SPATIAL AND TEMPORAL DYNAMICS OF DISTURBANCE INTERACTIONS ALONG AN ECOLOGICAL GRADIENT

by

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DEDICATION

This dissertation is dedicated to my grandfather Roderick O’Connor, an avid outdoorsman, conservationist, and teacher who introduced his family and generations of students to the sanctity of wild places and the need to understand and preserve them for future generations.

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ABSTRACT

Interactions among site conditions, disturbance events, and climate determine the patterns of forest species recruitment and mortality across landscapes. Forests of the American Southwest have undergone significant changes over a century of altered disturbance regimes, human land uses, and changing environmental conditions. Along steep vertical gradients such as those of southwestern Madrean Sky Island systems, where mountains rising out of the Sonoran Desert host biomes representing a latitudinal transect from Mexico to Canada, forests are especially vulnerable to changing dynamics of disturbances. In these vertically stacked systems, a change in one forest type can propagate changes into and across adjoining forest types. In the Pinaleño Mountains of southeast Arizona, a series of recent insect outbreaks and high-severity fires significantly reduced the extent of a remnant spruce-fir forest and raised concerns about the vulnerability of the surrounding forest to additional high-severity disturbances. A century of Euro-American influence and changes in longer-term climate patterns may have influenced the size and severity of recent disturbances by altering the species composition and structure of forests surrounding the spruce-fir system and increasing temperature and drought stress on overstocked forests. This study reconstructs the interactions between, fire, spruce beetle outbreaks, climate, and anthropogenic factors and their influence on the species composition, spatial extent, and structure of the four upper elevation forest types of the Pinaleño Mountains.

Reconstruction of historical fire events suggest that Euro-American settlement led to a significant decrease in fire spread but not fire ignition. Fire-climate associations changed following fire exclusion and recent high-severity fires occurred during less severe conditions than the single high-severity fire and several larger, lower severity fires in the historical record. Contemporary fires are burning with higher severity than similarly-sized historical fires, suggesting a shift toward stand-replacing fire over much of the upper elevation forest. This shift has significant ramifications for future forest structure and species. Accumulated fuels and more frequent climate conditions for fire spread suggest that additional large, high-severity fires can be expected without aggressive action to restore fire-adapted forest structure.

In the highest elevation forests, the area occupied by Engelmann spruce and corkbark fir doubled in size over the four decades following fire exclusion. Spruce beetle outbreak location and size lagged spruce extent by 40-90 years depending on the species composition of surrounding forests. Outbreak frequency averaged approximately 20 years regardless of changes to host distribution and climate conditions. The increase in outbreak size and severity in the 20th century appears to be linked to the significant expansion of host extent, accelerated growth of spruce in mixed-conifer forest, and incidence of warmer than average summer temperatures followed by up to a decade of lower than average precipitation. The most recent spruce beetle outbreak in the mid-1990s and fires in 1996 and 2004 reduced the extent of mature Engelmann spruce, postponing the risk of high-severity outbreaks for several decades. In other western forests where fire has not altered spruce extent, the trends toward warming, drying conditions are expected to increase the risk of future high-severity outbreaks, especially in locations of recent spruce population expansion.

Reconstruction of historical species dynamics suggest that the vulnerability of forest conversion from open, fire-adapted to closed, competition-adapted species is a function of site productivity. Species assemblages in the lowest and highest productivity sites were the most stable over the century following fire exclusion. Seedling recruitment in moderate productivity sites shifted from original fire-adapted species to secondary competition-adapted species within 20 years, resulting in significant changes to the structure and composition of these widespread forest types. Frequent low severity fires appear to have maintained the stocking of forests in moderate productivity sites well below their biological potential, conferring a degree of resistance to drought, insect outbreaks, and high-severity fire prior to fire exclusion. Current forests located on moderate productivity sites are now the most vulnerable to drought and future disturbance. Aggressive action to restore the historical species composition, stocking and fire component of these forests may return resilience to this system in the face of projected changes to fire and climate dynamics.

CHAPTER 1. INTRODUCTION

Explanation of Problem

Forests of the western United States have experienced major changes to the dynamics of fire, insect outbreaks, species composition and structure over the past century. Euro-American settlement in the mid-1800s resulted in an interruption of frequent, low severity fires in over much of the extent of dry pine and mixed-conifer forests adapted to a frequent, low-severity fire regime (Covington and Moore 1994, Grissino-Mayer et al. 1995, Swetnam and Baisan 1996a, Baisan and Swetnam 1997, Veblen et al. 2000, Taylor 2001, Beaty and Taylor 2001, Fry and Stephens 2006, Scholl and Taylor 2010). Settlement resulted in a sudden increase in animal grazing, logging, mining, road building and eventual fire suppression efforts that caused an abrupt decline in spreading fires and an infilling of previously open forest understory (Bahre 1998). Over the next several decades, forest regeneration shifted from fire-adapted, shade-intolerant species to competition-adapted shade-tolerant species (Minnich et al. 1995, Ansley and Battles 1998, Scholl and Taylor 2010). Changes to forest structure and species lowered the resistance of forests to drought and other climatically driven stressors (Breshears et al. 2005, McDowell et al. 2008, Breshears et al. 2009, Allen et al. 2010, Williams et al. 2013), and altered the behavior of fire (Parsons and DeBenedetti 1979, Heyerdahl et al. 2001, Miller et al. 2009, Miller et al. 2012a) and insect outbreaks (Ayres and Lombardero 2000, Logan et al. 2003, Raffa et al. 2008).

Fire exclusion changes to forests

Exacerbating the effects of fire exclusion on forest structure and species, a regional trend of increasing temperatures and prolonged droughts over the past several decades has resulted in a resurgence of spreading fire on landscapes that now support higher-severity fire behavior (Westerling et al. 2006, Miller et al. 2009). In pine-dominated forests of the southwestern United States, dramatic increases in stem densities as a result of successful seedling establishment without fire led to increased competition for water and nutrients between overstory and understory trees (Riegel et al. 1995) and the creation of a multi-tiered canopy with low canopy base heights that allow ground fire to spread to the overstory through continuous ladder fuels (Covington et al. 1997, Allen et al. 2002). In mixed-conifer forests, fire exclusion led to proliferation of shade-tolerant fir and spruce seedlings previously limited by fire (Taylor 2001, Fulé et al. 2003a, Fulé et al. 2009). Establishment of shade tolerant seedlings changed the composition of forest understories and hindered recruitment of less shade-tolerant seedlings representative of the pre-fire exclusion overstory trees (Scholl and Taylor 2010). In mountainous terrain with steep ecological gradients driven by elevation, aspect, and precipitation, removal of fire led to a homogenizing of forest species and structure as open fire-maintained forest structure was transformed to dense closed-canopy forest resembling the mesic subalpine ecosystems found at higher elevation sites (Cocke et al. 2005). Loss of forest heterogeneity removed the natural buffer to fire spread among different forest types, and increased the likelihood of large high-severity fires (Grissino-Mayer et al. 1995, Taylor and Skinner 2003, Swetnam et al. 2009).

Forest structure and climate effects on insect outbreaks

Insect outbreaks are the most significant biotic disturbances affecting western forests (Jenkins et al. 2012) and are influenced by a series of local and regional conditions. Defoliating and phloem-feeding insect populations can be influenced indirectly by fire exclusion as a result of increased stand densities that alter microhabitat conditions and increase the contiguous extent of available hosts (McCullough et al. 1998, Parker et al. 2006). *Dendroctonus* bark beetles, responsible for tree mortality in 4.3 million hectares of western forests over the past 25 years (Jenkins et al. 2012), are also influenced by several conditions affected by fire exclusion, including host tree size, stand composition, tree age, and growth rates (Schmid and Frye 1977, Werner et al. 2006, Wallin et al. 2008, Egan et al. 2010).

In addition to the increased risk of insect damage associated with forest structural changes, prolonged drought and warming temperatures that increase host tree stress can influence the prevalence and severity of outbreaks (Breshears et al. 2005). Drought-associated bark beetle outbreaks have been recognized for more than a century in pine forests (Powell 1969), and more recent evidence has linked drought to outbreak initiation in more mesic upper elevation forests (DeRose and Long 2012c, Hart et al. 2013). Cambial-feeding bark beetles benefit from host stress through a reduction of host defenses, whereas host stress may have mixed effects on the feeding behavior of foliar-feeding insects (Mattson and Haack 1987, Larsson 1989). In the southwestern States, outbreaks of western spruce budworm (*Choristoneura occidentalis*) were associated with pluvial conditions that may have increased host fitness and growth rates (Swetnam and

Lynch 1993, Ryerson et al. 2003), whereas in British Columbia and in parts of the cascade range of Oregon, outbreaks have been associated with dryer and warmer conditions (Campbell et al. 2006, Flower et al. In prep). As small poikilotherms, insect developmental and reproductive rates are influenced by ambient temperature (Werner and Holsten 1985, Hansen et al. 2001, Logan et al. 2003, Hansen et al. 2011) and are closely tied to host phenology (Aukema et al. 2008, Raffa et al. 2008, Bentz et al. 2010, Régnière et al. 2012). Warmer temperatures during larval stages are expected to increase the developmental rates of both defoliator and bark beetle populations (Logan et al. 2003), and warmer winter temperatures are expected to reduce the physiological limitations of overwintering insects (Raffa et al. 2008). Additional indirect effects on insect populations that influence outbreak success and may be influenced by fire exclusion and climatic variability include changes to predation and parasitism rates, interspecific competition, and presence of pathogens and other conditions that affect host fitness (Mitchell 1990, Raffa et al. 2008).

Interactions among multiple disturbance agents

Fires and insect outbreaks are often influenced by prior disturbances (Veblen et al. 1994, Ayres and Lombardero 2000, Dale et al. 2001, Bebi et al. 2003, Bigler et al. 2005, Cooke et al. 2007). For example, positive correlations have been found between bark beetle activity and fire risk (Lynch et al. 2006, Page and Jenkins 2007, Jenkins et al. 2008), insect pest range expansion and warming temperatures (Ayres and Lombardero 2000, Dale et al. 2001, Williams and Liebhold 2002, Logan et al. 2010), and high severity fire following periods of fire suppression due to increased woody fuels (Parsons and DeBenedetti 1979, Heyerdahl et al. 2001, Marlon et al. 2009). Climate trends of milder winters and more drought-prone summers have been linked to increased risk of fire ignition and spread, larger and more severe insect outbreaks, and significant changes to forest species composition and structure which in turn feed back onto one another (Ayres and Lombardero 2000, Logan et al. 2003, Raffa et al. 2008). These cumulative disturbances can have adverse effects on long-term stability of species assemblages if the frequency of disturbances is higher than the rate of recovery (Clark 1996, Frelich 2002), or disturbance size or severity impact the availability of viable seed sources (Frelich and Reich 1999).

These trends of interacting disturbances across dry forests of western North America are expressed strongly along the steep vertical gradients of the Madrean Sky Island system. The isolated sky island forests may be especially vulnerable to changes in disturbance frequency or severity because the likelihood of colonization from outside the system is low (Peterson et al. 1998). Species assemblages in montane sky islands are an example of geographically isolated populations where steep vertical gradients of precipitation and temperature limit the extent of forest assemblages. Desert valleys between widely dispersed mountain ranges function as “inland seas” that inhibit migration between montane populations (Warshall 1995). Vertical gradients within sky islands increase the diversity of species assemblages in a small area and can enhance or dampen the likelihood of disturbances spread from one forest type to another (Swetnam et al. 2009).

While individual components of forest change have been identified in western ecosystems, much less work has been done to examine the dynamic interactions between fire, forest structure, insect outbreaks, and climate through time. These interactions pose significant challenges for forest managers where changes to one component of the system may result in cascading effects on other forest types, predisposing a system to future disturbance, and altering stability of the system as a whole. Information detailing the series of changes to disturbance regimes and species assemblages before and after Euro-American settlement and through several centuries of climate conditions is essential for understanding current forest conditions. By gaining a better understanding of past forest and disturbance dynamics, we may be able to guide potential management actions to mitigate the risks of severe disturbances and bolster resilience of these highly interconnected ecosystems.

An additional challenge for sky island systems of the southwestern U.S. and northern Mexico is the accelerated rate of changing temperature and moisture regimes in relation to other western forest systems. Over the next century changing temperature and precipitation regimes along are expected to alter the distribution of suitable habitat for many tree species (Rehfeldt 2004, McKenney et al. 2007, Notaro et al. 2012). These changes in climate will not be the only stressors on forested ecosystems, however. Warming temperatures and more severe drought will increase the frequency of conditions appropriate for fire (Westerling et al. 2006, Crimmins 2011) and insect outbreaks (Logan et al. 2003, Bentz et al. 2010).

The predicted shift in climate and disturbance regimes of southwestern ecosystems away from historical conditions limits the long-term application of studies of historical species dynamics and disturbance interactions. While historical reconstructions are imperative for developing mechanistic relationships between climate conditions, forest dynamics, and disturbance events, the dynamic nature of each of these components limits our understanding of system feedbacks under changing conditions. In this context, using historical forest conditions to calibrate hybrid mechanistic and probabilistic ecosystem process models that can vary individual components in relation to one another, is one way to examine some possible trajectories of future forest and disturbance conditions where there is no historical analog.

Approach

In this dissertation I combine dendroecological methods, geographic information systems (GIS), multivariate statistics, and time series analysis to reconstruct the size, frequency, and spatial extent of historical disturbance events and changes to forest species dynamics through time. I test climatic relationships to fire, spruce beetle outbreaks, and seedling recruitment, and statistical changes to forest species assemblages in response to fire exclusion. I use the spatial and temporal dynamics of species distributions and fires to begin calibration of a spatially explicit ecosystem process model capable of reproducing patterns of fire size and severity similar to the pre fire-exclusion period on independent calibration and validation landscapes.

The first study used a combination of fire scar, cohort establishment, and snag death dates to reconstruct spatial and temporal components of fire history along a gradient of four forest types above 2,135 m (7,000 ft.) elevation. The gridded sampling design allowed for GIS interpolation of composited fire records to ascribe reconstructed spatial extent to 104 individual fire years in the study area. Combinations of cohort establishment and fire scar dates allowed for the interpretation of fire severity at each recording location, and comparison of the proportion of low, moderate, and high severity fires before and after the period of Euro-American settlement. We used superposed epoch analysis (SEA) to test for patterns of significant temporal lags between anomalous climate conditions and fires in three size classes before and after Euro-American settlement.

The second study focused on spruce-containing forests above 2,835 m (9,300 ft), using a multi-proxy approach, including growth release events from tree-ring width measurement, tree death dates, failed bark beetle attack scars, and historical documents to reconstruct the history of major spruce beetle outbreaks over a 319-year period. Outbreaks were further corroborated with a spatial reconstruction of host spruce establishment following a large high-severity fire in 1685. The spatial extents of individual spruce beetle outbreaks were projected onto the reconstructed spatial distribution of host spruce to determine the time lag between spruce establishment and initial outbreak. Superposed epoch analysis was used to test the effects of summer temperatures and spring drought on outbreak initiation and duration over a series of time lags.

The third study used a combination of tree and seedling establishment dates collected from the four forest types, and time since last seedling-killing fire to test the stability of species composition as a function of time since fire and effective energy and mass transfer (EEMT), an independent measure of site productivity. I reconstructed Importance Values of the six dominant conifer species at each site in the year 1870 and used a multivariate regression tree analysis to determine the amount of variance in species assemblages that could be explained by EEMT. I then used Importance Values from two additional time steps, 75 years after fire exclusion, and 115 years after fire exclusion to assess the relative stability of each forest type through time. I used a nonparametric multivariate test of dispersion to determine if species assemblages had changed significantly from one time step to the next.

Organization of the Dissertation

The dissertation is composed of three papers included as appendices. Formatting of each paper is determined by the target journal for submission. A separate literature cited section is included as a component within each appendix article.

Appendix A, titled “Fire severity, spatial extent, and climate associations diverge from historical precedent along an ecological gradient of the Pinaleño Mountains, Arizona, U.S.A” has been prepared for submission to *Forest Ecology and Management*. In this study I reconstruct the size, severity, spatial distribution, and climate associations of fires in for forest types over a 368-year period. I then test for differences between each of these components before and after Euro-American settlement of the landscape.

Appendix B, titled “Fire exclusion and climate affect spruce beetle outbreak size and duration” has been prepared for submission to *Landscape Ecology*. In this study I reconstruct the history of major spruce beetle outbreaks between high-severity fires in the Pinaleño Mountains. I reconstruct the dynamic distribution of host spruce as it expanded from refuge populations after a fire in 1685 and test the temporal lag between spruce establishment and spruce beetle outbreak as well as subsequent changes to outbreak size, severity, and duration as a function of spruce extent. Lastly I test for repeated patterns of warmer than average temperatures associated with outbreak initiation and lower than average precipitation associated with outbreak duration.

Appendix C, titled “Site productivity mediates stability of species assemblages following fire exclusion” was prepared for submission to *Ecology*. This study used records of seedling establishment and time since fire to examine the stability of forest assemblages during the period of fire exclusion. Stability was defined in ecological terms as the conversion of seedling recruitment from disturbance-adapted to competition-adapted species and structure. I then test the ability of site productivity to explain differences in assemblage stability through time.

CHAPTER 2. PRESENT STUDY

Detailed introduction, methods, results, and discussion are presented in each of the papers appended to this dissertation. A short summary of each paper is included below. The overarching thesis of this work was to investigate the spatial and temporal interactions among the disturbance events, forest species dynamics, climate, and human impacts. Reconstruction of historical disturbance regimes along a gradient of forest types provides context for the series of recent, high-severity fires and insect outbreaks affecting forests of western North America and their associations to human-caused changes to forest structure and disturbance regimes. Testing for historical climate-disturbance associations allows for the detection of deviations from historical patterns related to changing landscape conditions and changing climate.

Appendix A- "Fire severity, spatial extent, and climate associations diverge from historical precedent along an ecological gradient of the Pinaleño Mountains, Arizona, U.S.A"

Prior to Euro-American settlement, the steep vertical gradients of Madrean Sky Island mountain ranges maintained a series of distinct forest types and fire regimes in close spatial proximity. In dry, pine-dominated forests, fire was a frequent disturbance that caused little mortality of overstory trees and limited establishment of seedlings, thus maintaining relatively open canopy conditions (Swetnam et al. 2001). Dry mixed-conifer forests experienced a similar fire regime to pine-dominated stands where high canopy base heights and thick bark rendered mature trees highly fire resistant. The cooler, wetter conditions of higher elevation mesic mixed-conifer forests reduced the occurrence of wide-spread ground fires, and highly productive sites created higher fuel loadings that promoted less frequent and patchier mixed-severity fire that caused some mortality of overstory trees (Swetnam and Baisan 1996b) . In the highest elevation mesic sites, fire was rare and likely occurred as a stand replacing event during extreme drought (Margolis et al. 2011). Variability in site conditions may have served as an "ecological buffer" (Grissino-Mayer et al. 1995, Swetnam et al. 2009), limiting the spread of fires to sites with similar fuel and moisture profiles in all but the most severe drought conditions (Grissino-Mayer et al. 1995, Margolis and Balmat 2009, Margolis et al. 2011). Over the past two decades, a series of large mixed-severity fires have occurred in the region, providing an opportunity to contrast the size, severity, and climate associations of recent fires to historical events.

I used a grid of 58 georeferenced demography and fire history sampling plots spaced 1-km apart to reconstruct the spatial and temporal components of historical fires in pine, mixed-conifer, and spruce-fir forests of the Pinaleño Mountains of southeast Arizona. I used dendroecological techniques to determine the establishment dates of 1,222 trees and dated 1,201 fire scars collected from 241 trees to identify 231 unique fire years.

Small fires on the order of 100-200 hectares were frequent in pine and mixed-conifer forest before and after Euro-American settlement, however the majority of spreading fires stopped after 1880. Intervals between small fires (<1000 ha) doubled in pine and dry mixed-conifer sites after 1880 and not enough fires greater than 100 ha were recorded in mesic mixed-conifer forest after 1880 to calculate pre and post-settlement differences. Large fires recorded in 50% or more of sites averaged once every twenty years for the 240 years prior to Euro-American settlement but were absent after 1880. Recent fires affecting the spruce-fir and mixed-conifer forest have the highest proportion of high-severity burned area over the period of reconstruction. A single fire in the historical record with a comparable high-severity extent occurred during the most severe drought conditions of the reconstructed period. Recent high-severity fires were associated with persistent moderate drought conditions similar to conditions during five low-severity spreading fires in the pre-settlement period. Climate thresholds necessary for high severity fire appear to have shifted as a result of anthropogenically driven changes to forest structure and fuel loadings following a century of fire exclusion.

Appendix B- “Fire exclusion and climate affect spruce beetle outbreak size and duration”

The most damaging biotic agent in high elevation spruce-fir forests of the western U.S. is the spruce beetle *Dendroctonus rufipennis* (Kirby). Mortality attributable to spruce beetle varies widely, from individual trees under endemic beetle population levels (Veblen et al. 1991a) to near complete mortality of mature trees under epidemic conditions (Veblen et al. 1991a, DeRose and Long 2007). Conditions influencing spruce beetle outbreaks include tree size and age (Massey and Wygant 1954, McCambridge and Knight 1972), antecedent disturbance (Wygant and Lejeune 1967), climatic variation (Hebertson and Jenkins 2008, Waring et al. 2009, Hart et al. 2013), and anthropogenic influences (Raffa et al. 2008). Outbreaks are commonly associated with stands containing mature spruce >10 cm diameter (Veblen et al. 1991a) and with spruce basal area exceeding 35 m^2 ha^{-1} (152 ft^2 ac^{-1}) (Schmid and Frye 1977), although mortality in trees with bole diameter as small as 5 cm has been documented in severe outbreaks (DeRose and Long 2007).

Spruce beetle outbreaks are cyclical and tend to recur in the same stands at approximately 40-60 year cycles (Veblen et al. 1994, Berg et al. 2006). Severe outbreaks in recent decades have been linked with seasonal droughts and warmer than average winter and summer temperatures (Berg et al. 2006, DeRose and Long 2012d, Hebertson and Jenkins 2008, Hart et al. 2013), though similarly severe spruce beetle outbreaks documented from the late 19th and early 20th centuries are not correlated with climate anomalies (Massey and Wygant 1954). At the southernmost extent of spruce-fir forest in North America, two spruce beetle outbreaks are documented over the past century. The first, in the 1950s was a relatively long lasting, moderate severity outbreak affecting up to 30% of spruce timber volume (Bennett 1953). The second spruce beetle outbreak starting in the 1990s took place concurrent with outbreaks of two foliage-feeding insects and an outbreak of western balsam bark beetle *Dryocoetes confusus* (Swaine) and resulted in mortality of mature spruce exceeding 80%.

In this study I used dendroecological methods to reconstruct the history of spruce beetle outbreaks after the last stand-replacing fire in the spruce-fir forest of the Pinaleño Mountains. I used a multi-proxy approach incorporating growth releases detected from tree-ring measurements, spruce death dates, scars from failed spruce beetle attack, historical documentation, and a spatial reconstruction of dynamic host populations to determine the frequency and size of historical outbreak events as well as the host size and age conditions and climate factors associated with outbreak initiation and duration.

From 654 sampled trees and 591 measured series we identified 12 spruce beetle outbreak events over a 319-year period of reconstruction, with a mean outbreak interval of 19.7 years. Outbreak interval was not significantly different before and after Euro-American settlement; however outbreak duration doubled from 4.6 to 9.8 years. The change in outbreak duration coincided with a doubling of the extent of host spruce in the decades following fire exclusion from surrounding mixed-conifer forest. Spruce diameter growth was significantly faster in mixed-conifer than higher elevation spruce-fir forest ($p<0.001$). Outbreak size and duration increased with increasing host extent, reaching a peak in the 1950s outbreak. The 1990s outbreak was similar in size to the 1950s event but outbreak severity appears to have been the highest in the reconstructed period, coinciding with the greatest spatial extent of large diameter spruce in more than 300 years. Significant associations were found between outbreak initiation and warmer than average summer temperatures 1-3 years prior to outbreak detection, possibly coinciding with a developmental shift from semivoltine to univoltine life cycle; and with persistent dryer than average spring conditions and forest drought index for up to a decade following outbreak initiation. These results suggest that fire exclusion and the subsequent increase in host spruce extent, as well as 20th century climate patterns favoring outbreak initiation and persistence had significant effects on recent spruce beetle outbreak extent and severity.

Appendix C- "Site productivity mediates stability of species assemblages following fire exclusion"

In complex natural systems, resilience of a species assemblage can be characterized by the stability of the assemblage after a change to the system-adapted disturbance regime (Jasinski and Payette 2005, Girard et al. 2008). The loss of resilience within a system can result in a shift to an alternative state composed of different species and different conditions of disturbance (Holling 1973, Barton 2002, Jasinski and Payette 2005, Drever et al. 2006). The shift itself can be sudden, following a major stand replacing event, or delayed, through competitive interactions among long-lived species (Suding and Hobbs 2009). In the American Southwest, fire exclusion in the mid to late 1800s caused a significant shift to the system-adapted disturbance regime (Bahre 1991, Swetnam et al. 2001) , providing an opportunity to test the longer-term resilience of fire-adapted forests to the interruption of one of the primary processes driving species selection and forest structure. At timescales shorter than a century, stability of southwestern forest assemblages cannot be measured through changes to overstory species because trees are long-lived organisms that can be slow to reflect changes in their environment. A better indicator of changing conditions is the relative proportion of newly established seedlings that represent 1) the overstory species, or 2) a different set of species better suited to current environmental conditions. In fire-adapted pine and mixed-conifer forests, a switch in seedling recruitment from primary disturbance-adapted shade intolerant species to secondary competition-adapted shade tolerant species may reflect a reduction in the longer-term stability of the forest assemblage as a whole.

In this study I use dendroecological techniques to identify changes to forest species assemblages after the onset of fire exclusion along a gradient of site productivity. Using demographic data and composited fire histories from 41 fixed-area plots in pine, dry and mesic mixed-conifer, and spruce-fir forest types, I quantified changes to seedling species and abundance before and after the onset of fire exclusion. Effective energy and mass transfer (EEMT), an independent measure of site productivity (Rasmussen et al. 2011, Pelletier et al. 2013), explained 39% of the variance of forest types based on the six primary conifer species. Over the century prior to fire exclusion, seedling species reflected overstory species, and recruitment was limited to brief fire-free intervals in sites outside of the spruce-fir forest. In the first two decades following fire exclusion, seedling recruitment in moderate productivity dry mixed-conifer forest shifted from primary species to secondary species, reaching a peak of secondary species recruitment 50-60 years post fire-exclusion. Lowest productivity pine-dominated sites and highest productivity spruce-fir dominated sites were the most stable species assemblages after a century of fire exclusion, though seedling abundance increased significantly in pine-dominated forests. Seedling recruitment in high productivity mesic mixed-conifer sites included secondary species but was not dominated by them, and recruitment of secondary species was considerably slower than in dry-mixed conifer sites. These results suggest that fire maintained the stocking of moderate productivity forests well below their ecological potential, reducing competition for sunlight, moisture, and nutrients, and conferring a degree of resistance to drought and high-severity fire. Forests in moderate productivity sites are at the greatest risk of shifting toward an alternative state, either through continued fire exclusion and species competition, or through stand-replacing fire or drought-related die-off.

Summary

In this dissertation I examined a series of interacting ecological disturbance agents and environmental conditions affecting forest dynamics along a steep ecological gradient. I examined interactions between fire, human land use changes, climate, and site parameters in pine and mixed-conifer forests; and interactions between stand-replacing fire, forest distributions, spruce beetle outbreaks, and fire exclusion in upper elevation spruce-fir forests. Some of the key finding from this work are summarized below:

- Euro-American land uses (livestock grazing, road building, etc.) beginning in the 1880s led to a significant reduction in fire spread but not fire ignition.
- Contemporary fires are more severe than similarly sized fires prior to fire exclusion.
- Historical fire-climate associations have decoupled and recent large fires occurred under a different set of climate associations than large fires prior to fire exclusion. Significant changes to spatial patterns, frequency, and climate associations of spreading fires after 1880 suggest that fuel accumulation is no longer a limiting factor to fire spread. Fire ignition during moderate drought in dry forests with continuous fuels is now sufficient for mixed and high-severity fire.

- Fire exclusion in mixed-conifer forest had a significant impact on spruce and corkbark fir forest extent and spruce beetle outbreak dynamics. Spruce establishing in mixed-conifer forest grow at a significantly faster rate than spruce in cooler, denser pure spruce-fir stands, making them susceptible to outbreak sooner.
- Temperature thresholds necessary for spruce beetle population conversion from a two-year to a one-year life cycle are reached more frequently in lower elevation mixed-conifer forest than in upper elevation spruce-fir forest.
- Spruce beetle outbreaks at their southern range extent occur at a frequency two to three time that of outbreaks in cooler northern spruce-fir forests.
- Over the period of the instrumental record, spruce beetle outbreak initiation was consistently associated with above average summer temperatures prior to outbreak and persistent below average spring precipitation during outbreak.
- In the decades following fire interruption by Euro-American land uses, forests in the highest and lowest productivity sites had the greatest stability of species assemblages, suggesting that site-productivity is a primary control on species these sites. Forests located in moderate productivity sites had the lowest species stability, suggesting that fire was the primary control on forest composition and structure in these sites prior to Euro-American settlement.
- Fire maintained forests in moderate productivity sites below their stocking potential, providing an ecological buffer to drought and high-severity fire. These fully stocked forests are now at greatest risk of die-off from future disturbance.

CHAPTER 3. FUTURE RESEARCH DIRECTION

Modeling paleo fire-vegetation dynamics along a steep ecological gradient

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Introduction

Fire dynamics in western North America are mediated by interactions among vegetation, topography, and climate that occur at varying spatial and temporal scales. At seasonal to annual timescales, fire ignition and spread are determined by short-term weather trends, accumulated fine fuels, and physical landscape properties such as topography (Falk et al. 2011). At temporal scales of decades to centuries, these factors interact with longer-term climate modes to form repeated patterns of fire size, frequency, and severity at the landscape scale. The resulting fire regimes are a primary process driving forest structure, species selection, and demographic distributions (Dillon et al. 2011, Falk et al. 2011, McKenzie et al. 2011).

Observations of fire effects in contemporary forests and reconstructed patterns of historical fire frequency and severity associated with specific species assemblages have contributed to the development of fire regime concepts and the role of fire as a driver of forest species and structure (Falk 2006, Sugihara et al. 2006). In ponderosa pine-dominated forests of northern Arizona, demographic and fire scar evidence have been used to determine historical forest structure, species composition, and fire frequency and severity (Fulé et al. 1997a, Mast et al. 1999, Heinlein et al. 2005). In more complex forested ecosystems distributed along the steep vertical gradients of mountains in the U.S. –Mexico border region, forests with different species composition and structure were found to have very different fire regimes, often at close spatial proximity (Grissino-Mayer et al. 1995, Swetnam et al. 2001).

From more than a century of studying the role of fire in shaping the vegetation and structure of contemporary forests (Turner and Romme 1994, Agee 1998b), fire scientists have quantified a range of mechanistic and probabilistic relationships that explain the behavior of fire and its effects on forested systems (e.g.,. Rothermel 1972, Scott and Burgan 2005).

Combining these methods with demographic analysis (Heyerdahl et al. 2001, Margolis and Balmat 2009), researchers have assembled an understanding of fire as an ecosystem process in western forests over the past several centuries (Bowman et al. 2009, Falk et al. 2011, McKenzie et al. 2011, Swetnam et al. 2011). This process-centered understanding of fire and vegetation dynamics can be modeled with quantified relationships between forest structure and fuel profiles, topography, and annual to multi-decadal climate patterns that have remained robust even as each component has varied continuously through time (Keane et al. 2011). Using a rich dataset of reconstructed historical relationships between forest species, structure, and patterns of fire spread and severity on an individual landscape, it is possible to develop a the first spatially explicit model of paleofire that encompasses the range of historical variability in fire and species dynamics at the landscape scale.

Here we combine a comprehensive set of field-collected species and site parameters geo-referenced to a topographically diverse landscape into the ecosystem process model FireBGCv2 (Keane et al. 2011). We use a 300-year record of spatial vegetation dynamics to calibrate species successional processes, and a spatial reconstruction of historical fire frequency and spatial distribution to calibrate fuel models and initial landscape fire parameters. This calibrated fire-vegetation system is then validated against an independent landscape also with detailed spatial reconstructions of historical fire and vegetation dynamics. We use this process to determine the skill of the FireBGCv2 modeling platform to capture the natural range of variability in fire-climate interactions over a defined set of historical parameters.

Methods

FireBGCV2 landscape succession model

The FireBGCv2 landscape fire succession model (Keane et al. 2011) is a third generation spatially explicit tree to landscape scale vegetation dynamics and ecosystem process simulation model. FireBGCv2 merges vegetation simulation components from FOREST-BGC (Running and Gower 1991) and BIOME-BGC (Running and Coughlan 1988, Running and Hunt 1993, Thornton 1998), fire initiation and spread outputs from FIRESUM (Keane et al. 1989, Keane et al. 1990), and a series of updated or additional components that simulate weather streams and additional ecosystem processes (Keane et al. 2011).

Fire BGCv2 incorporates the strengths of several modeling approaches to balance output realism with computational efficiency. Empirical relationships based on measured data are used for tree and plot-level inputs. Deterministic functions based on generalized relationships are used to describe species traits such as fire resistance, shade tolerance, and seral stage. A stochastic modeling framework that draws from probability distributions is used to simulate biological processes at the tree level such as year of tree death and masting events, as well as stand-level processes such as fire ignition. Mechanistic components based on biological and physical relationships are used to explain gap dynamics and the allocation of carbon, water, and nitrogen in the specified landscape (Keane et al. 2011). The ability to simulate a series of biophysical settings along a gradient of elevation, and incorporate interactions among fire, vegetation and climate makes FireBGCv2 an appropriate modeling environment for ecologically and topographically complex systems.

Model development and calibration

Model inputs for *species, tree,* s*tand*, *fuel* and *site* files were generated from a combination of field-collected data, shared databases on southwestern species, and published literature on species-specific ecophysiological parameters and fuel traits. Plot-based field data from 56, 500 m^2 forest demography plots (O'Connor 2013) and 61 species verification locations were used to adjust LANDFIRE vegetation maps (LANDFIRE 2013) and to develop geo-referenced species and stand databases. Demographic plot data provided records of tree species, diameter, height, canopy base height, and age for all trees and snags greater than 19.5 cm diameter at breast height (DBH) and 1/3 of trees and snags from 1 cm to 19.4 cm DBH. Fuel parameters from Brown’s lines (Brown 1971) within each plot were supplied by collaborators from the Coronado National Forest (Wilcox personal comm.).

We developed a database of species parameters for each of the major stand components in piñon manzanita shrubland, Madrean pine-oak oak woodland, ponderosa woodland, dry mixed-conifer, mesic mixed-conifer, and spruce-fir forest types. Maximum and minimum population-level species parameters were calculated from field-collected demography plot measurements. Individual ecophysiological parameters and life history descriptions were developed from data provided by the USFS Fire Lab species parameter database (Loehman et al unpublished) and the Ecological Restoration Institute at Northern Arizona University (Laughlin Unpublished Data). Additional parameters for species life history traits and general conifer and deciduous species parameters were collected from *Silvics of North America* (Burns and Honkala 1990) and generalized BiomeBGC input parameters (White et al. 2000, Korol 2001, Hessl et al. 2004).

Development of input model components

To avoid an artificial "edge effect" along the exterior margins of the modeled landscape, a buffer area was added to the simulated landscape and then clipped from model outputs to focus on results only for the landscape of interest. To determine the size of the buffer necessary to model fire in the high elevation forests above 2,135 m, we overlaid spatial fire extents from the Coronado National Forest fire atlas for the extent of the mountain range (USDA Forest Service 2013a). The majority of the area affected by fires recorded in the Pinaleño Mountains over the past 75 years burned above 1,900 m elevation. To limit computation demand while promoting natural fire spread behavior over the landscape, we placed a 1-km buffer around the 1900 m elevational limit and used this buffered landscape at the basis for modeling species dynamics and fire.

FireBGCv2 draws on multiple input layers to determine tree, stand, site, and landscape –level processes and interactions. Tree-level processes are derived first from individual species parameter lists that detail species life history traits, ecophysiological limitations (drought tolerance, photosynthetic rates, minimum growing season), and biogeochemical relationships for allocation and utilization of carbon, and nutrients. We calibrated species parameter lists for 10 tree species, three shrub complexes representing lower, mid, and upper elevation species, and high-elevation grassy meadow.

Tree file inputs were derived from field-collected age, height, and diameter data from demography plots located in pine, dry and mesic mixed-conifer, and spruce-fir forest types. The *site* file, developed from LANDFIRE biophysical setting, was used to define the sub-landscapes that receive independent weather inputs. In a Madrean Sky Island system, ecotones represent individual *sites* along a gradient of increasing precipitation and decreasing temperature from bottom to top. We defined seven distinct sites based on biophysical setting of climax forest type and potential productivity, determined by soil composition and depth, maximum potential leaf area index, maximum stand basal area, and maximum seedling densities. The *site* file also includes mean fire size and mean frequency of fire ignition drawn from reconstructed fire history data. Native resolution for LANDFIRE raster data is a 30 meter pixel size which determines the minimum size of individual forest types on the landscape. From a modeling standpoint, the biophysical setting is designed to broadly determine weather streams and gradients of growing conditions, typically at a scale much larger than the 30 m pixel size. To address concerns of overly precise, though not necessarily accurate classification of biophysical setting, 31 similar forest classifications were combined by dominant forest type to produce seven major site classes modeled on the landscape. Continuity of individual sites was improved by generalizing patches of individual forest types to a minimum size of 150, 30m pixels (13.5 hectares). Patches smaller than 150-pixels were combined into predominant surrounding forest types.

Individual stands were generated by partitioning site-level inputs by maximum height classes developed from LiDAR measurements collected in 2008 (Mitchell et al. 2012). Height classes were used as a proxy of initial forest age and successional stage. Maximum canopy heights were partitioned into five classes. Grouped classes were filtered by the same minimum patch size used for forest sites. The classified stand height model was then combined with the forest site model to produce 603 stands with unique forest-type-height combinations. The stand file was then converted to a series of vector polygons and the centroid was computed for each polygon. Stand elevation, slope, and aspect were extracted to the centroid point location from the underlying digital elevation model. Soil water and snow water parameters were generated from the soil layer, and initial fuel characteristics were generated from field-collected fuels data from representative plots in each forest type. The 603 stands were then populated with individual trees with defined species, age, DBH, and heights representative of the successional stage appropriate for site-height classifications. For this step, five distinct permutations of individual stands representing the 35 unique site-height groupings were randomly assigned to corresponding locations in the *stand* map. The *stand* file was then updated to include the appropriate tree count assigned from the *tree* file.

Weather file generation

A separate daily weather stream is used in each of the seven sites determined from the *site* input file. Daily temperature (maximum, mean, and minimum), precipitation, vapor pressure deficit, and solar influx are generated by the MTCLIM microclimate simulation model (Hungerford et al. 1989, Thornton and Running 1999). Complete daily information was not available for a more than five-year period from the RAWS stations within the simulated landscape, so a complete 50-year daily weather record from the base of the mountain range was used as the initial input for the MTCLIM model. Total annual precipitation at each of the seven sites was interpolated from the last two decades of RAWS station data (Desert Research Institute 2013) cross-referenced with 30-year normals generated from PRISM (PRISM 2013). Site elevation, latitude, slope, and aspect were averaged over the entire site area. For model simulations runs, a continuous loop of 50 years of daily weather inputs was used over the period of simulation.

Model initiation and calibration

Once species and site parameters were entered for the study area, model initiation scaled parameters from plot to landscape level, dynamically modeling a series of biogeochemical processes for each 30 m pixel on the landscape (Keane et al. 2011). A subsection of the full landscape, containing six of the seven sites was used to calibrate species and fire characteristics (Figure FRD-1). Simulation calibration runs were conducted only on the subset of the full landscape. Annual outputs of net primary productivity, total carbon, and mortality in kg/m^2, were used to track model stability and adequacy of initial input parameters.

Initial calibration was based solely on vegetation succession dynamics. We modeled 300 years of vegetation growth without fire to check expected species distributions along gradients of moisture, temperature, and interspecific competition. Initial species parameters were adjusted to reflect physiological limits and competitive interactions among species. Multiple runs of identical initiation conditions yielded different results over 300 years of modeling because mature tree seed production and dispersal, seedling survival, and tree mortality are simulated stochastically from an independent probability distribution for each species (Keane et al. 2011). Initial species parameters were considered stable enough to move to the next calibration phase when 80% or more of modeling runs resulted in species assemblages similar to those that developed over the 20th century fire exclusion period. In general, shade tolerant, dense stands of fire intolerant species were expected to dominate the landscape over a 300-year fire free interval. For example, white fir was expected to proliferate over the mid-elevation sites, buffered by moisture limitations at the lower elevation threshold and temperature limitations at upper elevations. Subalpine species were expected to spread to lower elevation sites until limited by moisture and warm temperature thresholds. Shade intolerant ponderosa pine and aspen were excluded from regeneration, resulting in only large old pine and small isolated aspen stands over the 300-year simulation period.

Once species parameters were calibrated to the range of moisture and temperature conditions across the landscape, we calibrated fire dynamics based on a 370-year spatial reconstruction of fire history on the modeled landscape (O’Connor et al. 2013). Mean fire return intervals and fire sizes were used as initial *site* file fire parameters. Stand and site-level fuel depths were generated from plot measurements and fuel model classifications and initial inputs were drawn from Rothermel (1972). Live and dead fuel moisture parameters in mesic forest were increased to the moist forest levels published in Scott and Bergan (2005) to limit fire spread in mesic forests. After initial modeling runs, mean fire sizes in oak-manzanita and pine-oak forest types were increased to reflect point fire frequencies similar to reconstructed parameters for dry mixed-conifer forest. Conversely, in upper elevation mesic and spruce-fir sites, fire sizes were reduced to limit point fire return intervals to more accurately express the 100-300 year intervals determined in fire-history reconstructions. Modeled patterns of fire frequency across the landscape reflected the influence of topography, aspect, vegetation dynamics, and fuel conditions, similar to reconstructed spatial patterns of historical fire (Figure FRD-2).

Model validation

An independent sub-landscape of similar size and species composition to the calibration landscape was selected for model validation. *Site* and *stand* maps and their linked database files from the full landscape map layers were cropped to include only those polygons included in the validation landscape. Parameters for *species*, *stand*, *site*, and *fuel* files fitted to the calibration landscape were transferred directly to the file structure of the validation landscape.

Results from this modeling effort are pending final calibration of fire and vegetation input parameters.

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Figures

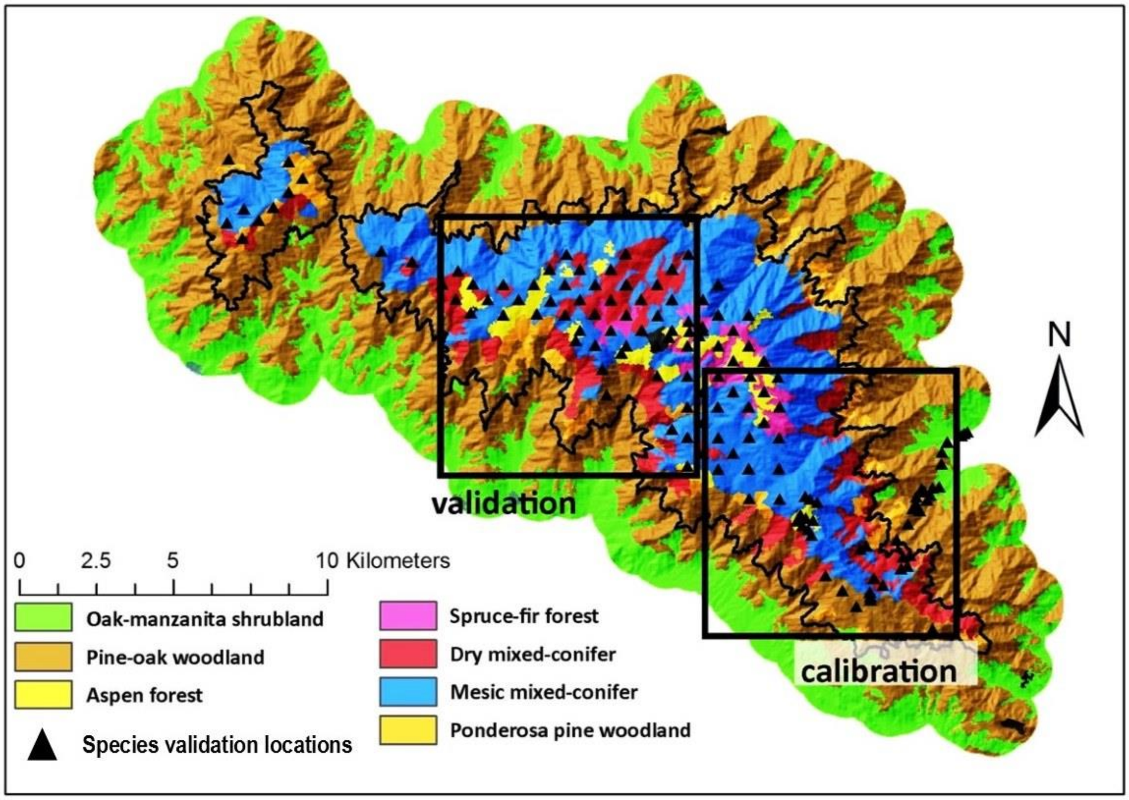

Figure FRD-1. Modeling landscape in the Pinaleño Mountains, Arizona, USA. Study Area above 2,135 m is outlined in black. Seven vegetation types on the map define sites layers with independent weather streams. Triangles represent species validation locations and demography sampling plots.

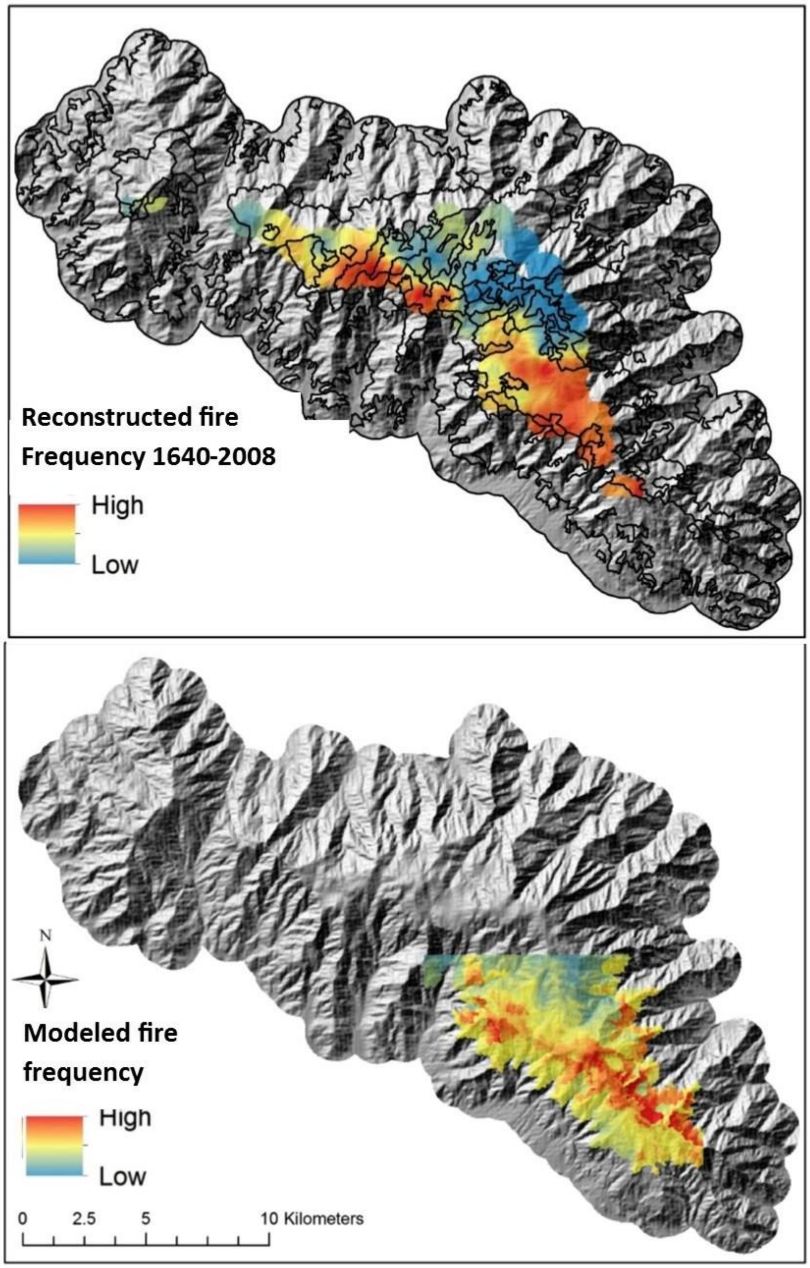

Figure FRD-2. Reconstructed and modeled patterns of fire frequency and spatial distributions. Reconstructed fire frequency spans calibration and validation site locations. Modeled fire frequency over a 300-year interval is limited to the calibration landscape.

APPENDIX A

FIRE SEVERITY, SPATIAL EXTENT, AND CLIMATE ASSOCIATIONS DIVERGE FROM HISTORICAL PRECEDENT ALONG AN ECOLOGICAL GRADIENT OF THE PINALENO MOUNTAINS, ARIZONA, U.S.A

Fire severity, spatial extent, and climate associations diverge from historical precedent along an ecological gradient of the Pinaleño Mountains, Arizona, U.S.A

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Abstract

Fire size and severity have been increasing over the past three decades in high elevation forests of the American Southwest. Ecological outcomes of these increases are difficult to gauge without a historical context for the role of fire in these systems prior to interruption by Euro-American land uses. Here we compare fire characteristics and climate associations between spreading fires before and after the onset of fire exclusion to determine the degree of similarity between past and recent fires. We use a gridded fire scar and demography sampling network to reconstruct spatially explicit estimates of fire extent and burn severity, as well as climate associations of fires from individual site to landscape scales from 1640 to 2008 C.E. (Common Era). We found that 1) Euro-American land uses (livestock grazing, road building, etc.) beginning in the 1880s led to a significant reduction in fire spread but not fire ignition; 2) contemporary fires are more severe than similarly sized fires prior to fire exclusion; 3) fire-climate associations have decoupled and recent large fires occurred under a different set of climate associations than large fires prior to fire exclusion; and 4) after a century of suppressing spreading low-severity fires, only the smallest and largest mixed and high-severity fires occur, and mid-scale spreading fires are absent.

Significant changes to spatial patterns, frequency, and climate associations of spreading fires after 1880 suggest that fuel accumulation is no longer a limiting factor to fire spread. Fire ignition during moderate drought in dry forests with continuous fuels is now sufficient for mixed and high-severity fire. Coinciding factors of extreme fuel loading and high fuel continuity as a result of fire exclusion, and projected lengthening of the fire season and prolonged drought support the conclusion that additional large high-severity fires, especially in mixed-conifer forests, can be expected without aggressive management action to restore fire-adapted forest structure and species composition.

Key Words

Spatial reconstruction, fire severity, fire-climate, elevation gradient, ENSO, PDSI, landscape fire

Introduction

The average annual area burned in wildfires in the Western U.S. has increased more than six fold over the past four decades (Westerling et al. 2006, Littell et al. 2009). The area affected by high severity fire is increasing as well (Eidenshink et al. 2007, Miller et al. 2009, Diaz and Swetnam 2013), although the proportional increase in high severity fire, in which most or all overstory vegetation is killed, is less consistent among western ecoregions and forest types (Dillon et al. 2011). While the human and natural resource costs of recent fires are indisputable, the degree of long-term ecological change resulting from recent fires is not yet known. In many dry forests of the interior West, fire was a keystone ecosystem process (Falk 2006) that shaped forest structure and species composition from stand to landscape scales (Swetnam and Baisan 1996a, Brown and Shepperd 2001, Fulé et al. 1997b, Fulé et al. 2009). In topographically diverse forests of the southwestern U.S., steep vertical gradients maintained distinct species assemblages and different fire regimes in close spatial proximity and often limited the spread of fire across distinct ecological boundaries (Grissino-Mayer et al. 1995, Stephens 2001, Margolis and Balmat 2009, Swetnam et al. 2009). Heterogeneity of forest types and fire regimes contributed to the landscape-scale resilience of forests within these systems by limiting the patch size of high-severity fire (Agee 1998b, Turner et al. 1999a, Taylor and Skinner 2003).

Euro-American settlement of the western states in the mid to late 19th century led to intensive livestock grazing, timber harvesting, and mineral extraction that interrupted natural fire cycles (Bahre 1998, Swetnam 2005). These actions initiated a series of changes that ultimately homogenized the structure and species assemblages of formerly fire-adapted landscapes via infilling of canopy gaps by shade tolerant species (Minnich et al. 1995, Allen et al. 2002, Fulé et al. 2003a). Conditions in many western forests now represent forest structure of assemblages adapted to infrequent, high-severity fire with multistoried canopies that promote fire crowning behavior as a result of fuel loading and development of understory ladder fuels (Agee 1998a, Allen et al. 2002). Recent fires in western forests may represent a returning of the system to historical patterns of fire size and severity following a century of fire interruption (Caprio et al. 1997, Marlon et al. 2012, Williams and Baker 2012a), or they may represent a new fire dynamic in which a legacies of fire exclusion are interacting with changing climatic conditions to produce fires uncharacteristic of those prior to Euro-American settlement (Seager et al. 2007, Seager and Vecchi 2010, Crimmins 2011, Garfin et al. 2013, Williams et al. 2013).

Forests of Madrean Sky Island systems are a microcosm of western forest types distributed along steep vertical gradients that mediate temperature and moisture regimes and maintain distinct species assemblages (Whittaker and Niering 1975, Van Devender and Spaulding 1979, McLaughlin 1993). The sky island region is expected to experience the ecological impacts of climate warming sooner than other parts of the west with similar forest ecosystems (Notaro et al. 2012, Garfin et al. 2013), providing an opportunity to observe changes to fire dynamics before they take effect in more northern forests. Historically, fire regimes were associated with ecological gradients. For example high frequency, low-severity fires were associated with pine and dry mixed-conifer forests, and lower frequency, higher-severity fires were associated with mesic mixed-conifer and subalpine forest types (Grissino-Mayer et al. 1995, Swetnam et al. 2001, Swetnam et al. 2009, Margolis and Balmat 2009).

In recent decades the region has been the locus of multiple large, mixed-severity fires, providing opportunities to compare current and historical fire regimes. Here we reconstruct the spatial, temporal, and severity patterns of fire at a landscape scale, spanning gradients of elevation and changing forest composition. The reconstruction covers a three century period of record in an area that subsequently experienced two large wildfires during the prolonged drought that began in the mid-1990s. We use the historical and contemporary fire record to examine whether there were differences in fire characteristics before and after fire exclusion including 1) frequency of isolated and spreading fires at landscape scale and within forest types; 2) associations between fire spread and climate conditions and periodic climate oscillations; and 3) fire size, spatial patterns, and proportion of low and high severity fire. These comparisons allow us to evaluate whether recent high-severity fires are within or outside the historical range of variability in terms of frequency, severity, and spatial extents.

Study area

The Pinaleño Mountains in southeast Arizona are the tallest of the Madrean Sky Island ranges, spanning a vertical gradient of more than 2,100 m from lowland desert at 1,150 m to spruce fir forest up to 3,268 m. Along this steep elevational gradient, the Pinaleño Mountains contain forest types representative of a latitudinal transect from Sonora Mexico to British Columbia Canada (Warshall 1995). Forests above 2,135 m are distributed along gradients of elevation and aspect (Figure 1). Lower forests are comprised of ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelmann), and several oak species (*Quercus spp.*) that transition to a dry mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirbel) Franco), southwestern white pine (*Pinus strobiformus* Engelmann), and ponderosa pine, with minor components of white fir (*Abies concolor* (Gor. & Glend.) Lindl. ex Hildebr.) and aspen (*Populus tremuloides*). Above 2,750 m mesic mixed-conifer forests are dominated by Douglas-fir and shade tolerant white fir with minor components of southwestern white pine, corkbark fir (*Abies lasiocarpa* var. *arizonica* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) (Martin and Fletcher 1943). At the highest elevations and along north-facing slopes, Engelmann spruce and corkbark fir are dominant species interspersed with occasional Douglas-fir. The Pinaleño Mountains contain the southernmost extent of spruce-fir forest in North America, and dense upper elevation forests serve as critical habitat for one endangered and several threatened wildlife species (Stromberg and Patten 1991, U.S. Fish and Wildlife Service 2004, Koprowski et al. 2005, Koprowski et al. 2006, Sanderson et al. 2009).

Disturbance history

Two fires in 1996 and 2004 burned a combined 14,160 ha in pine, mixed-conifer and spruce-fir forest, affecting 45% of the forested area above 2,135 m (USDA Forest Service 2013a). Prior to the 2004 fire, a series of insect outbreaks in the spruce-fir forest resulted in mortality of 83% of Engelmann spruce and 63% of corkbark fir greater than seven cm DBH (Lynch 2009, O'Connor 2013); this mortality, combined with the 2004 fire, resulted in a 66% reduction in the area occupied by spruce and corkbark fir (O'Connor et al. 2013). More than half of the area of these fires burned at moderate to high severity based on the relative difference normalized burn ratio (RdNBR); (Miller and Thode 2007, MTBS 2013). The only other contemporary fire in the Pinaleño Mountains of comparable extent to the recent events occurred in 1956; however no information is available on the fire severity of that event.

Prior to these recent fires, studies in two mixed-conifer and one spruce-fir site indicated that over the period 1575-1880 low-severity fire was frequent in parts of the mixed-conifer forest, occurring approximately every 4.2 years (Grissino-Mayer et al. 1995). No fire scars were found within the spruce-fir site and demographic evidence corroborated with fire scar dates from nearby mixed-conifer forest suggested that the spruce-fir site established after a stand-replacing fire in 1685 (Grissino-Mayer et al. 1995, Swetnam et al. 2009, Margolis et al. 2011). Grissino-Mayer et al. (1995) noted an abrupt decline in fire frequency in the mixed-conifer sites after 1880 and raised concerns that changes to forest structure and species could alter future fire behavior. This study expands upon earlier work with an unbiased, landscape-scale sampling of forest demography and fire history throughout the pine, dry and mesic mixed-conifer, and spruce-fir forests of the Pinaleño Mountains.

Methods

To reconstruct the spatial, temporal, and severity components of historical fire regimes in pine, dry and mesic mixed-conifer, and spruce-fir forest types, we used a systematic grid of 58 0.05-ha circular plots spaced one kilometer apart (Figure 1). A secondary grid of 15 supplemental plots offset 500 m northwest of fixed area plots was used to increase sampling resolution in and around the spruce-fir forest. Gridded sampling designs have been shown to more accurately capture spatial variability of simulated fire return intervals than random or stratified sampling designs (Parsons et al. 2007). Plot locations were determined through a GIS overlay in advance of field sampling. Two plots that included roads or other highly modified areas were relocated 50 meters in a direction away from the constructed feature. Increment cores or cross sections were collected from all trees, snags, and stumps 19.5 cm diameter at breast height (DBH) or larger. Trees between one and 19.4 cm DBH were sampled on a nested sub-plot equal to one third the area of the full plot (0.017 ha). Samples were taken within 20 cm of the soil surface whenever possible to minimize the need for sampling height correction of pith dates for tree age. In supplemental plots, cores or cross-sections were collected from the 10 spruce and 10 non-spruce trees nearest plot center with DBH greater than 15cm.

Fire-scarred material was collected from live trees, snags, and stumps within demography plots and while traveling among plots. All fire-scarred samples collected outside of demography plots were geo-referenced, and site characteristics were recorded and photographed. When appropriate, several samples from individual stumps and snags were collected to preserve as many fire dates as possible (Dieterich and Swetnam 1984). The original collections of Grissino-Mayer et al. (1995) were combined with the landscape-scale fire history reconstruction and coincide with four of the demography sampling locations.

Increment cores and cross-sections were mounted and sanded with progressively finer grits until the wood cell structure was observable. All samples were crossdated using a combination of visual pattern matching (Yamaguchi 1991), skeleton plots (Stokes and Smiley 1968), and statistical correlation analyses (Holmes 1983, Grissino-Mayer 2001a). On fire-scarred samples we recorded inner ring or pith date, year and season of fire (when determinable), outer year or bark date, and any scar of undetermined cause, and growth suppression or release dates. Scars of undetermined origin, injury-related growth suppressions, and outer ring dates corresponding to fire scars recorded within 500 m of a sample were recorded as fire dates; otherwise they were excluded from fire history analyses.

We used fire perimeter records from the Coronado National Forest fire atlas database for the period 1974-2008 (USDA Forest Service 2013a) and digitized the perimeter of the 1956 Nuttall fire from a hand drawn map from Forest historical archives. Fire perimeters prior to 1956 were reconstructed from the fire scar record.

Analysis

To differentiate ponderosa pine, dry mixed-conifer, mesic mixed-conifer and spruce-fir forest types we used the similarity of species assemblages, derived from “Importance Value” rankings (Taylor 2001). Importance values were calculated from the relative frequency and basal area of the six dominant conifer species in the year 1870 to account for changes to species composition, frequency, and basal area over the fire-interrupted period. Similarity of species assemblages, derived from the Importance

Value rankings, was used to perform a cluster analysis of plots. Douglas-fir was the most abundant species throughout all types of mixed-conifer forest, so Importance Values of pine species were double-weighted to enhance the differentiation between dry and mesic mixed conifer forest types. Hierarchical clustering was based on Ward's method of minimizing within-group variance among plots (Legendre and Legendre 1998) using the *hclust* package in the R statistical computing environment (R Core Team 2012). Prior to hierarchical clustering, the plot variable matrix was transformed to Jaccard distance to minimize the effect of zeros in the dataset on the clustering results (McCune et al. 2002). Demography plots without evidence of fire were grouped with nearest neighbors if fire history information was collected from at least three adjacent sides, or were otherwise excluded from the analysis (Supplemental Figure 1).

To observe patterns of fire spread, we used geo-referenced fire records composited at the site level. Fire dates recorded within 500 m of a plot center were ascribed to a single plot to allow direct comparison of discrete 1 km^2 spatial units (Dieterich 1980, Farris et al. 2010). A composite record of fire years from multiple samples over a discrete spatial unit produces a more complete record of fire occurrence because individual trees and samples are imperfect recorders of fire, and scars are sometimes eroded or burned off in subsequent events (Dieterich 1980, Dieterich and Swetnam 1984, Falk et al. 2011a, Farris et al. 2013). Compositing of fire records assumes topographic and ecological homogeneity within the specified scaling unit. While homogeneity at the kilometer scale cannot be assumed for all forest types and across the vertical gradient sampled in the Pinaleño Mountains, variability among one km^2 gridded cells was assumed to be greater than variability within cells. Compositing fire records by a standard spatial unit removes sampling bias generated by the natural aggregation of fire-recording sites and allows for an unbiased comparison of sites across a landscape (Farris et al. 2013).

Fire statistics by forest type

Initial fire scar formation requires a fire event of sufficient intensity to penetrate the bark and kill a section of the tree cambial layer (Gill 1974a). Once an exposed scar surface is formed, subsequent scar formation does not require a high-intensity fire because the cambial tissue near the original wound is no longer protected by thick insulating bark. For a site to record a low-severity fire, typically one or more trees already have an exposed scar-forming surface (Gutsell and Johnson 1996). We calculated fire frequency statistics for composited sites over the pre-fire exclusion period when 20% or more of sites were recording, and during the post fire-exclusion period after 1880. Individual analyses were performed for pine, dry mixed-conifer, mesic mixed-conifer and landscape-scale fire events. Mean and median fire intervals, Weibull median probability interval (WMPI), and minimum and maximum fire intervals were generated from the Fire History Analysis and Exploration System (FHAES) (Sutherland et al. 2013, Grissino-Mayer 2001b) for all fires, small fires recorded in up to 10% of sites, spreading fires recorded in 11 to 49% of sites and affecting one to two forest types, and landscape-scale fires recorded in 50% or more of sites and several forest types across the landscape. The Weibull model fitted to a frequency distribution of fire intervals has been shown to be a statistically more robust estimator of fire return interval in southwestern U.S. forests than mean interval values, because fire intervals tend to be right-skewed and include occasional extreme values (Grissino-Mayer 1999, Falk 2004). The standardized size of recording sites allows for a minimum spatial estimate of fire size based on the number of recording sites.

Climate associations with fire spread

Temporal relationships between drought conditions, ocean-atmospheric oscillations, and fires at the mountain range scale were identified with superposed epoch analysis (SEA) (Lough and Fritts 1987, Swetnam 1993). SEA tests for significant departures from the range of annual values in a continuous climate variable, in relation to a series of event years. In fire history analysis, values of a climate variable prior to and during individual fire years are compared with the distribution of values for the full time domain of the climate series. We tested the statistical significance of the fire year correlations to the climate variables with 1,000 bootstrapped random event years compared to actual event years (Holmes and Swetnam 1994). Fire size filters used for fire-climate analysis were the same fire classes used for analysis of fire statistics (small, spreading, landscape scale). Climate variables included reconstructed summer (June-August) Palmer Drought Severity Index (PDSI) for Southeast Arizona (Cook and Krusic 2004) and Niño3 index from Mexico and Texas (Cook et al. 2009) at annual lags of one to six years prior to a fire year. In the Southwest, drought in the spring and prior winter are correlated strongly with tree-ring reconstructed summer PDSI (St. George et al. 2010) which has been shown to influence fire probability during the Southwest pre-monsoon period (Baisan and Swetnam 1990, Swetnam and Baisan 1996a, Westerling et al. 2003). The Niño3 index is a tree-ring reconstructed proxy for the El Niño Southern Oscillation (ENSO) winter sea surface temperature in the Pacific Ocean (5^{o} N- 5^{o}S, 90^{o}-150^{o}W). A positive Niño3 index indicates warm sea surface temperatures associated with moist El Niño winter conditions in the Southwest U.S. and subsequent reduced likelihood of spreading fire. Conversely, a negative Niño3 index correlates with dry La Niña winter conditions in the Southwest U.S. and an increased likelihood of spreading fire (Swetnam and Betancourt 1990b, Diaz and Markgraf 2000, Margolis and Swetnam 2013, Swetnam and Betancourt 1990a).

To meet the statistical assumption of inter-annual independence for SEA analysis, we used an autoregressive model to remove year–to-year autocorrelation in PDSI and Niño3 index values (Heyerdahl et al. 2011, Margolis and Swetnam 2013). The autoregressive model residuals are a prewhitened version of the original index series that meets the statistical requirements for SEA analysis. There was no statistically significant differences in fire-climate relationships between raw and prewhitened climate indices. We compared fire-climate relationships in the pre-fire exclusion period (1640-1880) to the post fire-exclusion period (1881-2008) to determine changes as a result of fire exclusion and increasing mean temperatures.

Spatial reconstruction of fire size and severity

Fire severity terminology used in this study is based on degree of overstory tree mortality, in which low-severity fire is limited primarily to surface mortality of seedlings and shrubs, mixed-severity fire includes patches of canopy tree mortality but effects are primarily on surface vegetation, and high-severity fire describes complete or near complete mortality of canopy trees (Turner et al. 1999b). To reconstruct the size and severity of past fires we used a combination of composited fire-scar site locations (Iniguez et al. 2009, Farris et al. 2010) and demography plots (Margolis et al. 2007, Heyerdahl 1997, Heyerdahl et al. 2001, Brown and Wu 2005) (Supplemental Figure 2). The spatial extent of fire reconstructions was determined by applying a 750 m buffer to the grid of demography plots to generate a continuous fire reconstruction surface between spatially discrete composited fire records (Hessl et al. 2007, Swetnam et al. 2011). Interpolated surfaces of individual fire sizes and severities were based on inverse distance weighting of four nearest point locations with a power function of 2 and a raster cell size of 30 m (ESRI Inc. 2012).

Patterns of fire spread were examined by reconstructing the spatial pattern of fire frequency for spreading and landscape scale fires during the pre-settlement and post-settlement periods. Fire frequency was calculated for each composited plot by dividing the sum of fire events in an analysis period by the number of years in the respective period. A fire frequency surface was then interpolated over the sampled area to identify patterns of fire frequency in relation to forest types, landscape features, and period of analysis. Prior to 1955, fire perimeters were estimated by interpolating the area covered by the gridded sampling network. Fires after 1955 were mapped from fire atlas data.

To reconstruct severity of historical fires, a combination of fire scar, tree establishment dates, and tree death dates were combined into composited fire records. Composited point locations were coded as “No Data” until they began recording fire. Individual fire events were coded at point locations as “0” for no fire record, “1” for fire scar, indicating low to moderate-severity fire (Swetnam and Baisan 1996), and “2” for high severity fire. High-severity fire events were determined by demographic evidence of a recruitment pulse (Margolis et al. 2007) of four or more trees over a 20-year period without evidence of fire scar formation within a demography plot (adapted for 0.05 ha plots from Heyerdahl et al. 2011). A 20-year window of recruitment began with evidence of fire-caused tree death dates or the formation of fire scars in surrounding plots. We estimated the size of historical high-severity burn patches by reclassifying raster values of the interpolated reconstructed fire surface generated from coded composite point locations. Raster values greater than 1.7 were classified as high burn severity, 1.2-1.7 moderate severity, 0.3- 1.2 low severity and less than 0.3 as no fire. The size of high-severity patches in the 1996 and 2004 fires were determined from the RdNBR (MTBS 2013) reclassified to low, moderate, and high severity based on thresholds determined by Miller and Thode (2007) for dry inland forests. Plots classified as moderate and high-severity fire were verified by tree survivorship in the field. Sizes of moderate and high-severity patches prior to 1984 were reconstructed based on the coded composite point location method.

Results

Spatial and temporal reconstructions of historical fires were based on 1,201 crossdated fire scars collected from 146 trees at 130 fire recording locations, and 1,222 tree establishment dates from 2,178 crossdated samples. We identified 231 unique fire years over the period 1374-2008, but limited the spatial reconstruction of fires to the period 1640-2008 when 20% or more of sites were recording.

Fire at forest type and landscape-scales

At broad scales fire frequency varied little across pine and mixed-conifer forests prior to 1880 (Table 1A). Within the study area, small fires on the order of 100-200 hectares occurred every 3-4 years in pine, dry mixed-conifer and mesic mixed-conifer forest types. Spreading fires affecting two or more forest types averaged every 9-11 years. Larger landscape-scale fires were recorded most frequently in continuous dry-mixed conifer forest, somewhat less frequent in pine-dominated forest, and least frequently in mesic mixed-conifer forest.

In contrast to landscape trends, the majority of fires in pine forests were small, recorded in one or two sites (Table 1A). Larger fires occurred five to ten times less frequently than small fires. Spreading fires were more common in dry mixed-conifer forest where 61% of all fires were recorded in two or more sites and site connectivity was greater. In the mesic mixed-conifer ecosystem, fire return intervals were longer, but as in the dry mixed-conifer, most fires spread among multiple sites Proximity to other forest types influenced fire intervals in mesic mixed-conifer forest. Sites abutting dry forest recorded fire at 1-18 year intervals, whereas sites bordering on spruce-fir forest recorded fire infrequently at intervals of up to 44 years. Within the upper elevation spruce-fir forest, 10 sites had no evidence of fire scars but had strong demographic evidence of stand replacing fire in 1685.

After 1880 small fires continued to occur but fire return intervals began to shift significantly (Table 1B). Weibull median probability intervals were significantly more variable (*t*-test for difference in variance of the interval distributions, $p < 0.01$) and both small and spreading fire intervals increased significantly (*t*-test for difference in MFI assuming unequal variance, $p < 0.02$) compared to the pre-fire exclusion period. Small fires continued to affect pine and dry mixed-conifer sites at 6-8 year intervals but spreading fire was rare. Although half of all fires were recorded in more than one site, only 5% of fires were recorded in more than one forest type. No fires were recorded in pine, dry, and mesic mixed-conifer forest in the study area after 1863 (Table 1B). Within individual forest types, fire return intervals of spreading fires more than doubled, and consequently for some areas there were not enough spreading fires to calculate median probability intervals. At the landscape scale, the median interval between spreading fires increased four-fold and maximum fire-free intervals at individual sites surpassed 85 years.

The proportion of fires recorded in only a single site (<100 ha) increased from 4% prior to 1880, to 44% after 1880 (Table 2). Fires recorded in fewer than six sites (<600 ha) comprised 78% of all fires prior to Euro-American settlement and 94% of fires after settlement. The proportion of spreading fires decreased by more than two-fold after 1880 and no fires affecting more than 2,200 ha (50% of sites) of the reconstructed area were recorded after 1880.

Fire dates spanned the period from 1403-2004, with fire recorded in a single site in 1403 and a peak of 86% of sites recording by the year 1870. Our period of fire analysis began in 1640 when 20% of sites had recorded at least one fire (Figure 2a). The 10 mesic spruce-fir sites comprising 19% of the study plots had no fire-scars recorded over the study period. Fires affecting two or more sites were common over the period 1640 to 1880, but became less frequent in the 20th century when the average interval between small fires doubled and landscape-scale fires ceased (Figure 2b and c). After 1880 five fires were recorded in 10% or more of sites, and three fires affected two or more forest types. The 2004 fire was largest in 140 years and left little fire-scar evidence but was recorded in tree death dates and establishment of many aspen stems.

High-severity fire in 1685 was evident at several sites where fire was not recorded prior to 1700 (Figure 2B), indicating that the 1685 fire was stand replacing in several sites that subsequently recorded several lower severity fires. This is corroborated by demographic records from twelve sites indicating a pulse of seedling recruitment shortly after 1685 (O'Connor 2013). Five other fire dates had demographic evidence of mixed-severity fire in 1748 (1 site), 1773 (1 site), 1785 (2 sites), 1801 (1 site) and 1974 (2 sites); however, the higher severity components of these mixed fire years affected only 5-10% of the landscape and retained some living fire scarred overstory trees.

Fire and climate relationships at landscape and local scales

Regional drought and cool phase La Niña events were both significantly associated with spreading and landscape-scale fires prior to 1880 (Figure 3a-d). Smaller fires (not shown) were associated with moderate drought years but were not significantly correlated with PDSI or ENSO over this period. Spreading fires were more strongly associated with prior wet conditions, which probably indicate the importance of fuel limitations in dry forests (Swetnam and Baisan 1996b)(Figure 3a). Landscape scale fires were associated with extreme winter and spring drought the year of fire and a weaker pattern of antecedent wet conditions up to five years prior to the fire (Figure 3b). Spreading fires were consistently associated with the first year of strong sea surface cooling (La Niña conditions) following a prolonged 3-5 year period of warm-phase El Niño conditions (Figure 3c and 3d).

Similar to conditions prior to fire exclusion, small fires during the period 1881-2008 were associated with moderate drought but were not significantly correlated with PDSI or the Niño3 index (data not shown). Spreading fires were significantly correlated with drought the year of fire and persistent drought 1-2 years prior to fire (Figure 3e), but were not associated with prior wet conditions. Spreading fires after 1880 were not consistently associated with La Niña events in contrast to stronger associations that prevailed prior to 1880 (Figure 3f).

The two landscape fires that burned into and across spruce-fir areas in 1685 and 2004 occurred during very dissimilar drought and ENSO conditions (Figure 4). Conditions prior to and during the 1685 fire were similar to, but were extreme examples of, conditions associated with 10 other widespread landscape fires prior to 1880. The winter and spring drought in 1685 was the most severe in the more than 400-year period from 1586-2008 (PDSI -4.2) and followed a four-year pluvial period. The Niño3 index indicates that 1685 was the eighth strongest La Niña event (Niño3 index -1.6) in the past 400 years. In contrast, the 2004 fire occurred after a persistent drought during a warm phase El Niño event. The drought preceding the 2004 fire was the fifth most severe persistent drought (3-year mean of PDSI -3.1) during the period of reconstruction and the only persistent drought associated with wide-spread high-severity fire. The 2004 fire was the only spreading fire in the reconstructed period recorded during an El Niño event (in this case, a relatively weak event, i.e., Niño3 index 0.6).

Spatial reconstruction of fire

We reconstructed fire occurrence from fire-scar evidence in 43 plots and from demographic evidence in an additional 10 plots. Composite fire scar records averaged 5.2 fire-recording trees per plot (range 2 to 35 trees). Comparisons of relative fire sizes before and after the availability of 20th century fire maps were limited to the 6,470 hectare area that could be reconstructed from fire scar and demography plot evidence of fire.

Fire frequency and spatial distributions varied considerably before and after 1880 (Figure 5). Prior to 1880, the predominately southwest-facing pine and dry mixed-conifer sites recorded the most fire, forming a nearly contiguous corridor of fire spreading at 5-7 year intervals with a range of 1-11 years between fires (Table 1A) along the central plateau of the range (Figure 5a). Mesic drainages and mixed-conifer stands abutting the spruce-fir forest served as barriers to fire spread in the majority of fire years. Of 104 spreading fires over the 240 year period, only the 1685 fire breached these mesic mixed-conifer forests and burned into the spruce-fir zone. After 1880, fire frequency over the majority of the mountain range more closely resembled that of the mesic mixed-conifer and spruce-fir forest prior to 1880 (Figure 5b). Fire extent was no longer contiguous along the central plateau of the range, although fires continued to burn at lower frequency in predominately northwestern dry mixed-conifer and pine sites. Sites that sustained fire at 2-10 year intervals along the central and southeastern parts of the range prior to 1880 were affected by a maximum of two fires in the past 130 years, and nearly half of the pine and dry mixed-conifer forest experienced no fire after 1900.

From 1640 to 2008, 11 fires each burned more than 50% of the study area, affecting most of the pine and dry mixed-conifer sites and occasionally burning into mesic mixed-conifer and the edge of the spruce-fir zone (Supplemental Figure 3). These large fires appear to have spread from the southeast to northwest, burning across dry forests along south-facing aspects, assuming spread from sites with the highest number of recorded fires. A somewhat isolated pine forest on West Peak, on the northwest end of the range, rarely burned in large, widespread fires but burned frequently in smaller local fires, and these events were generally asynchronous with the rest of the pine and mixed-conifer forest on the main portion of the mountain range (Supplemental Figure 3).

The spatial footprint of the 1685 fire was similar to that of other spreading fires with the exception of the large high-severity patch in the spruce-fir and surround high-elevation mesic mixed-conifer forest (Figure 6a). The 1685 fire is recorded in fire scars as a low to moderate-severity event in pine and dry mixed-conifer forest types, and as a distinct pulse of seedling establishment in spruce-fir and adjoining mesic mixed-conifer forest, indicating stand-replacing severity (O'Connor 2013). Several small clusters of Douglas-fir trees dispersed throughout the spruce-fir forest survived the 1685 fire, but no sampled spruce or corkbark-fir predated the event. The extent of high-severity fire in 1685 fire was approximately 2,500-2,700 hectares within the reconstructed area, including the entire sampled area of the spruce-fir forest as well as 12 sites in the adjoining mesic and dry mixed-conifer forest. Sampling resolution limited our ability to reconstruct patchiness within the high-severity fire extent. Substantial growth suppression of seedlings establishing after 1765 indicated closed canopy conditions within 65 years of the fire. Canopy closure over this time interval suggests that the distance to seed sources was relatively short following the 1685 fire and that patches of mature surviving spruce and corkbark fir were distributed throughout parts of the high-severity burn area.

The proportion of total area burned that was classified as high-severity in 1685 is roughly comparable to that of the 1996 Clark Peak fire and the 2004 Nuttall Complex fire

(40, 23, and 47%, respectively). However, the spatial distribution of high burn severity was not consistent between historical and contemporary fires. High-severity burn patches in recent fires extend into dry and mesic mixed-conifer forest much farther than in the 1685 fire (Figure 6b). The lack of transition zone from high to moderate to low fire severity is indicative of fire-fighting efforts. For example, the large high-severity patch along the southeastern mesic mixed-conifer and spruce-fir zone was contained by fire line in 2004 (USFS 2004). The proximity of the fire break to additional mesic and dry mixed-conifer forest suggests that high-severity fire would have continued, likely burning an area equivalent to or larger than that in 1685 and with equal or higher severity.

Ecological effects of the 1996 and 2004 fires appear to have been more severe than in the 1685 fire. Within the perimeter of the 2004 fire, several Douglas-fir snags were found that died in the 2004 event but that had establishment dates 20-50 years prior to 1685. In addition, a site hosting the oldest known Douglas-fir snags on the mountain, undamaged by more than 800 years of fires (Grissino-Mayer and Fritts 1995), was incinerated during the 1996 fire (C. Baisan, personal communication), and the oldest known living Douglas-fir died shortly after 1996 from root damage sustaining during the fire (T. Swetnam, personal communication).

Discussion

Prior to fire exclusion, small and widespread fires followed regular patterns of size, frequency, distribution, severity, and climate associations. Under all but the most extreme drought conditions, fire frequently burned across pine and mixed-conifer forests at low to moderate severity but was excluded from the higher elevation mesic spruce-fir forest. The consistency of fire return intervals across vegetation types and strong fire-climate associations suggest that forest conditions and fire regimes were relatively stable for at least several centuries prior to 1880. Following Euro-American settlement, fire frequency and spread were altered substantially. Through the first half of the 20th century, small fires continued to burn at individual sites but spreading fires ceased. Fire-adapted pine and dry mixed-conifer forests of the Pinaleño Mountains would have been the most immediately affected by interruption of ground fires beginning in the late 1870s by livestock grazing, road construction, and logging activities (Bahre 1998). Spreading fires were completely absent for 70 years before returning to parts of the dry and mesic mixed-conifer forest at lower frequency and smaller size than in the past. Patterns of fire size and frequency were no longer distinct between pine, dry, and mesic mixed-conifer forests. The fuel-limited corridor of pine and dry-mixed conifer forest that experienced frequent fire along the south-facing plateau of the range, began to accumulate fuels (both living and dead trees) over more than 70 years without fire (O'Connor et al. In prep). Accumulated fuels and increased canopy connectivity during the 20th century removed what was essentially a "fuel-break" at the middle elevations, in terms of relatively open forests that promoted surface fires that could rarely ladder up into canopies, thereby limiting fire spread into the more mesic, higher elevation forests prior to Euro-American settlement (Swetnam et al. 2009).

Fire-climatology

Along steep ecological gradients, fire-climate interactions in the Pinaleño Mountains prior to 1880 were a microcosm of those across western forest types. Swetnam and Baisan (1996) identified a pattern of wetter than average conditions prior to years with widespread fire that is thought to have increased fine fuels and connectivity in fuel-limited systems. Several studies in other pine and dry mixed-conifer forests throughout the Southwest, including in this study prior to fire exclusion, identified similar patterns (Touchan et al. 1996, Brown and Shepperd 2001, Brown and Wu 2005, Margolis and Balmat 2009). In the Santa Fe Watershed in New Mexico, Margolis and Balmat (2009) found that frequent spreading fires in pine-dominated stands adjoining mixed-conifer forest appeared to be fuel limited as well, and occurred consistently during moderate drought only after two or more years of wet conditions. In the present study, spreading fires in adjoining mixed-conifer forest did not show evidence of fuel-limitation and were instead associated with more severe drought prior to the fire season. Fires in upper elevation mesic forests were also associated with extreme drought that would have overcome moisture- and temperature-driven limits to fire spread. A similar pattern of severe drought-driven spreading fires was noted in several upper-elevation forests of Arizona and New Mexico (Margolis and Swetnam 2013).

The 26% reduction in return intervals of small fires and cessation of spreading fires shortly after 1880 reflects the coincidence of early fire exclusion with a multidecadal switch from relatively dry to moist conditions throughout the region around 1900 that lasted approximately 40 years (Biondi et al. 2011, Griffin et al. 2013). Cessation of spreading fires was further aided by active fire suppression after ~1910, although the effectiveness of fire suppression is difficult to separate from the effects of livestock grazing and other land-uses in the “Sky Islands” during early decades of the 20th century. Additionally, the reduction in spreading fires would have affected the fire scar record, increasing the relative proportion of small fires more easily missed in the sampled fire scar network. After more than 70 years without spreading fires, a shift back to dryer climate conditions in the 1990s coupled with increased stand densities and accumulated fuels initiated the return of spreading fire to parts of the pine and dry mixed-conifer ecosystems. Spreading fires after 1950 occurred during periods of persistent drought with no consistent association with antecedent wet conditions.

The shift toward fires associated only with persistent drought suggests that the legacy of fire suppression (i.e., high fuel accumulations in dry forests) removed the fuel-limiting distinction between dry and mesic forest types (Margolis and Balmat 2009, Margolis and Swetnam 2013). Changes to the structure and species composition of dry mixed-conifer forest during the long fire-free interval (O'Connor et al. In prep) provide further support for the idea that former dry mixed-conifer forests now share structural and species characteristics with more mesic forest types that historically experienced mixed to high-severity fire regimes).

Climate conditions associated with recent spreading fires suggests that the drought threshold enabling fire to spread into mesic mixed-conifer and spruce-fir forest types has decreased as a result of an extended period of fire exclusion and consequent fuel accumulation. Drought conditions during the 1996 and 2004 fires were more similar to the conditions associated with the 10 widespread fires that burned around mesic forests in the reconstructed period. Multi-year drought conditions more severe than those in 2004 occurred five times in the reconstructed period prior to 1995, but did not result in fire spread to the spruce-fir forest.

The 2004 fire was unique in the fire record as the only spreading fire to occur during El Niño conditions. Warmer than average winter and spring temperatures accelerated snow melt (Koprowski et al. 2013) and may have resulted in earlier onset of fire weather conditions than would typically occur during El Niño years with above-average snow accumulation. Swetnam and Betancourt (1990a) noted a weakening of the relationship between the Southern Oscillation and area burned after the mid-1960s, and additional weakening through the mid-1980s, potentially indicating a shift away from past fire-ENSO relationships in the Southwest that could be accelerated with warmer winter conditions. At centennial timescales, fire-climate associations are known to fluctuate depending on decadal and longer scale temperature and moisture conditions (Grissino-Mayer and Swetnam 2000). The later part of the 20th century may represent such a change, as warming winter temperatures coupled with a shift from positive to negative Pacific Decadal Oscillation (PDO) in the late 1990s led to enhanced La Niña and dampened El Niño conditions contributing to persistent drought conditions across the American Southwest (Hoerling and Kumar 2003, Crimmins 2011). This is further supported by Yocom et al. (2010), who identified a recent switch from La Niña- to El Niño-associated fires in northern Mexico. These fires were also associated with anomalously warm temperatures during the shift in PDO. It would be worth exploring the relationship between ocean-atmosphere teleconnections and other large southwestern fires over the past several decades of warming temperatures to determine if fires during El Niño conditions are becoming more common as mean winter temperatures continue to increase.

Changes to fire severity

Prior to 1880, high-severity fire was rare, affecting less than 10% of burned area under all but the most extreme climate conditions. Fires in 1996 and 2004 were associated with moderate drought, but the proportion of area burned at high severity was two to four times that of most previous landscape-scale fires, even with extensive efforts to contain and suppress fire spread. The only event in the historical reconstruction with severity similar to the 2004 fire took place during the most extreme drought conditions in 400 years.

The ecological effects of recent fires appear to be more severe than those of any fire in the reconstructed period. This conclusion is supported by observations of tree mortality, fire scar formation, and post-fire recovery. Within the high-severity burn perimeter of the 2004 fire, most Douglas-fir trees that survived the fire in 1685 were killed in 2004 when the protective bark on these old trees would have been much thicker and canopy base heights much higher than in their previous encounter with fire. Fire scar evidence of the 1685 fire is well recorded along the high-severity burn perimeter, whereas fire scars recorded within or near the perimeter of the 2004 fire were rare. High tree mortality in the 2004 fire was responsible for the reduction in fire scar formation over much of the burned area, although for surviving trees, the 140-year fire free period would have increased tree size and bark thickness, reducing the probability of scar formation on those trees (Gill 1974). The rapid rate of recolonization of the spruce-fir zone following the 1685 fire (O'Connor et al. In prep), and evidence of canopy closure as early as the 1750s, indicate a mosaic of high and mixed fire severities that left a significant number of mature trees to serve as seed sources. Although no spruce or corkbark fir predating 1685 were found to confirm mixed fire severity, rapid seedling establishment suggests that seed sources were available. Surviving mature spruce and corkbark fir would most likely have died over the more than 300 years of subsequent spruce-beetle and western balsam bark beetle outbreaks recorded in this forest (O’Connor 2013). Within the perimeter of the 2004 fire, surviving trees in high severity areas are isolated to the outer margins, small groups of Douglas-fir along ridges, and spruce and corkbark fir in and around perennial springs. The majority of the area within high severity burned areas of the 2004 fire remains barren with extremely limited seedling establishment nine years after the event (Figure 7). In addition, where recent fires spread into dry and mesic forests, severity was higher than in any recorded fires during the period of reconstruction.

High tree mortality in recent fires is likely related to a combination of several factors. Increased stem densities and a shift toward fire-intolerant species promoted crown-fire in mixed-conifer forest surrounding the spruce-fir zone. Extended drought and the warmest winter and summer temperatures in more than a century increased tree drought stress and cured accumulated standing and downed fuels. The use of chemical accelerants during aggressive back-burning of fire lines consumed living trees and snags that had withstood centuries of past fires (USDA Forest Service 2004, Frye 1996). These firefighting tactics likely limited the size of high-severity burn patches by stopping the spread of fire while increasing the severity of fire in forests abutting fire lines. Finally, in the case of the 2004 fire, a preceding decade of compounded insect disturbances left 83% of the mature spruce and 63% of mature corkbark fir as standing snags with abundant fine fuels (O'Connor et al. 2013).

Management implications

Differences in fire severity and spread before and after 1880 are attributable to changes to forest structure and fuels as a result of management activities, decadal to multi-decadal climate variability, and a series of recent native and exotic insect outbreaks. Recent fires have had mixed effects on risk of future high-severity fires. In parts of the mesic mixed-conifer and spruce-fir forests, fire risk has been reduced because a significant proportion of available fuels have already been consumed. However over the majority of the area, fire suppression efforts preserved heavy surface fuels and dense canopy structure. Continuing efforts to suppress fires maintains these heavy fuel loads and heightens the risk of future high-severity fire, much like what has been observed in mesic and dry-mixed conifer forests in many areas of the western United States (Stephens et al. 2013).

Following high-severity fire in spruce-fir and mesic mixed conifer forest, recovery of the historical species composition remains uncertain. Distance to seed sources and degradation of soil substrates hinder the establishment of seedlings, and warming, drying conditions may make parts of the former spruce-fir forest no longer suitable for the species assemblage (Notaro et al. 2012). Efforts to re-establish spruce-fir seedlings through planting and to discourage encroachment by shrubs and other lower elevation species may be warranted (Stephens et al. 2013). Although there is little precedent for fire-induced conversion of spruce-fir to mixed-conifer forest, in nearby pine-oak communities, intense wildfire following fire-suppression has been shown to alter the long-term trajectory of post-fire species composition and structure for at least the next several decades to centuries (Barton 2002).

In historically fire-adapted dry forests, initial thinning of the understory and selective removal of encroaching non-fire-adapted species, followed by reintroduction of fire provides the best opportunity for restoring fire resilience to a system expected to experience more frequent fire under warming, drying conditions in the American Southwest (Hurteau et al. 2013, USDA Forest Service 2010). Breaking fuel continuity of dry forests would restore the buffer limiting fire spread from dry to wetter forests above them. Furthermore, allowing frequent low and mixed severity fires to burn across dry forests would maintain low fuel loadings without threatening higher elevation mesic stands. Returning heterogeneity of forest structure and fire frequency would provide protection to research infrastructure located in the spruce-fir forest and preserve habitat for the majority of threatened and endangered species in the Pinaleño Mountains that are dependent on dense cover in mesic forests for protection from predation and abundant food sources (Sanderson et al. 2009).

Conclusions

Large high-severity fire patches in the Pinaleño Mountains were rare and limited to only the most mesic, productive sites prior to fire exclusion. Interruption of spreading fires in the late 1800s led to changes in forest structure and species composition (O'Connor et al. In prep) that altered future fire behavior and fire-climate associations. More recent shifts in decadal to multidecadal climate modes coupled with warming temperatures may have accelerated changes in fire-climate relationships by lengthening the fire season and decoupling the effects of winter precipitation on reduced fire spread. Conditions during recent fires suggest that the drought thresholds necessary for fire to spread across multiple forest types have been reduced as a result of fuel accumulation and positive feedbacks from warming temperatures. Similar relationships have been identified in other western forests where the trend of increasing winter and spring temperatures is contributing to earlier snow melt and longer spring fire-weather conditions (Pederson et al. 2011). Over the past four years, record-setting fires in New Mexico, Arizona, and California are in line with the predictions of more frequent and larger fires in a warming, drying southwest (Attiwill and Binkley 2013). Fire-climate relationships appear to be changing; whether ecological communities can adapt to these new conditions remains to be seen.

Aggressive efforts to restore resilience to dry forests of the Southwest with thinning to reduce excessive fuel loads, followed by reintroduction of fire in the form of controlled burns and eventual wildfire use, may be the best option for retaining mature forests capable of adapting to future climate conditions (USDA Forest Service 2010, Stephens et al. 2013). Without restoration, inland forests of the western States are likely to continue to burn with increasing fire size and severity, with increased risk to human interests and sensitive species adapted to specific site conditions, such as the Mount Graham red squirrel. Restoring historical forest structure and fire regimes has been successful where it has been attempted (Hurteau and North 2008, Fulé et al. 2004, Fulé et al. 2001, Mast et al. 1999). Identifying and prioritizing restoration efforts to include landscapes like the Pinaleño Mountains where they are likely to produce the greatest benefit to natural and human interests will be key to successful landscape management in the future.

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Tables

Table 1. Fire interval statistics 1640-1880 and 1881-2008 by forest type. Statistics are from 241 fire-scarred trees on 43 1-km^2 composited sites. WMPI is Weibull Median Probability Interval.

A.

	Fire Statistics 1640 to 1880									
	Pine-dominated (11 sites)					Dry mixed-conifer (20 sites)				
	N	Mean FI	Median FI	WMPI	Min/Max FI	N	Mean FI	Median FI	WMPI	Min/Max FI
All Fires	97	2.4	2	2.1	1/11	98	2.4	2	2.0	1/11
Small	47	4.9	4	4.1	1/18	60	3.9	3	3.4	1/12
Spreading	20	10.8	12	10.3	3/21	24	9.3	10	9.0	3/18
Landscape	12	18.0	17	17.2	4/34	20	10.8	12	10.5	3/20
	Mesic mixed-conifer (12 sites)					All forests (43 sites)				
	N	Mean FI	Median FI	WMPI	Min/Max FI	N	Mean FI	Median FI	WMPI	Min/Max FI
All Fires	56	4.1	3	3.4	1/18	141	1.7	1	1.5	1/11
Small	34	6.8	5	5.9	1/21	104	2.2	2	2.0	1/11
Spreading	18	11.9	11	10.4	2/32	20	10.8	11	10.5	4/20
Landscape	9	23.9	24	21.6	4/44	11	19.6	16	18.6	8/44

B.

	Fire Statistics 1881 to 2008									
	Pine-dominated					Dry mixed-conifer				
	N	Mean FI	Median FI	WMPI	Min/Max FI	N	Mean FI	Median FI	WMPI	Min/Max FI
All Fires	25	4.6	4	3.9	1/15	28	4.3	2	3.0	1/27
Small	7	10.3	4	6.2	1/35	9	12.3	6	8.3	1/40
Spreading	1	*	*	*	*	1	*	*	*	*
Landscape	1	*	*	*	*	0	*	*	*	*
	Mesic mixed-conifer					All forests				
	N	Mean FI	Median FI	WMPI	Min/Max FI	N	Mean FI	Median FI	WMPI	Min/Max FI
All Fires	20	5.9	5	5.1	2/17	54	2.3	1	2.0	1/8
Small	2	*	*	*	*	27	4.6	3	3.3	1/25
Spreading	1	*	*	*	*	3	45.7	40	39.9	8/85
Landscape	0	*	*	*	*	0	*	*	*	*

* denotes not enough events to calculate fire statistics.

Table 2. Approximate size and count of reconstructed fire events 1640-2008.

Classification	Sites recording	Proportion of sites	Approximate size	Count of fires	% fire years
1640-1880					
Single site	1	≤ 2%	<100 ha	8	4%
Small	2-5	3-10%	100-500 ha	104	74%
Spreading	6-21	11-49%	600-2,100 ha	20	14%
Landscape	≥ 22	≥ 50%	> 2,200 ha	11	8%
1881-2008					
Single site	1	≤ 2%	<100 ha	24	44%
Small	2-5	3-10%	100-500 ha	27	50%
Spreading	6-21	11-49%	600-2,100 ha	3	6%
Landscape	≥ 22	≥ 50%	> 2,200 ha	0	0%

Figures

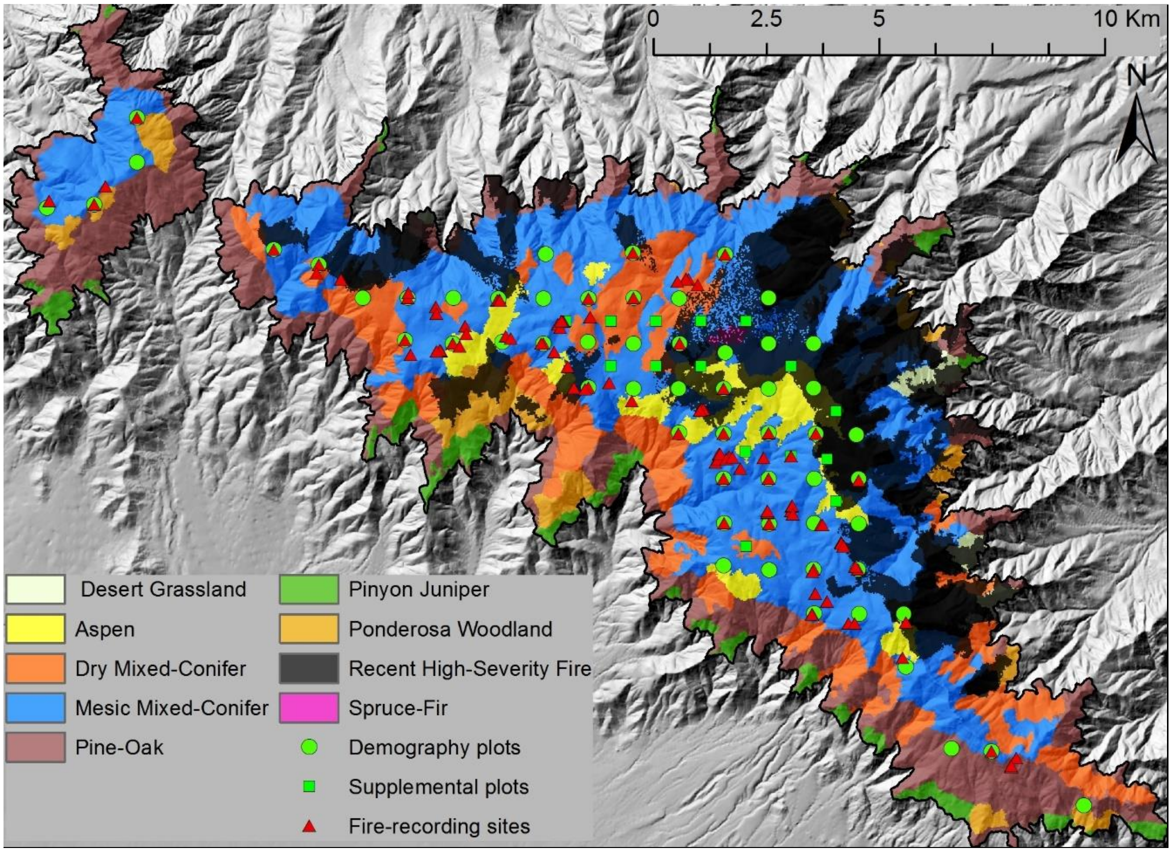


Figure 3. Pinaleño Mountain forest types and sampling locations. Colored area denotes elevation above 2,135 m. Distributions of forest types are from LANDFIRE rapid refresh 2008 (LANDFIRE 2012). High-severity burn patches are calculated from the relative difference normalized burn ratio (MTBS 2013) categorized according to Miller and Thode (2007). All raster values are generalized to a minimum patch size of 6.75 hectares.

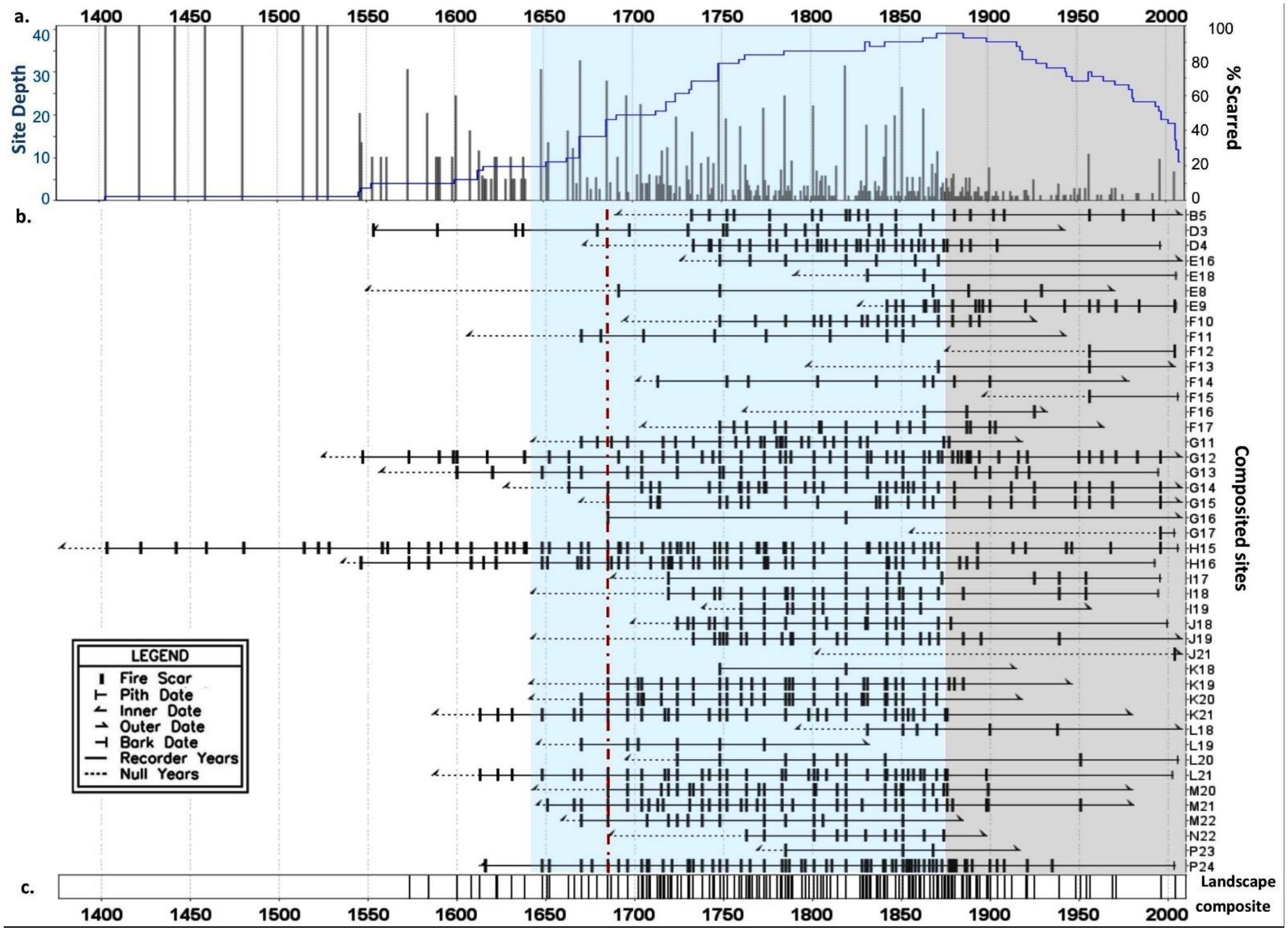


Figure 2. Landscape-scale fire history of the Pinaleño Mountains. Chart is based on 44 composited, 1-km^2 fire recording sites located above 2,135 m elevation. (a) Sample depth and percent of sites scarred. (b) Chronology of fires recorded at each composited site location; horizontal lines are time spans and vertical tick marks are fires recorded by all trees within each site. (c) The composite record depicts all fires events recorded in two or more sites. Periods of analysis from 1640-1880 and 1881-2008 are shaded in blue and gray, respectively. Stand replacing fire in 1685 is identified by a dashed red line. Sites are arranged along a spatial continuum from northwest (top) to southeast (bottom).

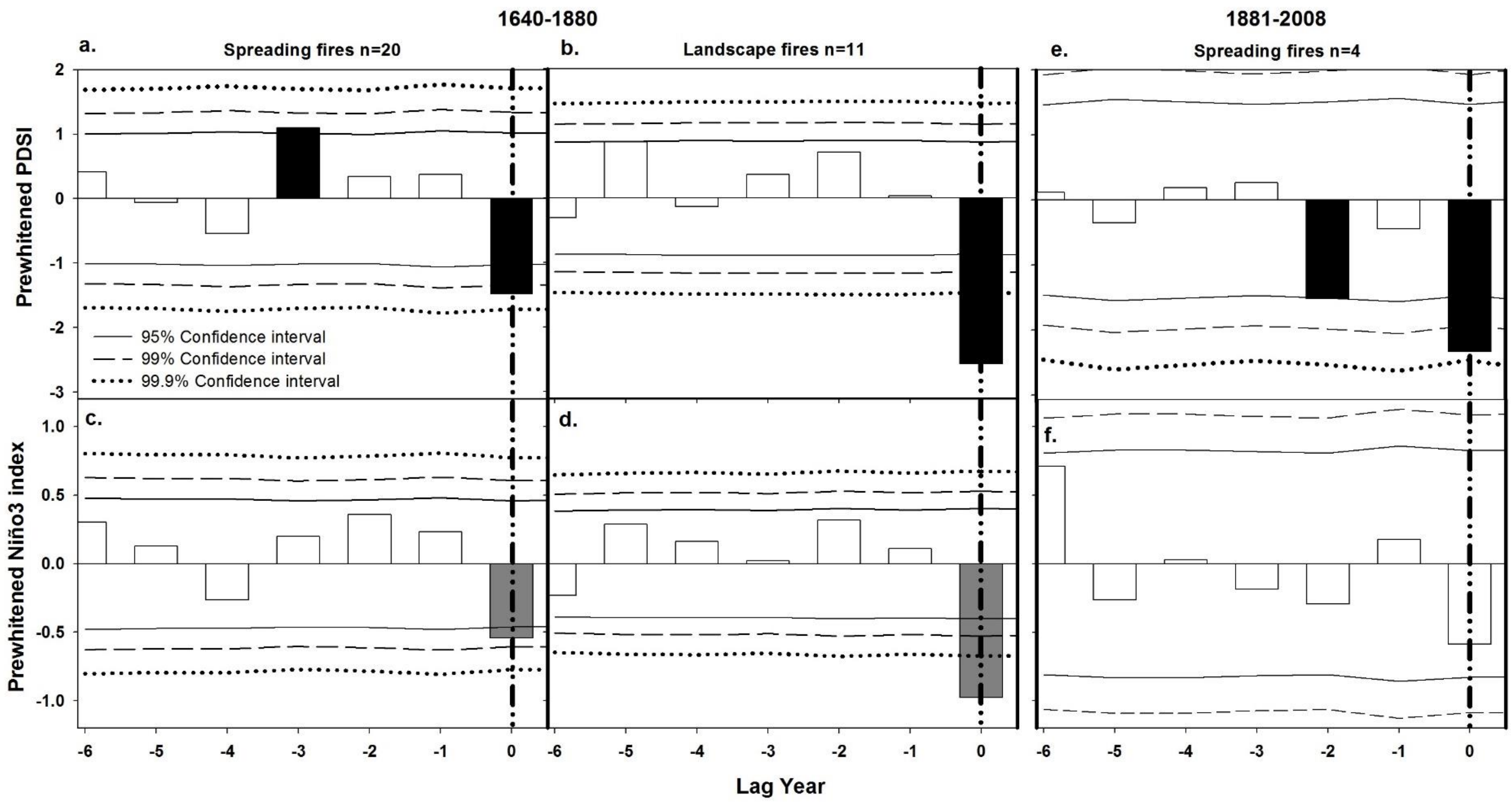


Figure 3. Fire-climate associations for spreading fires 1640-1880 and 1881-2008. Fires are reconstructed from 43 1-km^2 composited fire-recording sites. Climate relationships are lagged up to six years; vertical dashed lines indicate year of fire. Colored bars indicate significant relationship surpassing the 95% confidence interval. Palmer Drought Severity Index (PDSI) and Niño3 index were prewhitened to remove inter-annual autocorrelation. Spreading fires are recorded in up to 49% of sites and two forest types (20 fires pre-1880, 4 fires post 1880). Landscape fires are recorded in more than half of sites and three or more forest types (11 fires). No landscape scale fires are recorded after 1863.

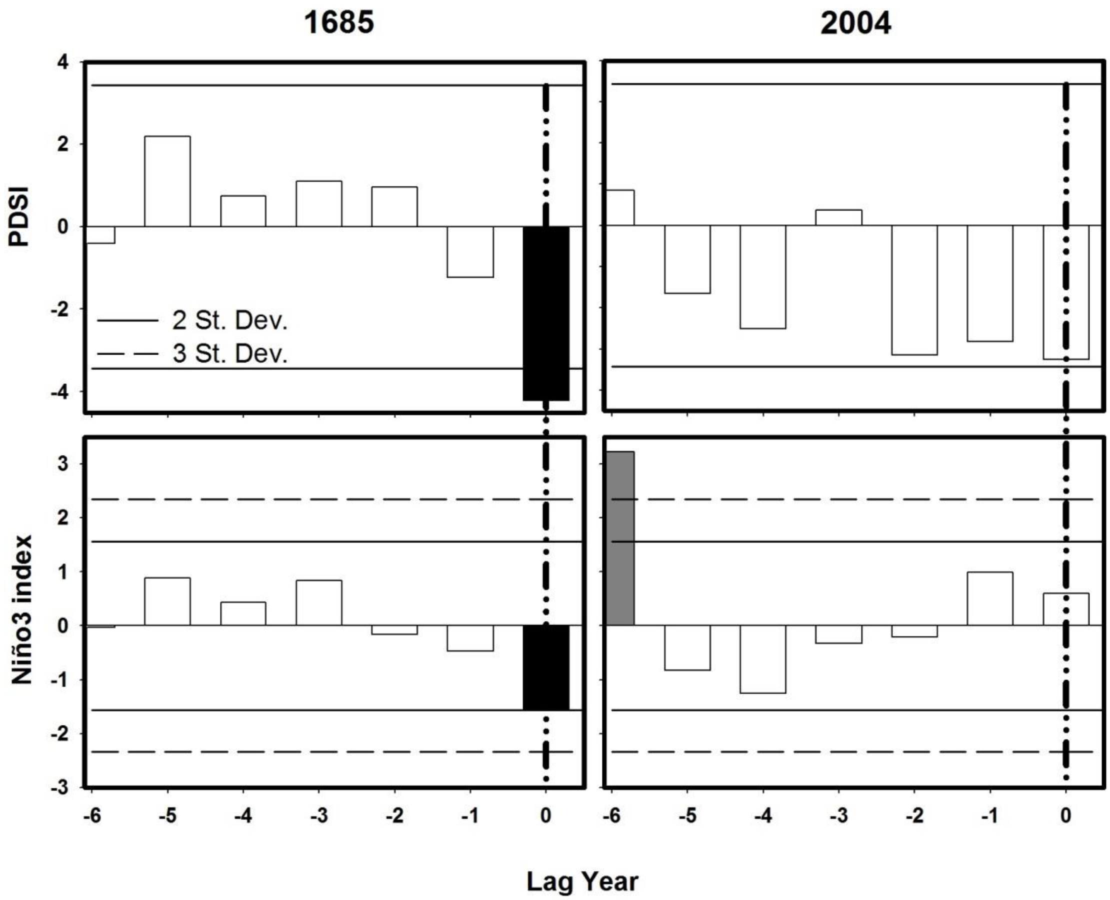


Figure 4. Drought and ENSO conditions before and during the two high-severity fires in the spruce-fir forest. Vertical dashed line indicates year of fire. Palmer Drought Severity Index (PDSI) and Nino3 index are raw series from (Cook and Krusic 2004) and (Cook et al. 2009) respectively. Reference lines are drawn for two and three standard deviations calculated over the period 1684-2006.

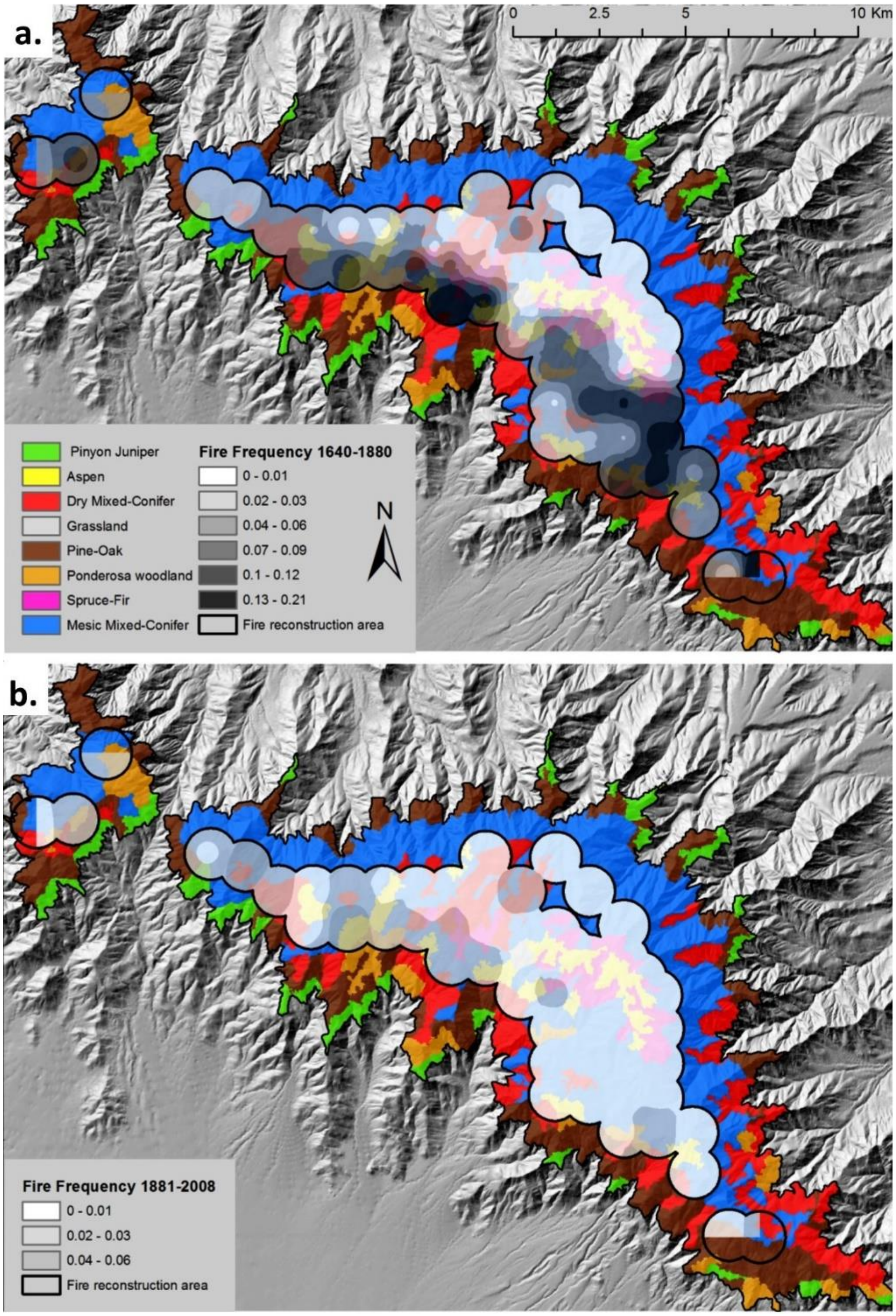


Figure 5. Spatial reconstruction of fire frequency 1640-1880 (a) and 1881-2008 (b). Fire frequency (fires yr^{-1}) surface is based on inverse distance weighting of 53 composited fire-recording sites using four nearest neighbors with a power factor of two. Fire frequency is calculated from fires recorded in two or more sites from 1640-1880 (n = 104) and 1881-2008 (n = 27).

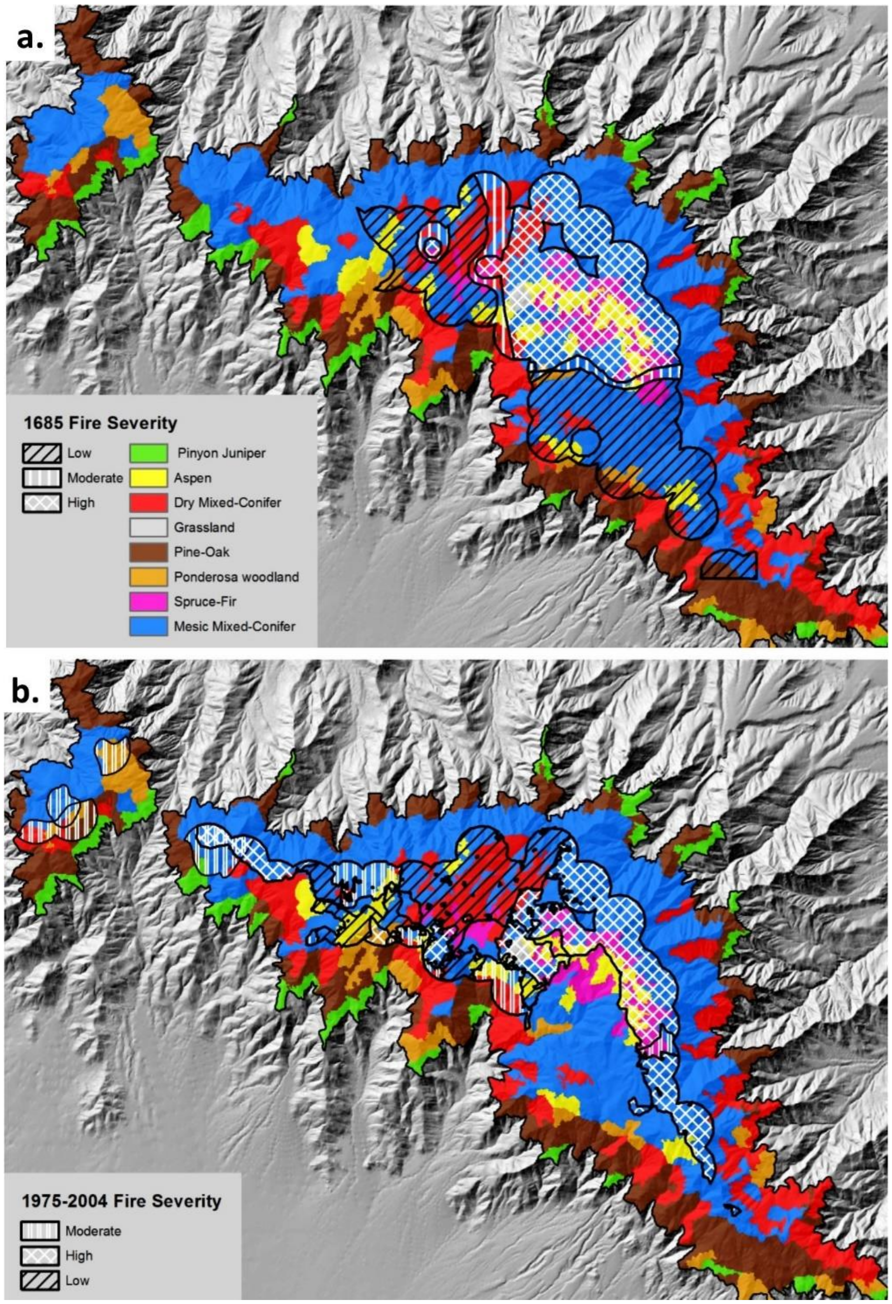
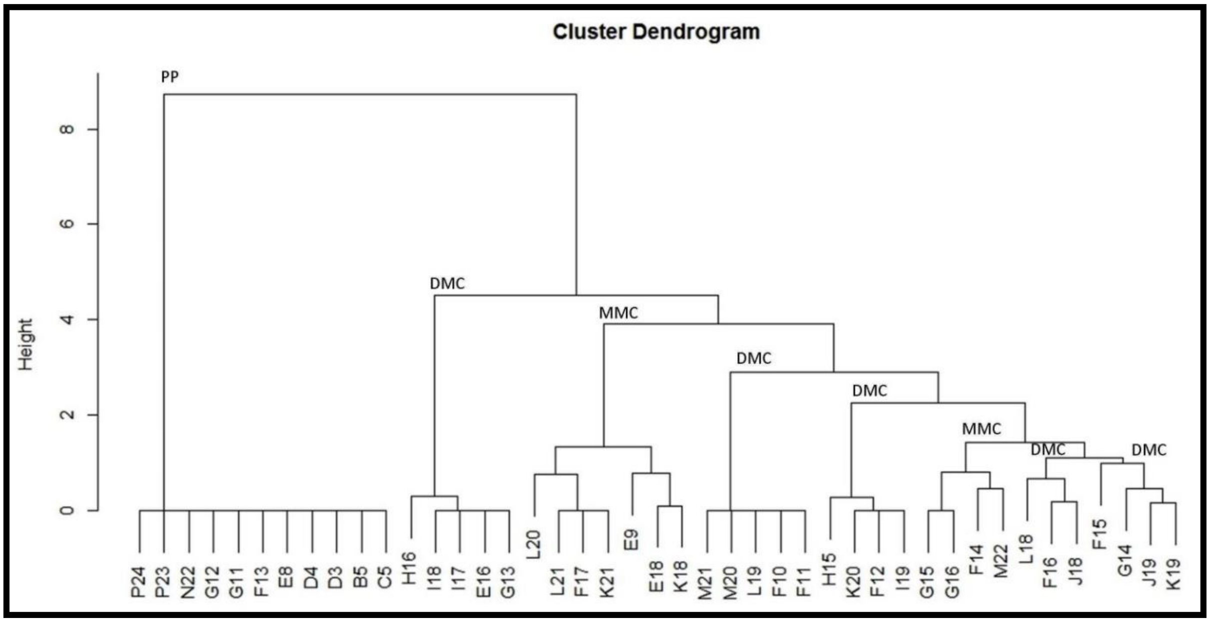


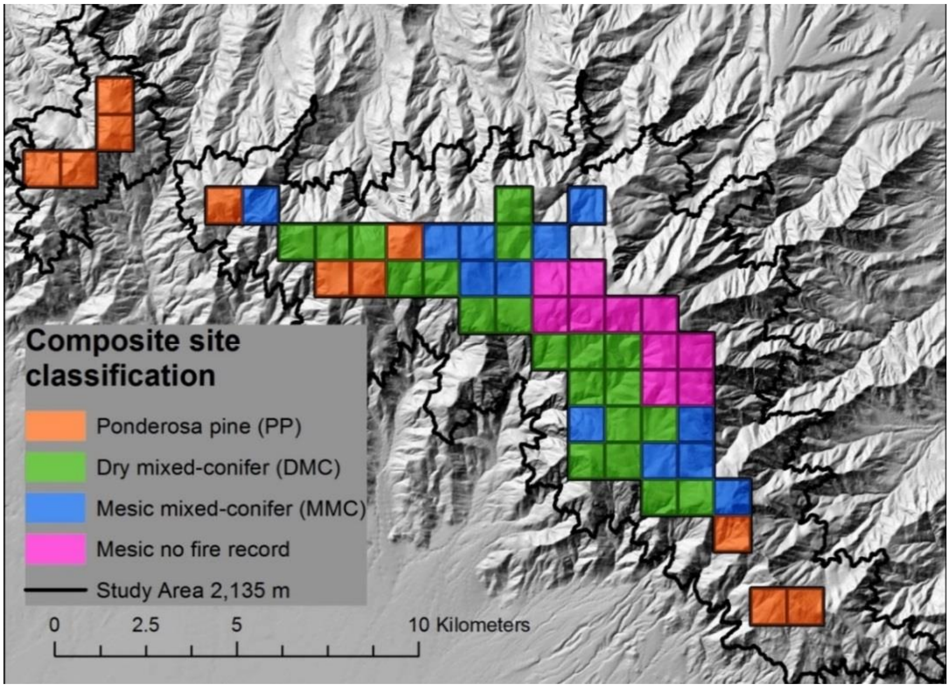
Figure 6. Spatial extent and burn severity of historic and contemporary mixed-severity fires. Severity of the 1685 fire (a) is reconstructed from 41 composited point locations with fire-scar records, and 12 demography plots indicating establishment post 1685. Polygons are interpolated from inverse-distance weighting of four nearest neighbors with a power function of two. Modern fire severities (b) are reclassified from relative difference normalized burn ratio for fires after 1984 (Miller and Thode 2007, MTBS 2013), and fire scar and demographic evidence associated with fire perimeters (Coronado NF GIS 2013) from 1975-1983. No fires larger than 200 ha were recorded in the study area from 1881 to 1955.

Figure 7. A high severity burn patch eight years after the 2004 Nuttall Complex Fire. Photo: C.D. O’Connor. June 12, 2012.

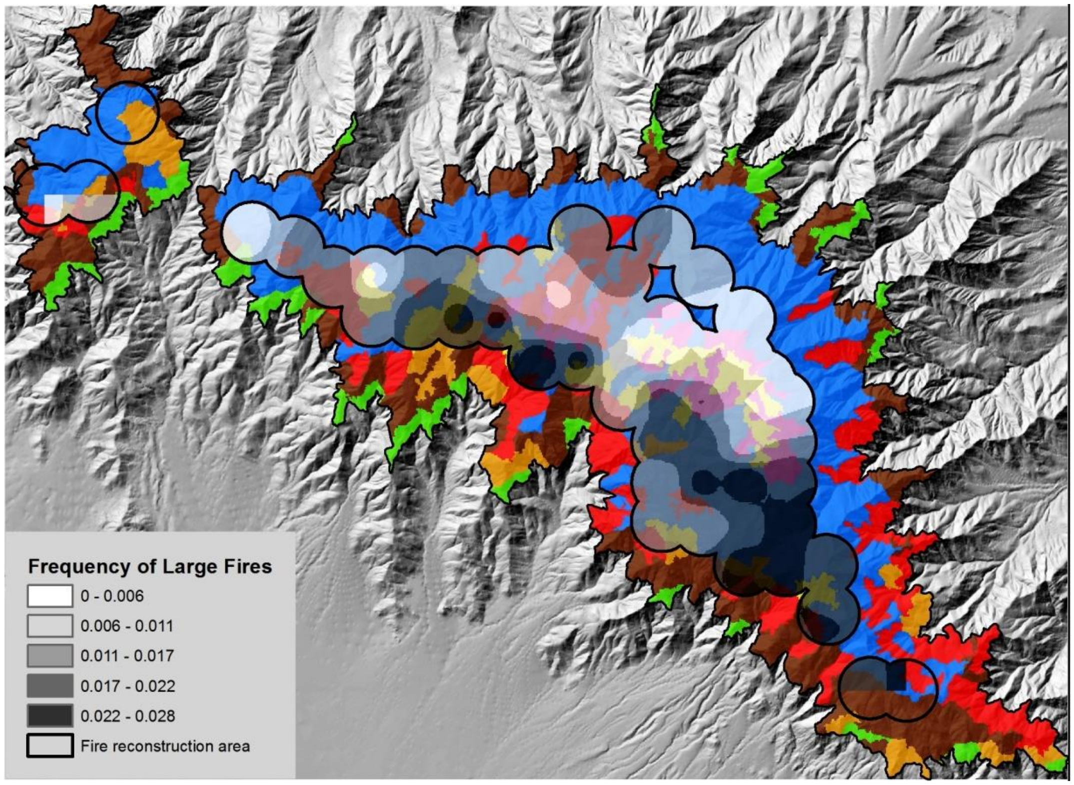
Supplemental Materials



Supplemental Figure 1. Dendrogram of plot groupings used to define forest types for fire history analysis. Cluster nodes are labeled by forest type: PP (Ponderosa pine), DMC (Dry mixed-conifer), MMC (Mesic mixed-conifer). Cluster ends are individual demography plot labels. Groupings are based on Ward's method of minimizing within-group variance for Jaccard-distance transformed species Importance Values in the year 1870. Importance values of pine species were doubly weighted to enhance differentiation the between dry and mesic mixed-conifer forests. The broad distribution of ponderosa pine is responsible for four mesic sites grouping with the majority of dry mixed conifer sites.



Supplemental Figure 2. Forest classification of fire recording sites and demography-only sites, based on plot groupings in Supplemental Figure 1.



Supplemental Figure 3. Frequency of Landscape-Scale fires 1640-1880. Fire frequency surface is based on inverse distance weighting of 53 composited fire-recording sites using four nearest neighbors with a power factor of two. Fire frequency is calculated from 11 fires recorded on 50% or more of sites.

APPENDIX B

FIRE EXCLUSION AND CLIMATE AFFECT SPRUCE BEETLE OUTBREAK SIZE AND DURATION

Fire exclusion and climate affect spruce beetle outbreak size and duration

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Key words: spruce beetle, disturbance, range expansion, tree-ring, fire suppression

Abstract

Recent spruce beetle outbreaks in the western United States are some of the largest and most severe on record. To put these recent events into a historical perspective, we reconstructed the spatial and temporal dynamics of past spruce beetle outbreaks in relation to the dynamic distribution of host Engelmann spruce on an Arizona sky island mountain range over a 319-year period of record. We examined the effects of host species' distribution and growth rates on initial spruce beetle outbreaks and subsequent outbreak frequency and extent. We examined the effects of summer temperature as it relates to physiological thresholds of spruce beetle development, and spring drought as it relates to host stress and outbreak proliferation. Spatial reconstructions of host spruce range and inclusion of failed attack scars and tree death dates improved the temporal and spatial resolution of two historically documented outbreaks and corroborated the growth release records of ten other undocumented events. We found that in the decades following fire exclusion, the area occupied by Engelmann spruce and corkbark fir doubled in size, coinciding with the first wide-spread outbreaks and a two-fold increase in outbreak duration. Spruce beetle outbreaks tend to lag spruce establishment by 40-90 years depending on forest type and time period and were significantly correlated with antecedent warm summer temperatures followed by up to a decade of persistent spring drought. Spruce diameter growth, a factor affecting host susceptibility, was significantly faster in mixed-conifer forest than in historically spruce-fir dominated sites. Increasing size and severity of outbreaks appears to have been influenced by host range expansion due to fire suppression, coupled with increasing incidence of warm summer temperatures associated with persistent spring water stress. The combined effects of expansion of spruce into mixed-conifer forest as a result of fire exclusion and trend toward warming, drying conditions in the Southwest are expected to increase the incidence of conditions conducive to extensive spruce beetle outbreaks in upper elevation forests across the western states.

Introduction

Subalpine spruce-fir forests comprised primarily of Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and corkbark fir (*Abies lasiocarpa* (Hook.) Nutt.), are the highest elevation forest type in the southwestern United States and comprise approximately 1% of the land area of Arizona, New Mexico, Colorado, and Utah (Thompson et al. 1999, Vankat 2013). Species dynamics in spruce-fir are mediated by fire, insect outbreaks, avalanches, rockslides, and blow-down events (Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003, Bigler et al. 2005). Infrequent mixed and high-severity canopy fires at 200 to 1000-year intervals (Arno 1980, Romme and Knight 1981, Kipfmueller and Baker 2000) are the typical stand-replacing disturbances in this forest type because mature stands tend to form closed canopies with low canopy base heights that retain dead lower branches (Burns and Honkala 1990). Fires in spruce-fir in the southwestern United States have been associated historically with extreme drought conditions mediated by decadal to multidecadal ocean-atmosphere oscillations at centennial to millennial timescales (Margolis and Swetnam 2013). During extended periods between fires, spruce beetle (*Dendroctonus rufipennis* Kirby) and western balsam bark beetle (WBBB) (*Dryocoetes confusus* Swaine) are the most important drivers of forest species composition, structure and age distribution of upper elevation forests (Schmid and Hinds 1974, Aplet et al. 1988, Veblen et al. 1991a, Vankat 2013).

Over the past two decades the size and severity of spruce beetle outbreaks have increased throughout the western states (Dymerski et al. 2001, DeRose and Long 2007, Raffa et al. 2008, DeRose and Long 2012a). A variety of factors at local and regional scales have been identified as potential contributors to recent outbreaks, including large contiguous stands of mature spruce (Berg et al. 2006, DeRose et al. 2009), warmer than average mean winter and summer temperatures (Berg et al. 2006, Hebertson and Jenkins 2008, Raffa et al. 2008, Bentz et al. 2010, DeRose and Long 2012b), persistent drought and increased vapor pressure deficit (DeRose and Long 2012a, Williams et al. 2013, Hart et al. 2013), and decadal to multidecadal scale climate variability (Sherriff et al. 2011, Hart et al. 2013).

While regional climate and stand characteristics may act as precursors to spruce beetle outbreak, an inciting factor that allows the endemic beetle population to move into incipient and outbreak modes is still necessary (Schmid and Frye 1977). Using the analogy of spreading fire, in which conditions appropriate for fire ignition and spread occur more often than spreading fire itself, spruce beetle outbreaks may require synchrony among a series of local host and beetle population factors and regional climate conditions to move from simply being present in the system to becoming a significant agent of spruce mortality (Raffa et al. 2008).

Patterns of spruce beetle outbreak size and severity are poorly understood, due mainly to the short length of the historical record and the relatively long time intervals between repeated outbreaks on the same landscapes. Several recent studies have examined potential natural controls on outbreak size, severity, and inciting factors (Berg et al. 2006, Hebertson and Jenkins 2008, Sherriff et al. 2011, DeRose and Long 2012, Hart et al. 2013); however, no spatially explicit reconstructions of spruce beetle outbreak history have examined changes in outbreak size and severity through time as a function of changes to stand conditions, host range distributions, and regional climate patterns.

Here we use a spatially explicit gridded sampling design to reconstruct changes to the distribution, age structure, and stand characteristics of a spruce-fir forest in relation to spruce beetle outbreaks on an isolated mountain range in southeastern Arizona, USA.

We use demographic reconstructions of seedling establishment, species composition, spatial extent, and age structure to track the suitability of spruce-inhabited forest for spruce beetle outbreak over a 319-year period between stand-replacing fires. We use a multiproxy reconstruction of spruce beetle outbreaks based on 1) growth release events in surviving trees, 2) encapsulated scars from failed spruce beetle attacks, 3) death dates from spruce beetle-killed trees, and 4) historical documentation of outbreak events, to reconstruct the spatial and temporal components of major spruce beetle outbreaks. We examine 1) the impact of fire exclusion and subsequent range expansion of spruce and corkbark fir into surrounding mixed-conifer forest, 2) the effect of this expansion on the size and severity of spruce beetle outbreaks, and 3) associations between spruce beetle outbreak initiation and seasonal temperature thresholds associated with accelerated larval development in spruce-fir and mixed-conifer forests.

Study area

The spruce-fir forest of the Pinaleño Mountains represents the southernmost extent of the forest type in North America (Stromberg and Patten 1991) and is situated at the top of a vertical gradient spanning approximately 2,100 meters (McLaughlin 1993). The study area above 2,835 m (9,300 ft) is located on gently sloping Typic Dystrochrepts (Natural Resources Conservation Service, USDA 2012) populated by Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and corkbark fir (*Abies lasiocarpa* var. *arizonica* (Hook.) Nutt.) with occasional Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirbel) Franco), southwestern white pine (*Pinus strobiformus* Engelmann), and aspen (*Populus tremuloides*) (Figure 1). The forest surrounding the study area along the central plateau of the range is primarily mixed-conifer forest that also includes white fir (*Abies concolor* (Gor. & Glend.) Lindl. ex Hildebr.) and ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelmann). The mixed-conifer forest transitions abruptly to pine and oak forest (*Quercus* spp.) on the steep slopes below 2,135 m (McLaughlin 1993).

The contemporary spruce-fir forest originated from a stand replacing fire in 1685 that also burned parts of the surrounding mesic mixed-conifer forest with high severity (O'Connor 2013). Small patches of surviving spruce and fir began to repopulate the upper elevation forest shortly after the fire, and much of the spruce-fir zone was under closed canopy conditions by the mid to late 1700s (O'Connor 2013). No fires entered the spruce-fir forest for 311 years until the 1996 Clark Peak fire burned a small area of the upper elevation spruce-fir forest with high severity. Shortly thereafter the 2004 Nuttall Complex Fire burned over the majority of the remaining spruce-fir forest with more than 70% moderate to high burn severity (Figure 1).

Spruce beetle activity in the Pinaleño Mountains is documented from an outbreak from 1943-1952 that caused a loss of approximately 18-20% of spruce timber volume (Bennett 1953), and another outbreak from 1998-2002 that was preceded by a series of defoliation events by other insects and resulted in much higher mortality of mature Engelmann spruce throughout the spruce-containing forest extent (O'Connor et al. 2013). The endemic population of spruce beetles began to build in the spruce-fir forest following a winter storm in 1993 that caused a modest amount of tree breakage and blowdown (Frank and Fairweather 1994). Beetle population density then increased rapidly in trees defoliated in 1996-1999 by *Nepytia janetae* (Rindge), a native Geometrid. Bark beetle-related mortality was first noted in 1999 (USDA Forest Service 2000). The same year, the introduced spruce aphid *Elatobium abietinum* (Walker) was first detected in the Pinaleño Mountains, damaging spruce of all size classes (Lynch 2009). From 1999-2002 the bark beetle outbreaks and spruce aphid infestation spread throughout the species extents of spruce and corkbark fir (Lynch 2009). Drought years in 1996, 2000, and 2002 and continued insect damage were likely contributors to the severity of spruce beetle and WBBB outbreaks.

Methods

To reconstruct the spatial and temporal dimensions of spruce-containing forest and bark beetle outbreaks, we used tree establishment and growth records from a primary grid of 14 fixed area (0.05 ha) tree demography plots spaced 1-km apart supplemented with a secondary grid of 21 fixed sample size plots offset 500 meters from demography plot locations. In demography plots, trees greater than 19.5 cm DBH were sampled over the full plot area, trees from 1 cm to 19.4 cm were sampled in a sub-plot equal to one third the total plot area (0.017 ha), and seedlings <1 cm DBH were cut at the soil surface. In fixed sample size plots, the nearest 10 spruce trees and 10 non-spruce trees >15 cm DBH were sampled around plot center. In all plots, up to three increment cores were removed from live trees within 20 cm of mineral soil. Radial cross-sections were collected from stumps and fallen logs, and quarter round wedges were removed from snags as close to the root collar as possible.

Sample Processing

Increment cores and cross-sections were mounted and sanded with progressively finer grits until individual cell structure was observable. Samples were cross-dated using a combination of visual pattern matching (Yamaguchi 1991), and skeleton plots (Stokes and Smiley 1968). A master chronology (Stokes and Smiley 1968) developed from Douglas-fir within the spruce-fir zone had the highest series inter-correlation among all high elevation species and was used to validate crossdating. On samples that did not include pith, concentric ring pith locators (Applequist 1958) were used to estimate pith dates if ring curvature indicated pith was within 10 years of the innermost ring. Ring-width measurements were recorded with J2X measuring software on a Velmex TA system® with sensor accuracy of one micron (VoorTech 2010). Crossdating of individual trees was checked with COFECHA crossdating analysis software (Holmes 1983). Cores that did not correlate with the plot-level chronology at a level of 0.3 or higher were removed from the analysis (Grissino-Mayer 2001a).

Bark beetle outbreaks are commonly inferred by growth releases in surviving trees (Veblen et al. 1991b, Eisenhart and Veblen 2000, Berg et al. 2006). Raw measurements from individual trees at each plot location were analyzed for growth release events with the program JOLTS (Holmes 1999). We used documented spruce beetle outbreaks from 1948-1954 and 1998-2002 as well as internal scarring evidence of failed spruce beetle attack (Craighead 1925) (Figure 2) and spruce death dates to calibrate the sensitivity of growth release detection. Failed attack scars are commonly found on trees in early and late stages of spruce beetle outbreak when the beetle population is not sufficient to overcome tree defenses, or in trees too small in diameter for successful brood development (Schmid and Frye 1977). Scars form as a result of lesions caused by spruce beetle attack and larval gallery formation that is then encapsulated in callus tissue and incorporated into an annual growth ring. Lesions are highly variable in size, ranging from one to several centimeters in length, and tend to be aggregated around the lower bole of the tree (Schmid and Frye 1977). This is the first study we are aware of to use failed attack scars to corroborate growth release evidence of spruce beetle outbreak in the historical record.

Growth releases were recorded as a minimum of 67% increase (JOLTS ratio of 1.5) in the 10-year running mean of ring widths with minimum time between releases of 15 years, to focus on initiation of bark beetle outbreaks. Growth releases were composited by plot to determine the proportion of outbreak-recording sites. We used a threshold of a minimum of 25% of recording plot locations recording growth release over a five-year period to define likely spruce beetle outbreaks. Growth releases occurring within 500 m and up to five years after fire or known logging operations were excluded from the analysis (O'Connor et al. 2013).

Use of a 10-year running mean excludes the first and last decades of measurement series, and caused a problem with detecting growth releases associated with the most recent insect outbreaks because high-severity fire in 2004 killed the majority of trees that would have experienced growth release. To reconstruct the spatial and temporal progression of insect-caused tree mortality for the 1990s insect outbreaks, we used tree death dates determined from the last ring of growth. Samples with charred outer rings were not used for the analysis of tree death dates. We did not attempt to differentiate between bark beetle, defoliator, or pathogen-caused mortality in the 1990s series of outbreaks.

We used a spatial reconstruction of spruce and corkbark fir establishment following the 1685 stand-replacing fire to verify the potential for spruce beetle or WBBB outbreaks at each plot location through time. An interpolated surface of spruce and corkbark fir establishment was generated through inverse distance weighting of earliest establishment dates from the four nearest plots with a power function of two (ESRI Inc. 2012). Establishment dates were based on the minimum inner ring date if pith was not present or could not be estimated within 10 years.

Spatial reconstruction of bark beetle outbreaks

To reconstruct the approximate size and spatial distribution of spruce beetle outbreaks recorded in 25% or more of recording sites, we used the grid of composited growth release events. Plots recording growth release in 10% or more of trees (minimum of two trees) over a five-year period during identified outbreaks were labeled as recording the outbreak. Approximate spatial extent of outbreak events was determined through inverse distance weighting, a deterministic method for multivariate spatial interpolation (Shepard 1968), of outbreak presence or absence based on values of four nearest neighbor plots with a power function of two. A maximum interpolation distance of 500 m was used to limit the possibility of over-predicting outbreak area (Hessl et al.

2007) and interpolated surfaces were clipped to the spruce range extent above 2,835 m elevation.

Outbreak initiation and climate

The approximate onset of spruce beetle outbreak was identified as the first year of concurrent growth release in 25% of recording sites. Initial outbreak years were tested statistically against seasonal records of precipitation and summer temperature, as well as annual forest drought stress to identify associations to local and regional climate conditions. We used superposed epoch analysis (SEA) (Lough and Fritts 1987) with EVENT software (Holmes and Swetnam 1994) to test for significant departures from mean climate ten years before and after the initial year of outbreak. SEA tests for significant departures from the range of annual values in a continuous climate variable, in relation to a series of event years (Swetnam 1993, DeRose and Long 2012). Values of a climate variable prior to, during, and after outbreak initiation were compared with the distribution of values for the full time domain of the climate series. We tested the statistical significance of outbreak initiation correlations to the climate variables with 1,000 bootstrapped random event years compared to actual event years (Holmes and Swetnam 1994). The relationship between outbreak patterns and summer temperatures (which affect larval development (Hansen et al. 2011)) was tested using mean maximum summer temperature (June-August) (PRISM 2013). The effects of host drought stress during the period of beetle flight (Massey and Wygant 1954) was tested with spring precipitation anomaly (January - June), regional, tree-ring reconstructed annual Forest

Drought Severity Index (FDSI) (Williams et al. 2013), and Palmer Drought Severity Index (Cook and Krusic 2004). Summer temperature and spring precipitation records were limited to the period 1896-2012. Tree-ring reconstructed annual PDSI and FDSI were available for the entire reconstructed period. Reconstructed PDSI values were averaged from the two nearest gridded PDSI locations surrounding the Pinaleño Mountains (Points 105 and 120, Cook and Krusic (2004)).

Results

We collected samples from 654 trees in 35 plots, including 296 Engelmann spruce, 111 corkbark fir, 103 Douglas-fir, 76 southwestern white pine, 33 aspen, 29 white fir, and six ponderosa pine. We were able to successfully crossdate 87 % of samples (709 of 815) and to date or estimate pith date on 76% of samples (617 of 815). From 591 measured series we detected 1,205 growth release events, averaging 2.04 growth release events per tree.

Immediately following the stand-replacing fire in 1685, the distribution of Engelmann spruce was restricted to a few small areas on north facing fire-sheltered valleys and surrounding moist springs (Figure 3). By the late 1700s spruce seedlings had established in the space between earlier isolated populations and formed a nearly contiguous forest in the highest elevation sites, including a small isolated population on a peak southeast of the main spruce-fir forest. Additional expansion of the original spruce population into sites that experienced infrequent fire (O'Connor et al. In prep) continued after 1840, including two additional isolated spruce populations to the south and west of the main spruce-fir forest. With the onset of fire exclusion in surrounding mixed-conifer forest circa 1870 (O'Connor 2013), the area occupied by spruce seedlings almost doubled from 1,095 ha to 2,168 ha by expanding into mixed-conifer forest to the southeast and west from 1886 to 1930, eventually occupying 89% of the area above 2,835 m (Figure 3). Mean DBH of spruce sampled from plots containing spruce prior to fire exclusion (32.2 cm) was nearly identical to that of spruce in the mixed-conifer forest where spruce established after fire exclusion (32.5 cm). However, mean ring width (0.19 cm) of spruce growing in in the pre-fire exclusion spruce range was approximately half that of spruce growing in mixed-conifer forest (0.39 cm) (two-tailed paired *t*-test with unequal variance $p<0.001$). Mean spruce age in mixed conifer forest (78.4 years) was significantly younger than in original spruce-fir forest (173.9 years) (two-tailed paired *t*-test with unequal variance $p<0.001$).

Corkbark fir followed a similar pattern of wave-form range expansion (Frelich 2002) following stand replacing fire, although establishment of fir lagged that of spruce (Schmid and Hinds 1974, Aplet et al. 1988) (Figure 4). Corkbark fir was slow to expand out from three original sites also occupied by Engelmann spruce prior to 1750. The first large expansion of corkbark fir extent occurred from 1840-1885, approximately 50 years after spruce establishment over the same general area. The extent of corkbark fir also nearly doubled from 1886-1930 with the onset of fire exclusion in surrounding mixed-conifer forest and continued to expand into other sites already occupied by spruce over the next 40 years (Figure 4). Bark beetle outbreaks prior to 1996 do not appear to have negatively impacted the overall spatial extent of spruce or corkbark fir over the past 300 years.

Spruce beetle outbreak dynamics

Twelve growth release events affecting 25% or more of spruce-containing sites were detected from 1700 to 2008 (Table 1). The first growth release did not occur until 94 years after the fire in 1685 and 77 years after confirmed spruce establishment. While the interval between outbreaks remained relatively constant before and after fire exclusion, the average duration of spruce beetle outbreaks almost tripled, from 3.4 years to 9.9 years. Outbreak duration was significantly shorter over the first two centuries of spruce range expansion following the 1685 fire (paired *t*-test with unequal variance p= 0.025) (Table 1).

Outbreak events recorded in 25% or more of sites are corroborated with failed spruce beetle attack scars (Figure 2) during nine of the 12 periods of growth release, including the two earliest recorded outbreaks in 1779 and 1803 (Figure 4a). Failed spruce beetle attack scars were recorded in 18% of spruce cross sections and quarter rounds and were not found in increment cores. More recent outbreaks are confirmed with attack scars and outer ring dates of dead spruce corresponding to each of the major outbreaks after 1920, and a detailed temporal record of the 1990s outbreak (Figure 4b). Growth release events at individual sites were common throughout the reconstructed period (Figure 4d); however the 25% filter clearly demarks large-scale spruce beetle outbreaks (Figure 4c).

Spatial reconstruction of outbreak events

After 1780, release events occurring in two or more sites were common. Aggregated release event dates at individual plot locations demonstrate the spatial and temporal variability of release events across the upper elevation forest. Spruce beetle outbreaks tracked the expansion of the spruce population starting 90 years after stand replacing fire and remained relatively small, affecting 3-5 sites over the next century (Figure 6). The 1880-1890 outbreak was approximately twice the size of any previous event in the record, and was the first to affect all three spatially distinct satellite spruce populations outside of the main forest. After 1890, outbreaks tended to alternate between smaller and larger events. Records of repeated outbreaks in sites where suitable host trees persisted for several centuries provide evidence for relatively low outbreak severity for at least the first 260 years following stand-replacing fire. The outbreak that began in 1949 was the longest and one of the most widespread events affecting the spruce population. During this outbreak trees within individual sites exhibited staggered release dates every 3-5 years from 1949 to 1966. The early part of this outbreak was documented in 1952 by aerial and ground surveys (Bennett 1953). The outbreak continued at a low level for more than a decade, eventually affecting approximately three times the area of the original aerial survey boundary. A single site that hosts corkbark fir but not spruce exhibited a growth release during the 1949-1966 outbreak, suggesting that a concurrent outbreak of WBBB, noted as a minor mortality agent in the Bennett (1953) report, also occurred during this period. A minor outbreak detected from growth releases from 1972-1981 was not noted in aerial surveys but is confirmed by a series of spruce death dates and failed attack scars (Figure 4a and 4b).

Growth release and death date records of the most recent spruce beetle outbreak from 1996 to 2002 are confounded by concurrent damage from *N. janetae* (which also affected corkbark fir) and from spruce aphid, both of which caused significant mortality of understory spruce (Lynch 2009) and may have delayed the growth release of surviving understory spruce and corkbark fir. The spatial extent of the confounding insect damage signals was limited to the oldest stands of spruce and corkbark fir over the duration of the outbreak, but spruce aphid affected spruce throughout the spruce extent. During the most recent outbreak, 94% of spruce-containing sites recorded growth release and mortality of overstory spruce. Corkbark fir mortality from WBBB was also recorded from 1993-2003 in 23% of sites. By 2002 the number of sites containing living spruce greater than 15 cm DBH was reduced from 97% to 72% of sites, and then further reduced to 49% of sites following the 2004 fire. In the five demography plots that were not affected by the 2004 fire, the proportion of living basal area occupied by corkbark fir increased by an average of 28% (range 16 to 44%) in four plots and decreased by 27% in one plot from 1996 to 2008. This suggests that in the absence of fire, the spruce-fir forest would have undergone a shift toward corkbark fir dominance to a degree not seen in prior spruce beetle outbreaks.

Climate conditions associated with widespread release events

The six outbreak events recorded from 1896-2010 were consistently associated with a temporal sequence of several years of antecedent warm summer temperatures, followed by persistent high forest drought severity (negative FDSI) and low spring precipitation the decade after outbreak initiation (Figure 6). Mean maximum summer (June to August) temperatures 0.4 to 1.2 °C above the 114- year mean were associated with each of the five years prior to outbreak initiation (Figure 6a). Following outbreak initiation, summer temperature no longer expressed a consistent pattern. Conversely, regional FDSI and spring (January-June) precipitation showed no consistent pattern prior to spruce beetle outbreak but the year of outbreak detection and subsequent decade were associated with persistent negative annual FDSI values and poor spring precipitation (Figure 6b and 6c). Values of FDSI and spring precipitation were below average for eight out of the ten years following outbreak initiation, and up to two years deviated significantly (95% confidence) from the 114-year mean of each variable. Spring precipitation anomalies over the decade following outbreak initiation were associated with two or more years in which precipitation was more than 10 centimeters below average. A significant period of high moisture eight years prior to outbreak detection occurred in both recent and historical reconstructions.

Comparable seasonal reconstructions of temperature and precipitation for the region of southern Arizona were not available for the spruce-fir forest type prior to 1896, however regional reconstructions of cool season precipitation (Ni et al. 2002) and annual temperature (Wahl and Smerdon 2012) remain to be explored. Spruce beetle outbreaks prior to 1896 did not exhibit consistent relationships with annual tree-ring reconstructed temperature from the southern Colorado Plateau (Salzer and Kipfmueller 2005) or annual tree-ring reconstructed PSDI for the gridded points nearest the Pinaleño Mountains. Outbreaks were associated with negative values of regional FDSI prior to 1896; however the period of negative FDSI values following outbreak was shorter (up to six years) than that associated with outbreaks over the 20th-21st centuries (Supplemental Materials Figure 2).

Discussion

Spruce beetle outbreaks tracked the size and age distribution of available spruce following the stand-replacing fire in 1685 (O'Connor 2013 Appendix A). Outbreaks were generally smaller and of shorter duration prior to the onset of fire exclusion when the extents of spruce and corkbark fir were approximately half of their post-fire-exclusion maximum. The continuous expansion of spruce-fir forest range after 1685, with accelerated expansion after 1880, and relative stand dominance of Engelmann spruce over corkbark fir suggest that outbreak severity remained relatively low for almost three centuries following stand-replacing fire. The most recent spruce beetle outbreak beginning in 1996 was triggered by outbreaks of two foliage-damaging insects and was compounded by a concurrent outbreak of WBBB. This combination of biotic factors, dense mature forest conditions, and climatic stressor resulted in the largest and highest severity spruce beetle outbreak in the reconstructed period. Outbreaks of similar or higher severity are documented in other western North American forests (ex. Berg et al. 2006, DeRose and Long 2009). The 2004 fire further reduced the spatial extent of spruce-fir forest, leaving the majority of mature spruce and corkbark fir in mixed conifer forest, outside of the pre-fire exclusion range of either species (Supplemental Figure 1).

Effects of fire suppression on Engelmann spruce and corkbark fir distribution

Fire exclusion over much of the 20th century in the southwestern United States had the most obvious effects on fire-dependent pine and mixed-conifer forest types where forest structure has changed dramatically (ex. Minnich et al. 1995, Allen et al. 2002). However, increased numbers of spruce and corkbark fir in surrounding mixed-conifer forests has been documented in several locations (Habeck and Mutch 1973, Cocke et al. 2005). Prior discussion of this expansion has been focused on the increased risk of high-severity fire in mixed-conifer forest, and spread of canopy fire from the mixed-conifer to the spruce-fir, as a result of changes to species and structure (Grissino-Mayer et al. 1995, Swetnam et al. 2009). In this study we identify a series of factors that may contribute to the size and severity of biotic disturbances affecting spruce colonizing mixed-conifer forest. Spruce expansion into mixed-conifer forest was accompanied by a doubling of diameter growth rates, accelerating the suitability of these trees as spruce beetle resources in future outbreaks. Younger large diameter trees contributed a significantly larger resource for spruce beetle outbreaks following fire exclusion in comparison to slow growing spruce within the pre-fire exclusion range.

Outbreak reconstruction methods and outbreak frequency

Tree-ring growth thresholds used to reconstruct spruce beetle outbreaks in previous studies (Veblen et al. 1991b, Eisenhart and Veblen 2000, Berg et al. 2006, DeRose and Long 2012a, Hart et al. 2013) were not used here because they were found to be overly conservative for capturing the onset of documented outbreaks in the early 1950s and mid-1990s. The 67% increase in tree-ring growth over a 10-year period used in this study identified growth changes one to two years earlier than the more conservative 100% increase method suggested by Berg et al. (2006). A potential problem with lowering the growth release threshold is an increase in Type 1 error (false positives). To address this potential source of error, additional filtering of detected growth releases to include only those events detected in a minimum of 10% of trees in the same plot over a five year period, and the requirement of 25% or more sites in release in the same five-year interval, was used to reduce the possibility that widespread release events were not the result of spruce beetle outbreak.

This study was unique in the use of multiple proxy records to corroborate growth release events as actual spruce beetle outbreaks. The combination of spatial reconstructions of host spruce range and inclusion of failed attack scars and tree death dates improved on the temporal and spatial resolution of two historically documented outbreaks and corroborated the growth release records of ten other undocumented events. Additional screening of recorded growth releases after Euro-American settlement in the area to remove potential effects of logging, road improvements, and building construction further reduced the possibility of false positives. The twelve events detected from 1779-1996 were all associated with locations where spruce establishment occurred a minimum of 90 years previously. Growth releases detected in mixed-conifer forest recently colonized by spruce may also have been subject to outbreaks of Douglas-fir beetle, and Douglas-fir tussock moth, though there is no record of tussock moth in the Pinaleño

Mountains prior to 2003 (USDA Forest Service 2013b and similar reports). Although other insects cannot be ruled out as a potential cause for growth release in spruce-containing mixed-conifer forests, concurrent spruce beetle outbreaks in nearby spruce-dominated forest suggest that spruce beetle is the most likely cause of growth release in both forest types.

Detecting the initiation of spruce beetle outbreaks from changes in the growth patterns of surrounding trees remains an imperfect method. Determining the specific year of growth change is subject to the methods used and the minimum threshold defined as a growth release. Moving average window methods with or without tree growth trend removal (Veblen et al. 1991b, Berg et al. 2006), detection of changes to growth trend (Rodionov and Overland 2005, Hart et al. 2013), and correction for non-insect-induced growth changes (*sensu* Swetnam and Lynch 1993) can all be applied to the same tree-ring sample and produce a variety of outbreak onset dates depending on the amount of trend removal and threshold of growth release. Adding to the uncertainty, the degree of outbreak severity and other environmental stressors can result in loss of needles in attacked trees and subsequent growth release in surrounding trees over a variable period of one to four years (Schmid and Frye 1977) with some reported release events occurring up to seven or more years post outbreak (Sherriff et al. 2011). Continued development of improved methods to detect growth trend changes in tree-ring series and to isolate the causes of these changes, such as the recent work of Druckenbrod et al. (2013), will further improve our ability to define the temporal windows of spruce beetle outbreaks and relate these to local and environmental conditions that may provide improved predictive power to assess future outbreak risks. Tuning growth release detection methods to more temporally precise proxy records such as tree death dates or failed attack scars will add to their utility.

The temporal progression of spruce-fir stand development and spruce beetle outbreaks is similar to the model proposed by Schmid and Hinds (1974). Following a high severity fire in 1685, the spruce-fir forest was relegated to a few relict populations that survived the fire and provided progeny that eventually colonized most of the upper elevation area. Growth releases detected at multiple sites within the limited area occupied by spruce approximately 100 years after stand-replacing disturbance suggests that the stand conditions necessary for spruce beetle outbreak were achieved considerably faster in southern Arizona than the 200-year window proposed for the southern Rocky Mountains and Utah based on size and structural traits (Schmid and Hinds 1974). The 100-year period to develop appropriate size and structure for spruce beetle outbreak in the highest elevation sites is consistent with the findings of Bebi et al. (2003) that risk of spruce beetle outbreak was low for the first 60-70 years following high-severity fire. Spruce beetle is one of a few aggressive bark beetle species capable of depleting host resources once an outbreak is established (Raffa et al. 2008). The rapid growth rate of spruce in mixed-conifer forest would make these trees vulnerable to outbreak more quickly than in older dense stands of spruce where outbreaks are more likely to initiate (Reynolds and Holsten 1994).

Intervals between repeated outbreaks in this study are considerably shorter than those reported from more northern study sites. Intervals between spruce beetle outbreaks were more than 100 years in two reconstructions of Engelmann spruce-subalpine fir forest dynamics in northwestern Colorado and central British Columbia (Veblen et al. 1994, Zhang et al. 1999). On the Kenai Peninsula of Alaska, mean return intervals in white spruce (*Picea glauca*) forests were 52 years (Berg et al. 2006), and in multisite reconstructions from the Colorado Front Range outbreak return intervals in Engelmann spruce forests varied from 40-60 years (Hart et al. 2013). Each of these areas likely has a considerably shorter growing season than southeastern Arizona, making it likely that the rate of spruce growth may be linked to outbreak frequency. Methods used to reconstruct outbreaks in these studies were also more conservative than those used in this study. It is possible that use of less strict criteria defining a growth release event may have resulted in shorter outbreak intervals in some of these previous studies as well.

Spatial reconstruction of spruce beetle outbreak

The spatial and temporal lag of spruce beetle outbreaks behind spruce establishment and diameter growth further supports the likelihood that growth releases are associated with spruce beetle outbreak. The increase in host distribution after 1880 combined with accelerated diameter growth in some sites provides a set of conditions appropriate for the increase in outbreak size, duration, and severity over the 20th century.

Spruce beetle physiology and climate associations to outbreak initiation

Recent studies identifying associations between two spruce beetle outbreaks during the past two decades of exceptionally warm winter and summer conditions (Berg et al. 2006, DeRose and Long 2012b) indicate the possibility of a physiological shift from semivoltine to univoltine reproductive life cycles that may be necessary for high-severity spruce beetle outbreak (Werner and Holsten 1985, Hansen et al. 2001, Hansen et al. 2011). These studies were not able to identify similar temperature anomalies associated with previous outbreaks and did not examine patterns of summer temperatures specific to developmental thresholds for the onset or bypassing of larval diapause between third and fourth instar life stages that is responsible for the univoltine, outbreak-associated life-cycle switch (Hansen et al. 2011). Warmer than average winter temperatures have also been associated with outbreak conditions due to a reduction in overwintering beetle mortality (Hebertson and Jenkins 2008). Minimum winter temperature was not a significant factor in the Arizona study because the temperature threshold for winter spruce beetle mortality of -40 °C (Holsten et al. 1999) has not been reached in the mountains of southern Arizona during the instrumental record.

Although host susceptibility to spruce beetle outbreaks is associated with several factors, including stand conditions and host size and stress, outbreak initiation is generally associated with an inciting event that allows endemic spruce beetle populations to build (Massey and Wygant 1954). In this study, disturbance events such as wind or ice storms were not reconstructed, but the six most recent spruce beetle outbreaks were associated with persistent warm summer temperatures prior to extended drought. Prior to the most recent outbreak, mean monthly summer temperatures of 15.5-17.8 °C from June through August during the period of spruce beetle flight, gallery excavation, and larval development (Massey and Wygant 1954, Schmid and Frye 1977), is within the 15-17 °C threshold triggering a shift in developmental cycle from semi-voltine to univoltine life cycle for a portion of the developing beetle population (Werner and Holsten 1985, Hansen et al. 2001, Régnière et al. 2012). Mean summer temperatures associated with outbreaks on the Kenai Peninsula in Alaska (10.5 -11.5 °C) were significantly lower than those in the Pinaleño Mountains of Arizona. Persistent tree stress following a period of temperatures favorable to spruce larval development and population growth sets up an ideal temporal sequence for a spruce beetle population shift from endemic to incipient to outbreak stages. Although temperature may trigger outbreak initiation through a physiological change in the spruce beetle life cycle, drought may be what enables outbreaks to continue. If accelerated spruce beetle development does not coincide with an abundance of susceptible hosts shortly after outbreak initiation, the outbreak may not continue because host conditions are not favorable. Likewise if tree drought stress is not preceded by a warm period that allows the spruce beetle population to escape the semivoltine life cycle, beetle abundance may not be high enough to overcome even diminished host defenses. Favorable spruce beetle development conditions combined with unfavorable host characteristics or vice versa are responsible for the record of failed spruce beetle attacks over the period of reconstruction.

Although data were not available to reconstruct summer temperatures prior to 1896, earlier outbreaks were associated with shorter periods of negative FDSI following outbreak initiation (Supplemental Figure 2). Consistently shorter periods of drought following outbreak initiation may have contributed to shorter outbreak durations prior to the 20th century. The increase in outbreak duration after 1880 may also be attributable to the increased distribution and growth rate of available host trees, allowing beetle populations to spread over a larger area over several years or to re-infest the same sites as beetle population dynamics change over the course of an outbreak (Bentz et al. 2010). Longer outbreak duration may also be a factor of the increase in the number of trees available to record growth release events as a result of fire exclusion.

A consistent pattern of an anomalously wet spring eight years prior to each of the 20th century outbreaks may be random chance or may be a signal of extreme winter storms or other weather event that contributed to the availability of damaged host material. Wet periods prior to outbreaks are know from studies of several western bark beetle species in certain locations and during individual events, however, no tree or bark beetle physiological signal has been identified to explain significant rainfall as a trigger for spruce beetle outbreak (Powell 1969). An opposite pattern of severe drought six to seven years prior to growth release in spruce on the Markagunt Plateau of Utah was reported by DeRose and Long (2012), though other than short-term drought stress, no trigger of spruce beetle outbreak was identified.

Spruce growth response to climate

Annual patterns of moisture and temperature were unlikely to cause the patterns of growth release in spruce populations of the Pinaleño Mountains. In a study of Engelmann spruce growth response to climate in sky islands of Arizona and New Mexico, (Buckley 1989) found that spruce growth was negatively affected by warm summer temperatures and drought conditions, suggesting that growth release could be associated with a prolonged switch from hot, dry conditions to cool, moist conditions. During the 12 growth release events identified in this study, temperature and moisture conditions were opposite those that would be associated with a climatically-triggered growth release in Engelmann spruce. For comparison, the growth release events reported by DeRose and Long (2012) occur during a period of reduced drought stress, suggesting that an increase in available moisture may have contributed to detected growth releases.

Western balsam bark beetle in the spruce-fir forest

During the most recent spruce beetle outbreak, significant mortality of corkbark fir was caused by a concurrent outbreak of WBBB. Outbreaks of WBBB are generally considered secondary to spruce beetle outbreaks because susceptibility of corkbark fir to mortality from WBBB is generally limited to trees >200 years of age with diameter > 32 cm (Bleiker et al. 2003). Mortality from WBBB has also been linked to infection by *Armillaria* root fungus that is typically found in older senescing corkbark fir in the southwestern states (Negrón and Popp 2009). These conditions associated with “old” corkbark fir have been present only during the past 50 years in the Pinaleño Mountains, suggesting the corkbark fir has only recently become susceptible to outbreaks of WBBB. Therefore it is unlikely that WBBB to have contributed to growth release events prior to the past 50 years.

Conclusions and summary

The spatial and temporal reconstruction of spruce-fir demography and disturbance yielded several consistent patterns relating forest dynamics, spruce beetle outbreaks, and fire over the past three centuries. Initial spruce beetle outbreaks occurred approximately 90 years after spruce establishment for the first two centuries of spruce expansion following a stand-replacing fire in 1685. The onset of fire exclusion in surrounding mixed-conifer forest resulted in a doubling of the extent of host distribution over a 40-year period. A shorter interval from spruce establishment to initial spruce beetle outbreak in mixed-conifer forest coincides with faster spruce growth rates and shorter time to suitable diameter for beetle attack. After initial outbreak, subsequent outbreaks occurred at ~ 20 year intervals regardless of host distribution and stand conditions, suggesting that the recurrence of spruce beetle outbreaks is accelerated in warmer, low latitude forests. Outbreaks over the last century were associated with a pattern of warm summer conditions prior to outbreak paired with persistent spring drought and forest stress during outbreak. Warm temperatures suggest that a switch from semivoltine to univoltine life cycle is associated with outbreak initiation, but once a successful outbreak begins, the univoltine life cycle is no longer necessary. Instead, outbreak persistence appears to be associated with drought-driven prolonged host tree stress. Longer outbreak duration over the past century may also be related to the increased abundance and spatial extent of suitable host trees following fire exclusion.

Restoring the fire-adapted structure of the mixed-conifer forest and allowing natural and prescribed fire back into the system has been proposed as a way of promoting the long-term stability of theses diverse ecosystems (USDA Forest Service 2010). However, the legacy of spruce and corkbark fir in mixed-conifer forest poses a challenge for restoration efforts. The majority of the area occupied by spruce and corkbark fir post 2004 is classified as mesic mixed-conifer forest where fire return intervals ranged from 10-25 years prior to 1870 (O'Connor 2013) (Supplemental Materials Figure 1). Returning fire to these forests would reduce available spruce and corkbark fir seed sources and may slow the rate of recovery of the upper elevation forest. Climate conditions projected for the next century may not be favorable to spruce establishment and survival (Notaro et al. 2012) so the rate of seedling establishment over the next few decades may determine the composition of the upper elevation forest for several centuries.

Warmer temperatures and increased forest drought stress projected for the region (Seager and Vecchi 2010, Garfin et al. 2013, Williams et al. 2013) will continue to affect the developmental rates of multiple insect pests (Raffa et al. 2008, Bentz et al. 2010) and may lead to persistent conditions favorable to accelerated insect development and reduced host defenses. Without a climatic threshold to overcome, host range distribution and density may become the most significant limits to the size and severity of future insect outbreaks. The reduced density of surviving spruce and corkbark fir in mixed-conifer forest are likely to reduce the size and severity of future bark beetle outbreaks in the short term. Future outbreak dynamics will depend on the effects of restoring fire to the mixed-conifer forest and success of reestablishment of spruce-fir forest within the perimeter of the 2004 fire.

Throughout the southwestern states, warmer temperatures are expected to lengthen the window of favorable fire conditions (Crimmins 2011, Williams et al. 2013). In other mixed-conifer forests across the western states, the 20th century incursion of spruce as a legacy of fire suppression increases both the risk of crowning fire and portends more frequent and potentially larger and more destructive spruce beetle outbreaks. The majority of recent research efforts have focused on climate-driven changes to spruce beetle dynamics which are an important component of future outbreak risk. This study identifies the expansion of spruce range as an additional factor likely to exacerbate already increased risk of outbreaks and fire. Under this scenario, it seems unlikely that the forests of the future will bear much resemblance to those of the 20th century, let alone those of the past.

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Tables

Table 1. Spruce beetle outbreak events 1779-1996. Horizontal line at 1880 indicates the onset of fire exclusion in surrounding mixed-conifer forest and the start of range expansion of Engelmann spruce and corkbark fir.

Outbreak start	**Outbreak end**	**Duration (Years)**	**Interval (Years)**
1779	1783	4	
1803	1806	3	24
1824	1829	5	21
1842	1845	3	18
1866	1868	2	24
1880	1890	10	14
1896	1910	14	16
1923	1932	9	27
1940	1944	4	17
1949	1966	17	9
1972	1981	9	23
1996	2002	6	24
Pre 1890	**Mean**	**4.6**	**20.2**
	Std. dev.	2.9	4.3
Post 1890	**Mean**	**9.8***	**19.3**
	Std. dev.	4.9	6.6

Figures

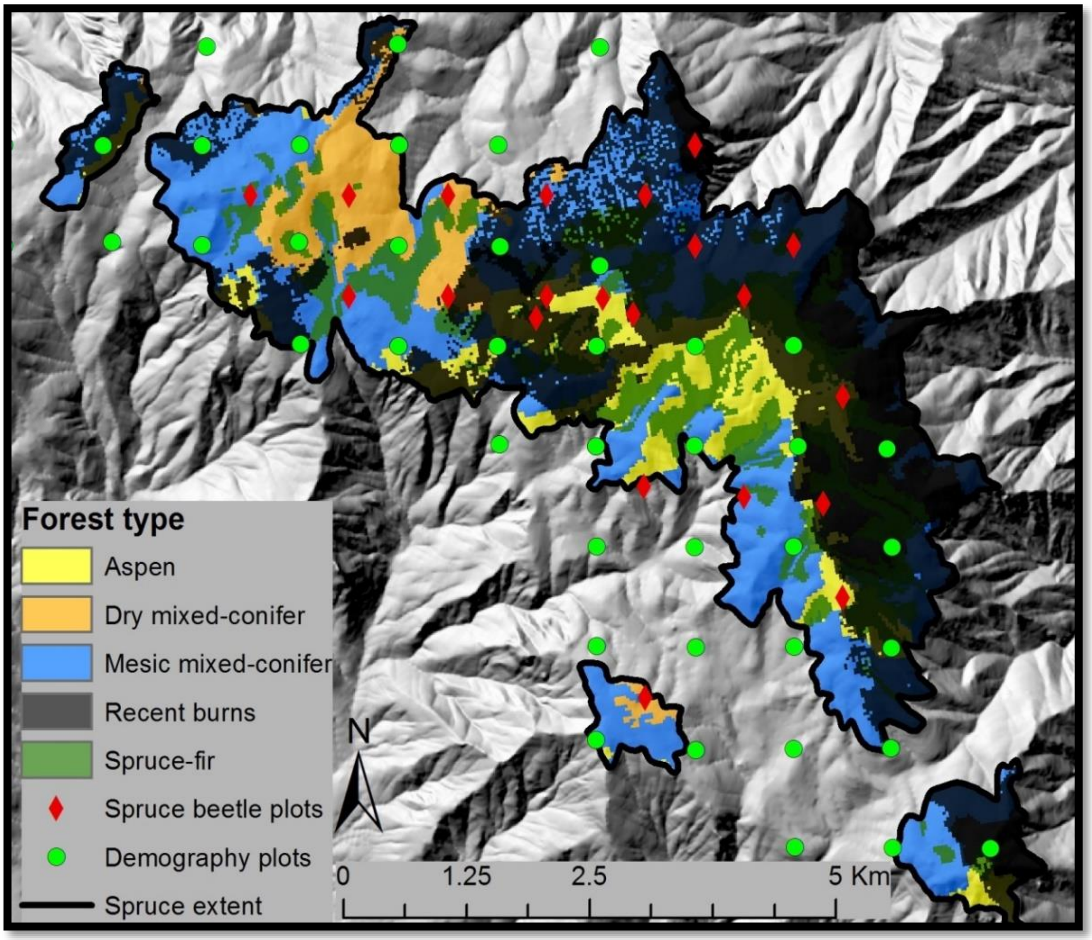


Figure 4. Gridded sampling design and distribution of spruce-containing forest in the Pinaleño Mountains, Arizona, USA. Colored area denotes elevation above 2,835 m. Distributions of forest types are from LANDFIRE biophysical setting (LANDFIRE 2013). Burn patches are calculated from moderate and high severity vegetation burn ratings from reclassified relative difference normalized burn ratio (Miller and Thode 2007, MTBS 2013). All raster values are generalized to a minimum patch size of 6.75 hectares.

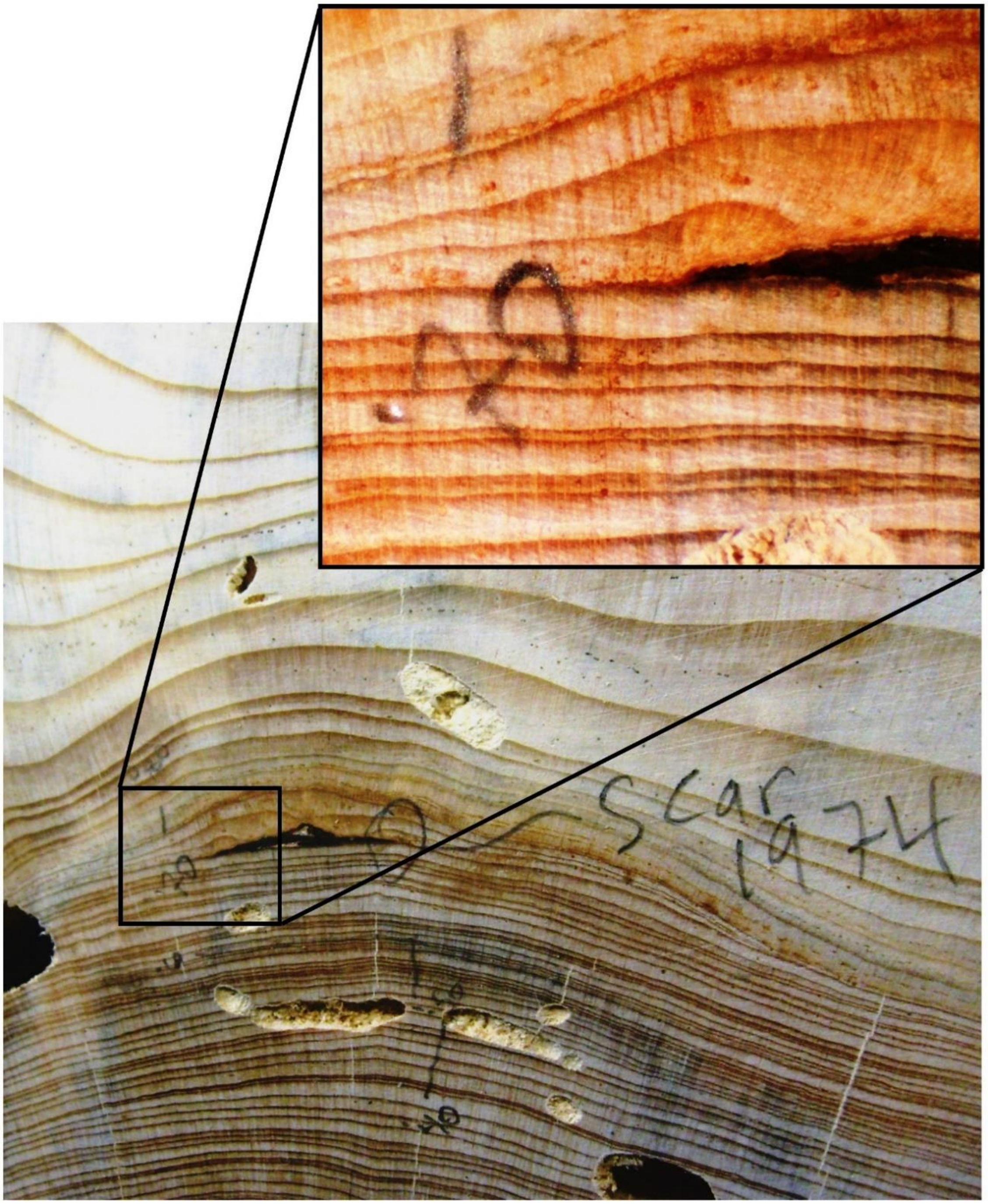


Figure 5. A scar formed in 1974 from a failed spruce beetle attack on a suppressed understory Engelmann spruce in the Pinaleño Mountains, Arizona. The upper right photo is the magnified image of the same scar depicted in the lower left. From the position of the wound within the ring, it appears that attack occurred early in the growing season, i.e., probably May or June. The failed attack occurred four years prior to the onset of growth release in 1978.

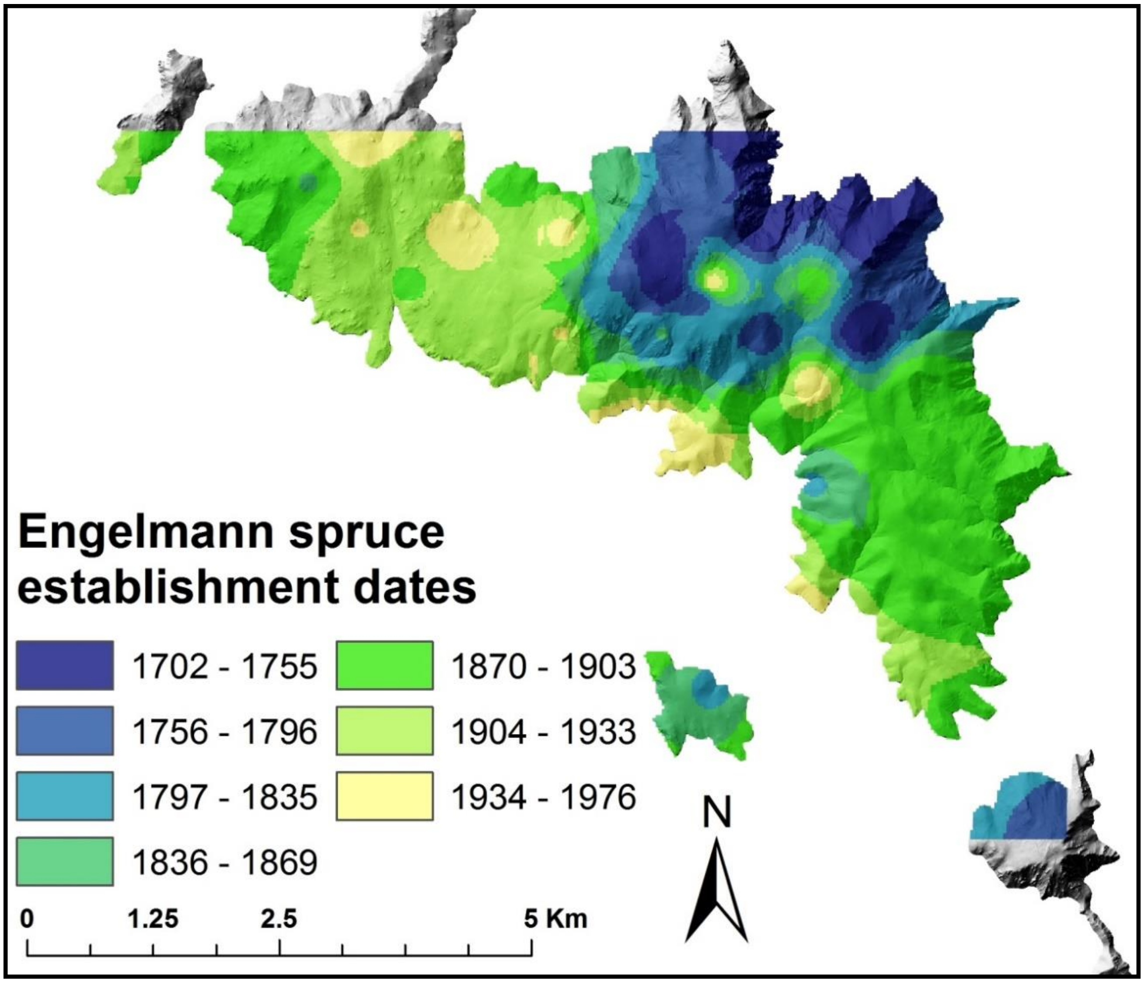


Figure 3. Temporal progression of Engelmann spruce establishment following 1685. Interpolated spruce stand age surface is based on inverse distance weighting of minimum tree establishment dates from 44 gridded point locations. Interpolation algorithm uses four nearest point locations with a power function of two.

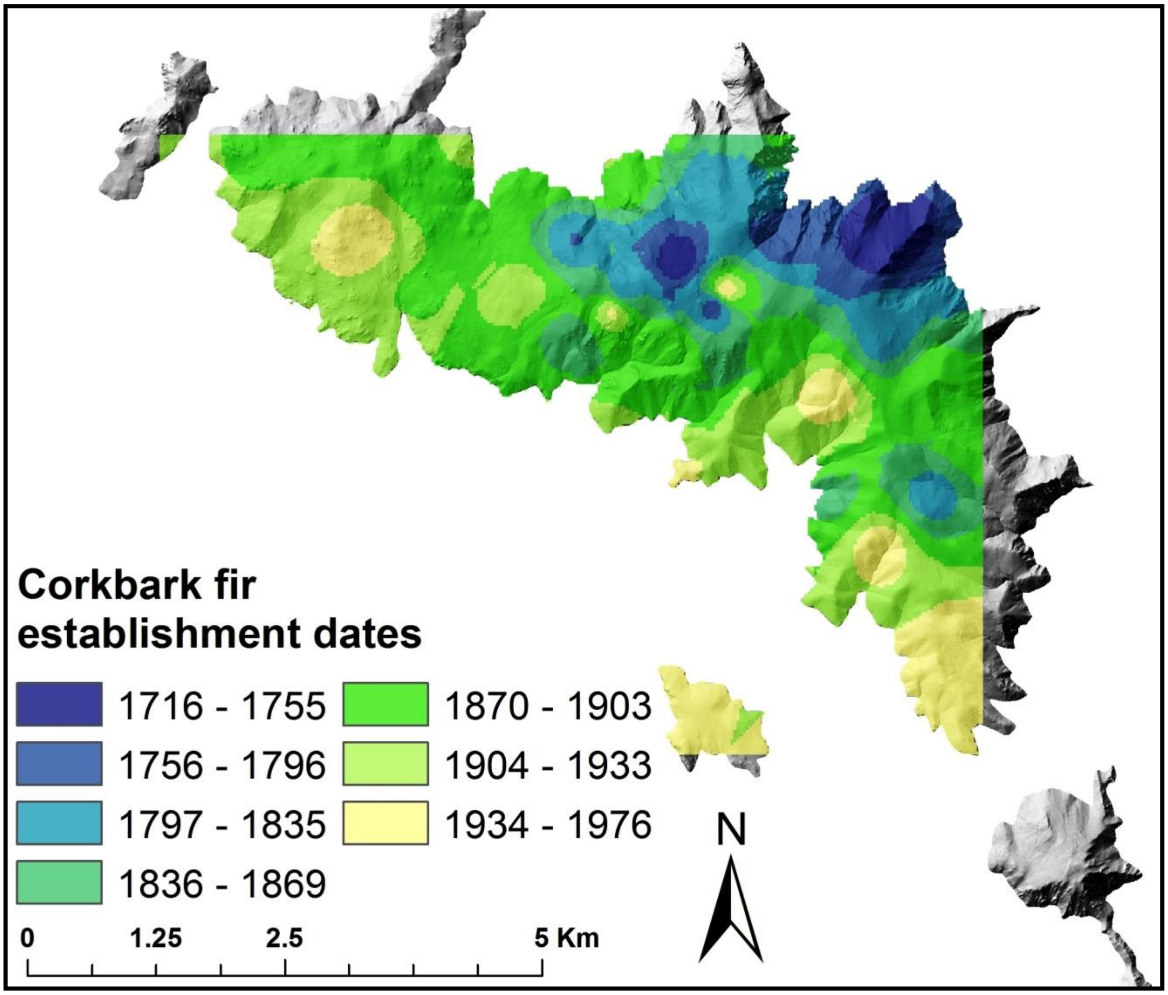


Figure 4. Temporal progression of corkbark fir establishment following 1685. Interpolated corkbark fir age surface is based on inverse distance weighting of minimum tree establishment dates from 37 gridded point locations. Interpolation algorithm uses four nearest point locations with a power function of two.

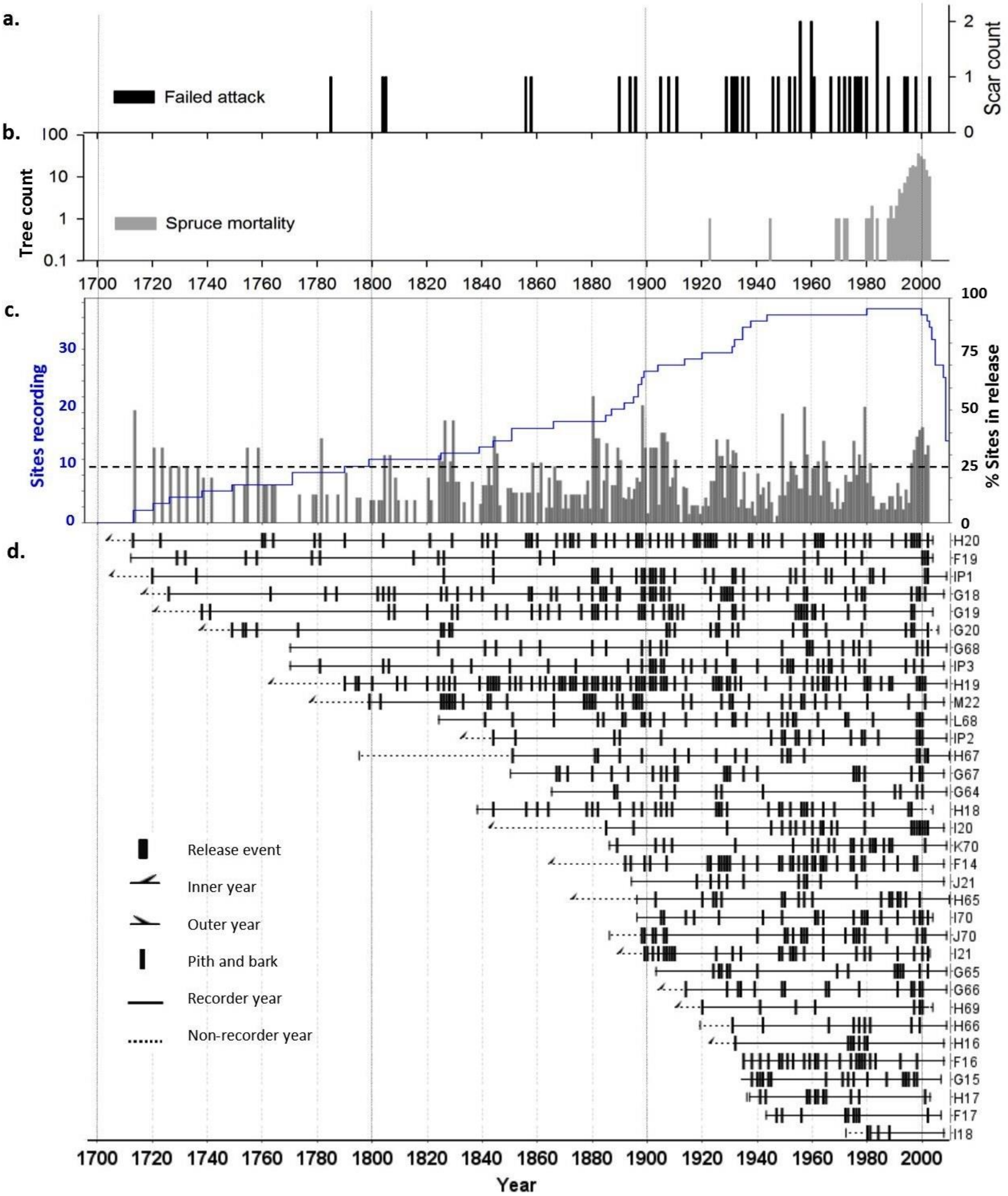
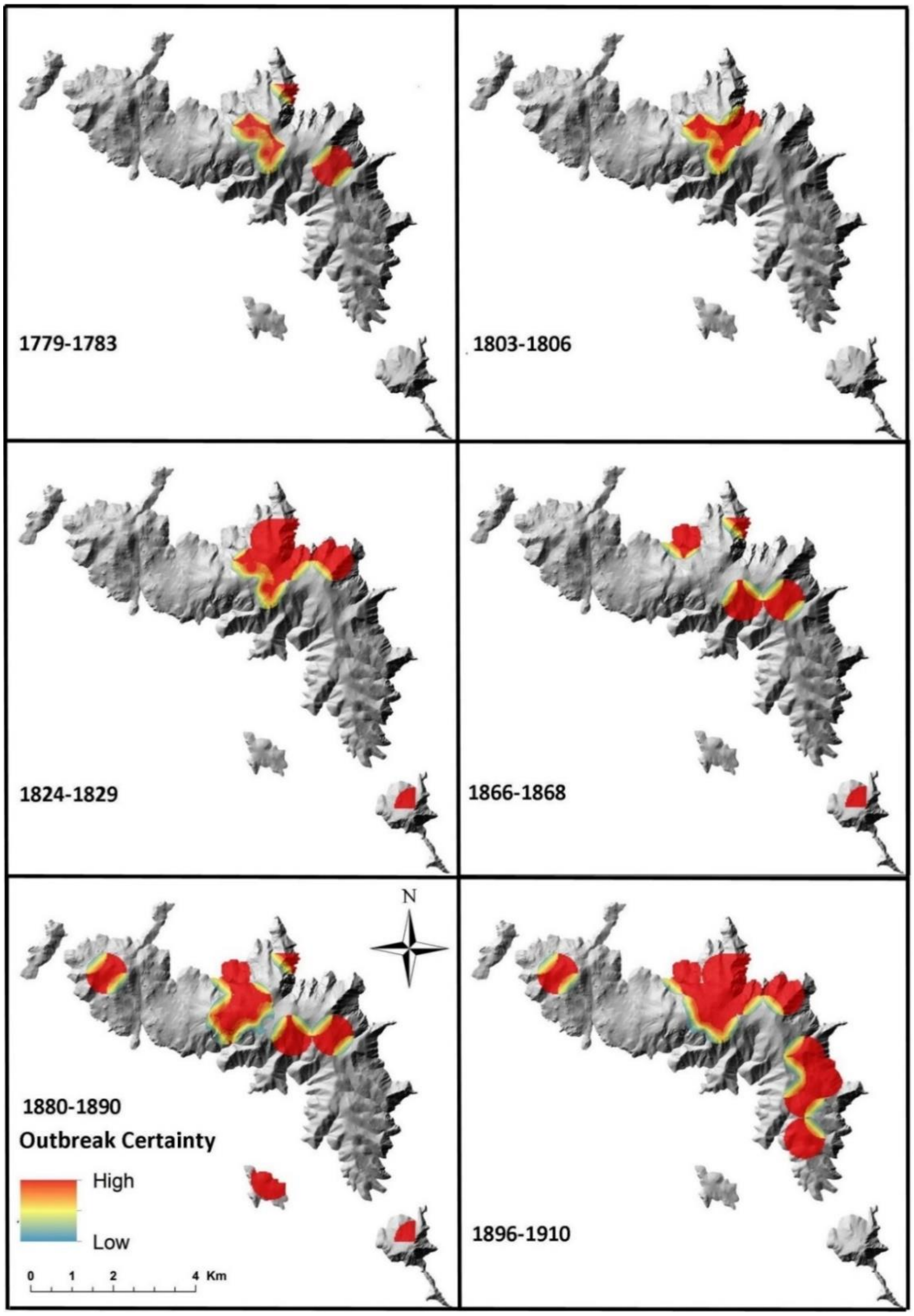


Figure 5. Multiproxy reconstructions of spruce beetle outbreaks in the Pinaleño Mountains 1700-2008. (a.) Bark beetle failed attack scars within individual growth rings of surviving trees. (b.) The outer growth ring of beetle killed trees. (c.) Index plot of 34 composited site records recording growth release; the dashed horizontal line indicates 25% of sites (used to differentiate outbreaks from other ecological factors). The earliest growth release attributed to spruce beetle outbreak is in 1779 with nine sites (26% of sites) containing spruce. (d.) Site-level record of growth release events occurring in two or more trees over a 5-year period.


1779-1783
1803-1806
1824-1829
1866-1868
N
1880-1890
Outbreak Certainty
High
Low
0
1
2
4 Km
1896-1910

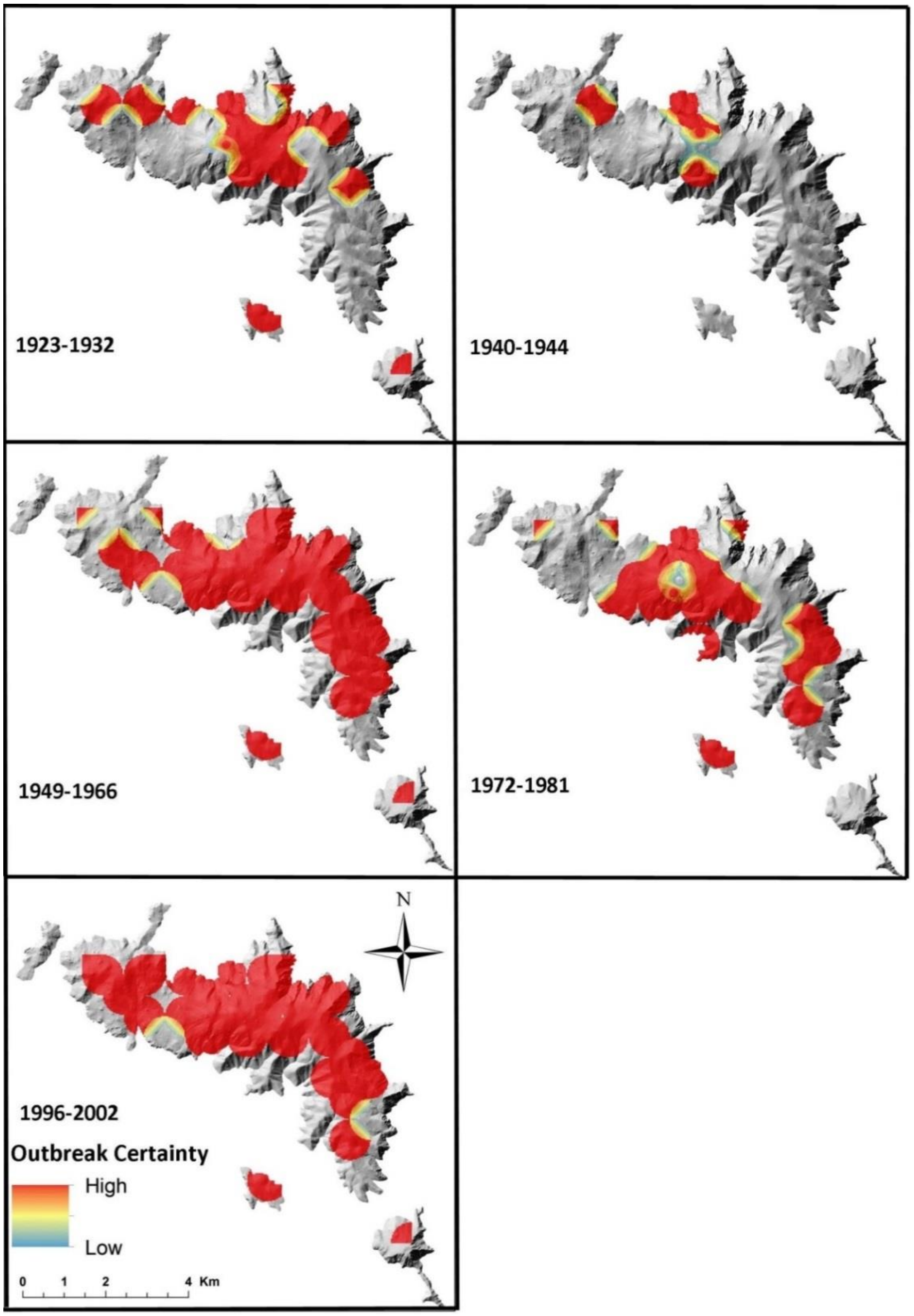


Figure 6. Spatial progression of spruce beetle outbreaks recorded in 25% or more of sites from 1779-1996. Outbreak events are reconstructed from growth releases detected in a minimum of 10% of trees over a five-year period at each of 34 spruce-containing sites. Interpolated outbreak certainty surface is based on inverse distance weighting of four nearest point locations with a power function of two. The underlying surface is the spruce extent in the Pinaleño Mountains circa 1995.

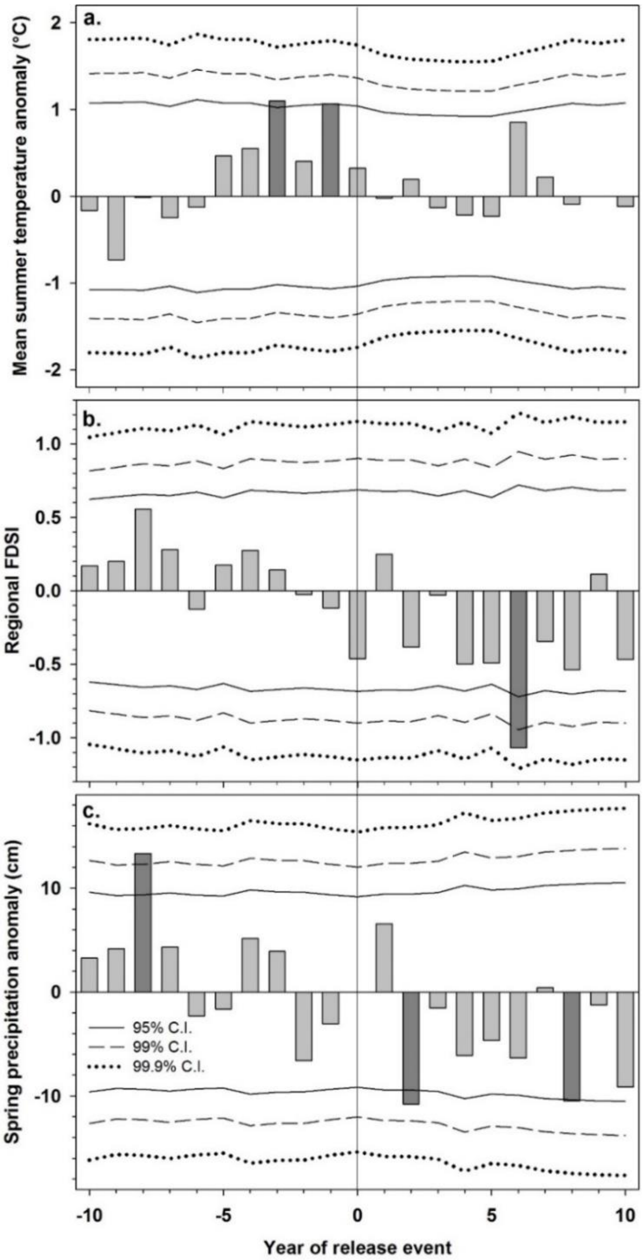
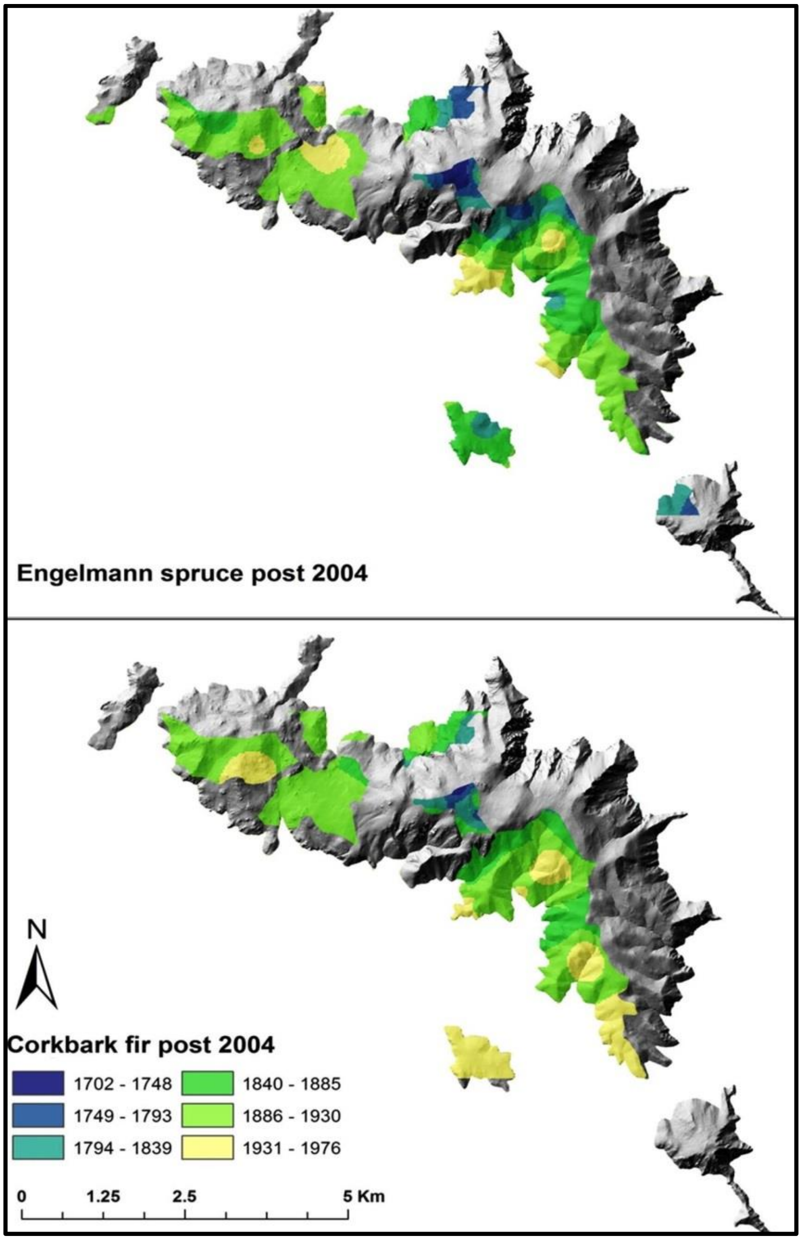


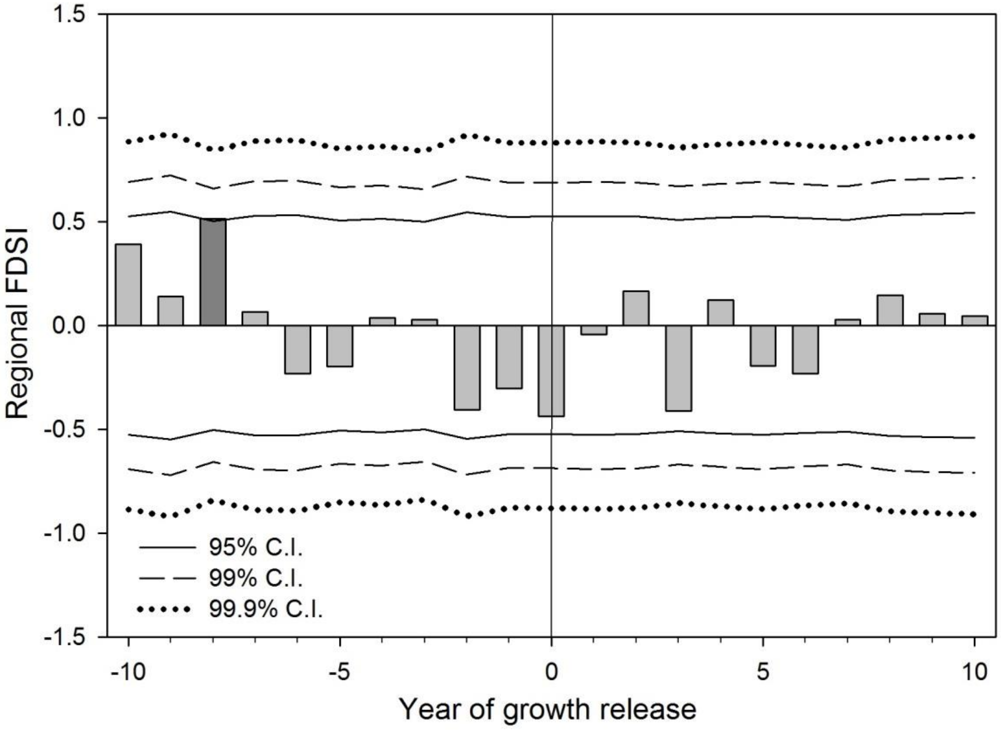
Figure 7. Associations between spruce beetle outbreaks and seasonal climate variables for 1896-2008, as determined with superposed epoch analysis. (a.) June-August maximum temperature anomaly in relation to initial growth release, (b.) Regional Forest Drought Severity Index (Williams et al. 2013) in relation initial growth release, and (c.) January-June precipitation anomaly in relation to initial growth release. The vertical line at year zero indicates the year for which 25% or more of sites were experiencing growth release. Bars to the left of this line relate to the years prior to 25% of stands experiencing growth release, while bars to the right are after that time reference. The dark bars are statistically significant deviations from 114-year mean value of the climate series.

Supplemental Materials


Engelmann spruce post 2004

Corkbark fir post 2004

Supplemental Figure 1. Post-2004 age distribution of Engelmann spruce and corkbark fir. Interpolated establishment date surface is based on inverse distance weighting of minimum tree establishment dates from 44 gridded point locations. Interpolation algorithm uses four nearest point locations with a power function of two. The majority of remaining spruce and corkbark fir established after the onset of fire exclusion in 1880 in areas with historical fire frequencies incompatible with primary species of the spruce-fir ecosystem.



Supplemental Figure 2. Association of six spruce beetle outbreaks with regional Forest Drought Severity Index 1770-1896. Year zero is the year of detection of growth release. Negative FDSI values are not significant but are persistent prior to and shortly after outbreak detection. The short period of elevated forest drought stress (negative values) before and after outbreak detection may be related to shorter outbreak intervals prior to 1900. Ecological significance of the favorable growth period eight years prior to outbreak are is not known.

APPENDIX C

SITE PRODUCTIVITY MEDIATES STABILITY OF SPECIES ASSEMBLAGES FOLLOWING FIRE EXCLUSION

Site productivity mediates stability of species assemblages following fire exclusion

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O’Connor, C.D., D.A. Falk, A.M. Lynch, T.W. Swetnam, C.P. Wilcox. Site productivity mediates stability of species assemblages following fire exclusion. ***To be submitted to*** **Ecology**

Abstract

Dry inland forests of the southwestern U.S. have transformed from open, fire-adapted landscapes to dense, competition-mediated forests during a century of fire exclusion. Recently fire has returned to many southwestern landscapes in the form of large, high-severity events that raise concerns about forest resilience and the future of forested landscapes in this region. Changes to forest species and structure are variable across gradients of forest type and site productivity. Here we document the conversion from fire-mediated to competition-mediated seedling recruitment immediately following fire suppression across a productivity gradient of pine, dry and mesic mixed-conifer, and spruce-fir forest types. Low and high productivity sites were the most stable in terms of species composition immediately following fire exclusion and for the next 100 years, although stem densities increased significantly in low productivity sites. Moderate productivity mixed-conifer forest was the least stable forest type following fire exclusion. Primary seedling recruitment in these forests shifted from fire-adapted to shade-tolerant, competition-adapted species within 20 years, resulting in extreme shifts in species composition and structure over the following century. Although the mixed-conifer ecosystem is currently the most altered forest on this landscape, historically, fire maintained this forest type well below its maximum stocking potential, providing a

degree of drought and fire resistance that did not exist in lower and higher productivity forests.   Aggressive efforts to return fire-adapted forest structure and species to mixed-conifer forests have the potential to restore resilience to this system in the face of projected increases in drought and fire conditions.

Introduction

The onset of fire exclusion in the western United States began one of the largest and most effective landscape ecology experiments in human history. From the mid to late 19th century onward, exclusion of fire caused extensive structural and species changes, especially in mid-elevation pine and mixed-conifer forests of western North America (Swetnam et al. 2001, Minnich et al. 1995, Bahre 1991) . The legacies of these changes transformed how these forests now respond to natural and anthropogenic disturbances (Allen et al. 2002, Fulé et al. 2004b, Moore et al. 2004, Fulé et al. 2009). Over the past two decades, fire exclusion practices have begun to fail as a century of accumulated ecosystem changes, particularly increased fuel loads and stand densities, contribute to a trend of more frequent high-severity wildfires (Minnich et al. 1995, Miller et al. 2009, Scholl and Taylor 2010, Miller et al. 2012). At fine scales, fire exclusion led to infilling of the understory by fire-sensitive seedlings and shade-tolerant species, resulting in high fuel loads with vertical connectivity (Allen et al. 2002, Taylor 2001, Fulé et al. 2009). At coarse scales, loss of structural heterogeneity contributed to crown fire spread, creating the potential for a larger high-severity burn footprint than occurred with fires in the pre-suppression period (Parsons and DeBenedetti 1979, Miller et al. 2012). These changes to forest structure, species composition, and fire behavior affect forest resilience, long-term stability, and adaptability to the higher temperatures and reduced precipitation amounts that are predicted in climate projections (Cocke et al. 2005, Fulé et al. 2003b, Seager et al. 2007, Fulé et al. 2009, Allen et al. 2010, Williams et al. 2010, Williams et al. 2013).

Forests of the Southwest U.S. are particularly prone to changes in fire behavior as a result of altered forest structure and species assemblages because multiple forest types coexist at close proximity due to topographic relief. Structural and species changes that affect fire behavior and longer term stability of forest assemblages are driven by patterns of seedling recruitment. Shifts in recruitment patterns can be sudden, following a major stand replacing event, or delayed, through competitive interactions among long-lived and niche-adapted species (Chesson and Warner 1981, Suding and Hobbs 2009). Frequent disturbances affecting seedlings but not overstory seed sources, such as ground fires in western forest, function as a selection mechanism for fast-growing seedlings adapted to abundant resources redistributed by fire. Interruption of frequent disturbances causes a shift in selective mechanism toward stable competition-adapted seedling recruitment. Shifts in understory seedling recruitment occur on much shorter time scales than shifts in overstory species. While these shifts may not affect the species and disturbance trajectory of the system over the short term, persistent interruption of disturbance, such as the 20th century legacy of fire exclusion, can cause the system to cross a hysteretical threshold (May 1977) requiring a disproportionate increase in ecosystem inputs (such as fuels treatments) prior to reintroduction of disturbance (fire) or risk conversion to a degraded alternative state (Turner 2010).

Species and structural characteristics of current southwestern forests are relatively well characterized (LANDFIRE 2012, Miles et al. 2001, USFS FIA 2013) and several studies have compared pre-fire exclusion stand conditions to present conditions (Fulé et al. 1997a, Taylor 2001, Moore et al. 2004, Heinlein et al. 2005, Fulé et al. 2009). However, little work has been done to characterize the changes to seedling recruitment that occurred immediately after fire exclusion. Patterns of seedling recruitment in the decades that followed early 20th century fire exclusion set the successional and fire behavior trajectory for current forests. Differences between seedling recruitment patterns before and after fire exclusion can thus help to elucidate the ecological role of fire in maintaining past species assemblages and how forest structure and species recruitment shifted from disturbance-mediated to competition-mediated controls.

Patterns of seedling recruitment and survival vary considerably with fire frequency. Under frequent fire conditions, the persistence and longevity of mature trees, physiological adaptations to survive fire, continuous seed production, and the ability of seedlings to establish during fire-free intervals contribute to the stability of species assemblages (Clark 1996). Seedling survival after establishment is limited by site productivity, variability in temperature and precipitation, resource competition, and frequency and severity of subsequent fires (Barton et al. 2001, Larocque et al. 2000, Johnstone and Chapin III 2006). Herbivory in western forests tends to promote conifer seedling survival (Belsky and Blumenthal 1997). In systems that experience less frequent fire, timing of seedling recruitment is important because initial recruits tend to dominate forest basal area for several centuries (Kneeshaw and Burton 1997). In the absence of fire or other disturbance, competition for water, nutrients, and sunlight are the primary controls on seedling survival (Atzet and Waring 1970, Mitchell 2001, Plamboeck et al. 2008). In these systems, species succession allows early- and late-seral species to coexist for decades or centuries of recruitment, conferring a degree of stability to the system (Shea 1985, Veblen 1986, Aplet et al. 1988).

In this study we use the abundance and species composition of seedling recruitment following the start of fire exclusion to characterize the rate of conversion from disturbance-mediated to competition-mediated seedling recruitment along a gradient of site productivity. Throughout this paper we refer to primary species as those existing in a stand prior to fire exclusion and secondary species as those that successfully establish and persist in a stand only after fire exclusion. The process of species conversion begins with the successful recruitment of secondary species and continues until secondary species dominate seedling recruitment (Figure 1). The 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 in the period immediately following fire exclusion. Stability of species assemblages before, immediately following, and decades after fire exclusion is a proxy for forest dependence on fire and potential changes to future fire behavior and assemblage recovery with subsequent reintroduction of fire. We propose that stability of species assemblages following fire exclusion is a function of site productivity. Assemblages adapted to low productivity sites with high fire frequency should quickly monopolize limited resources after fire to maximize reproductive success during short fire-free intervals, resulting in inhibition of secondary species encroachment (Davis et al. 2000). Assemblages adapted to high productivity sites with infrequent fire are already excellent resource competitors and should also be resistant to encroachment by secondary species. Between these two extremes are forests that should be most vulnerable to conversion, where frequent fire maintained species and structure consistent with lower productivity sites (Figure 2). Thus a change in seedling recruitment from primary to secondary species would constitute a shift from disturbance to competition-mediated control of seedling establishment with ramifications for longer-term community stability (Frelich and Reich 1999). Here we test the role of site productivity in determining species assemblage stability following fire exclusion.

Study area

To test this hypothesis we used a varied montane forest landscape in the Pinaleño Mountains of southeastern Arizona (Figure 3). The Pinaleño Mountains and nearby sky island ranges were central to the development of early theories about elevational gradients and local constraints on species distributions (Shreve 1922). The vertical distribution of vegetation in the Pinaleño Mountains is representative of interior western forest types along a latitudinal transect from Mexico to Canada and (Whittaker and Niering 1975, McLaughlin 1994). The study area above 2,135 m is comprised of montane conifer forest distributed along an elevational gradient of low to high productivity (Pelletier et al. 2013) and frequent to infrequent historical fire regime (Grissino-Mayer et al. 1995, Swetnam et al. 2009). Lower elevation pine-oak communities comprised 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 strobiformus* Engelmann), and ponderosa pine, with a minor component of white fir (*Abies concolor* (Gor. & Glend.) Lindl. ex Hildebr.) (Martin and Fletcher 1943). Above 2,750 m, precipitation and temperature regimes favor mesic mixed-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*) (Martin and Fletcher 1943). Above 3,000 m and along north-facing slopes, Engelmann spruce and corkbark fir become dominant forest species interspersed with occasional Douglas-fir (Figure 3).

Disturbance history

Fire was a relatively common occurrence in pine and mixed-conifer forests of the Pinaleño Mountains prior to Euro-American settlement of the area in the 1870s (Grissino-Mayer et al. 1995, Bahre 1991). A study from two sites near the center of the range reported median fire return intervals of 4.2 years in mixed-conifer forest, and more than 300 years in the nearby spruce-fir forest over the period 1575-1880 (Grissino-Mayer et al. 1995). The timing of initial fire exclusion was variable across the mountain range, depending on accessibility for livestock grazing, logging, and recreational use (Bahre 1998). The spruce-fir forest probably established after a stand-replacing fire in 1685 (Stromberg and Patten 1991, Grissino-Mayer et al. 1995, Swetnam et al. 2009, Margolis et al. 2011). After nearly a century without widespread fire and a series of extensive insect outbreaks, fires in 1996 and 2004 burned 14,367 ha of mixed-conifer and spruce-fir forest at moderate to high severity (O'Connor 2013), including more than two thirds of the former spruce-fir extent (Koprowski et al. 2005).

Methods

We established a systematic grid of 41, 0.05-ha circular plots spaced one kilometer apart to collect demographic and fire history information across the landscape. Trees ≥ 20 cm diameter at breast height (DBH) were sampled over the whole plot area; trees and saplings smaller than 20 cm DBH were sampled on a nested sub-plot equal to one third 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 need for sampling height correction of tree ages. Cross sections were taken from snags and stumps. Seedlings and saplings less than 1 cm DBH were sampled at ground level in the subplot and were tallied by species over the full plot area.

Fire-scarred material was collected from live trees, snags, and stumps within demography plots and while traveling among plots. Fire history information from the Grissino-Mayer et al. (1995) collection coincided with two of the 41 demography sampling locations and is included as part of the mountain-wide fire history reconstruction.

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 (Stokes and Smiley 1968), and statistical pattern matching (Holmes 1983, Grissino-Mayer 2001a). Pith dates were estimated on samples that did not include pith but with enough ring curvature to uses 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

Recruitment dates from trees with DBH smaller than 20 cm were normalized to equivalent density over the full plot area (Table S-1). Recruitment dates were binned by 5-year intervals to account for variability in age at sampling height. Species Importance Values (IV) were calculated for each demography plot by averaging the relative frequency and basal area of the six conifer species (Taylor 2001). We used Wards method of hierarchical clustering to group plots based on IV rankings (*hclust* package, (R Core Team 2012). Prior to clustering, IVs were transformed to Jaccard distance to minimize the effect of zeros in the dataset (McCune et al. 2002). Clusters computed for the year 1870 were used to determine pre-fire exclusion forest types, which were then tracked for changes through time.

Plot-scale fire histories were reconstructed from all fire-scarred material within 500 m of plot center. Onset of fire exclusion was determined for each plot by selecting the nearest fire date prior to continuous seedling establishment. To analyze demographic response in relation to fire date, tree establishment dates were scaled to the last recorded fire date within each plot before being pooled by forest type present in the year 1870.

Intervals from the start of fire exclusion to peak seedling recruitment and from fire exclusion to establishment of secondary species were calculated at each plot. A peak in primary species establishment was defined as the 5-year 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-year bins in which species not present during the pre-fire exclusion period established and persisted.

To test the effects of inter-annual precipitation and drought on seedling establishment, we plotted 5-year means of annual precipitation index for southeast Arizona (Griffin et al. 2013) and summer Palmer Drought Severity Index (PDSI) grid point 105 (Cook and Krusic 2004) against seedling establishment over the period spanning 100 years prior to and 100 years following fire exclusion (Figure S-2).

To estimate the frequency of fire occurrence at each plot location we used the Weibull median probability interval (WMPI) (Grissino-Mayer 1999, Sutherland et al. 2013) calculated from the composite record for all fires recorded within 500 m of a demography plot (Brown and Wu 2005, Falk et al. 2011). The WMPI is a robust measure of central tendency in distributions of fire intervals which are often skewed (Grissino-Mayer 1999, Falk 2004) and provides an index of fire interval as an independent variable in analyzing changes in species selection and seedling recruitment. If no fire-scarred material was recovered within 500 meters of a demography plot but information was available for two or more adjacent plots, WMPI was interpolated from surrounding plot locations.

Fire-recruitment relationships

Time to secondary species establishment along the gradient of site productivity was used to test the hypothesis that conversion from disturbance-mediated to competition-mediated recruitment is greatest in moderate productivity sites (Figure 2). Short time interval to secondary species establishment indicates rapid conversion from primary to secondary species, low assemblage stability, and high dependence on fire to determine the composition of the species assemblage. Longer time to secondary species establishment indicates greater assemblage stability and reduced influence of fire on species selection. To determine if a bimodal distribution could be used to explain the species-stability to site productivity relationship, a cubic polynomial was fitted to the scatter plot of time to secondary species establishment vs. EEMT.

Site productivity

Effective energy and mass transfer (EEMT), a pedogenesis measure derived from precipitation, temperature, and vapor pressure deficit (Rasmussen et al. 2011, Chorover et al. 2011), was used as an independent proxy for site productivity. EEMT, expressed in megajoules per m^{-2} yr^{-1}, is correlated strongly with terrestrial biomass (Rasmussen et al. 2011). EEMT 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 to 2009 (Pelletier et al. 2013).

To test the relationship between 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 all sites in the year 1870 (De'Ath 2002) (Figure S-1). The Hellinger transformation is robust to zero-inflated data and is back-transformable to retain individual species' contributions to tree splits (Legendre and Legendre 1998). To quantify the changes within forest types over time, we used a nonparametric multivariate test of dispersion in the program PermDisp2 (Anderson 2004) to test for changes in dispersion of the Jaccard distance-transformed IV matrix at three time steps. We used pairwise t-tests to determine the significance of changes to the dispersion (centroids and median values) of IVs in low, moderate, and high productivity sites in 1870, 1955, and 1995 (Table S-2). Site productivity groups were defined by the 1870 classification of plots based on EEMT (Figure S-2). Paired *t*-test statistics and *p*-values were based on 4999 permutations of IV and site productivity values. To account for possible Type 1 error as a result of multiple pairwise tests, a conservative Bonferroni correction equal to α/3 was used to determine significance of *p*-values (Gotelli and Ellison 2004).

The distribution of species assemblages in projected species space in the year 1870 was compared to assemblages in 1955 and 1995 with nonmetric multidimensional scaling (labdsv package, R Core Team 2012). The IV matrix at each time step was transformed to Jaccard distance and projected in two dimensions with a gradient of EEMT fit to the solution for reference to site productivity.

Results

Fire exclusion was a variable process over about 30 years starting in wet high-productivity sites as early as 1864 and in dry low-productivity sites as late as 1901. 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 (Table S-3). Five sites in the mixed-conifer forest had historical WMPI values much higher than surrounding forests with similar EEMT values, suggesting that local topography limited the ability of fire to spread into these “fire-sheltered” stands. For demographic analysis, these forests were grouped 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.

Pooled seedling establishment dates indicate that the initial pulse of seedling recruitment associated with the start of fire exclusion coincided with a 30-year period of below-average precipitation in the late 1800s (Figure S-2). Establishment continued through a 30-year period of above average precipitation, reaching a peak in the 1930s. Following the pluvial (wet) period seedling recruitment persisted through an additional 40-years of below-average precipitation at a rate 3-6 times greater than in the pre-fire exclusion period (Figure S-2). Seedling recruitment was not significantly associated with the 5-year average of climate indices over the entire period of study (linear regression of recruitment on precipitation $R^2=0.01$, $p>0.46$), indicating that climate controls were much less important than fire regime interruption.

In the century following fire exclusion, stability of forest assemblages varied widely along a gradient of forest productivity. Low productivity forests dominated by ponderosa pine in 1870 were still pine-dominated in 1996, and fewer than half of plots contained secondary species after a century of fire exclusion. Recruitment pulses in these stands peaked in the first decade following fire regime disruption and then declined nearly as abruptly (Figure 4a). Stem densities increased rapidly for the first 25 years after fire exclusion, after which additional recruitment occurred only after additional fires, and the pine-dominated species assemblage remained intact.

Moderate productivity mixed-conifer sites were the least stable species assemblages following fire exclusion. In these forests, conversion from primary to secondary species began shortly after the median fire return interval of 9.2 years was surpassed, and continued for another 60 years (Figure 4b). Over this period seedling recruitment and increased stem density rates remained relatively constant. Within five decades of fire exclusion, stem densities were highest in moderate productivity dry mixed-conifer forests; however the time to peak recruitment was considerably longer (50 years) than in lower productivity pine-dominated sites (15 years).

Higher productivity mesic mixed-conifer (Figure 4c) and fire-sheltered mixed-conifer (Figure 4d) sites were more resistant to assemblage conversion. Both forest types eventually developed significant understories of more shade tolerant species, and recruitment in 25% of Douglas-fir-dominated mesic mixed-conifer sites switched to secondary species within 60 years (Figure 4c). Median tree densities increased 18 fold in mesic mixed-conifer sites and 11 fold in fire-sheltered white fir-dominated sites during the century of fire exclusion (Figure 4 c and 4d).

The high-elevation cool, moist, high productivity spruce-fir forest did not exhibit a post fire-exclusion shift in recruitment (Figure 5). Species dynamics in these sites correspond to establishment after the stand replacing fire in 1685 followed by more than 250 years of periodic disturbance and seedling recruitment unrelated to fire. 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 a bark beetle outbreaks and other smaller scale disturbances (Schmid and Hinds 1974, Veblen et al. 1991a, O'Connor 2013).

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 secondary species did not successfully establish in more than half of sites in the century following fire exclusion (Figure 6). Average time to secondary species establishment was lowest (15 years) in moderate productivity dry mixed-conifer forests, followed by mesic mixed-conifer (40 years) and fire-sheltered mixed conifer (60 years) sites (Figure 6).

Dispersion of forest type groupings in IV space, a proxy for variability within forest types, was not significantly different in the years 1870, 1955 and 1995 in the high and low site productivity classes (Table S-2). In contrast, moderate productivity sites underwent significant change from 1870 to 1955 and 1870 to 1995 ($p<0.001$, Table S-2).

Changes to the IVs of individual plots and forest types reflected changes to dispersion along the gradient of EEMT (Figure 7). Pine-dominated sites exhibited almost no change in species from 1870-1995 in the lowest productivity sites and some shift in species in the more moderate-productivity sites. Dry mixed-conifer sites were tightly clustered in 1870 but were much more dispersed by 1955 and continued to disperse through 1995. Spruce-fir, mesic mixed-conifer, and fire-sheltered-mixed conifer sites had the least amount of spatial dispersion through time in the highest EEMT sites and showed some evidence of dispersion down the gradient of EEMT toward moderate productivity sites.

Discussion

Prior to the period of fire exclusion, fire functioned as a strong control on seedling establishment and survival in all but the highest productivity sites. Under historical surface fire return intervals of 3-10 years, post-fire seedling recruitment increased linearly between fires. In a prolonged fire-free period, recruitment eventually reached a saturation point in which the space available for seedling growth of the primary species assemblage was filled. Occurrence of fire during the period of continuous recruitment or near the point of seedling saturation would promote system resilience by returning the forest to its pre-fire state. However, under continuous fire exclusion, seedling recruitment switches from the primary species assemblage to secondary species that can fill previously unoccupied niche space. This second wave of seedlings may alter system resilience by changing species composition and forest structure in a way that alters the behavior of future fires (Stephens and Moghaddas 2005) and selects for species adapted to competition on sites ultimately subject to increasing fire frequency (Seager et al. 2007, Flannigan et al. 2009, Fulé et al. 2009, Crimmins 2011).

Lowest productivity sites tended to experience the most frequent fire, reached peak seedling recruitment within the median fire return interval, and were among the least likely to undergo conversion to secondary species. Similarly, high productivity sites experienced the least frequent fire return intervals and had a low likelihood of conversion to secondary species.

Species assemblages in which the interval to peak seedling recruitment is shorter than the interval to seedling-killing disturbance tend to be the most ecologically stable (Clark 1996). In this study, the lowest productivity pine sites and the highest productivity spruce-fir sites tended to reach peak seedling recruitment within their respective median fire return intervals. In pine dominated sites, low site productivity and reduced moisture availability confer a degree of resistance to invasion by shade-tolerant secondary species. In spruce- and fir–dominated sites, high site productivity, extreme shade tolerance of the existing dominants, and infrequent seedling-killing disturbance make this assemblage highly resistant to invasion by secondary species. Moderate-productivity dry and mesic mixed-conifer sites underwent the most significant conversion from fire-mediated to competition-mediated species assemblages. Within the mixed-conifer forest, mesic Douglas-fir- and white-fir-dominated stands were the most resistant to secondary species recruitment. Dry mixed-conifer forests comprised of a mix of southwestern white pine, ponderosa pine, and Douglas-fir, were more susceptible to conversion to secondary species.

Conversion from disturbance-adapted to competition-adapted forest types followed two distinct mechanisms. The widespread recruitment of white fir into moderate productivity sites following fire exclusion represents the local expansion of a population that persisted at low numbers in fire refugia and along riparian corridors during the pre-fire exclusion period (Burns and Honkala 1990). These populations were suppressed by frequent fire, and recruited into forests whenever there was a prolonged fire-free interval. This locally persistent population was able to quickly establish seedlings over broad areas following the exclusion of fire. Lower productivity pine-dominated sites did not support local populations of white fir, making these sites considerably more resistant to forest conversion. The second form of forest conversion represents a migration of species from higher productivity sites, where fire was historically less frequent, into surrounding forest types following fire exclusion. Wave form-type succession (Frelich 2002) was identified by Cocke et al. (2005) in the San Francisco Peaks of northern Arizona where Engelmann spruce seedlings from upper elevation forests eventually expanded into previously mixed-conifer forest over several decades. This mechanism explains the eventual expansion of spruce and corkbark fir into mesic and dry mixed-conifer forests of the Pinaleño Mountains following fire exclusion.

Forest restoration in the southwestern United States has been driven primarily by concerns about structural changes to ponderosa pine and other dry forest types (Covington et al. 1994, Covington and Moore 1994, Swetnam et al. 1999) that affect fire behavior, and the effects of warming and drying temperatures on habitat suitability for subalpine forest types (Notaro et al. 2012). Until recently, less attention has been given to restoration of mixed-conifer forests (but see Evans et al. (2011) and Reynolds et al. (2013)), a type that in topographically diverse southwestern landscapes may be most responsible for the increased size and severity of recent forest fires (Miller et al. 2009). Structural and species changes in mixed-conifer systems increase canopy closure, ladder fuels, and the likelihood of high-severity fire (Stephens and Moghaddas 2005). Swetnam et al. (2009) discuss the role of natural heterogeneity of forest structure and species assemblages along steep vertical gradients in sky island systems in creating a fire buffer around spruce-fir ecosystems. Loss of heterogeneity in the mixed-conifer forests surrounding the spruce-fir ecosystem allowed fires in 1996 and 2004 to breach the fire buffer that had been in place for more than 300 years, burning into and across most of the spruce-fir forest. The loss of structural heterogeneity in mixed-conifer forests throughout the Southwest poses a major challenge for limiting the size and severity of future fires.

Restoring mixed-conifer forests to fire-adapted species composition and structure could also increase the resilience of these montane forests to changing temperature and precipitation regimes. Moderate-productivity sites maintained at a level below their maximum stocking potential through fire or mechanical thinning are less likely to experience significant tree die-off during prolonged drought or extreme heat (McDowell et al. 2007, McDowell et al. 2008), and may be less susceptible to defoliator outbreaks (Carlson et al. 1983, Swetnam and Lynch 1993, Muzika and Liebhold 2000). Lower and higher productivity sites supporting forests where tree densities are closer to their biological limits, are most vulnerable to climate-induced mortality. Low productivity forests will be more affected by recurrent drought (Allen et al. 2010, Williams et al. 2013) and higher productivity forests may be more likely to experience stand-replacing fire (Westerling et al. 2011). While pine and spruce-fir species assemblages were least affected by fire exclusion, they may be most vulnerable to expected changes to climate patterns in the Southwest U.S. Fire will be an important part of this vulnerability if continuous fuels allow it to spread across long ecological gradients. Returning heterogeneity to forest structure and fire to low and moderate productivity sites may be the best option to mitigate some of the effect of a warmer, dryer future.

Application to forest management

Documenting the timing and conditions associated with forest change as a result of fire exclusion is an important part of creating science-based restoration prescriptions that prioritize the risk of crown fire and deviation from historical stand conditions (Falk 2006). Allen et al. (2002) described 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 structure and the use of controlled burns to maintain ecological function in pine-dominated forests have been implemented successfully across the southwestern U.S.

(Pollet and Omi 2002, Covington et al. 1997, Fulé et al. 2004a, Stephens and Moghaddas 2005, Van Mantgem et al. 2011) although determining the rotation of additional treatments is problematic. Reliance on historical WMPI may not be appropriate under contemporary forest and climate conditions and simulating the high frequency of historical fires may be impractical for planning and budgeting considerations. Basing treatment rotation intervals on the rate of forest change after fire may be a more practical option. EEMT can be computed at broad spatial scales (Rasmussen et al. 2011) and may be useful to guide the timing of subsequent controlled burns, wildland fire use, or additional thinning operations following initial restoration. Under a site-productivity-based management scheme, pine and mixed-conifer-dominated forests with higher EEMT values would receive higher treatment priority based on their ability to accumulate fuels and increase canopy connectivity at a higher rate than lower productivity sites. Fire itself may be the most effective restoration tool to retain species assemblages and structure most adapted to future fire (Hunter et al. 2011, Fulé et al. 2012, Korb et al. 2012).

In a series of recent reconstructions of fire severity in dry inland forests of the western U.S. (Sherriff and Veblen 2007, Sherriff and Veblen 2006, Heyerdahl et al. 2011, Williams and Baker 2012b), combinations of fire-scar evidence and cohort structure within forested plots was used to indicate the relative frequency and severity of past fires. In these studies, identified cohorts of trees were used as evidence for mixed- or ‘higher”-severity fire events. In some cases tree cohorts were the primary evidence presented for a complete change of forest restoration policy and argument that current fire events are within the range of natural variability for pine and mixed-conifer fire events (Sherriff and

Veblen 2007, Williams and Baker 2012a, Williams and Baker 2012b); however, see Fulé et al. (2013) for a rebuttal of Williams and Baker's papers by 19 fire scientists.

In the present study we demonstrate that lack of fire can be a strong a driver of cohort formation in fire-adapted landscapes. Specifically, on low and moderate productivity sites where fire is the primary limiter of seedling survival and stem density, it is appropriate to examine climatic or other factors that may have temporarily interrupted the fire regime. It is possible that some of the cohorts detected in previous studies can be attributed to temporary fire exclusion instead of high-severity fire; a finding supported by Brown and Wu (2005) where cohorts of mature ponderosa pine in southwest Colorado were associated with pluvial conditions that temporarily excluded fire from the landscape.

Understanding the complex interactions between fire, forest dynamics, and climate is necessary to provide the best available science for restoring resilience to western forests. Twentieth century fire exclusion in the American West provided a set of conditions that helped to identify the interactions between disturbance events such as fire, and conditions at the site level that determine the structure and species composition of forest assemblages. Applying this understanding to guide management and to adapt to dynamic forest conditions will be essential to maintain healthy, functional ecosystems.

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Figures

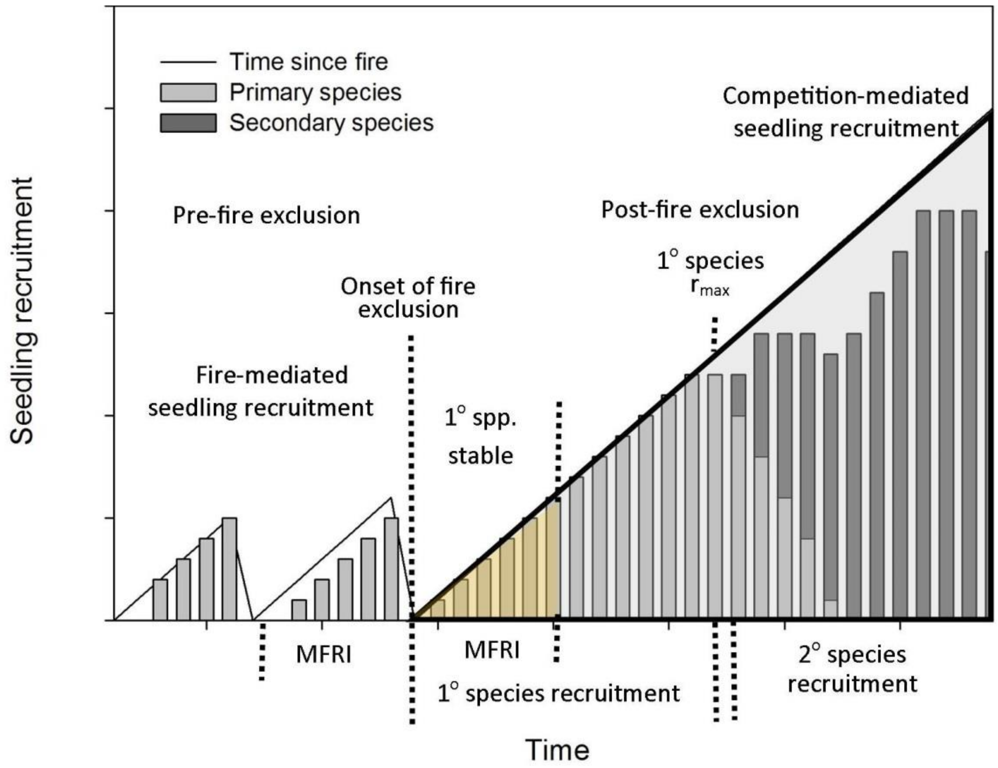

Figure 1. Graphical model of transition from fire-mediated to competition-mediated seedling recruitment as a result of fire exclusion. MFRI is the Weibull median probability interval (Grissino-Mayer 1999). Maximum recruitment of primary species (1^{o} species r_{max}) and secondary species recruitment (2^{o} species recruitment) are measured from the onset of fire exclusion.

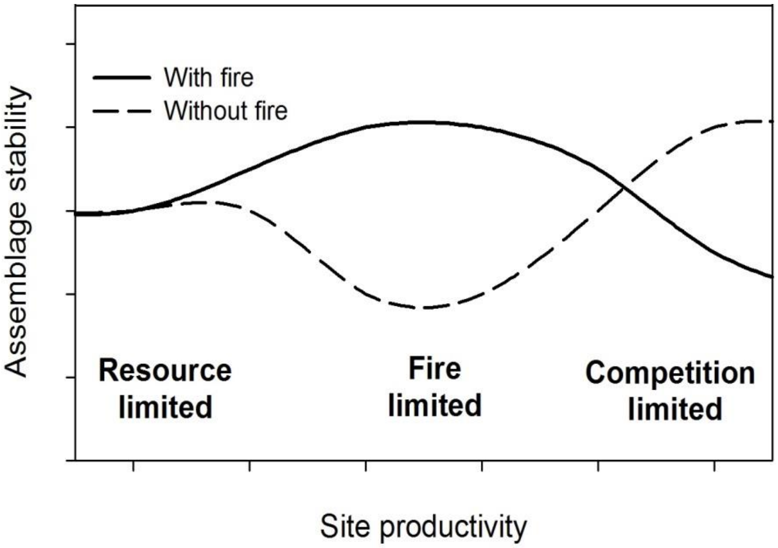

Figure 2. Theoretical relationship between forest assemblage stability and site productivity with and without fire. Assemblages adapted to limited resources or competition are least affected by fire removal. Fire-limited systems shift most quickly toward competition-mediated species assemblages. Assemblage stability with fire is represented by a unimodal quadratic function. Assemblage stability without fire is represented as a bimodal polynomial function.

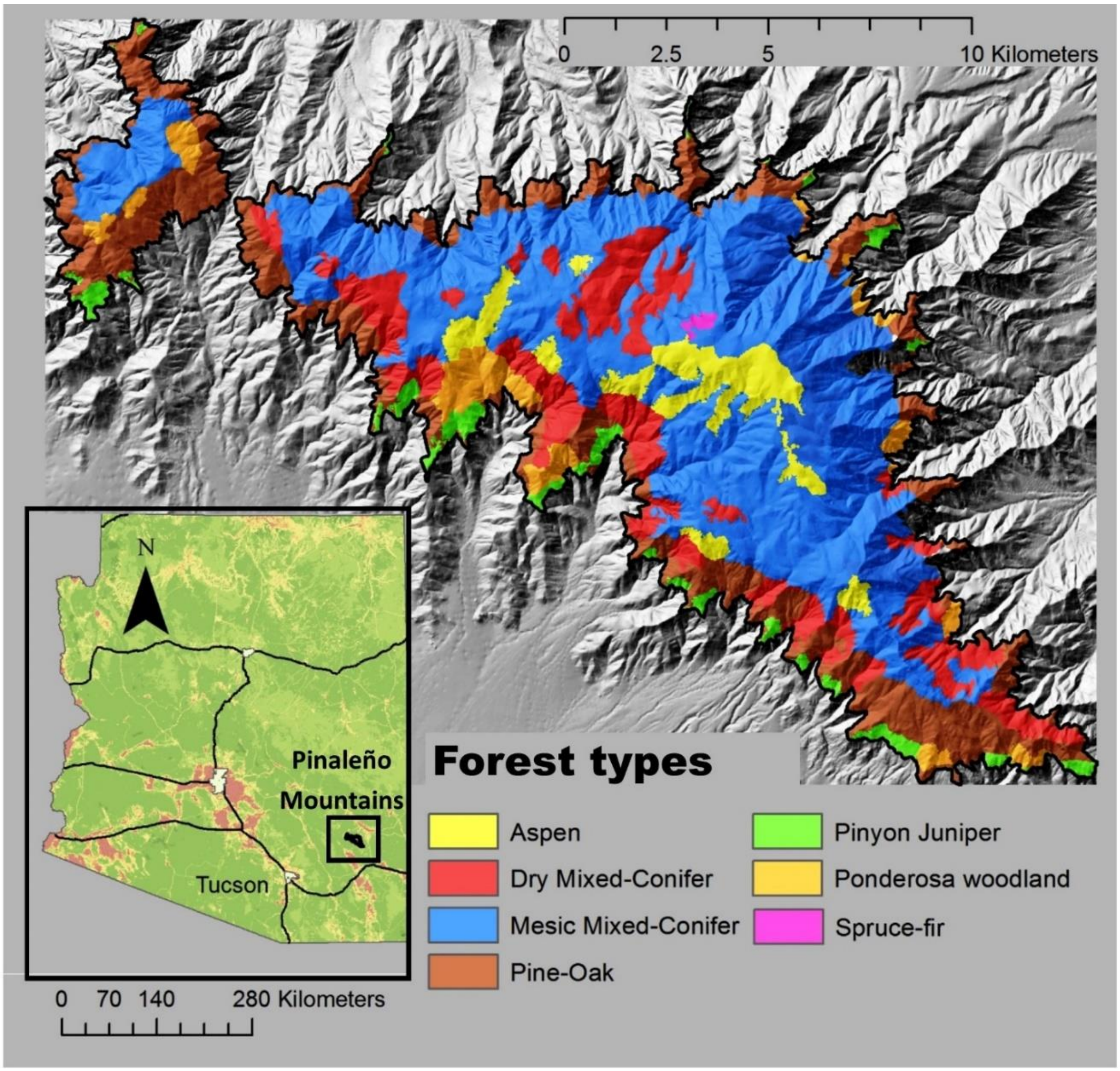

Figure 3. Vegetation of the Pinaleño Mountains above 2,135 m. Distribution of vegetation varies by elevation and aspect. Pine-oak woodlands near the lower elevation limit abut dry and wet mixed-conifer forests along the elevation gradient leading to the central high-elevation spruce-fir forest, much of which is currently dominated by aspen and post-fire herbaceous vegetation. Data are reprocessed from LANDFIRE existing vegetation type rapid refresh 2008 (LANDFIRE 2012) with a minimum patch size of 6.75 hectares.

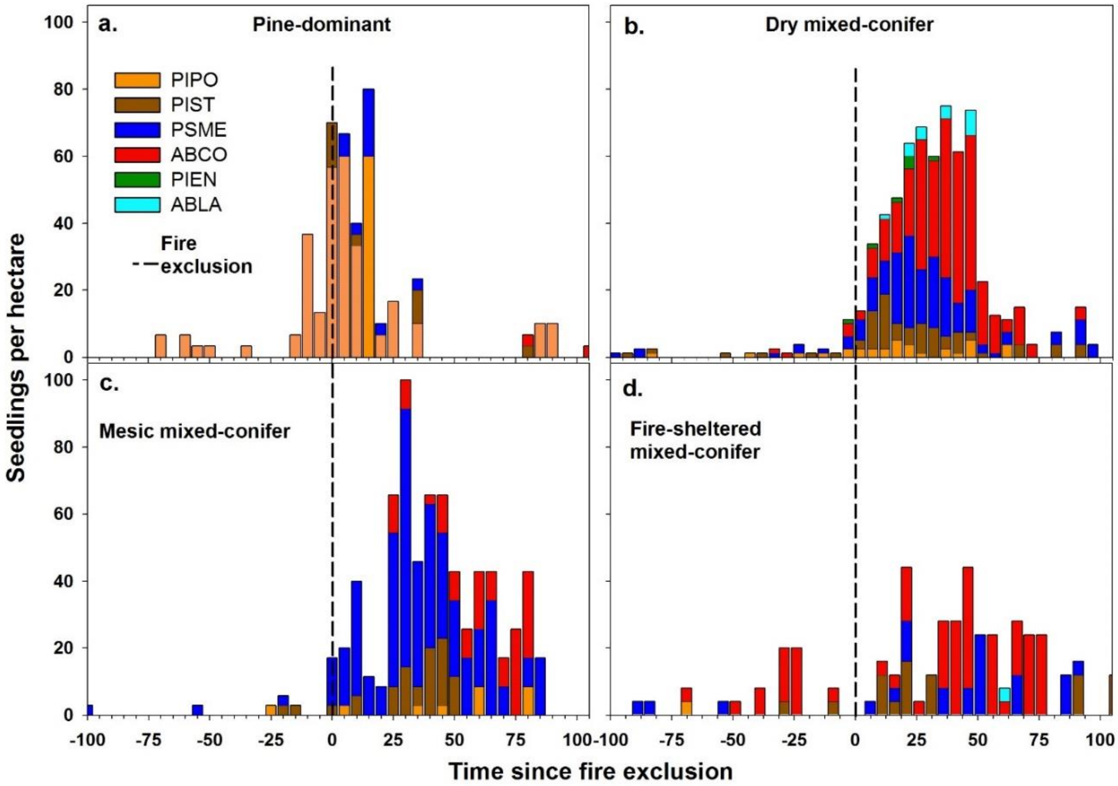

Figure 4. Patterns of seedling recruitment along a gradient of site productivity. Tree establishment dates are standardized to the start of fire exclusion within each plot (year zero). Four forest types are arranged from low to high site productivity: pine dominated, n=6 plots (a), dry mixed-conifer, n=16 plots (b), mesic mixed-confer, n=7 plots (c), and fire-sheltered mixed-conifer, n=5 plots (d). Species codes are: PIPO= ponderosa pine, PIST= southwestern white pine, PSME= Douglas-fir, ABCO= white fir, PIEN= Engelmann spruce, and ABLA= corkbark fir.

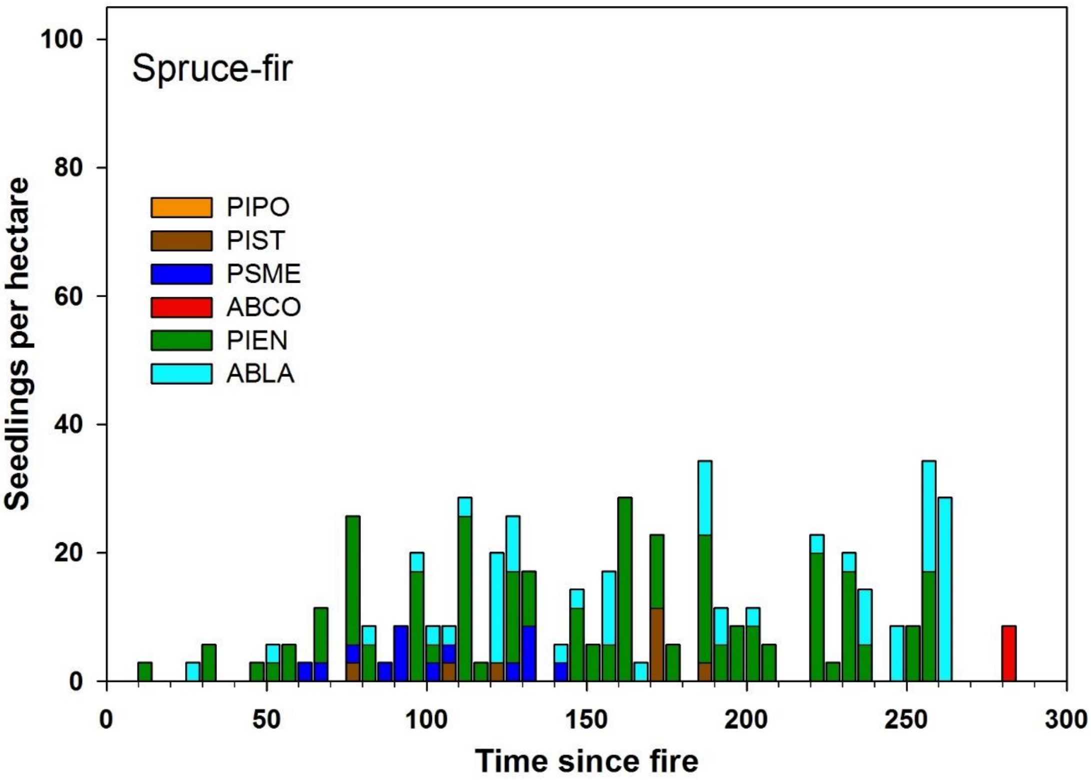

Figure 5. Seedling recruitment in high productivity spruce-fir forest. Year zero represents a stand replacing fire in 1685, fire exclusion in surrounding forest begins around year 195. N= 7 demography plots. Species codes are: PIPO= ponderosa pine, PIST= southwestern white pine, PSME= Douglas-fir, ABCO= white fir, PIEN= Engelmann spruce, and ABLA= corkbark fir.

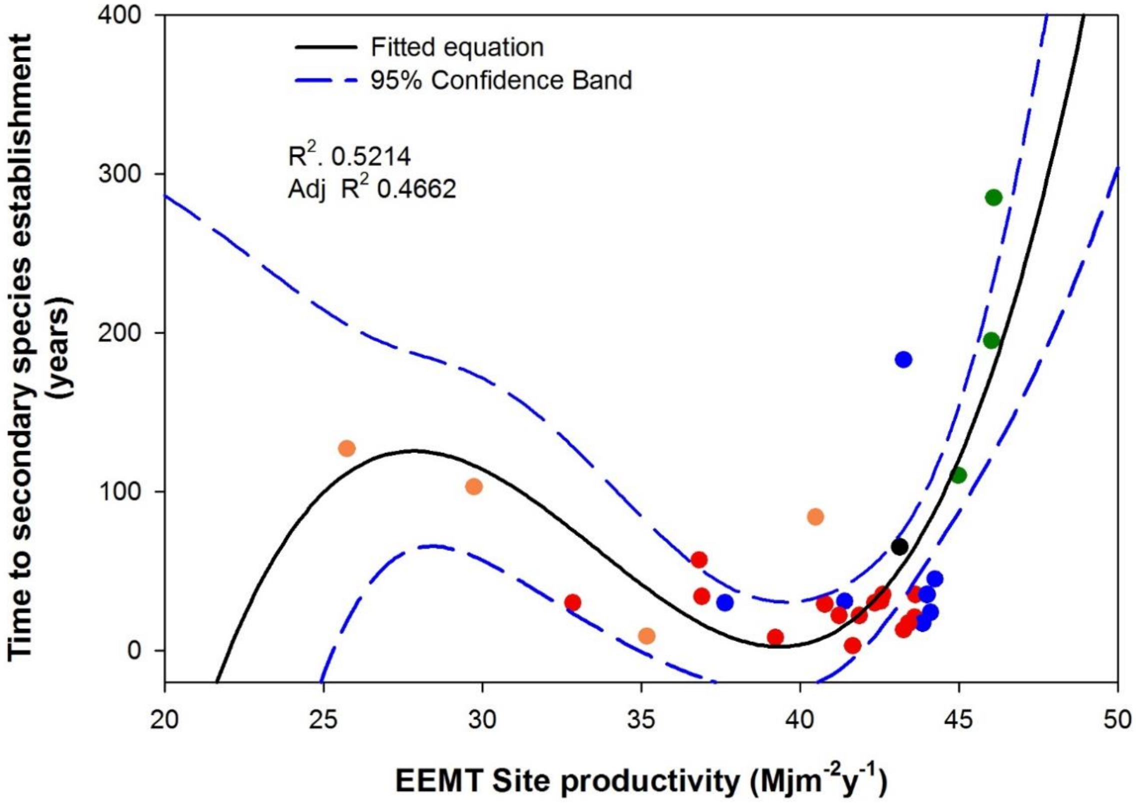

Figure 6. Time to secondary species establishment as a function of site productivity, based on 30 sites with secondary species establishment. The black line is the fitted equation explaining 52% of the variance in secondary species establishment with effective energy and mass transfer (EEMT); dashed blue line represents the 95% confidence interval. Dot colors represent forest type in the year 1870: orange = ponderosa pine, red = dry mixed-conifer, blue = mesic mixed-conifer, black = fire-sheltered Mesic mixed-conifer, dark green = spruce-fir. Polynomial fit represents the theoretical bimodal distribution of species stability following fire exclusion.

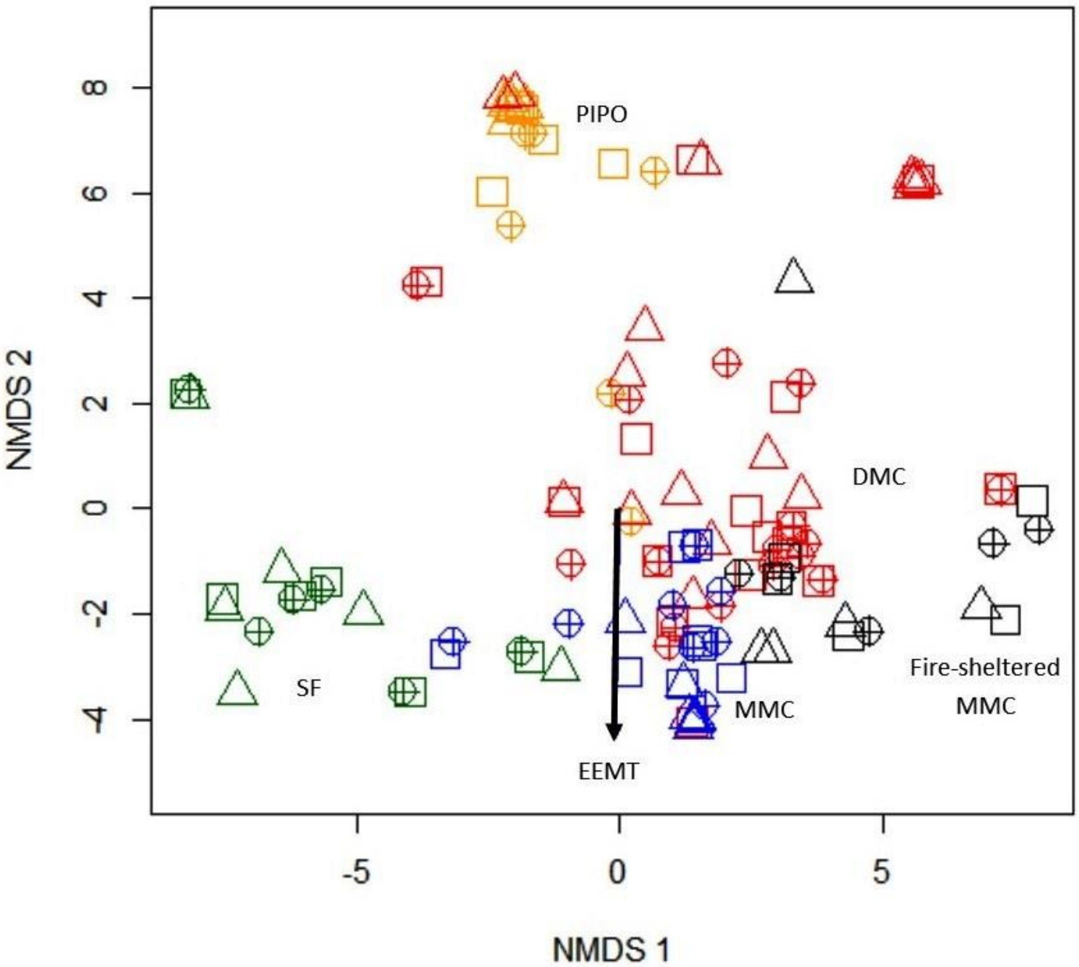

Figure 7. Nonmetric multidimensional scaling of site Importance Values (IV). IV scores were transformed to Jaccard distance prior to NMDS analysis. Sites are constrained to two dimensions with a final stress of 19.3. Raw scores of the site productivity variable EEMT are scaled to the NMDS solution. Colored points represent IV scores in 1870 (triangles), 1955 (squares), and 1995 (crossed circles). Close proximity or overlap between symbols of the same color indicates that the species assemblage is stable through time. Colors represent the forest type that was present in 1870: orange = ponderosa pine, red = dry mixed-conifer, blue = mesic mixed-conifer, black = fire-sheltered mesic mixed-conifer, dark green = spruce-fir.

Supplemental Tables

Table S-1. Count of trees and species used in demographic analysis. Trees in the 0.05 ha plot are weighted by 1; small trees on the 0.017 ha subplot are weighted by 3 to normalize to equal area.

Genus and species	**Species label**	**Plot weight**	**Tree count**	**Weighted tree count**
Abies concolor	ABCO	1	102	
		3	68	
				306
Abies lasiocarpa var. *arizonica*	ABLA	1	90	
		3	30	
				180
Picea engelmannii	PIEN	1	194	
		3	36	
				302
Pinus ponderosa var. *scopulorum*	PIPO	1	122	
		3	24	
				194
Pinus strobiformus	PIST	1	165	
		3	25	
				240
Populus tremuloides	POTR	1	17	
		3	25	
				92
Pseudotsuga menziesii var. *glauca*	PSME	1	281	
		3	68	
				485
Unknown (advanced decay)	UNK	1	23	
		3	7	
				44
Total			**1,277**	**1,843**

Table S-2. PermDisp nonparametric multivariate pairwise test for significant difference of dispersion in low, moderate, and high productivity sites in 1870, 1955, and 1995. Significant differences are indicated in bold text.

Low EEMT sites pairwise test for differences in dispersion among groups

Groups	Centroid t	P(tables)	P(perm)	Median t	P(tables)	P(perm)
1870x1955	1.5241	0.1534	0.3872	1.4188	0.1814	0.2212
1870x1995	2.2083	0.0474	0.0754	2.2301	0.0456	0.0392
1955x1995	1.2965	0.2192	0.2524	0.7896	0.4451	0.3452

Moderate EEMT sites pairwise test for differences in dispersion among groups

Groups	Centroid t	P(tables)	P(perm)	Median t	P(tables)	P(perm)
1870x1955	2.8528	**0.0062***	0.0202	2.3704	0.02151	0.0236
1870x1995	3.6917	**0.0005***	**0.0036***	3.0619	0.00348	**0.0056***
1955x1995	0.7008	0.4866	0.5822	0.5574	0.57967	0.6074

High EEMT sites pairwise test for differences in dispersion among groups

Groups	Centroid t	P(tables)	P(perm)	Median t	P(tables)	P(perm)
1870x1955	2.3875	0.0440	0.0582	2.1357	0.0652	0.0428
1870x1995	2.4901	0.0375	0.0392	2.1991	0.0591	0.0304
1955x1995	0.1166	0.9101	0.8960	0.1671	0.8715	0.9162

Bonferonni correction for multiple pairwise comparisons.

alpha to reject null hypothesis is 0.016667

Table S-3 part 1. Last recorded fire data, time to primary species peak, and time to secondary species establishment in relation to EEMT.

Plot	**EEMT**	**Last recorded fire**	**Time to 1° spp peak**	**Time to 2° spp peak**
E9	27.5	1900	45	NA
L21	43.1	1901	39	NA
L20	43.2	1898	42	NA
H17	44.3	1685	265	55
G17	45.0	1685	90	40
H18	45.4	1685	255	NA
G18	45.4	1685	100	NA
H19	46.0	1685	175	NA
H20	46.1	1685	130	110
B2	12.6	1895	5	NA
D4	24.7	1892	3	NA
E8	25.7	1868	12	NA
D3	27.0	1891	4	90
B5	27.5	1901	4	NA
P23	29.7	1904	6	80
G12	35.2	1956	19	NA
F13	40.5	1871	9	30
N22	41.7	1887	38	15
L19	41.9	1898	37	15
G13	39.2	1922	3	30
E14	40.0	1956	4	25
I17	40.8	1916	4	30
E16	41.2	1903	17	30
K19	42.4	1885	25	NA
G14	42.6	1880	30	NA
I18	43.6	1954	26	NA
F12	37.6	1925	15	25
K18	41.4	1924	46	NA
H15	41.7	1893	42	NA
F14	43.9	1863	22	80
I19	44.0	1895	55	10
F15	44.1	1956	19	NA
F11	32.8	1925	15	15
L18	36.8	1898	42	15

Table S-3 part 2. Last recorded fire data, time to primary species peak, and time to secondary species establishment in relation to EEMT.

Plot	**EEMT**	**Last recorded fire**	**Time to 1° spp peak**	**Time to 2° spp peak**
E18	41.1	1903	27	NA
J18	42.4	1966	19	NA
J19	43.3	1885	40	NA
F16	43.6	1900	25	25
M22	43.9	1776	24	NA
K20	44.2	1885	50	35
F10	28.0	1894	6	70
G11	32.5	1894	41	NA
P24	35.8	1908	22	NA
M20	36.9	1876	14	40
M21	42.5	1899	31	0
F17	43.2	1889	31	60
H16	43.4	1913	12	35

Supplemental Figures

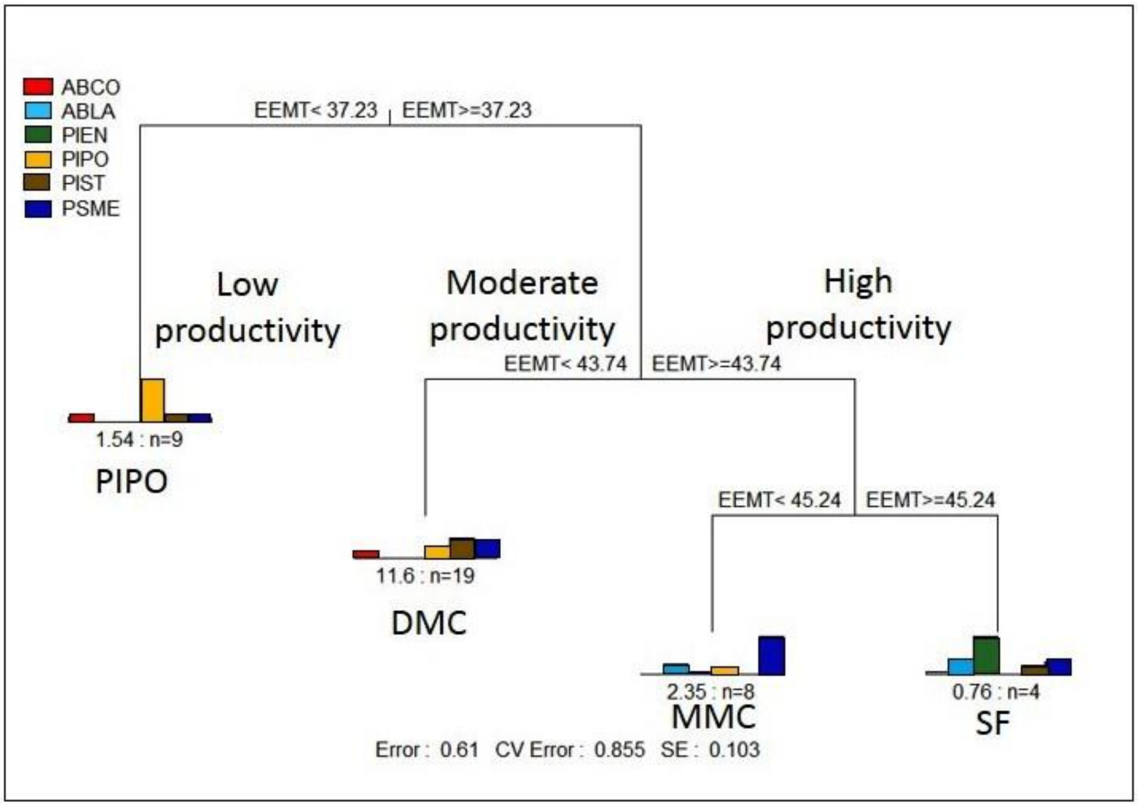

Figure S-1. Partitioning of forest types by Effective Energy and Mass Transfer. Partitioning is based on the species Importance Values (IV) of 40 demography plots in the year 1870. Multivariate regression tree is based on the best fit to minimize cross-validated error based on 1000 permutations. Resulting groups define the ponderosa pine, dry and mesic mixed-conifer, and spruce-fir plot groupings. EEMT explains 39% of the variance in the distribution of species IVs.

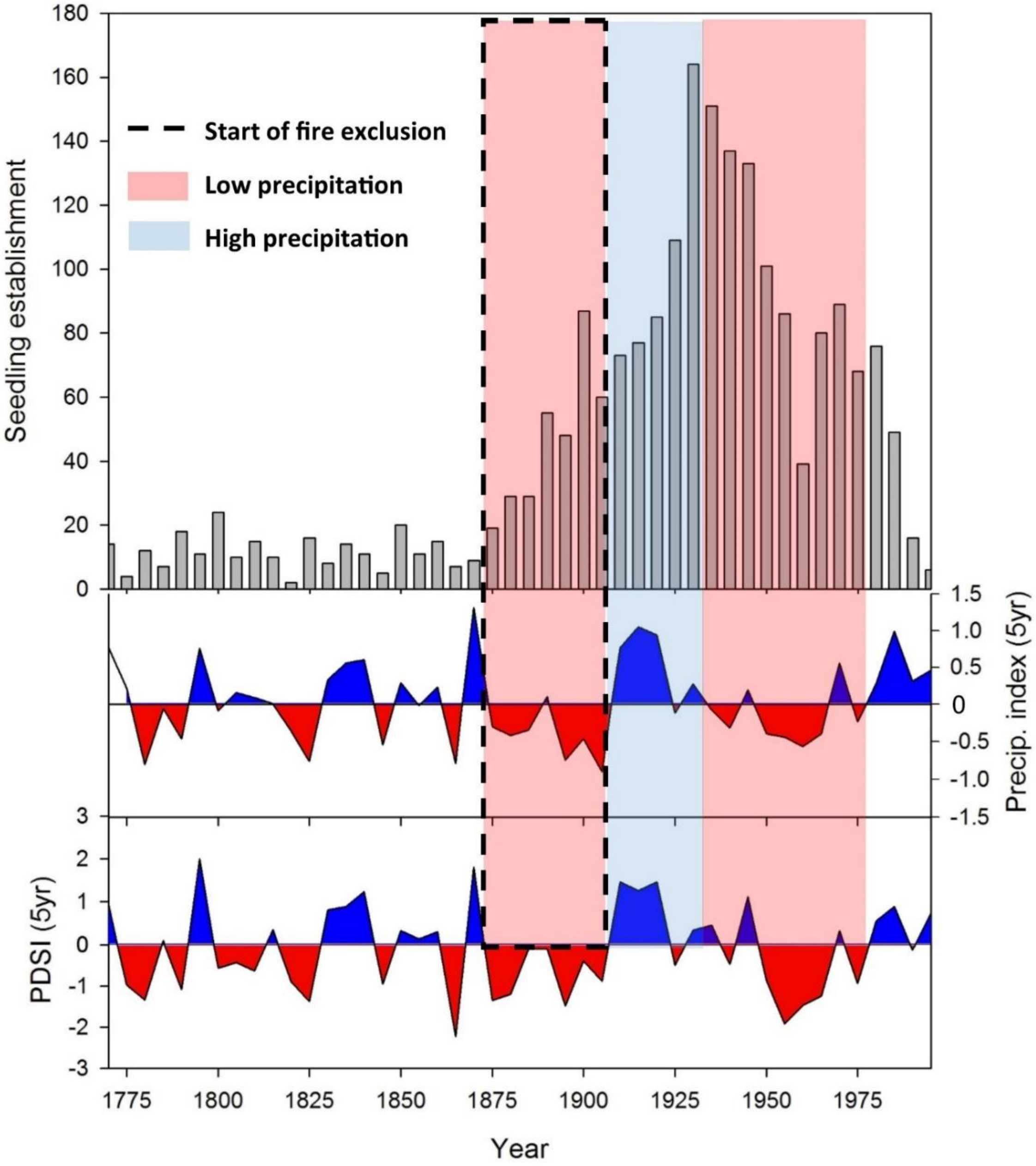

Figure S-2. Association between seedling establishment, annual precipitation, and drought. Seedling establishment is binned in 5-year intervals. Precipitation index is adapted from Griffin et al. (2013). Palmer drought severity index (PDSI) is adapted from Cook and Krusic (2004) grid point 105 for southeast Arizona. Dashed polygon denotes start of fire exclusion across the landscape. Red polygons indicate period of lower than average annual precipitation. Blue polygons indicate periods of high than average annual precipitation.