallow acidic soils and lower moisture availability (Pelletier et al. 2013, Boness 2015) probably limited the suitability of historically pine-dominated sites for secondary, competition-adapted fir species. Similarly, in the highest productivity spruce- and corkbark-fir-dominated sites, colder temperatures, a short growing season, and other biophysical conditions such as a thick O-horizon, seed pathogens that limit seedling germination (Daniel and Schmidt 1972, Whipple 1978, Wicklow-Howard and Skujins 1980), extreme shade tolerance of the existing dominants, and infrequent understory disturbance likewise make this assemblage resistant to invasion by secondary species.

In contrast, intermediate-productivity mixed-conifer sites underwent significant changes to species composition following fire exclusion. The relatively high rate of transition from primary to secondary species in mixed-conifer forests most closely follows the proposed transitional model and suggests that site productivity was not limiting in these forests. Frequent disturbance was necessary to maintain fire-adapted species and to mask the potential for site productivity to support a more diverse array of species and higher stem densities than lower productivity sites. This suggests that forests occupying intermediate productivity sites are in a state of unstable equilibrium, with the potential to transition either way depending on the frequency and severity of disturbance. A comparison between fire-sheltered and more typical mixed-conifer forest provides further evidence for disturbance-mediated control of mixed-conifer forest on intermediate productivity sites. Species assemblages adapted to longer disturbance intervals remained compositionally stable, even as adjacent forest with similar potential productivity and much higher historical fire frequency expressed a near complete transition to secondary species (Fig. 4c). Fire-sheltered mixed-conifer sites are comparable to the “safe sites” identified in forest regeneration studies in northern

Arizona and northern Mexico (White 1985, Meunier et al. 2014), suggesting that these small patches of forest with distinct ecological characteristics may be an important contributor to landscape-scale heterogeneity.

Changes to species composition following fire exclusion followed two distinct mechanisms. The widespread recruitment of secondary species into intermediate productivity sites appears to be a spatial expansion of species historically present in topographically fire-sheltered sites that were embedded within the fire-adapted landscape (Fig. 4d; O’Connor 2013). These populations would have been constrained by frequent fire, successfully recruiting into adjacent forests only during prolonged fire-free intervals. Locally persistent populations of competition-adapted species, such as white fir, were able to establish seedlings over broad areas shortly after the exclusion of fire (Fig. 4b, c). Lower productivity pine-dominated sites did not support these local populations of competition-adapted species (Fig. 4a), making them more resistant to forest conversion even after fire exclusion.

The second mechanism of forest transition represents a slow migration of species from higher productivity sites, where fire was historically less frequent, into surrounding forests following fire exclusion. This wave-form-type recruitment pattern (Frelich 2002) was also identified along an elevational gradient of the San Francisco Peaks of northern Arizona where competition-adapted Engelmann spruce seedlings from higher elevation forests eventually expanded into previously mixed-conifer forest over several decades (Cocke et al. 2005). This mechanism explains the slow but steady expansion of spruce and corkbark fir into mesic and dry mixed-conifer forests of the Pinaleno Mountains following fire exclusion (O’Connor et al. 2015).

In the present study, we demonstrate that interruption of the fire regime can promote cohort formation in fire-adapted landscapes. Prolific seedling establishment associated with prolonged fire-free periods has been noted in other demographic studies in pine and dry mixed-conifer forests from northern Sonora, Mexico and southwest Colorado, USA (Brown and Wu 2005, Meunier et al. 2014), although these recruitment pulses represented cohort dynamics without the additional shift in species presented here.

Our results suggest that sustained recruitment and changes to species composition are a consequence of extended interruption of the natural disturbance regime. This conclusion is closely aligned with studies suggesting that fire exclusion-driven changes to fuel structure in many western forests is increasing the risk of high-severity fire and drought-related die-off beyond conditions experienced in these systems over the past several centuries (Collins et al. 2015, McDowell and Allen 2015, Steel et al. 2015, Stevens et al. 2016). Some studies over the past decade have interpreted late 19th century and early 20th century recruitment pulses in several pine-dominated and mixed-conifer forests of the southwestern United States as evidence of mixed- or high-severity fire, with effects

comparable to more recent mixed-severity fires in these landscapes (Sherriff and Veblen 2006, Williams and Baker 2012, Odion et al. 2014). The strong association between fire-free interval and formation of recruitment cohorts in fire-adapted landscapes documented in this study suggest that periods of prolific seedling recruitment should not be interpreted as evidence of a historical legacy of mixed- or high-severity fire in similar dry interior forests.

#### *Limitations and considerations for interpretation of results*

While this study was spatially constrained to a single mountain range in the southwestern United States, the distribution of species along a vertical gradient of forest types and potential site productivity represents a microcosm of species assemblages along a latitudinal gradient spanning Northern Sonora, Mexico to British Columbia, Canada. Similarly, the changes to this landscape catalyzed by livestock grazing, resource extraction, nearby settlement of cities, and eventual formal fire suppression policies is representative of anthropogenic changes to forests across western North America, and in many other forests. The effects of timber harvesting in the first part of the 20th century prompted us to exclude the results from approximately 25% of the material we collected, resulting in a sample size of 41 plots to characterize changes to a 15220-ha landscape spanning 1133 m in elevation. While total plot counts in each forest type were modest, the spatially explicit dendrochronological reconstruction of species dynamics across a gradient of forest types represents the most detailed and comprehensive effort known by the authors to reconstruct demographic and disturbance dynamics at a mountain range scale. Each plot was designed to represent a 1-km<sup>2</sup> area, thus the 6-km<sup>2</sup> area of spruce–fir forest used for demographic reconstructions was the smallest sampled area and the 16 km<sup>2</sup> of dry mixed-conifer forest was the largest.

While significant effort was made to select a site and series of forest types representative of many of the forested ecosystems of western North America, localized topography, species assemblages, climate patterns, and disturbance legacies are likely to modify the relationships demonstrated here when applied to other forested ecosystems. Just as the vertical structure of Sky Island mountain ranges facilitates interactions between very different forest types and may propagate disturbance across ecotones, the balance between species assemblages constrained by site productivity, disturbance frequency and severity, and competitive ability is likely to manifest somewhat differently on landscapes with different species mixes, soil characteristics, and topography. Expansion of this work to include a broader range of geographic locations, forest types, productivity gradients, and disturbance histories, would serve to elucidate the strength of the productivity thresholds identified here and to test the transferability of interpretations.

#### *Implications for forest management*

Restoration of historical forest structure in the western United States and Canada has been driven primarily by concerns about extreme fire behavior and fire effects associated with structural changes to ecosystems adapted to surface fire regimes (Covington et al. 1994, Swetnam et al. 1999, Gower et al. 2015). These forests have been used as a model system for alternative stable states theory (Beisner et al. 2003), in which resilience is maintained by a negative feedback loop of frequent surface fires that select for large, old, fire-tolerant trees (Larson et al. 2013). Resilience of these disturbance-adapted forests is threatened when changes to fuel loading and vertical structure, driven by ecological changes from fire exclusion, increase fire severity (Moore et al. 2004, Keane et al. 2006, Falk 2013, Parks et al. 2014) and intensify drought-related stress (Linares et al. 2010).

Alleviating some of these concerns about loss of resilience, Larson et al. (2013) found that unlogged ponderosa pine forests remained resilient to reintroduced fire if primary species remained the dominant seed sources following a return to frequent fire. In this study, the maintenance of a ponderosa-pine-dominated canopy over the extended fire-free period was limited to lower productivity sites, which also exhibited little change in understory species composition. Changes to species composition in higher productivity mixed-conifer forest with equivalent frequency of historical fires suggest that while disturbance is an important control of species assemblage membership, it is the interaction between disturbance and site productivity that determines the relative stability, and likely the resilience, of disturbance-adapted ecosystems.

Increased fuel continuity attributable to fire exclusion in mixed-conifer forests (Keane et al. 2002, Collins et al. 2010) has been associated with larger and more severe fires in several regions of western North America (Miller et al. 2009, Mallek et al. 2013, O'Connor et al. 2014). Returning structural heterogeneity and fire-adapted species assemblages to mixed-conifer forests could help to reduce extreme fire activity (Evans et al. 2011, Reynolds et al. 2013), but may also promote the resilience of these montane ecosystems to changing temperature and precipitation regimes. Intermediate-productivity sites maintained at a level of stocking below their maximum potential, through fire or mechanical thinning, may be less susceptible to tree die-off during prolonged drought or extreme heat (Kolb et al. 2007, McDowell et al. 2007, 2008), and may be less susceptible to defoliator and bark beetle outbreaks (Carlson et al. 1983, Swetnam and Lynch 1993, Kolb et al. 1998, Fettig et al. 2007). Dry forests with relatively low biological productivity are already experiencing tree mortality associated with greater frequency and intensity of recurrent drought (Breshears et al. 2009, Allen et al. 2010, Williams et al. 2013, McDowell and Allen 2015), and higher productivity forests may be more likely to experience stand-replacing fire (Westerling et al.

2011). While species assemblages at both ends of the site productivity distribution were least affected by fire exclusion, they may be more vulnerable than intermediate productivity species assemblages to projected increases in mean temperatures, moisture variability and lengthening of fire seasons (Seager et al. 2007, Flannigan et al. 2009, Fulé et al. 2009, Crimmins 2011, Jolly et al. 2015). The low productivity sites occupied by pine forests have little water holding capacity and are likely to experience elevated vapor pressure deficits and extreme moisture stress conditions sooner than intermediate productivity forests, especially at current high stocking levels (Williams et al. 2013). Breaking up vertical fuel structure and returning fire to forests located on low and intermediate productivity sites may be the best option to promote more fire-adapted species and structure, increase available moisture, and mitigate some of the effects of a warmer, dryer future (Collins et al. 2014).

Species assemblages constrained to the highest productivity sites near the top of elevational gradients are likely to experience longer growing seasons, though this may be offset by increasing moisture stress, shrinking suitable habitat, and more frequent exposure to fire and insect outbreaks (Bentz et al. 2010, Notaro et al. 2012). For these assemblages constrained by a shrinking climatic envelope, management options are more limited.

Documenting the timing and magnitude of forest changes resulting from fire exclusion is an important part of creating science-based restoration prescriptions that prioritize the risk of uncharacteristic crown fire and deviation from historical stand conditions and associated ecological function (Falk 2006). Allen et al. (2002) describe a series of principles to guide restoration of ecological function to southwestern ponderosa pine forests, and many of these criteria are directly applicable to other forest types adapted to frequent fire. Restoration of forest species and structure through the use of mechanical thinning, prescribed fire, or managed wildfire, has been implemented successfully in many conifer-dominated forest types (Pollet and Omi 2002, Fulé et al. 2004, van Mantgem et al. 2011, Fernandes 2015). However, determining the appropriate intervals between subsequent treatments under current fuel accumulation rates and climate conditions is problematic. Carrying out restoration treatments at intervals that mimic the high frequency of historical fires may be impractical for planning, budgeting, and social considerations, and managing for mixed-severity fire regimes presents additional challenges.

Basing treatment rotation intervals on the rate of forest assemblage transition after fire may be a more practical option for pine and mixed-conifer forest types. EEMT can be computed at broad spatial scales (Rasmussen et al. 2011) and may be useful to determine appropriate intervals between controlled burns, managed use of wildfire, or additional thinning operations following initial restoration efforts. Under a site productivity-based management system, forests historically adapted to frequent surface fire but with higher EEMT values would

receive higher treatment priority based on their ability to accumulate fuel and increase vertical fuel connectivity at a higher rate than forests on lower productivity sites. Under this system as with current forest restoration efforts, care should be taken to identify historically fire-sheltered locations and to preserve the heterogeneity of stand structure and species assemblages afforded by these unique ecological features.

In this study, potential site productivity is used to characterize and explain the relative compositional stability or transition of forested systems to alternative states following a change in disturbance regime. A logical extension of this work would be to use EEMT or another independent proxy for site productivity to predict ecosystem response to current or projected disturbance regimes. Using potential productivity thresholds to pre-identify locations where species assemblages are expected to be relatively stable or dynamic has potential application for predicting and understanding forest changes, accumulation of biomass, carbon sequestration, shifts in wildlife habitat, and changes to tree species distributions.

The complex interactions between disturbance, forest dynamics, site conditions, and climate pose a series of challenges for science-based management of forests. Twentieth-century fire exclusion altered the interactions between biological mechanisms and physical landscape characteristics that determine forest structure and species composition in many forest types. Understanding and leveraging these interactions to guide forest and fire management decisions and to adapt to dynamic future conditions is a first step toward maintaining resilient, functional ecosystems.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1492/full>

## DATA AVAILABILITY

Data associated with this paper have been deposited in the USFS Research Data Archive: <https://doi.org/10.2737/RDS-2017-0001>