

PATTERNS AND PREDICTORS OF CROWN FIRE INDUCED
TYPE CONVERSION IN DRY CONIFER FORESTS

By Collin M. Haffey

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Approved:

Thomas D. Sisk, Ph.D., Chair

Andrea E. Thode, Ph.D.

Jose Iniguez, Ph.D.

ABSTRACT: PATTERNS AND PREDICTORS OF CROWN FIRE INDUCED TYPE CONVERSION IN DRY CONIFER FORESTS

COLLIN M. HAFHEY

Since 1996, high-severity crown fires in Southwestern ponderosa pine forests have produced large treeless areas, which are unprecedented in the regional historic record. Other dry conifer forests, similar to ponderosa pine, are also experiencing extensive high-severity crown fires that are creating conditions unique in the evolutionary history of these forests. Recent crown fires have reset large portions of southwestern forest landscapes, creating opportunities for successional vegetation communities to alter ecological trajectories away from a return to the pre-fire forest type, which can lead to type conversion. I conducted a synthesis of the peer-reviewed scientific literature and carried out an empirical and modeling study to examine patterns of landscapes change and predictors of ecosystem type conversion.

For the literature review and synthesis, I examined general post-fire response patterns from studies completed following crown-fires in dry conifer systems. I determined that severely burned areas are often set on successional trajectories that lead to conversion from conifer forest ecosystem types to a non-forested types by following one of three pathways: 1) climate change or prolonged drought limits moisture availability, which prevents regeneration of the pre-fire conifer species, favoring more drought-adapted shrublands or grasslands; 2) changes to the fire regime of the area as a result of early successional ecosystem establishment excludes conifer regeneration; or 3) post-fire interspecific competition favors the persistence of early successional plant communities, to the exclusion of conifer regeneration. The complex linkages among particular land use histories, landscape changes in vegetation and ‘fuels’, climate variability and change, and differing fire patterns along with variation through time and across geographic space in different landscapes, leads to interactions between the 3 ‘pathways,’ which will likely increase the probability of type conversion in any given landscape.

For my empirical and modeling study, I hypothesized that the hottest and driest areas within the burned area would be most likely to convert from forest to a non-forest ecosystem type, because the post-fire areas are recovering in a climate period that is warmer than when the forest established. To test this, I created a spatially explicit landscape model based on topographic variables: elevation, slope position, and aspect. I developed the model using empirical field data collected from nine areas in Arizona and New Mexico. The results show low elevation, xeric sites are more likely to type convert than higher elevation sites with more mesic conditions, indicating a shift toward post-fire climate conditions that limit pine regeneration. Additionally, areas far away from a viable seed source have a high probability of type conversion, even if those areas are favorable for pine germination. This model provides a spatially explicit illustration of landscape vulnerability to type conversion. The field survey shows a wide variety of post-fire ecological responses following stand-replacing crown fire. Together, these research results provide a greater understanding of landscape change in the face of climate warming, and I hope that they will contribute meaningfully to informed land management decisions regarding adaptation or mitigation strategies.

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TABLE OF CONTENTS

ABSTRACT: PATTERNS AND PREDICTORS OF CROWN FIRE INDUCED TYPE CONVERSION IN DRY CONIFER FORESTS.....	II
ACKNOWLEDGEMENTS	IV
TABLE OF CONTENTS	V
TABLE OF TABLES	VII
TABLE OF FIGURES	IX
PREFACE.....	XII
CHAPTER 1: A LANDSCAPE APPROACH	1
CHAPTER 2: A REVIEW OF POTENTIAL PATHWAYS TO LONG-TERM ECOSYSTEM TYPE CONVERSION IN DRY CONIFER FORESTS	5
ABSTRACT.....	5
VULNERABILITY OF SEMI-ARID FORESTS TO TYPE CONVERSION	6
<i>Pathways to type conversion.....</i>	<i>7</i>
SCOPE AND METHODS	7
PATHWAYS TO ECOSYSTEM TYPE CONVERSION.....	9
1. <i>Climate pathway.....</i>	<i>9</i>
2. <i>Competition pathway.....</i>	<i>11</i>
3. <i>Fire regime shift pathway</i>	<i>13</i>
REVIEW SUMMARY	13
CONSEQUENCES OF LONG-TERM TYPE CONVERSION	15
<i>Effects on carbon sequestration</i>	<i>16</i>
<i>Hydrologic cycle</i>	<i>16</i>
<i>Wildlife effects.....</i>	<i>17</i>
MOVING FORWARD WITH MANAGEMENT AND SCIENCE	18
<i>The future of forest vulnerability and the need for active management.....</i>	<i>18</i>
<i>Additional research needs.....</i>	<i>19</i>
CHAPTER 3: A MODELING AND FIELD STUDY OF CROWN-FIRE INDUCED ECOSYSTEM TYPE CONVERSION IN SOUTHWESTERN PONDEROSA PINE FORESTS	21
ABSTRACT.....	21

INTRODUCTION	21
<i>Objective and question:</i>	23
<i>Type conversion studies (micro-review)</i>	23
<i>Climate's role in type conversion</i>	25
<i>Patch size is a major driver of type conversion</i>	25
<i>Hypotheses</i>	26
METHODS.....	27
<i>Predictor variables</i>	27
<i>Field data collection</i>	29
<i>Burn severity data</i>	30
<i>Field sampling</i>	30
<i>Model comparison and averaging</i>	32
RESULTS.....	32
<i>Modeling results</i>	32
<i>Spatially explicit model representation</i>	33
<i>Forest regeneration</i>	34
<i>Post-fire landscape potentials</i>	35
MODEL DISCUSSION.....	36
<i>Limits to regeneration</i>	36
<i>Next steps in model development</i>	37
MANAGEMENT IMPLICATIONS AND APPLICATIONS	38
<i>No "steady march"</i>	38
<i>Spatial strategies</i>	39
CONCLUSION: HOW CAN WE ADAPT TO RAPIDLY CHANGING LANDSCAPES?	42
ACCEPTANCE	42
LOCAL & ACTIVE SCIENCE-POLICY INTERFACE.....	43
ASSISTED ADAPTATION.....	44
COMMUNITY DEVELOPMENT	45
REFERENCES.....	47
TABLES AND FIGURES	58

TABLE OF TABLES

Table 3-1 - List of fires in this study - ID numbers correspond to map in Figure 3. The acreages of the fire and the acres burned at high severity (HS) are listed, along with the year of the burn and general location.	58
Table 3-2 - Model comparison results - Model Variables: Seed = a continuous variable measured in meters for each plot location to nearest viable seed source (10+ mature trees); Elev = scaled (0-1) elevation range of ponderosa pine, values are relative for each burned area such that the highest elevation = 0 and lowest elevation = 1; TPI = topographic position index scaled for each burned area, Aspect = deviation from NE cosine transformation and scaled (0-1) aspect where SW (225°) = 1 and NE (45°) = 0, ‡ = mixed effects model that included random effects of each burned area, Site RE = mixed effects model with random effects of each burned area and intercept. K = number of parameters (including intercept). AIC = Akaike information criterion. ΔAIC = difference in AIC values of other models from 'best fit' model. 4.10 E-10 = relative likelihood of null model is better fit than model with lowest AIC value.	59
Table 3-3 - Parameter Coefficients - Standardized model-averaged regression coefficients (column 2), unconditional standard errors (SE), and Z-statistics for physical variables used to predict relative probability of type conversion. Greater Z values give a relative importance of each variable to type conversion predictability.	60
Table 3-4 - Plots per fire - Number of plots per fire, number of plots where <i>Pinus ponderosa</i> (PIPO) was present, and number of planted plots within each fire area. Planted plots were determined from forest service spatial information and personal communication with personnel involved in post-fire reforestation efforts. Cerro Grande was so extensively reforested that it was determined all of the sample plots lie within potential planting zones, though there was only living PIPO on 6 plots.	61
Table 3-5 - Breakdown of tree regeneration by species and the nurse structure the seedling germinated under/near - PIPO = ponderosa pine (<i>Pinus ponderosa</i>), PSME = Douglas-fir (<i>Pseudotsuga menziesii</i>), POTR = aspen (<i>Populus tremuloides</i>), JUDE = alligator juniper (<i>Juniperus deppeana</i>), ABLA = Subalpine fir (<i>Abies lasiocarpa</i>), ABCO = white fir (<i>Abies concolor</i>), JUMO = oneseed juniper (<i>Juniperus monosperma</i>), and JUOS = Utah juniper (<i>Juniperus osteosperma</i>)	62
Table 3-6 - Number of trees by species found at each fire - totaled by row and column. PIPO = ponderosa pine (<i>Pinus ponderosa</i>), PSME = Douglas-fir (<i>Pseudotsuga</i>	

menziesii), *POTR* = aspen (*Populus tremuloides*), *JUDE* = alligator juniper (*Juniperus deppeana*), *ABLA* = Subalpine fir (*Abies lasiocarpa*), *ABCO* = white fir (*Abies concolor*), *JUMO* = oneseed juniper (*Juniperus monosperma*), and *JUOS* = Utah juniper (*Juniperus osteosperma*) 63

Table 3-7 - Summary of dominant cover type - Table shows percent dominant vegetation type within each fire, row total = 1 (100%). Dominant vegetation type assigned to each plot using a qualitative process that involved a combination of photos and quantitative plot cover data. Mesic tall shrubs = *Quercus gambelii* and *Robinia neomexicana*; Xeric tall shrub are all other *Quercus* species.....64

Table 3-8 - Mean percent cover and mean percent exposed surface of each classification type for each fire area - Means calculated from cover class midpoints for all plots in a burned area. CWD = coarse woody debris, mainly downed logs.....65

TABLE OF FIGURES

Figure 2-1: Conceptual diagram of three potential pathways to type conversion -

Purple dots represent a “climate-induced pathway” where immediately following the initial stand-replacing crown fire the system slowly recovers biomass (y-axis) and drought (or climate change) eliminates any post-fire regeneration and alters the successional trajectory toward non-forest. The red dashed line shows the “change in fire regime pathway,” where the initial post-fire the successional trajectory is rapidly approaches a return to forest (e.g. ‘hyper-dense’ regeneration from Savage and Mast (2005)), but subsequent fires occur (at each peak of the red line) kill young trees and establish a ne fire regime for the system that supports non-forest communities. The green line represents the “competition pathway” to type conversion, where vigorous post-fire successional communities of shrubs and grasses establish rapidly and largely exclude conifer regeneration. 66

Figure 2-2: Chart of various pathways identified from studies in this review -

Most studies implicated competition as a reason for type conversion. Climate (including drought) was the next highest pathway to type conversion. Fire regime change was the least implicated pathway. 40% of the studies cited multiple pathways interacting as the reason for type conversion. 67

Figure 2-3: The total number of studies using various methods -

Observational with modeling was most common approach. Observation alone was nearly as common. Note the lack of experimentation.....68

Figure 3-1: Palmer Drought Severity Index average for study area, 1915 to 2013 -

data from www.wrcc.dri.edu accessed Jan 2014. The recent period of dry (negative) conditions since 1996 to present is one of the most extreme multi-year windows of persistent drought in the past century (Daly et al. 1994; Schwalm et al. 2012). 69

Figure 3-2: Diagram of dry forest type conversion risk -

illustrating how post-fire regeneration to pre-fire forest type (small trees) only occurs where nearby tree seed sources (large trees) coincide with landscape locations that are climatically favorable (green shading) along topographic and elevation gradients. Red shading indicates areas that are climatically unfavorable for pine germination. This general “model”, while not spatially explicit, presents the idea in an easily understandable way. 70

Figure 3-3: Map of the field study region across northern Arizona and New Mexico

- Studied fire areas shown in red, with descriptions of each fire in Table 3-1. Study was spread across AZ and NM to capture regional patterns of post-crown-fire landscape response. 71

Figure 3-4: Topographic variables and their related hypothetical probabilities -

Diagram of relative probabilities of type conversion used in model development and hypothesis testing; a) type conversion probability decreases as the percent of maximum elevation approaches 100%, b) categorized topographic positions (TP) show decreasing probability of type conversion moving from ridges to valleys, for each burned area TP was calculated as a continuous variable and rescaled (0-1), for illustrative purposes the continuous variables on the x-axis have been replaced with TP categories, with the scaled continuous values in parentheses; c) probability of type conversion based on aspect azimuth values, where aspect values represent a deviation from NE (45°), a cosine transformation was then applied to represent the circular value from 0-1, with the highest probability of type conversion being SW (225°). 72

Figure 3-5: Plot layout with nested subplots - Outer subplots separated by 120° from an initial randomly generated azimuth. Inner nested plot is 3m in diameter and used for vegetation cover classification. Larger subplot is 6m in diameter and used for regeneration survey.....73

Figure 3-6: Spatial model output, topographic variables only - Spatial representation of weighted model outputs. This representation of the model removes distance to seed source a parameter, essentially creating a vulnerability assessment that can be applied for pre-fire planning. Here I show the Rodeo-Chediski (a) and Cerro Grande (b) fires. Greens and yellows indicated mesic topographic conditions; reds and yellows are more xeric areas. Notice the difference in probabilities between the two fires, the Cerro Grande fire burned through steep elevation and at the lower end of the local elevation range for ponderosa. The Rodeo-Chediski fire burned at higher local elevations and on relatively smooth terrain. Gray areas are areas not covered by ponderosa pre fire, and the area burned by the fire.....74

Figure 3-7: Spatial Model output with patches of high severity - Spatial representation of weighted model outputs, this time including distance to seed source for the Rodeo-Chediski (a) and Cerro Grande (b) fires. Greens and yellows indicated low probability of type conversion; reds and yellows are higher relative probability of type conversion. In the Rodeo-Chediski fire, areas that burned in areas with low type

conversion probability are now high at high risk for type conversion due to the large patch size and far distance to seed sources. In the case of Cerro Grande the largest high severity patches burned in areas of high or moderate type conversion probability, the large patch size and far distance from seed sources reduces the likelihood of forest regeneration even further. Gray areas are areas not covered by ponderosa pre fire, and red lines show the perimeter of the fire. 75

Figure 3-8: Natural ponderosa pine regeneration - Shows regenerating trees per plot relative to distance to the nearest seed source. Seed source defined as a group of reproductive trees, generally 10 or more. No natural regeneration was observed outside of 250m from a viable seed source with most regeneration occurring within 150m of seed source, half of the sampled locations were outside of 150m 76

Figure 3-9: Proportion of Dominant Plot Cover per Fire - proportion of plots from each fire dominated by grass, shrubs, bare ground, or tree regeneration. Shrub and grass dominated areas are the most common followed by bare ground and tree regeneration. 77

Figure 3-10: Logistic Regression Output - Output from logistic regression (blue line) with sample plots represented as blue dots. On the x-axis values near 0 are the areas predicted to have a low probability of type conversion, with values near 1 being the highest probability. On the y-axis 0 = not type converted (i.e. more than 2 ponderosa pine found at the site) 1 = type converted (i.e. fewer than 2 ponderosa found on a plot). Notice the large amount of sites that type converted despite being at areas with low probability of type conversion, indicating complex dynamics result in type conversion. ..78

Figure 3-11: Number of regenerating ponderosa per plot along type conversion probability scale - Post fire ponderosa regeneration shown as number of ponderosa per plot. Notice the large amount of regeneration near 0, the more favorable sites. The planted areas (green x's) are near the least favorable (1) end of the probability gradient indicating planting helps cross the germination "hump," but not always. 79

PREFACE

Because I plan to submit each chapter in the near future for peer-reviewed publication, I formatted each chapter as a stand-alone journal article. I plan to publish in journals that focus on landscape scale ecological modeling, forest ecology and land management. Because of the overlap of research for each chapter, I have combined the references into one reference list for the entire document.

CHAPTER 1:

A LANDSCAPE APPROACH

The goal of this thesis is to understand the patterns and predictors of crown-fire induced ecosystem type conversion, specifically from ponderosa pine forest to non-forested ecosystems. I have divided the thesis into two main parts. First, I use a literature review to investigate broad patterns and underlying mechanisms driving type conversion in the western United States. Second, I explore my own experimental study of type conversion following recent high severity fires in ponderosa pine forests of Arizona and New Mexico. I conclude the thesis by exploring the shifts in regional and local land management necessary for communities to adapt to rapidly changing landscapes.

This project takes a broad perspective and attempts to understand general patterns that are occurring over a large portion of the distribution of ponderosa pine. The loss of any foundation species such as ponderosa pine will have cascading effects on the overall ecology and evolution of the landscape (Ellison et al. 2005). Determining the broad patterns of pine regeneration or ecosystem type conversion following a major disturbance such as crown fire is important in order to understanding the future landscape dynamics and the evolution of future ecosystems (Connell 1978). Regardless of whether the landscape returns to ponderosa pine forest or transitions to alternative vegetative communities, there is potential for significant evolution following such a disturbance (Whitham et al. 2012). Because of the significance of the effects of these impacts to forested lands and the communities that rely on them, I feel it is appropriate to take a landscape approach for this research. I have been drawn to the approaches of "macroecology" as outlined by Brown (1995), who argued for a focus, "more on the form and magnitude of variation than average trends," (p.227) and the identification of broad-scale patterns. I have incorporated these principles into my research project insofar as my goal is to explain a large proportion of the variability in the system using foundational ecological principles and simple analytical and modeling approaches. My goal with this research is to explore new ideas and applies fundamental concepts to advance understanding of broad spatial and temporal dynamics following disturbance in the context of a changing climate, rather than explain the fine scale patterns and drivers of site-specific of type conversion

To gain a better understanding of regional patterns of type conversion, I performed a review of relevant literature. From a synthesis of the literature review, I identified three unique 'pathways' to type conversion: climate, competition, and changes to fire regimes. All pathways interact with spatial and temporal patterns to increase the risk of type conversion as the size of the treeless patch increases. I used literature from regions with forests that support, or historically supported, frequent low intensity fire regimes, similar to ponderosa pine. Areas included in the review are: the Southwest US, the Mediterranean Basin, Sierra Nevada Range, and the Central and Northern Rocky Mountains.

A large body of research has shown climate to be a major limiter to pine regeneration, with several studies finding little or no regeneration at the warmest and driest ends of the pre-fire forest ranges (*Chapter 2*). This could be in response to long-term regional droughts or global change. Current research projects an increase in both short and long-term drought as the climate warms (IPCC 2013).

Vegetation community dynamics, such as fire regimes and competition among dominant species in the post-fire communities, are likely to further limit pine regeneration, even in areas that may otherwise be favorable. Post-fire vegetation communities often have very different fire regime characteristics from ponderosa pine. Dense resprouting shrublands can develop into a chaparral-like, extremely fire-prone, system. The frequency and intensity of chaparral-like fire regimes are too extreme to support pine regeneration. Competition on more mesic sites may limit the amount of pine regeneration by limiting the amount of exposed soil, out competing pine germinates for water or other nutrients, or creating an inhospitable allelopathic environment.

Alterations to the vegetation community will have consequences for the regional, local and social systems that depend on the forest for various ecosystem services. Large fires directly affect ecosystem services such as carbon sequestration, recreation, and municipal water sources. Toward the end of Chapter 2, I briefly outline the long-term social consequences of ecosystem type conversion from forest to non-forest.

I designed my field study to understand the vegetation community potentials and biotic and abiotic bottlenecks to pine regeneration following large stand-replacing fire. I examined how far from the seed source trees are able to germinate, and the vegetation

composition in areas not regenerating to pine. My field surveys should help land managers answer the question "what comes next?" after large stand-replacing fire in ponderosa pine forests.

In my empirical study of type conversion, I hypothesize that tree regeneration is restricted at the warmest and driest ends of their pre-fire distribution, due to a warming climate, and the biophysical constraints affecting seed dispersal. To examine these hypotheses, I chose to use topographic variables as a proxy for climate information. Using topographic variables as climate proxies dates back to Whitaker (1967) and has proven to be an extremely useful heuristic and generally predictive tool. Because the climate has warmed over the past century, areas that are already at the lowest end of the topographically controlled moisture gradient may already have warmed to a point that post-fire tree regeneration at those sites is unlikely.

The short distance ponderosa pine seed travels from the seed source has been hypothesized as a limit to forest recovery in large treeless patches following stand-replacing fire, but has never been explicitly tested. I test this hypothesis by collecting regeneration data using a stratified random sample design, with the goal of determining likelihood of type conversion for any given distance from a viable seed source.

The result is a spatially explicit model of relative likelihood of type conversion. Managers or policy makers could use this model to optimize pre- and post-fire management strategies (e.g. restoration, tree planning), and to identify areas where such practices are doomed to failure. Combined with, other data such a crown fire hazard maps, or local monitoring of post-fire succession patterns and tree regeneration, management strategies could target specific areas where they have a highest probability of success in the 'new-normal' of changing landscapes and warmer climates.

The last chapter of the thesis is a call to action for land managers, community leaders, and policy makers managing a drying and warming West. I acknowledge the fact that large once-forested areas are likely to remain treeless for several human generations, and call on leaders to seriously address the possibility that many pine forests undergoing severe crown fires in the coming decades will never return to the pre-fire forests. Land managers and community planners should begin planning for a future with fewer forests. I believe research such as this, aimed at predicting some aspect of future landscapes, is a

preliminary step toward helping policy makers, land managers, and communities adapt to future change.

CHAPTER 2:

A REVIEW OF POTENTIAL PATHWAYS TO LONG-TERM ECOSYSTEM TYPE CONVERSION IN DRY CONIFER FORESTS

Abstract

In dry conifer forests, where frequent surface fires dominated the historical fire regimes, high severity crown fires are creating conditions unique in the evolutionary history of these forests. Recent crown fires have reset large portions of the landscape, creating opportunities for successional vegetation to develop into ecological communities different from the pre-fire forest. I examined general patterns from the review of 28 studies completed following stand-replacing fires from the western United States and Europe. From a synthesis of the review literature I determined that severely burned areas are often set on a successional trajectories that lead to conversion from conifer forest ecosystem type to a non-forested ecosystem type by following one of three pathways: 1) climate change or prolonged drought limits moisture availability, which prevents regeneration of the pre-fire conifer species, and favors more drought-adapted shrublands or grasslands; 2) changes to the fire regime of the area as a result of early successional ecosystem establishment excludes conifer regeneration; or 3) post-fire interspecific competition favors the persistence of early successional communities to the exclusion of conifer regeneration. Once post-fire communities develop positive feedbacks to sustain the successional community for the long term the area can become 'type converted'. Individually, all three pathways can lead to type conversion, but interactions among all three pathways across a landscape are likely to increase along with the time since fire or geographic scale of the crown-fire disturbance. Interactions between the pathways may increase the probability of type conversion. Globally, forests are undergoing rapid change to non-forest communities that could persist for decades to centuries. Land managers and scientists must learn more about the drivers of fire induced type conversion to make informed management decisions and predict type conversion in a fire-prone future.

Vulnerability of semi-arid forests to type conversion

Globally, large areas of dry coniferous forests, historically dominated by frequent surface fire regimes, have transitioned to stand structures that make forests vulnerable to high-severity crown fires (Stephens et al. 2013). Following high-severity fires, these areas often convert to shrubland or grassland ecosystems. Ecological community dynamics, such as species composition, competition, evolution, and physical structure begin developing immediately following a stand-replacing fire event. Post-fire climate conditions and subsequent disturbance (e.g. erosion, salvage logging, subsequent fires) lead to establishment of vegetative communities that are often very different from the forest that initially occupied the site (Foxx 1996; Savage & Mast 2005; Savage et al. 2013; Anderson-Teixeira et al. 2013; Foxx et al. 2013). Soil moisture, seed availability, and other conditions required for conifer regeneration may not obtain immediately post-fire, essentially giving the non-forested community a head start down the road toward long-term establishment of a post-fire community that is markedly different from the pre-fire forest. Instead, the post-fire landscape is set on an different ecological trajectory that will influence the future of the system and could lead to long-term ecosystem type conversion.

It is important to understand the underlying processes and patterns, or ‘pathways,’ that drive post-fire systems to non-forest ecosystems once a large, high-severity, crown fire resets the landscape. Following the resetting of the landscape, successional communities, typically composed of herbaceous plants or shrubs quickly establish in the area and begin to develop in areas previously dominated by conifer forest. Early successional communities can alter the ecological trajectory away from forest and toward an ecosystem dominated by non-forest species, typically toward grasses or shrubs, whose functional properties and fire regimes often differ dramatically from the pre-fire forest type. The area becomes type converted once ecological feedbacks are in place that preclude reestablishment of forest and sustain the successional community over the long-term. Spatially, type conversion occurs at the size of an ecological patch. Patch size is determined by the scale of the high severity fire, and can range from sub-stand level (dozens of ac.) to near landscape scale (> 1,000 ac.). The processes that alter the ecological trajectories of a specific landscape will determine the areas that ultimately type

convert within an area of high severity fire. The patches of type conversion will alter the overall landscape structure, increase heterogeneity, and affect many ecological processes, including future fire regimes, across the landscape.

Pathways to type conversion

From a review of post-fire tree regeneration literature, I synthesized three pathways that lead to long-term conversion in post-fire ecosystems. Bio-climatic conditions are warmer and drier than when the forest established; without adaptation to the new climate, regeneration is impossible in areas that are too warm/dry. 2) The successional community prohibits pre-fire conifer germination or seedling survival through interspecific competition (e.g. tall shrubs or thick grass). 3) A fire regime characteristic of the post-fire community prohibits sustainable conifer regeneration (e.g. through increased fire severity or frequency). Interactions between the three pathways could further increase the likelihood of type conversion (e.g. grass out competes conifers and changes fire regime). **Figure 2-1** shows a conceptual diagram of the three pathways. Spatial and temporal patterns will influence the interactions by multiplying relative effects of each pathway. For example, a persistent drought immediately following the fire that lasts for several years could favor more drought-tolerant grasses, essentially giving the grassland a temporal advantage toward gaining a competitive superiority over conifer regeneration once conditions shift back to those favorable for conifer germination. Similarly, large patches can provided the successional communities near the center of the patch, those far away from a seed source, longer to develop a competitive advantage if the forest recovers from the edge of the patch and moves into the burned area.

I conclude the synthesis by discussing some of the potential ecological and social consequences of crown-fire induced type conversion, the management challenges in a post-fire landscape, and important research needs.

Scope and methods

Because most of the literature focuses on regeneration rather than type conversion, I reviewed the modest body of peer-reviewed literature focusing on tree regeneration in dry conifer forests of the western United States. I consider type conversion to be the inverse of forest regeneration; therefore, I interpret post-fire

regeneration studies and type conversion studies to be one in the same. This review is centered on conifer forests that have evolved with a frequent low severity surface regime (e.g. *Pinus ponderosa* and *P. jeffreyi* dominated systems), because the historic fire regimes of most dry conifer forest types in the western US are well known, and known to be changing due to climate warming (Fulé et al. 2006; Swetnam & Baisan 1996; Brown et al. 1999; Westerling et al. 2011). Given the departure from historic fire regimes and several recent large fires as examples, dry conifer forests are at highest risk of fire-induced type conversion. The understanding of historic fire regimes provides us a foundation from which to base the current trends of high-severity fire and assess the precedence for landscape-scale resets caused by crown fire, within the context of historic fire regimes.

I found relevant literature by 1) searching academic databases (Web of Science and Google Scholar) for combinations of key words (e.g. high severity fire, ponderosa pine, Jeffery pine, type conversion), 2) pulled references from the literature and cited sections of articles reviewed previously, and 3) targeted more articles citing the most relevant of the literature I reviewed in stages 1 and 2. I categorized the methods or evidence used for each study into four categories: observation, observation and modeling, long-term monitoring, and review.

I attempted to be as thorough as possible when reviewing literature from the western United States (US) and the review of the literature from this region should be considered comprehensive. Because the research on type conversion in the western US is a relatively new field, published literature is scant. Therefore, I have included all relevant peer-review research from the western US. Additionally, I looked to other geographic regions to find similar patterns of crown fire induced type conversion in coniferous forests. My search identified a fair amount of additional sources, particularly in the Mediterranean Basin. I used global research to supplement and reinforce the findings from the literature focused on Western North America. For the purposes of this review, I used only the strongest research papers from the Mediterranean Basin, i.e. those that had been cited the most, or ones published in journals that are more prestigious. For each study, I identified the pathway to long-term establishment of the post-fire ecosystem, or

type conversion. In some cases, the authors clearly identified one or multiple pathways, but more often, I identified the pathway using information provided in the study.

I synthesized the reviewed literature to identify pathways of type conversion, to make management recommendations, and to suggest avenues of continued research. In order to make the most relevant research suggestions, those that would most efficiently inform type conversion science and management or policy decisions, I summarized several long-term consequences of type conversion. I selected these example effects to highlight the cascading effects type conversion can have on ecological and social systems and to emphasize the need for continued research and active management of type-converted landscapes. I used the literature synthesis and summary of consequences to determine management recommendations and highlight a small number of specific management challenges. I used the management challenges to prioritize research needs that address specific management challenges and informed type conversion science.

Pathways to ecosystem type conversion

1. Climate pathway

Climate change is causing longer dry seasons leading to an increase of intra-annual drought stress of conifer trees, longer fire seasons, larger patches of high severity fire, and more opportunities for forest type conversion (Westerling et al. 2006; Miller et al. 2009; Allen et al. 2010). Changes to regional weather patterns caused by shifts in the polar or subtropical jet streams that result in longer precipitation free periods will increase drought stress and fire risk (Frierson et al. 2007; Francis & Vavrus 2012). Increases in frequency or duration of drought could lead to an increase in the amount of high severity fire in forests of the western US; large crown fires in mesic conifer forests have been tied to severe droughts using dendrochronological methods (Margolis & Swetnam 2013). Areas may be more likely to type convert following major disturbance such as fire or drought than they were in the past as the climate is projected to continue to warm and forest health is projected to decline (IPCC 2014).

Conifer establishment is closely tied to periods of high moisture availability favorable to conifer germination and seedling recruitment (e.g. Savage et al. 1996, Brown and Wu 2005) which, under current climate predictions, are likely to occur less

frequently and across smaller proportions of forested landscapes (IPCC 2013). Research of recent post-fire regeneration identifies specific precipitation requirements for successful regeneration following high-severity fires (Feddema et al. 2013; Savage et al. 2013). Forecasts of the same models using climate projections indicate a reduced likelihood of suitable conditions for post-fire establishment of ponderosa pine (Savage et al. 2013; Feddema et al. 2013). The likely increase of long-term drought will reduce the regeneration capacity of forests following stand-replacing fire. In the Black Hills of South Dakota, long-term drought is blamed for the lack of regeneration of ponderosa pine forests (Bonnet et al. 2005; Keyser et al. 2008; Lentile et al. 2007). Likewise, drought in the Sierra Nevada and Alps is inhibiting conifer regeneration (Collins & Roller 2013; Moser et al. 2010).

As the climate warms, the bioclimatic envelopes of most conifer species are predicted to shift geographically into cooler or wetter sites (Colwell & Rangel 2009). Major disturbances can induce a shift in geographical range of coniferous forests, moving the driest ends of the range ‘uphill,’ as the species track their acceptable bioclimatic envelopes (Allen & Breshears 1998; Breshears et al. 2005). Large mature trees are resistant to some level of drought and seasonally dry conditions. Shading from adjacent trees and mulching from litter can create microsites that allow for germinate survival within, or nearby, a forest stand. Following a crown fire, treeless patches create microsite differences that are warmer and drier than the adjacent intact forests (Meyer et al. 2001). Germinates in open areas are often found only in favorable microsites, such as growing next to a log, or from under a protective cover of litter mulch (Roccaforte et al. 2012; Bonnet et al. 2005). Conifer regeneration has been observed in moderate or low severity burned areas (i.e. those areas with mature forest canopy), but regeneration was drastically reduced or non-existent in high severity (i.e. treeless) areas of the same burn, indicating strong microsite-climate effects (Lentile et al. 2005; Crotteau et al. 2013).

Topographic variables, such as elevation and aspect, are often used as proxies for climate conditions and can be useful when comparing the likelihood of type conversion along a topographic gradient (Whittaker 1967; Allen & Breshears 1998). Following a 2002 crown-fire in Oregon that burned a ponderosa forest, Dodson and Root (2013) observed a complete lack of ponderosa pine germination at the lowest elevations of the

burn. If this pattern holds into the future, ponderosa pine in that portion of the Eastern Cascade Range will have shifted its range permanently up in elevation. Similarly, lower regeneration densities were observed at lower elevations following crown-fire in the Mediterranean Basin (Gracia et al. 2002; Retana et al. 2002; Vilà-Cabrera et al. 2012). Additionally, post-fire regeneration was significantly lower or absent on southerly exposures following a fire in the southern Cascades in northern California (Crotteau et al. 2013). The geographic range shift of forest regeneration creates a vacuum that will be occupied by other species, often drought-tolerant shrubs or grasses that could alter the ecological trajectories and establish a climate driven pathway to ecosystem type conversion (Foxx et al. 2013; Dodson & Root 2013; Barton 2002; Savage & Mast 2005).

2. Competition pathway

Following stand-replacing fire, competition with the successional vegetation can limit conifer germination success or seedling establishment and set the ecosystem on a pathway to ecosystem type conversion. Forest research long ago identified that interspecific competition – for light, moisture, or through allelopathic effects – with shrubs or grass limits conifer growth and germination success (Clark & McLean 1975; Coop & Givnish 2011; Elliott & White 1987; Harrington 1987; Rietveld 1975; White 1985). In general, many species in arid forests are shade intolerant and susceptible to mortality from competition with multiple species commonly associated with post-fire successional vegetation (Bonnet et al. 2005).

Following a stand-replacing fire in southern Arizona, Barton (2002) identified shrub competition as a potential reason for lack of Apache pine (*Pinus engelmannii*) regeneration. Resprouting shrubs, mainly oak (*Quercus* spp.) had grown taller, than adjacent Apache pine germinates and Chihuahua pine (*P. leiophylla*) regrowth, outcompeting the conifers for light (Barton 2002). In northern New Mexico and Arizona, several oak species and New Mexico locust (*Robinia neomexicana*) vigorously resprout following high severity fire and outcompete ponderosa pine germinates and seedlings (Haire & McGarigal 2008; Haire & McGarigal 2010; Savage & Mast 2005; Roccaforte et al. 2012; Foxx et al. 2013; Foxx 1996; Savage et al. 2013). *Arctostaphylos* spp and

Ceanothus spp shrubs reduce post-fire conifer establishment in California systems (Collins & Roller 2013; Goforth & Minnich 2008).

Following high severity fire, shrubs are often the early successional species in the Mediterranean Basin and are able to outcompete the *Pinus nigra*, which is adapted to a low severity, high frequency fire regime (Gracia et al. 2002; Crotteau et al. 2013). Rodrigo (2007) studied fires in the northeastern Iberian Peninsula and found high mortality in *Pinus nigra* seedlings that germinated after the fire once the oak shrub cover became tall enough to shade out the germinates. The long-term type conversion of Mediterranean conifer forests to oak-dominated woodlands is contrary to conventional wisdom and may be a novel phenomenon (Rodrigo et al. 2004).

Resprouting shrubs can gain a competitive advantage over any potential conifer germination by their ability to establish vigorous regrowth shortly after the fire. The shrub species of the genera *Quercus* and *Robinia*, mentioned in this review, resprout from root stores, and can grow more than 30cm within the first weeks following a fire without any precipitation (*personal observation*). Increased CO₂ has been shown to enhance the vigor of resprouting shrubs, particularly nitrogen fixing shrubs, which is thought to produce a fertilizing effect (Poorter & Navas 2003). The same fertilization effect was not observed for trees (Poorter & Navas 2003). Strom and Fulé (2007) modeled forest structure using climate projections and a Forest Vegetation Simulator and forecast an increase in shrub domination following large, high severity fires in ponderosa pine forests.

Competition with grass species also limits post-fire conifer establishment (Dodson & Root 2013). Areas once dominated by ponderosa pine forests in northern Arizona are now dominated by robust grasslands (Stevens-Rumann et al. 2013). According to Dodson and Root (2013), the competitive advantage of grass may come from its ability to thrive in warmer and drier areas.

In all cases, conifer competition with grasses or shrubs will not favor the conifer species if the successional shrubland or grasslands develop to the point where the successional communities alter the fire regimes toward frequent, high intensity fires.

3. Fire regime shift pathway

Changes to the vegetation cover and species composition drive change in landscape-scale fire regimes, which may result in a fire regime that excludes conifer regeneration and ecosystem type conversion. Once established, the successional vegetation communities are reinforced by subsequent fire, which leads to long-term type conversion (Bond & Midgley 2001). Post-fire type converted areas can exclude or eliminate any conifer regeneration during subsequent fires, even when that fire is several decades after the initial high-severity fire (Nagel & Taylor 2005; Foxx et al. 2013). Furthermore, areas that burned with high severity in the initial fire could burn at high severity during subsequent fires, particularly in the case of shrublands and chaparral, due to the rapid accumulation of biomass, and change in fuel structure following the initial fire (Holden et al. 2010; van Wagtenonk et al. 2012). There is evidence that resprouting shrubs have evolved into a stand-replacement niche that allows them to maintain site dominance through frequent, intense, fire (Bond & Midgley 2001; Keeley et al. 2011)

In successional grass communities, ecosystems can shift toward low-severity, high frequency fire that can exclude pine regeneration (D'Antonio et al. 1992; Stevens-Rumann et al. 2012). Even in low severity fires, tall saplings (>1.3m) are at risk of fire-induced mortality because of overly dense regeneration patterns or downed coarse woody debris (logs and branches) that resulted from the initial high severity fire (Savage & Mast 2005; Stevens-Rumann et al. 2012; Roccaforte et al. 2012). Climate change will alter fire regimes in a way that is likely to increase fire-induced mortality of conifer forests and conifer regeneration in western North America and the Mediterranean Basin (Rodrigo et al. 2004; Pausas et al. 2008; Westerling et al. 2011; Savage et al. 2013). Similar to resprouting shrubs, grasses have evolved with fire and their adaptations allow them to maintain dominance in places with high frequency fire regimes (Bond & Keeley 2005).

Review summary

I identified competition, in 61% of the 28 papers reviewed, as the most common pathway to long-term type conversion. The climate pathway was identified in 43%, and changes in fire regime was determined as a pathway to type conversion in 39% of the

research articles (**Figure 2-2**). Interactions between pathways could also favor type-conversion, though most of the papers reviewed here (60%) implicated a single pathway.

In an example of an interaction between type conversion pathways, an area that burns in the middle of a prolonged drought may recover to drought tolerant grassland. This grassland will outcompete the conifer seedlings that are able to germinate in the dry conditions. Next, a fire may burn over the area killing any seedlings that managed to establish between the grasses. If the fire frequency is rapid enough, the changing fire regime will likely support increased growth of grass, further increasing its competitive advantage over the conifer germinates (e.g. Stevens-Rumann et al. 2012, *Chapter 3*). Additionally, the interaction between non-forest herbaceous cover, soil microbes, and nutrient cycling can reinforce the herbaceous non-forest system and create dynamics that establish long-term type conversion (Kurth et al. 2014). Understanding the interactions between pathways, as well as the iterations in time and space, is essential for predicting those areas most likely to type-convert.

Of the 28 papers reviewed, 10 studies reported distance to seed source to be, at least potentially, a limiting factor for conifer regeneration. One paper did not find distance to seed source to be a significant factor but the overall lack of regeneration may have influenced the results (Collins & Roller 2013). Large patches may lead to type conversion if there is no seed source available, even in otherwise favorable sites.

Larger patches of stand-replacing fire are more likely to experience type conversion, when compared to small treeless patches, for each of the type conversion pathways. Larger patches have less shading from sun and wind and are therefore drier and warmer than nearby forest patches (Meyer et al. 2001; Bonnet et al. 2005). In the interior of a treeless patch, far from a conifer seed source, shrub or grass communities are able to establish in the absence of conifer competition. Larger patches increase the interaction between multiple pathways by increasing the time available for the successional community to develop free of potential conifer competition. The large seed size of many dry conifer species prohibit long distance travel from the seed source (Shepperd & Battaglia 2002). Because of this, post-fire conifer establishment is initially limited to a small area near a viable seed source.

Time since disturbance can act as a positive feedback mechanism for each of the individual pathways. For example, following high severity fire, longer time since fire allows more biomass to accumulate and increases the likelihood of high severity fire, during a subsequent fire (van Wageningen et al. 2012; Holden et al. 2010). Prolonged drought may favor the successional community by creating a “regeneration delay [that] may allow alternative vegetation to dominate the site for some period of time and alter community flammability,” (Savage et al. 2013). Even if the drought weakens and climate shifts back towards conditions favorable for conifer germination and establishment, the site may have adopted a fire regime that cannot support conifer establishment, or be so dense with vegetation that shade intolerant conifers are unable to compete.

Once dry conifer forests are gone, large portions of the landscape will not return to the pre-fire forest type. The recovery of forests post-fire is likely in some areas but will type conversion will likely be permanent in others. Type conversion from forest to non-forest is could be an example of ‘regime shift,’ (Scheffer et al. 2001) and may take several centuries of forest regeneration, or massive reforestation efforts, to shift back to forest. Even if the regime shift is temporary, with shrublands or grasslands establishing on the landscape for some time (Elmqvist et al. 2003), and then the pre-fire landscape dominates, the trajectory of recovery will result in a system with different ecological dynamics, even if it appears superficially the same (Falk 2013).

Consequences of long-term type conversion

As climate changes, it will become even more important to understand the interrelationships of species and ecosystems so that society can better manage or adapt to the consequences of ecological change (Walther 2010). Better understanding of threshold effects and cascading feedbacks associated with broad, landscape scale type conversion will enhance understanding of the ecological consequences and inform efforts to mitigate them (Allen 2007). More is known about the short-term ecological and social consequences of “mega-fires” than the long-term effects of type conversion (Stephens et al. 2014). The consequences of type conversion highlighted below will have cascading and long-term effects on the connected ecological and social systems (Keane et al. 2002)

Effects on carbon sequestration

Conversion from forest to non-forest ecosystem type will have significant effects on the amount of carbon the landscape is able to sequester. Large fires release large amounts of carbon into the atmosphere, turning areas that burn from carbon sinks to carbon sources (Dore et al. 2008). This switch from carbon sink to source happens extremely rapidly as the area burns and the area can potential remain a carbon source decades after stand-replacing fire as the remaining wood rots (Dore et al. 2008). A single fire event in Eastern Oregon produced an estimated amount of carbon that was equivalent to 2.5% of the state's anthropogenic carbon emissions (Meigs et al. 2009).

The rapid emission of carbon into the atmosphere combined with the switch from sink to source is likely to have a significant positive feedback effect well into the future. As crown fires and drought increase, western North America will likely turn from a net sink of (non-anthropogenic) carbon to a net source by the end of the current century due to changes in vegetation (Schwalm et al. 2012). Globally, there is risk that fire, and other climate induced forest mortality, could switch once-forested areas from net sinks to sources of carbon (Allen et al. 2010). As forests decrease in their ability to sequester carbon, or even turn from sinks to sources, this will exacerbate global warming, and increase the risk of crown fire and type conversion. From an economic standpoint, many carbon sequestration programs are dependent on forests to meet carbon-offset goals. Reduction of carbon sequestration capacity due to an increase in the amount of area that has undergone long-term type conversion of forest to non-forest will reduce the ability of carbon offset programs to meet their sequestration goals (McKinley et al. 2011).

Hydrologic cycle

Many communities, particularly in the western United States, rely on forested landscapes for much of their drinking water. Large fires can alter the hydrologic cycle and result in increased peak flows, increased erosion, and altered nutrient cycling (Ice et al. 2004). Debris flows and large erosion events can redistribute large amounts of sediment post-fire (Wondzell & King 2003). These effects are all generally isolated to short durations following a fire and should stabilize as the watersheds recover. Type-conversion can alter hydrologic processes such as infiltration, erosion, and runoff, as well

as soil formation processes, but long-term studies on the subject are scarce (Shakesby & Doerr 2006).

Changes to the hydrologic cycle can create a positive feedback that favors the successional, post-fire, community; particularly if there was significant erosion immediately post-fire. Soil loss will affect the type of successional community that can establish and persist at the site. The vegetation community will also influence the runoff, evapotranspiration, and infiltration rates. Reductions in the infiltration or runoff amounts could negatively impact the local communities that depend on the landscape for freshwater.

Wildlife effects

Habitat heterogeneity created by patches of high severity fire can increase wildlife biodiversity by increasing the availability and diversity of ecological niches (Bond et al. 2012). Bond et al. (2012) reviewed literature and listed many species of insect, bird, and plant that thrive in habitats created by high severity fires. Following a crown fire in Oregon, bird species composition and richness was found to be greater in areas that burned at high-severity compared with those that were unburned or burned at low severity (Fontaine et al. 2009). When ponderosa pine grows adjacent to Gamble oak (*Quercus gambelii*), a common resprouting shrub in the southwestern United States that occupies burned areas, bird abundance and diversity increases (Jentsch et al. 2008).

The heterogeneity and landscape complexity created by patches of type conversion can create diverse wildlife habitat (Bond et al. 2012). Bird species composition is likely to be different in the open area created by high-severity fire when compared with that of the still intact forest (Ries et al. 2004; Ries & Sisk 2010). This could increase bird species diversity depending on the spatial complexity of the type converted area. The landscape heterogeneity caused by large patches of high-severity fire can also affect the behavior of butterfly species by altering the microclimate and creating edges between forested and non-forested areas (Meyer et al. 2001), which could have cascading effects through the ecosystem. The post-fire vegetative community will likely have an effect on the abundance and distribution of large mammals as well because of the structural alteration in available habitat and the change in food type and availability.

Long-term type conversion will alter wildlife habitat, heterogeneity, and connectivity, which will almost certainly have ensuing changes to connected social and ecological systems. For example, the ‘favorite spots’ of hunters and bird watchers will need to change to follow the novel patterns of wildlife as they respond to habitat changes.

Moving forward with management and science

The future of forest vulnerability and the need for active management

Increasingly, land managers must address new long-term challenges associated with post-fire landscapes. The level of uncertainty surrounding post-fire landscapes is exceptionally high. Better understanding the potential patterns and predictors of the post-fire landscape is necessary if managers are to make informed and pragmatic decisions to increase the ecosystem health of the area they manage. Science should work to address these pressing questions as the number of forest hectares and number of people affected by large, high-severity fires will increase in the future. Land managers and scientists must also come to the realization that we may not be able to "restore" our way out of the problem. We must accept that, at least a significant portion of our landscape is likely to undergo significant change in the near future. We must increase our knowledge about post-fire landscapes, and our understanding of the pathways to type conversion, so we can make better decisions for the future.

Many post-fire areas, even given a long period of climate stability, no longer seem suitable for the pre-fire forest type. Climate change undoubtedly exacerbates the prohibition of forest regeneration. Spatial patterning also limits tree regeneration. Understanding the potential pathway that a post-fire landscape may take can assist managers in developing management strategies. For example, if the management goal were reforestation, managers need to overcome the challenges brought about by the different type conversion pathways. Areas that are best suited climatically to support successful reforestation are likely to be the areas with the highest levels of competition, particularly from tall shrubs, (Dodson & Root 2013). Because of the high amount of biomass produced by the shrubs, these areas are also at the greatest risk of burning

intensely during subsequent fires (Holden et al. 2010). Therefore, land managers must look for areas of ‘middle ground’ where competition and reburn risk is low but moisture availability is high enough to support establishment and growth.

Identifying the specific areas that are likely to follow one pathway or another can help in developing pre-fire management strategies. A spatial representation of which type conversion pathways were likely to dominate across a given landscape could provide managers with information on what the post-fire ecosystem could be. By determining areas that are likely to result in undesirable conditions (e.g. increased fire intensity), managers could identify areas with the greatest need for restoration treatments in order to maintain the desired forest cover. On the other hand, a spatial representation of the different pathways to type conversion could identify areas where facilitating the natural transition from forest to grassland or shrubland could be the best course of action. This could result in a increased landscape heterogeneity and biodiversity.

Conversion from forest to non-forest is likely to increase in frequency and area given the projected climate warming and increased forest drought stress (Westerling et al. 2006; McDowell et al. 2008; Williams et al. 2012). Because most fires occur during drought years, the initial post-fire community must establish during dry conditions. The dry post-fire conditions could favor drought-tolerant, resprouting vegetation types such as many oak species and perennial bunchgrass species. The selection pressure applied by the drought during development of the successional community is likely to have long-term effects over the genetics of the entire community (Whitham et al. 2006). The trajectory of the community succession is also likely set in the first few years following large disturbances such as fire (Whitham et al. 2012). If the years following a large fire event are consistently dry and warm, this will favor drought-tolerant species and the likelihood of competition and fire regime change.

Additional research needs

Most of the studies I reviewed relied on observational approaches, with half of those supplemented with statistical modeling (**Figure 2-3**). Few of the models addressed spatial interactions of the pathways that lead to type conversion, aside from measuring distance to seed source. None of the studies performed experiments to assess the relative

importance of any one pathway of change. Two of the reviewed studies used long-term monitoring plots. Observational studies are useful but it seems that even in its infancy, the type conversion body of research has outgrown the usefulness of observation alone. The modeling studies greatly added to the interpretability of the observations and allowed for hypothesis testing. The next steps might include modeling of physical variables, including temperature and moisture availability reducing reliance on topographic variables as proxies for the mechanistic drivers of plant stress and seedling survival.

Experimentation would greatly improve our understanding of the various type conversion pathways and dynamics. This would allow for the development of baseline pre-fire data and establishment of control areas. Finer scale experiments on post-fire competition would also be extremely informative, such as removal of grass or shrubs following high severity fire to determine competitive effects. Water supplementation experiments could help to tease out climate or drought effects. Controlled experimental burns could help understand change in fire regimes. Controlled burn studies could help managers to better understand the best way to maintain dominate forest species or assist the transition of forested landscapes to grasslands or shrublands in a warming future.

Most studies examined only one pathway to type conversion. Future studies should focus on interactions between multiple pathways, space, and time; similar to Haire and McGarigal (2010) who examined the spatial relationships with topographic, and competitive relationships. Studies that deal with the interactions of type conversion pathways will be most useful when designed with spatially explicit predictions as a key objective. From a management perspective, predicting the likelihood of type conversion is an important outcome of any study on post-fire succession.

The consequences of long-term type-conversion are still relatively unknown. How type conversion of a particular landscape will affect the broader mountain range or region is important to understand. Long-term consequences will have the greatest impact on the human communities that depend on the forests and the ability to predict the effects of type conversion on a community will help policy makers and community leaders develop more 'fire adapted' communities.

CHAPTER 3:

A MODELING AND FIELD STUDY OF CROWN-FIRE INDUCED ECOSYSTEM TYPE CONVERSION IN SOUTHWESTERN PONDEROSA PINE FORESTS

Abstract

Since 1996, high-severity crown fires in Southwestern ponderosa pine forests have produced large treeless areas, which are unprecedented in the historical record of ponderosa pine. The post-fire areas are recovering in a climate period that is likely warmer than when the forest established. I hypothesize that the hottest and driest areas within the burned area are most likely to convert from forest to non-forest ecosystem type. To test this, I developed a spatially explicit landscape model based on topographic variables: elevation, slope position, and aspect. I validated the model using empirical field data collected from nine areas, burned between 1996 and 2007, in Arizona and New Mexico. The results show xeric sites are more likely to type convert than areas with more mesic conditions, indicating a shift toward post-fire climate conditions that limit post-fire pine regeneration. My model provides a spatially explicit illustration of landscape vulnerability to type conversion. My field survey shows a wide variety of post-fire ecological responses following stand-replacing crown fire. This research could lead to a greater understanding, and more informed management decisions, regarding the vulnerability of landscapes to type conversion in a changing climate.

Introduction

Since the 1970s, the frequency and size of wildfires in the Southwest United States (SWUS) has been increasing (Westerling et al. 2006; Miller et al. 2009), likely due to a wide variety of factors including uncharacteristically dense and homogeneous forest structure (Covington 2000), drought stress (Williams et al. 2012), and natural fluctuations in weather driven by the El Niño Southern Oscillation and other ocean currents (Swetnam & Betancourt 1990; Swetnam & Betancourt 1998; Margolis & Swetnam 2013). Whatever the causes, the increasing frequency and size of stand-replacing fire results in a proliferation of large treeless areas, with few remnant live trees to serve as seed sources for forest regeneration. Ponderosa pine forests have evolved under low severity, high

frequency surface fire regimes (Covington & Moore 1994; Swetnam & Baisan 1996). Researchers have described fire histories in nearly every ponderosa pine forest and mountain range in Arizona and New Mexico, and all have shown similar results of low-severity, high frequency fire regimes (Falk et al. 2011). Fires burned through ponderosa pine forests at a frequency of surface fire every 5-25 years (Swetnam & Baisan 1996; Touchan et al. 1996; Grissino-Mayer & Swetnam 2000; Reynolds et al. 2013). Historically, crown fires were likely spread throughout the distribution of ponderosa pine (Baker & Ehle 2001). Unlike crown fire patches of recent decades, historic crown fire patches were likely small, discontinuous, and much less common (Fulé et al. 2006; Fulé et al. 2013).

During the most recent drought, *c.* 1996-present, several large, high-severity fires in the ponderosa pine forests of Arizona and New Mexico have resulted in many thousands of contiguous hectares of high severity fire. Of all the area burned in Arizona and New Mexico between 1984 and 2011, nearly 13% burned with high severity, totaling more than 218,000 hectares (Eidenshink et al. 2007, MTBS.gov). These areas, largely treeless, are recovering under dry climate conditions and potentially establishing ecological trajectories that move away from a return to historically forested landscapes. In the Southwest, areas burned in a crown fire generally recover to either shrublands or grasslands with varying amounts of bare ground (*Chapter 2*). The conversion from forest to shrubland or grassland could be a short-term, intermediate landscape as the pre-fire forest recovers, or these areas could become established for the long-term (Falk 2013).

The long-term establishment of non-forest ecosystems represents a "regime shift" (Scheffer et al. 2001) or ecosystem type conversion from one ecosystem type, in this case forest, to a grassland or shrubland ecosystem type. Large crown fires represent threshold events, driven by land use histories and background climate warming. Once the threshold is crossed it may be impossible for the landscape to return to the pre-disturbance state (Peters et al. 2004; Allen 2007). If the climate has shifted to long-term warmer conditions across the distribution of ponderosa pine, then areas that are already relatively hotter and drier should fail to recover to the pre-fire forest type as the climate envelope moves 'up hill' leaving large areas once suitable for pine forests outside of the germination envelope. Non-climate factors, such as lack of available seed source,

competition with resprouting shrubs or perennial grasses, or shifts in fire regimes, may further restrict reestablishment of pre-fire forest stands.

Objective and question:

Recent crown fire patches within large wildfires in the Southwest and the treeless areas they leave behind have driven us to ask the question: what are the landscape level patterns and predictors of type conversion following crown fire in southwestern US ponderosa pine forests? I set several objectives for this research project. First, I developed testable hypotheses of type conversion following crown fires in SW ponderosa pine forests. I developed my hypotheses from post-fire literature, expert opinion, and based them largely on ecological first principles. Second, I developed a spatially explicit landscape model to test the hypotheses. I evaluated the spatial model using field data collected during the 2013 field season. Lastly, I combined the landscape model outputs with post-fire empirical data and use the combination of information to take a ‘big-picture’ look at the post-fire landscapes.

I argue the results of this study point to a need for management in a post-restoration world where land managers should consider assisting the landscape in adapting to a changing world. I do not argue that restoration of ponderosa forest has no purpose in land management, only that crown fire creates areas in which ponderosa is unlikely to return. Managers and scientists should start actively deciding the fate of these landscapes in a, post-restoration, post-ponderosa world.

Type conversion studies (micro-review)

To determine the extent of current knowledge on post-fire successional patterns, I reviewed the relatively small volume of literature on succession following crown fires in southwestern ponderosa pine forests. Since the early 1900s, fires have reportedly created large treeless areas (Keeley & Zedler 2009). Most research has focused on fires that burned before 1990 for the simple reason that those areas have had more time to recover. Most studies on successional patterns in southwestern ponderosa pine have been observational and do not address *a priori* hypotheses for mechanisms or drivers of post-fire patterns.

Savage and Mast (2005) examined burn scars in Arizona and New Mexico and found a variety of responses that included ‘hyper-dense’ ponderosa pine regeneration, shrublands, and grasslands. Savage and Mast found pine regeneration occurring at all crown fire sites, with “densities ranging from moderately dense to very dense,” (Savage and Mast 2005). The authors intentionally chose to study crown fires several decades old to maximize post-fire germination potential. Because the study focused on areas that burned more than 40 years ago, it captured climate periods that favored germination of pine seedlings (i.e. the 1980s, **Figure 3-1**) which may be less frequent in the future due to climate change (IPCC 2013): for ponderosa pine, current drier than average climate conditions will lead to decreased germination success, or adaptation to the drier conditions.

Haire and McGarigal (2008; 2010), found that regeneration was limited to areas near seed sources with specific microsite environments that favored germination. They studied two fires: the 1960 Saddle Mountain fire which burned on the Kaibab Plateau near Grand Canyon National Park and the 1977 La Mesa fire which burned areas in and outside of Bandelier National Monument on the Pajarito Plateau near Los Alamos, New Mexico. The researchers found that after several decades post-fire, forest regeneration extended roughly 200m into the burned area, with random individual trees occurring beyond 200m (Haire & McGarigal 2010). At the time of their study, the oldest cohorts of post-fire regeneration for La Mesa and Saddle Mountain were 20 and 30 years old respectively, indicating that post-fire germination was delayed until climate conditions favored pine establishment (Haire & McGarigal 2010).

In southern Arizona, research has pointed to shrub competition and drought as the explanation for lack of seedling regeneration in Apache pine (*Pinus engelmannii*) and Chihuahuan pine (*P. leiophylla*) dominated systems (Barton 2002). Barton (2002) found most areas free of pine germinates. Where resprouting pine was present, it was much smaller than the vigorously resprouting oak species.

Other studies in the Southwest have noted the conspicuous absence of tree regeneration, though specifically the studies focused on other aspects of the post-fire landscapes. Following the 1977 La Mesa fire, Terry Foxx started one of the first and longest running studies of vegetation dynamics following crown fire in ponderosa pine

forests. In two reports, she has noted the low amounts of tree regeneration and the low survival rates of ponderosa germinates (Foxx 1996; Foxx et al. 2013). Similarly while studying post-fire coarse woody debris, Roccaforte et al. (2012) found just over half of the sites sampled to be completely lacking of any pine regeneration.

Outside the Southwest region of the US, research has found likelihood of encountering post-fire regeneration is zero at the lowest elevations of ponderosa's range and increases with increasing elevation (Dodson & Root 2013). In the Sierra Nevada, shrubs have replaced dry mixed conifer species following uncharacteristically large stand-replacing fires (Collins & Roller 2013). Other research done in European Scots pine (*P. sylvestris*) forests has shown post-fire regeneration decreases at the drier and warmer ends of the pine species range (Vilà-Cabrera et al. 2012).

Climate's role in type conversion

Climate change projections point to an increasingly warm and dry southwestern North America (IPCC 2013). Projected warming is forecast to increase drought stress in southwestern forests making them more vulnerable to crown fire (Williams et al. 2010; Williams et al. 2012). Global climate warming notwithstanding, following a fire, local changes to microsite-climate in the non-forested areas may be significant enough to inhibit tree regeneration, even given several decades (Meyer et al. 2001; Foxx et al. 2013). Post-fire weather patterns are extremely important for successful pine germination and establishment, and the suitable conditions for pine regeneration are forecast to become less common (Savage et al. 2013; Feddema et al. 2013; Puhlick et al. 2012). Microsite-climate changes coupled with regional and global climate change may create conditions very different than when the forest initially established (Savage et al. 1996; Brown & Wu 2005).

Patch size is a major driver of type conversion

Crown-fire patches (i.e. treeless areas) have increased in size since at least the 1980s in the SWUS and Sierra Nevada range of California (Miller et al. 2009; Thode 2012). Personal communication with long time fire managers also suggests that crown-fire patches are increasing in frequency and size (Gary Kemp Fire Management Office Bandelier National Monument 30 years wildland fire experience). Increases in patch size

alone will probably limit the ability of ponderosa pine forests to recover completely to the pre-fire forest type, because ponderosa pine has a limited seed dispersal range (Shepperd & Battaglia 2002). Therefore, ponderosa pine is not well adapted to recolonize large areas following stand-replacing fire. Ponderosa germinates require bare mineral soil to germinate (Oliver & Ryker 1990). Previous research has found that ponderosa pine does not germinate to any significant degree more than 200m from a seed source, or intact forest edge (Dodson & Root 2013; Haire & McGarigal 2010). Patch size and shape will control the amount of edge between forest and non-forest. The differences in micro-sites between forest and non-forest ecosystems will be very different with the non-forested area being warmer than the forest (Meyer et al. 2001). In certain cases, the non-forested edge can act as a barrier for certain species and create suitable habitat for other species that will freely cross the forest edge (Ries et al. 2004). Whether those species transport pine seeds from the forest to the open non-forested area will change the availability of pine seed for regeneration. Thus, any increase in crown fire induced patch size that increases the amount of area far away from a seed source will influence pine regeneration.

Hypotheses

Based on my review of the appropriate literature, and my understanding of ecological first principles, I have developed two hypotheses based on a potential climate driven process and a biophysical pattern of type conversion in ponderosa pine systems. H1) Pine regeneration will be lower on those sites at the fringe of the ponderosa pine bioclimatic envelope, for example lower elevations and southern aspects. H2) Seedling establishment will be limited to a narrow band that extends away from seed trees into the burned area. Favorable areas far from a seed source will fail to reestablish ponderosa pine. H0) An alternative hypothesis is that seedling regeneration will be random across the severely burned areas where ponderosa pine forests dominated pre-fire. See **Figure 3-2** for a conceptual diagram of my hypotheses.

Methods

Predictor variables

I developed spatially explicit topographic variables to evaluate my hypothesis that type conversion is a result of bioclimatic conditions warming across a landscape to a point at which pine regeneration is not possible in specific areas (H1). I have chosen to use three independent topographic landscape variables as a proxy for local climate differences: elevation, aspect, and a topographic position index (TPI) that delineates ridges, valleys, and slopes. Using an information-theoretic approach (Burnham & Anderson 1998) I developed, tested, and compared statistical models from a combination of physical variables to predict the relative likelihood of type conversion following a large crown fire. I created spatial representations of the best-fit model using model coefficient averaging. Each spatial model shows the relative likelihood of type conversion for a specific landscape.

This approach assumes several conditions. First, I assume that climate change is occurring uniformly across a given landscape. In other words, I assume the background climate conditions across a landscape have warmed but the forest is keeping sites artificially cool. Following the fire, the landscape rapidly shifts into the background climate conditions due to lack of shade, moisture retention, etc. Additionally, I assume land use histories have generally followed the same pattern of extensive logging, overgrazing, and fire suppression and will affect each burned area uniformly (Covington & Moore 1994). Finally, I assume ponderosa regeneration is possible at any given location within its pre-fire distribution (null model) and the only limitations are seed availability and short-term climate patterns. I predict that if the background climate has warmed, then following a large crown fire, type-conversion should be more likely on the warmest and driest sites on the landscape because seedling germinates are unable to survive the warmest climate conditions without facilitation from the mature parent trees.

I examined nine of the largest wildfires that burned through the ponderosa pine forests of Arizona and New Mexico from 1996-2006. **Table 3-1** lists the fires selected for this study, their location, year, and acreage. To gain a regional understanding of the patterns and predictors of post-fire type conversion I selected fires ranging from east-

central AZ and west-central NM to the northern portions of each state (**Figure 3-3**). I accessed fire perimeters from the US Forest Service spatial fire perimeter database (USFS 2013), extracted the relevant fire perimeters, and buffered each individual fire by 2 km using a geographic information system (GIS; ESRI 2011). I buffered the fire perimeters to eliminate “edge noise” when calculating the topographic variables and allow for a broader search area when determining the maximum and minimum values for each spatial variable (see below). I then calculated all model variables individually for each fire within the buffered perimeter to account for local adaptation. The variables represent moisture and temperature gradients (Whittaker 1967; Parker 1982; Allen 1989; Kelly & Goulden 2008) and I hypothesize that the areas most likely to type convert are the relatively hottest and driest (H1). I scaled each variable between zero and one – to represent relative likelihood of type conversion – with values near 1 being the hottest and driest and thus with the greatest likelihood of type conversion and values near 0 being the wettest or coolest and being the least likely to type convert. For example, I predict the highest elevation in a burned area to have a lower likelihood of type conversion – a value near 0 – compared to the lowest elevation areas within the same burned area, which would have a value near 1. I developed each individual topographic variable using the following methods.

Elevation

Using a 30m digital elevation model (DEM) accessed from the LANDFIRE database (USGS 2013) I determined the local elevation range of ponderosa pine. Ponderosa pine distribution was determined using the SWReGap vegetation classification map (Prior-Magee et al. 2007). For fires that occurred before the creation of the ReGap map in 2000, I interpolated ponderosa pine distribution from the surrounding vegetation types that burned at moderate or low severity. After separating the distribution of ponderosa pine from the rest of the vegetation, I determined the local elevation range for ponderosa pine within each buffered burn perimeter. Finally, I rescaled each raster layer between zero and one. The higher number indicates a higher likelihood of type conversion, and warmest and driest location (i.e. lowest elevation). See **Figure 3-4a** for a graphical representation of the elevation model.

Topographic position index

The topographic position index (TPI) was developed using the methods outlined in Jenness et al. (2013). TPI is correlated with soil development and has been shown to relate to soil moisture availability (Parker 1982). The TPI uses a DEM and a moving window to assess the topographic position of each individual pixel and assigns a relative value to each pixel where low numbers indicate valley or canyons, and higher values represent steep slopes and ridge tops. For each burned area, the TPI values were reclassified from the output values to a range from near zero to one, representing the relative probability of type conversion, where ridge tops were determined to be the driest locations and assigned values near one (i.e. most likely to type convert), and valleys were determined to be the wettest areas so they were assigned values near zero (i.e. least likely to type convert). See **Figure 3-4b** for a graphical representation of the likelihood of type conversion for TPI.

Aspect

To assign probability of type conversion for any given aspect, I created a scaled (0-1) deviation from northeast (45°). I began with azimuth values from the LANDFIRE aspect data set (USGS 2013) and determined the distance in degrees each azimuth was from 45° . Based on research that showed increased productivity of forest stands I determined 45° aspects to have the lowest likelihood of type conversion and aspects of 225° to have the highest type conversion likelihood (Trimble & Weitzman 1956; Beers et al. 1966). I then converted each azimuth to radians using the ArcGIS raster calculator. Next, I took the cosine of each pixel, now represented as n radians from NE, to convert the radians into a linear -1 to 1 scale. Finally, I converted the -1 to 1 scale to a 0 to 1 scale representing probabilities of type conversion (i.e. SW = 1, NE = 0). See **Figure 3-4c** for a graphical representation of the likelihood of type conversion for aspect.

Field data collection

To gather data for model validation, I examined the largest treeless patches resulting from high severity fire in my study area. The current regional drought represents some of the driest years of the past century and PDSI values for the study region being

constantly negative since 1996 (**Figure 3-1**) (Daly et al. 1994, Schwalm et al. 2012, Abatzoglou 2013, data from: Abatzoglou and Redmond accessed Jan 2014). I selected fires that burned during this period, as these years potentially represent the future climate normal of the southwestern US (Williams et al. 2012). Data collected during this time is informative for interpreting ecological processes during warm and dry periods, without interference from cooler, wetter periods.

Burn severity data

To determine the spatial extent of high severity burn in each fire, I used the Relative Differenced Normalized Burn Ratio (RdNBR), derived from the Monitoring Trends in Burn Severity dataset (MTBS.gov) which uses Landsat imagery (Eidenshink et al. 2007). The RdNBR method is more accurate at delineating high severity areas in drier vegetation types than the standard dNBR method, and is therefore preferred in most dry forest types (Thode & Miller 2007). I used RdNBR values greater than 640 for my delineation of high severity fire. Within areas identified as high severity, I created sampling bands using the Euclidian distance tool in ArcGIS. These bands were intervals of 0-50m, 50-100m, 100-150m, 150-250m, and greater than 250m. After creating sample bands for all high severity areas, I visually identified and selected the largest contiguous patches of high severity fire that burned in ponderosa pine. The pre-fire ponderosa pine stands were determined using the ReGap vegetation map (Prior-Magee et al. 2007). I extrapolated ponderosa pine distribution for pre-2000 fires similar to the elevation model variable. Within the remaining area, I randomly assigned each sample band 10 points, for a total of 50 points. My goal was to collect at least 30 points within each fire. Given uncertainties of travel time and road conditions at many of the fire locations, I determined that 50 potential sample points would be a sufficient number to allow us to abandon unsuitable or inaccessible sites and increase the probability of collecting enough points at each location.

Field sampling

Each sample point was located using a Garmin 60CSx GPS unit with an estimated accuracy of ± 3 meters. Each sample location was determined viable as long as it met the following criteria: 1) it was in an area that supported ponderosa pine pre-fire, 2) it was

one hundred meters from a low, moderate, or high use road, 3) it was not directly on an abandoned or very low use road, 4) it was not in a drainage bottom, 5) it had not been significantly or unnaturally disturbed since the fire. If the site did not meet these criteria, I attempted to move the sample point to another nearby location, identified by blindly tossing a survey stake toward a more suitable location. If it proved impossible to move the sample point to a suitable location, I abandoned the sample point.

At each sample location, I established a multipart plot. Each plot consisted of four circular radial subplots, each separated by 120° from an initial randomly selected bearing, and 13m from the center plot, **Figure 3-5**. Each subplot was a nested plot that consisted of an inside plot with a 1.5m radius and an outside plot with a 3 m radius. At each subplot, canopy cover was classified within the 1.5 m nested plot based on physiognomic characteristics (grasses, forbs, tall and short shrubs, trees, or logs) in seven different percentage cover classes: 0, 0-5, 5-25, 25-50, 50-75, 75-95, and 95+. Exposed ground surface (litter, bare ground, or rock) was classified using the same classes. Within the 3 m subplot, I measured all trees ≥ 15 cm tall and recorded species, height, and nurse structure. I felt that this height of seedling was old enough to have survived several seasonal droughts and cold seasons. For junipers only, I recorded the number of stems.

Using a Nikon Prostaff 3 rangefinder (range 500 m, accuracy ± 1 m), I measured distance to the nearest ponderosa pine seed source at each subplot. I defined seed source as any group of reproductive trees. Generally, ten or more trees qualified as a group, but exceptions were made if smaller groups were producing copious amounts of cones. If the seed source was outside of the range of the rangefinder or not visible from the plot, the distance from the plot to a seed source was later estimated using 1 m resolution aerial imagery from the National Agriculture Imagery Program in a GIS (USDA 2013).

Following the field sampling, I used Forest Service Region 3 geospatial data (USFS 2013) to determine the locations of reforestation efforts. One fire (Cerro Grande) received extensive replanting, with most of my study plots falling in the planting area. I happened to sample a single planted area in two other burned areas (Ponil and Rodeo-Chediski). In the other burned areas, forest restoration plantings were non-existent or obvious (e.g. fences around the planted areas) and easy to avoid. I excluded planted areas from the model evaluation.

Model comparison and averaging

I determined a sample location was type converted if there were fewer than 2 post-fire ponderosa pine trees greater than 15 cm tall. Based on my plot size of $\sim 113\text{m}^2$, 2 trees per plot represents roughly 175 seedlings/ha which results in a high density of trees for a Southwest ponderosa pine forest when compared with pre-settlement reconstructions (Moore et al. 1999). However, because of the randomness and high mortality risk associated with the establishment of a single tree, it seems appropriate to use more than a single tree.

Within the statistical program R (R Core Team 2013), I used logistic regression with a binomial distribution and compared Akaike's Information Criterion (AIC) values from multiple models. Using all possible variable combinations, including models with random effects and combinations of interactions, I created 95+ unique models of type conversion likelihood. I compared the random effects of individual fires and burned areas, defined burned areas as those where fires were in close proximity (<10 km) to each other. I determined an AIC difference of at least 10 below the null model, and the model(s) with the lowest AIC are the model(s) that best fit to the observed data (Burnham & Anderson 1998). I used model averaging of the individual models with a ΔAIC of less than 2 using a process developed by Burnham and Anderson (1998). Model averaging allows for a better model fit by determining the weighted contribution from each parameters based on their importance to the model rather than simply choosing the single model, or combination of variables, that happens to fit the data best. The result is a weighted average of the coefficients with standard error and Z-values for each parameter.

Results

Modeling results

Topographic variables combined with the distance to seed source resulted in the model that best fit the empirical type conversion data (**Table 3-2**). Table 3-2 lists the small subset of models that best fit the data or demonstrate the importance of separate parameters. The random effects of burned area (i.e. forest or mountain range where the fires burned) were included in the final, best fit, model. The distance to seed source was

by far the most important individual model parameter. With elevation, aspect, and topographic position index added, the model better fit the empirical data. Because the difference in AIC values is less than 2 for the models that included elevation and the other topographic variables, it is impossible to determine which model is absolutely the best fit. Therefore, I used model averaging to create a model that best fit the data and used each important variable. The final model resulted in a weighted average of distance from seed source, elevation, aspect, and topographic position index. The coefficients for this model are shown in **Table 3-3**.

Based on the coefficient for seed source, I show a positive relationship between distance to seed source and likelihood of type conversion. Elevation and topographic position index (TPI) show agreement (positive sign) with the hypothesized (**Figure 3-4**) relationship (i.e. at the hypothesized high probability locations, the model results in a higher likelihood of type conversion). The coefficient for aspect has the opposite relationship with the hypothesized curve (**Figure 3-4**), showing that type conversion is less likely on NE slopes than SW slopes. However, this relationship is weak and has a coefficient less than 1, which results in a nearly flat curve and similar likelihoods for all aspects.

Spatially explicit model representation

The model average results provide a spatially explicit, landscape scale representation of relative type conversion vulnerability. The spatial representation of the model shows specific areas where type conversion is more likely to occur. These are the areas that are already the warmest and driest in the local distribution of the ponderosa pine. This suggests a process of bioclimatic processes restricting conifer germination at the warmest ends of its range, and is in line with other studies on shifts in species ranges (e.g. Allen and Breshears 1998, Kelly and Goulden 2008) which fit the model of species niche shifts upslope, to cooler more mesic environments, in response to climate change (Colwell & Rangel 2010).

Using only the topographic variables, the model predicted a higher likelihood of type conversion at lower elevations (**Figure 3-6**). The model predicted the lowest likelihood of type conversion to be at the higher elevations. The low importance of TPI

and aspect in the averaged model can be seen in the spatial expression of the model; there are fewer obvious patterns of lower type conversion risk in valleys or on certain aspects.

Some burned areas had less area predicted to be of high type conversion likelihood than other burned area due to topographic differences between sites. For example, the high severity sample points in the Rodeo-Chediski (Figure 3-6a) fire burned on relatively flat, high elevation lands above the Mogollon Rim. The highest likelihood of type conversion is in the low elevation canyons and valleys. The model predicted most of the area above the rim to have moderate to low likelihood of type conversion. In other burned areas, such as the Cerro Grande fire (Figure 3-6b), the majority of areas are predicted to have high likelihood of type conversion because most of the fire was at low elevation and on rugged terrain.

Because of the large patch sizes in many fires and the importance of distance to seed source in the averaged model, type conversion likelihood is high, even in areas that are otherwise favorable. Both examples in Figure 3-7, the Rodeo-Chediski and Cerro Grande fires, have large patches of stand-replacing fire. In the Rodeo-Chediski (**Figure 3-7a**), several large high severity patches (large red areas) are in locations that would otherwise be low probability of type conversion (**Figure 3-7a**). In the case of Cerro Grande, most of the high severity fire burned in areas where type conversion was predicted to be moderate or high (**Figure 3-7**). In this case, the greater distance to a viable seed source only slightly increased the likelihood of type conversion.

Forest regeneration

Of the 202 total plots, 51 plots (25%) had ponderosa pine regeneration, either natural or planted. Of the 179 unplanted plots, 43 had natural ponderosa regeneration (24%). Within a distance of 150m from a seed source, 41 of the 107 plots had natural regeneration (38%). I did not observe any natural regeneration further than 250m from a seed source. In all but two plots with natural regeneration, the distance to seed source was less than 150m (**Figure 3-8**), **Table 3-4** has a list of the total number of plots, the number of plots with ponderosa regeneration, and the number of reforested plots for each burned area.

I found that nearly half of ponderosa pine seedlings germinated under some sort of nurse structure. **Table 3-5** lists the different nurse structures by tree species. Short shrubs and bunch grasses occasionally provided cover as a nurse structure, and a small portion of the regeneration occurred under oak shrubs. Logs and large branches served as the most common nurse structure. Branches and logs seem to provide enough shade for germination, and do not compete with the tree for other resources, making them ideal nurseries for young pine.

Other than ponderosa pine, the most common tree species were Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and alligator juniper (*Juniperus deppeana*). I also found subalpine fir (*Abies lasiocarpa*), white fir (*A. concolor*), oneseed juniper (*Juniperus monosperma*), and Utah juniper (*J. osteosperma*) on my sample locations. **Table 3-6** lists the total number of each tree species found in each burned area.

Post-fire landscape potentials

Grassland systems were the most common post-fire ecosystem type. Grass dominated over 60% of all plots (**Table 3-7, Figure 3-9**). On all plots, grass canopy cover averaged roughly 40% (**Table 3-8**) cover and varied from a trace cover to complete coverage, but was present on all plots. Complete ($\geq 95\%$) plot coverage was more common in areas dominated by rhizomatous grasses such as western wheatgrass (*Pascopyrum smithii*). Areas dominated by bunchgrasses, mainly Arizona fescue (*Festuca arizonica*) and mountain muhly (*Muhlenbergia montana*), tended to have more exposed ground due to the interspaces between individual grass bunches. Cheatgrass (*Bromus tectorum*) and smooth brome (*B. inermis*), common invasive grasses in SW forests, rarely dominated large areas and were absent on most plots appearing on only 25 and 10 percent of plots, respectively.

I found tall shrubs, identified as New Mexican Locust (*Robinia neomexicana*), and species in the Oak (*Quercus*) genera, at nearly half (47%) of the total plots, see **Table 3-8**. Tall shrubs were absent from half of all plots visited, and completely absent from some fires. Tall shrubs dominated 33% of all plots **Table 3-7**. Occasionally, tall shrubs completely covered sample plots. More commonly, I observed areas of grass, forbs, or bare ground between the shrub canopies. It is likely that these shrubs will increase in

ground cover percent and connectedness during the coming years (*Chapter 2*). At xeric locations, I found tall shrubs from of multiple members of the hybridizing *Quercus* genus, wavy leaf oak (*Q. undulata*), and shrub live oak (*Q. turbinella*), and rarely, New Mexico locust.

I found members of the genera *Arctostaphylos* and *Ceanothus* to be the most common species in the short shrub category, though the two species were never collocated. Together, short shrubs dominated just 2% of all plots (**Table 3-7**) and averaged just 6% cover on all plots (**Table 3-8**). In more xeric areas, short shrubs had very little vegetation between the canopies and very little topsoil. In more mesic environments, short shrub communities, dominated most commonly by *Ceanothus* sp., tended to have a higher percentage of canopy cover and grass and forbs between canopies.

Areas covered in rock, litter, or bare soil, and free of vegetation cover, were categorized as bare/open. These areas dominated only 5% of all plots (**Table 3-7**, **Figure 3-9**). On average, exposed surface was $\approx 32\%$ of the plot with 21% bare ground, 3% litter, and 8% rock (**Table 3-8**).

Model Discussion

Limits to regeneration

The results from the model comparison provide evidence that supports my hypotheses. The most important model parameter was distance to seed source. This supports my hypothesis (H2) that viable seed sources are important to pine regeneration and lack of seed source has a high likelihood of resulting in type conversion. Adding the topographic variables, particularly elevation, created a model with the best fit. Elevation was the most important topographic variable – which I used as proxies for moisture and temperature – and supports my hypothesis (H1) that type conversion was most likely at the hottest and driest locations (i.e. lowest elevations). The modeling results suggest the alternative hypothesis of random regeneration (H0; $\Delta AIC = 43$) is not a robust predictor of type conversion. Accounting for the random effects of burned area enhanced the fit of the model. This is not surprising due to the large number of influencing variables that I did not measure (e.g. soil type, land use history, etc.). The negative (opposite)

relationship of aspect (**Table 3-3**) from the hypothesized probabilities could be due to the increased competition on the cooler and wetter, more NE, aspects. Alternatively, the overall lack of regeneration results in many type converted sites in areas where the model predicts forest regeneration, resulting in high standard error.

The model generally under predicts type conversion. **Figure 3-10** shows the sampled binary type conversion value (i.e. whether or not a sample location actually type converted) compared to the predicted probability of type conversion for that location from the final averaged model. There was little regeneration (sampled value = 0, i.e. not type converted) in areas beyond 0.6, there was however many sample locations that type converted (sampled value = 1) where the model predicted a low probability (<0.5). This indicates complicated dynamics involved post fire tree regeneration. Factors such as land use history, local pre-fire vegetation differences, and local soil types likely play a significant role in determining the probability of type conversion following stand-replacing fire.

Next steps in model development

The topographic variables used in the model are all proxies for moisture availability or temperature gradients. The model fit could be improved if the current variables were combined with, or substituted for, broad-scale temperature and moisture models. Topographic position could be substituted with finer scale hydrologic catchment models that are able to discern the areas where more moisture may be available. Solar radiation might be an appropriate replacement for aspect, but that requires an understanding of which period of solar insolation is most important to pine and other successional vegetation, which may be difficult to incorporate into this simple and general model of type conversion. Developing a soil moisture model to use a predictor variable in the model may also improve model predictions.

Incorporating pre-fire vegetation or understory data into this study would likely increase the predictability of the model. The simple step of using a local, more precise, vegetation map that would allow for separate analysis of pure pine forests and ecotones, and potentially identify patterns of type conversion based on pre-fire vegetation characteristics. I lacked equal distribution of samples across the temperature and moisture

gradient for all fires. This would require more focused sample stratification. Increased sample size would allow for better fit of the model. Likewise, I lacked the sample depth to determine the exact distance from viable seed sources regeneration is probable. Again, increased sample size and focused stratification would mitigate this problem.

Management implications and applications

No “steady march”

This study reinforced the findings from a previous study (Haire & McGarigal 2010) that found regeneration occurring within 250m of the forest edge. Other researchers (e.g. Haire & McGarigal 2010; Puhlick et al. 2012) suggests that following a high severity fire, ponderosa pine will begin a “steady march” out from a seed source into the center of the treeless patch, eventually recolonizing the burned area. For several reasons I believe this not to be the general case. Because ponderosa cones are not serotinous and seeds do not survive fire, regeneration must rely almost completely on post-fire seed production (Oliver & Ryker 1990). In my study, I did not find regeneration beyond 250m from a seed source. In recent fires, high severity patch sizes are so large that much of the post-fire landscape is further than 250m, or even 500m, from a viable seed source. The “steady march” idea suggests the initial post-fire cohort begets subsequent cohorts until the entire treeless area is reforested.

I suggest that during the 30+ years it might take the initial post-fire cohort to reach reproductive age, the vegetation outside the forest regeneration has been establishing its own community dynamics, for example, changing fire regimes and intraspecific competition could act as a positive feedback for the newly set ecological trajectories (see *Chapter 2* for discussion on the separate pathways to type conversion). In the post-fire shrublands and grasslands, fire regimes are likely to become more severe, more frequent, or both (Nagel & Taylor 2005). Frequent fire in grasslands can limit ponderosa expansion (Allen 1989; Coop & Givnish 2007). Reburns of older burn scars recovered to shrublands have resulted in complete mortality of pine regeneration and even mortality of adjacent stands that survived the initial fire (C.D. Allen *unpublished data*). Even though invasive species were not found to be widespread in this study, they have been shown to alter the fire regime of other areas and prevent conifer germination

(D'Antonio et al. 1992). Pine germination facilitated by a flammable nurse structure such as a log or shrub may lead to mortality during a subsequent fire (Roccaforte et al. 2012). Shrub and grass nurse structures may facilitate germination of seedlings at drier sites, but this interaction could switch to competition at more mesic locations (Sthultz et al. 2007). Thick grass and shrubs could compete for sunlight, nutrients, and space with the shade intolerant ponderosa pine germinates.

Shade tolerant Douglas-fir on the other hand, seems to be relatively well adapted to stand-replacing fire. Douglas-fir (and other firs) can germinate and survive under the tall shrubs that tend to dominate the more mesic locations. The species is able to germinate in areas once dominated by ponderosa forests (e.g. Bear fire; **Table 3-6**). This could lead to competitive pressure on ponderosa pine establishment in the upper, more mesic ends of its distribution. Firs may be better suited than ponderosa pine to adapt to projected future conditions, because of its comparative lack of germination limitations.

Spatial strategies

Both the modeling effort and field study show broad, non-random patterns of tree regeneration. In other words, type conversion is predictable. This preliminary step is an important one toward better anticipating ecosystem changes. Given the mounting evidence that landscapes are moving into a “no-analogue” future (Williams et al. 2012), with large amounts of uncertainty about the exact process and timing, any level of predictability will help guide decision-making.

The model results provide managers with spatially explicit information about where type conversion is likely to be permanent, and the spatial distribution of areas that could return to ponderosa forests. Even under the most optimistic projections of a “steady march” of trees into the treeless patches, the crown fire areas in this study will largely remain type converted for many decades to centuries.

The model is a first step toward incorporating type conversion into post-fire management decisions. The model describes the relative probability of post-fire type conversion on a landscape scale. This model, combined with other models, local monitoring data, or spatial data, that explore different post-fire processes or patterns, can help initiate the management conversations in a spatially explicit manner. For example,

planting germinated (2-3 year old) trees avoids the biotic and abiotic bottlenecks of regeneration. Trees that survived planting, observed in this study, appeared to be healthy even in more xeric locations, suggesting the planted trees have an ability to survive in locations inhospitable to natural regeneration (**Figure 3-11**). While site-specific type conversion predictions are outside the scope of this study, the model shows the spatial distribution of areas that are unsuitable for ponderosa germination and establishment. The decision to attempt reforestation or manage for the post-fire landscape should be approached using a data driven methodology and I feel the model developed here, or one similar to it, could assist in such decisions.

This model could be used before a fire to assess the vulnerability of a landscape and may be particularly useful if combined with crown fire hazard maps to identify areas of likely restoration success or areas where strategies might be developed to facilitate the transition from forest to shrubland or grassland. This model of type conversion vulnerability could be combined with other data in a landscape assessment (e.g. Sisk 2007) to identify areas where type conversion may have the greatest impact on other elements of the ecosystems or cultural values, such as endangered species habitat or municipal watersheds.

An example of such a discussion could incorporate a landscape assessment that includes probability of type conversion might identify areas that may serve as future ponderosa pine refugia. Refugia in this case are defined as small pine stands isolated from larger stands by crown fire similar to those described by Camp et al. (1997), in which there may locally adapted genetic genotypes, that could reestablish forests better adapted to dry conditions than current the forest. Using a model of type conversion probability one might identify refugia in one of two ways. First, before a fire, managers could map out potential refugia by identifying areas with the highest risk of type conversion from the local ponderosa distribution and overlay those areas with other variables that may allow for small stands of ponderosa forest to survive a fire such as extremely rocky terrain that may not carry surface fuels. After identifying these areas, management strategies could be set in motion to further protect the potential refugia and prevent crown fire from destroying the stands. Second, post-fire analysis could identify surviving stands of ponderosa forest that are located in locations of high probability of

type conversion. In this case, local managers could conduct field surveys to determine the *in situ* reproductive capacity of the xeric stand. If the survey discovers young ponderosa, or evidence of seedlings killed by surface fire, these sites may potentially harbor the genetic capacity to germinate in the current drought conditions. Monitoring plots could then be established, and seeds collected for use in common garden experiments to quantitatively determine the genetic capacity for germination and growth in arid environments (Ikeda et al. 2014). This would represent another step in determining the adaptive capacity of ponderosa pine (Lesser et al. 2013).

Climate projections in the Southwest point to increased severity of drought conditions in the coming decades. Further climate conditions could reduce the potential distribution of ponderosa pine, pushing the area suitable for germination and establishment in areas of higher up along an elevation gradient. Models similar to the one created here, combined with future climate projections, would help to further explain spatial patterns of areas likely to type convert. Understanding the broader implications, positive and negative, of type conversion on ecosystems and social values could help to bring management decisions to the landscape level and create a system amenable to a discussion of possible active management decisions regarding ecological and social adaption in the face of global change.

CONCLUSION: HOW CAN WE ADAPT TO RAPIDLY CHANGING LANDSCAPES?

Acceptance

The first step toward adaptation to changing landscapes is accepting the fact that there is a high probability that many areas are going to change significantly and permanently in the near future. In ponderosa pine for example, once crown fire kills all the mature trees over a large section of the landscape, ponderosa forests are unlikely to return in many areas. Instead the previously forested landscapes will be replaced with some combination of shrublands, grasslands, or other woody species.

The conversion from forest to non-forested ecosystem has wide ranging implications for the rest of the mountain range. From an ecological perspective, loss of forests will result in the loss of species that depend on them, some of which are threatened or endangered such as the Mexican spotted owl, or northern goshawk. The shrublands and grasslands that establish following the fire can outcompete the new tree seedlings. The successional ecosystems can alter the fire regime of the landscape such that fires burn hotter and more frequently than the forest was adapted to. In either case, the forest can be excluded from reestablishing following high severity fire for a long time. Humans depend on forests for recreation, clean water, spiritual needs, economic sustenance, and many other ecosystem services. Large stand-replacing fires can devastate a community, and stress the social structures of the community to the breaking point.

It is important to realize that crown-fire induced landscape changes are not all "bad" from a human or ecological perspective. Crown fire can "punch holes" in the overgrown and contiguous forested landscapes that have resulted after a century of fire suppression. Provided crown fire creates a balance of "holes" and leaves enough forest, the resultant landscape heterogeneity can create habitat for species that require areas of high severity fire, such as the black-backed woodpecker. The successional shrublands and grasslands provide habitat diversity and support different species of flora and fauna than the overgrown forest, which can become relatively species 'poor'. The heterogeneity

of burned areas can create natural firebreaks and reduce the risk of crown fire to the adjacent forest stands for decades.

Local & active science-policy interface

For managers, it is important to understand which areas are most likely to convert from forest to non-forest on their landscapes. Too much science on post-fire succession is done to explain observations of small, specific, locations, with little or no heuristic capacity. This information is difficult to use in areas without the exact set of parameters collected for the research, which are not consistent across space and time. To be useful for land managers and policy makers, scientists should work to develop general models that have regional application and transferability. Scientists should work directly with local managers to adapt the models by incorporating local information and data, applying local ecological knowledge from a specific landscape. This process can transform general models into robust predictive, spatially explicit, models that are viewed as legitimate by local decision makers.

Wildfires and land managers are operating at scales far broader than most studies and contemporary restoration efforts. Using broad-scale, spatially explicit information, managers can develop post-fire strategies based on local evidence which is more likely to succeed than those developed on the "best practices" from another forest or landscape, which often take specific ideas and attempt to pull generalities from them. General succession models, combined with local information, can be applied following a fire to determine post-fire management strategies. This approach could be used before a fire to assess the vulnerability of an area to "type conversion" or ecosystem changes from forest to non-forest following a stand-replacing fire. Managers and scientists can work together to develop management plans to reduce the type conversion vulnerability of a particular landscape. Combined with other information regarding ecological functions and social values and needs, this information could be used to prioritize areas where management actions such as forest restoration have the highest need and highest chance of success. Once the areas at highest risk of type conversion are identified, we can ask the question: should we step into this process and assist with the ecological adaptation?

Assisted adaptation

The landscape is adapting to new conditions brought about by climate change and land use histories. We have an opportunity to assist in the adaptation of landscapes and to facilitate the succession of more resilient ecosystems to replace the current forests. We can avoid going from “denial to despair without pausing on the intermediate step of actually solving the problem,” (Al Gore, 2005). Assisted adaptation must take a landscape approach and should be a combination of ecological restoration in some areas, natural succession in others, and assisted migration in the areas that lack any kind of ecologic foundation to establish a successional trajectory. Assisted adaptation should be an active process to reduce the “shocks” to the ecologic and social systems following the abrupt and violent changes brought about by stand-replacing fire.

The scale of the fire, particularly stand-replacing fire in recent years (Shultz, Wallow, Las Conchas, Rodeo-Chediski, Little-Bear, Warm), demands a landscape approach to management (Sisk et al. 2005). Just as the attempts to mitigate crown fire risk through restoration strategies (Stephens et al. 2013; Stevens-Rumann et al. 2013; Allen et al. 2002) require a broad, landscape scale perspective, so to do any post-fire management response. Often, as a result of such mitigations, areas that do not burn at high severity generally resemble the pre-fire forest type with little change to ecosystem function (Keyser et al. 2008; Lentile et al. 2007). Large treeless patches are unprecedented in the recent history of ponderosa forests, change ecosystem function dramatically, and may require innovative management techniques. Large amounts of energy and capital will be required to rapidly return these areas to the pre-fire forest type. Perhaps the best management action is to take no action and allow the natural systems to recover on their own. There are advantages to the “no action” response. Large treeless patches, distributed across a landscape, reduce crown fire risk to extant forests by breaking up the continuity of the fuels that have been building since the early 1900s. The heterogeneity from patchy crown fire has the potential to ease the landscape into the “new-normal” instead of abruptly shifting into a novel system. The “no-action” response is certainly a viable option, especially given the current amount of uncertainty surrounding ecosystem response moving into a warmer future, but this decision should be

made *actively*, not settled upon as decision makers watch landscapes evolve faster than the local social structures can adapt.

Assisting in landscape adaptation may take the form of larger (>20,000 acre) prescribed burns with recommendations to allow crown fire to create large “holes” in the forest canopy. Another strategy could be aggressive thinning to create fire breaks and allow the successional communities to develop in the understory of the remaining large trees. In certain areas where fresh water security may be the highest priority, plans to significantly and rapidly reduce fire risk while preventing increasing water infiltration may require drastic reduction in forest density and active maintenance of the successional vegetation using frequent fires that favor more open grasslands. To become incorporated into pragmatic land management, the science of exactly how and where to assist adaptation of landscapes must be developed using information from completed and future type conversion studies. Therefore, it will be important for scientists to learn from these aggressive actions through experiments and observation.

Community development

Assisted adaptation strategies cannot be done without strong community support. Resilient communities are necessary to create more resilient landscapes. The scientific outcomes and management strategies are only one, potentially tiny, piece of the puzzle that is land management in a time of rapid landscape change. Developing strong social structures and communities will be a necessary part of any land management action.

A potential strategy for developing community support is for scientists to outline a series of likely future scenarios, using local information to create spatial models of potential landscape change in the ‘backyards’ of local people. Allowing the public to see the consequences of attempting to maintain the status quo, and to educate them that changes to their landscape are inevitable, will help to create the need for action. Allowing community members to participate in the assisted adaptation decision-making process can create legitimacy of the information and support for recommended actions. Moving from support to action will require long-term commitment by managers and scientists to maintain the ‘social capital’ developed during the decision-making process.

Social research should also be conducted to determine the best way to create a fire adapted community that embraced some level of type conversion. This research

could provide land managers with a benchmark or limit to the amount of forest communities are willing to sacrifice in order to save the rest of it. This will assist managers and community leaders in developing robust community structures that will lead to resilient landscapes.

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TABLES AND FIGURES

Table 3-1 - List of fires in this study - ID numbers correspond to map in Figure 3. The acreages of the fire and the acres burned at high severity (HS) are listed, along with the year of the burn and general location.

Fire	Location	Year	Total Acres	High Severity Acres (% of fire)
Bridger-Knoll	Kaibab Plateau, AZ	1996	35,478	7,148 (20%)
Pumpkin	San Francisco Mts, AZ	2000	16,086	3,536 (22%)
Horseshoe	San Francisco Mts, AZ	1996	8,289	1,783 (22%)
Hochderffer	San Francisco Mts, AZ	1996	13,206	2,332 (18%)
Rodeo-Chediski	White Mountains, AZ	2002	461,753	169,042 (37%)
BS	Gila National Forest, NM	1998	4,475	1,978 (44%)
Bear	Gila National Forest, NM	2006	34,703	8,383 (24%)
Cerro Grande	Jemez Mountains, NM	2000	44,280	14,504 (33%)
Ponil	Sangre de Cristo Mts, NM	2002	89,085	27,276 (31%)

Table 3-2 - Model comparison results - Model Variables: Seed = a continuous variable measured in meters for each plot location to nearest viable seed source (10+ mature trees); Elev = scaled (0-1) elevation range of ponderosa pine, values are relative for each burned area such that the highest elevation = 0 and lowest elevation = 1; TPI = topographic position index scaled for each burned area, Aspect = deviation from NE cosine transformation and scaled (0-1) aspect where SW (225°) = 1 and NE (45°) = 0, ‡ = mixed effects model that included random effects of each burned area, Site RE = mixed effects model with random effects of each burned area and intercept. K = number of parameters (including intercept). AIC = Akaike information criterion. ΔAIC = difference in AIC values of other models from 'best fit' model. 4.10 E-10 = relative likelihood of null model is better fit than model with lowest AIC value.

Variables	K	AIC	ΔAIC
Seed+Elev+Aspect ‡	4	105.53	0.00
Seed+Elev ‡	3	105.83	0.30
Seed+Elev+Aspect+TPI ‡	5	106.84	1.31
Seed+Elev+TPI ‡	4	107.11	1.57
Seed+Aspect ‡	3	109.34	3.81
Seed ‡	2	110.36	4.83
Seed+TPI+Aspect ‡	4	111.15	5.62
Seed+Aspect ‡	3	112.18	6.64
Seed	2	125.72	20.19
Site RE Only	1	132.47	26.94
Intercept Only	1	148.76	43.23

Table 3-3 - Parameter Coefficients - Standardized model-averaged regression coefficients (column 2), unconditional standard errors (SE), and Z-statistics for physical variables used to predict relative probability of type conversion. Greater |Z| values give a relative importance of each variable to type conversion predictability.

Parameter	$\tilde{\beta}$	SE	Z
Distance to Seed Source	0.016	0.00	3.64
Elevation	5.839	6.30	0.93
Aspect	-0.685	0.83	0.82
Topographic Position Index	1.130	1.74	0.65

Table 3-4 - Plots per fire - Number of plots per fire, number of plots where *Pinus ponderosa* (PIPO) was present, and number of planted plots within each fire area. Planted plots were determined from forest service spatial information and personal communication with personnel involved in post-fire reforestation efforts. Cerro Grande was so extensively reforested that it was determined all of the sample plots lie within potential planting zones, though there was only living PIPO on 6 plots.

Fire	Total Plots	Plots w/ PIPO	Planted Plots
Bear	31	2	-
Bridger Knoll	17	2	-
BS	5	3	-
Cerro Grande	25	6	25
Hochderffer	8	1	-
Horseshoe	17	2	-
Ponil Complex	30	3	1
Pumpkin	30	13	-
Rodeo-Chediski	39	19	1
Total	202	51	27

Table 3-5 - Breakdown of tree regeneration by species and the nurse structure the seedling germinated under/near - PIPO = ponderosa pine (*Pinus ponderosa*), PSME = Douglas-fir (*Pseudotsuga menziesii*), POTR = aspen (*Populus tremuloides*), JUDE = alligator juniper (*Juniperus deppeana*), ABLA = Subalpine fir (*Abies lasiocarpa*), ABCO = white fir (*Abies concolor*), JUMO = oneseed juniper (*Juniperus monosperma*), and JUOS = Utah juniper (*Juniperus osteosperma*)

Organic Structure								
Species	Branch Log	Grass Shrub	Live Tree	Oak	Resprout	Rock	None	Total
Abco	11%						89%	9
Abla	100%							1
Jude	9%		3%		70%	1%	16%	74
Jumo	33%					33%	33%	3
Juos	17%						83%	6
Pipo	27%	10%	4%	2%		1%	56%	293
Potr	8%				92%			89
Psme	19%						81%	164
Total	20%	5%	2%	1%	10%	1%	62%	639

Table 3-6 - Number of trees by species found at each fire - totaled by row and column. PIPO = ponderosa pine (*Pinus ponderosa*), PSME = Douglas-fir (*Pseudotsuga menziesii*), POTR = aspen (*Populus tremuloides*), JUDE = alligator juniper (*Juniperus deppeana*), ABLA = Subalpine fir (*Abies lasiocarpa*), ABCO = white fir (*Abies concolor*), JUMO = oneseed juniper (*Juniperus monosperma*), and JUOS = Utah juniper (*Juniperus osteosperma*)

Fire	Pipo	Abco	Abla	Jude	Jumo Juos	Potr	Psme	Total
Bear	2	7		5		11	163	188
Bridger Knoll	10							10
BS	7	2	1				1	11
Cerro Grande	24			3	3	71		101
Hochderffer	1					100		101
Horseshoe	3				6			9
Ponil Complex	6					1		7
Pumpkin	74			1		6		81
Rodeo-Chediski	166			68				234
Total	293	9	1	77	9	189	164	742
Percent	39%	1%	0%	10%	1%	25%	22%	

Table 3-7 - Summary of dominant cover type - Table shows percent dominant vegetation type within each fire, row total = 1 (100%). Dominant vegetation type assigned to each plot using a qualitative process that involved a combination of photos and quantitative plot cover data. Mesic tall shrubs = *Quercus gambelii* and *Robinia neomexicana*; Xeric tall shrub are all other *Quercus* species.

Fire	Grass	Mesic Tall Shrubs	Xeric Tall Shrubs	Bare/Open	Short Shrubs	Tree
Bear	0.65	0.13	-	0.19	-	0.03
Bridger Knoll	0.41	0.53	-	0.06	-	-
BS	0.20	0.80	-	-	-	-
Cerro Grande	0.21	0.44	0.23	0.12	-	-
Hochderffer	0.94	-	-	-	-	0.06
Horseshoe	1.00	-	-	-	-	-
Ponil Complex	0.40	0.20	0.40	-	-	-
Pumpkin	0.83	-	-	0.07	0.07	0.03
Rodeo-Chediski	0.51	0.13	0.15	-	0.13	0.08
Average	0.57	.25	.09	.05	.02	.02

Table 3-8 - Mean percent cover and mean percent exposed surface of each classification type for each fire area - Means calculated from cover class midpoints for all plots in a burned area. CWD = coarse woody debris, mainly downed logs

Fire	Canopy Cover						Exposed Surface		
	Grass	Forb	Tall Shrub	Short Shrub	Tree	Logs	Bare	Rock	Litter
Bear	39.80	10.85	3.93	1.39	1.94	9.38	28.67	0.81	15.67
Bridger Knoll	32.28	11.88	34.23	5.85	0.04	10.11	14.45	2.72	11.80
BS	56.25	12.50	18.50	8.50	1.00	10.00	17.38	0.25	4.50
Cerro Grande	13.65	6.55	21.90	3.85	1.55	12.88	32.35	5.70	5.03
Hochderffer	57.69	12.75	0.00	12.13	3.35	17.49	21.96	0.00	0.58
Horseshoe	54.55	11.30	0.00	4.23	0.10	11.78	28.19	1.03	1.00
Ponil Complex	37.54	11.92	17.56	2.19	0.06	8.94	22.46	3.56	6.50
Pumpkin	46.73	19.67	0.00	9.83	1.44	11.83	8.44	6.85	2.83
Rodeo-Chediski	28.08	21.46	8.38	11.28	3.51	7.77	16.54	0.03	14.82
Average	40.73	13.21	11.61	6.58	1.44	11.13	21.16	2.33	6.97

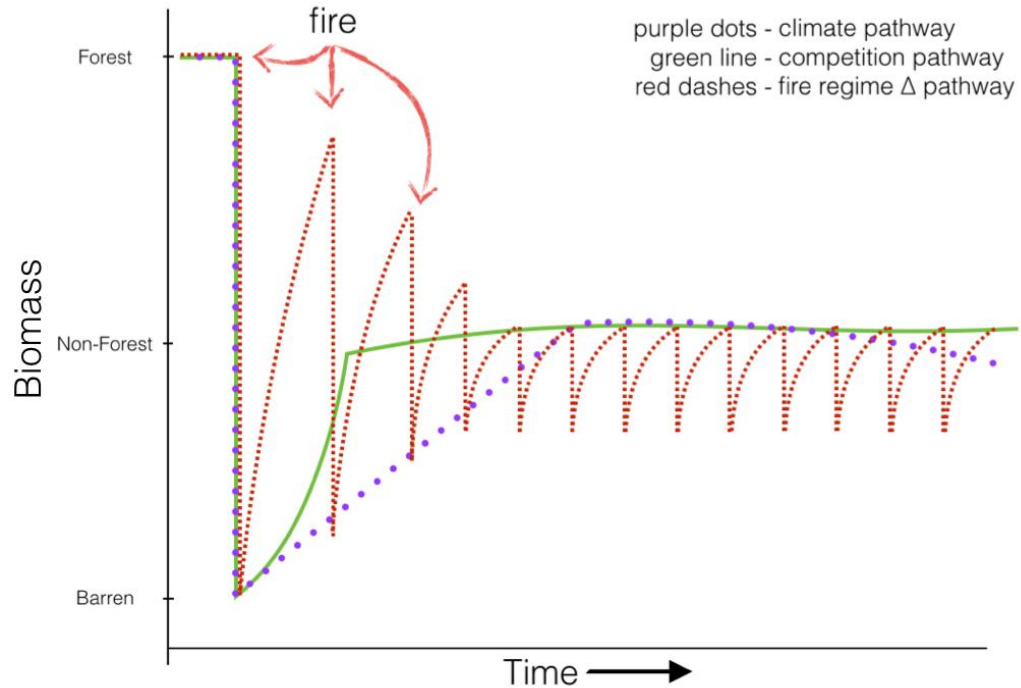


Figure 2-1: Conceptual diagram of three potential pathways to type conversion -

Purple dots represent a “climate-induced pathway” where immediately following the initial stand-replacing crown fire the system slowly recovers biomass (y-axis) and drought (or climate change) eliminates any post-fire regeneration and alters the successional trajectory toward non-forest. The red dashed line shows the “change in fire regime pathway,” where the initial post-fire the successional trajectory is rapidly approaches a return to forest (e.g. ‘hyper-dense’ regeneration from Savage and Mast (2005)), but subsequent fires occur (at each peak of the red line) kill young trees and establish a ne fire regime for the system that supports non-forest communities. The green line represents the “competition pathway” to type conversion, where vigorous post-fire successional communities of shrubs and grasses establish rapidly and largely exclude conifer regeneration.

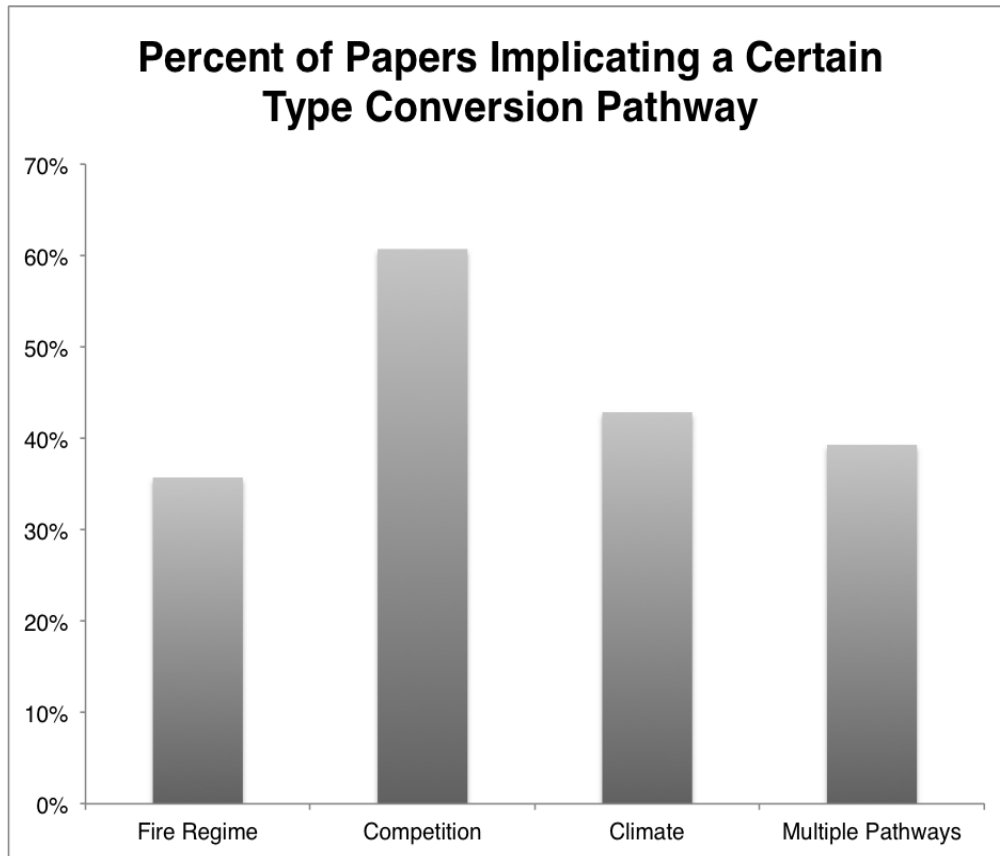


Figure 2-2: Chart of various pathways identified from studies in this review - Most studies implicated competition as a reason for type conversion. Climate (including drought) was the next highest pathway to type conversion. Fire regime change was the least implicated pathway. 40% of the studies cited multiple pathways interacting as the reason for type conversion.

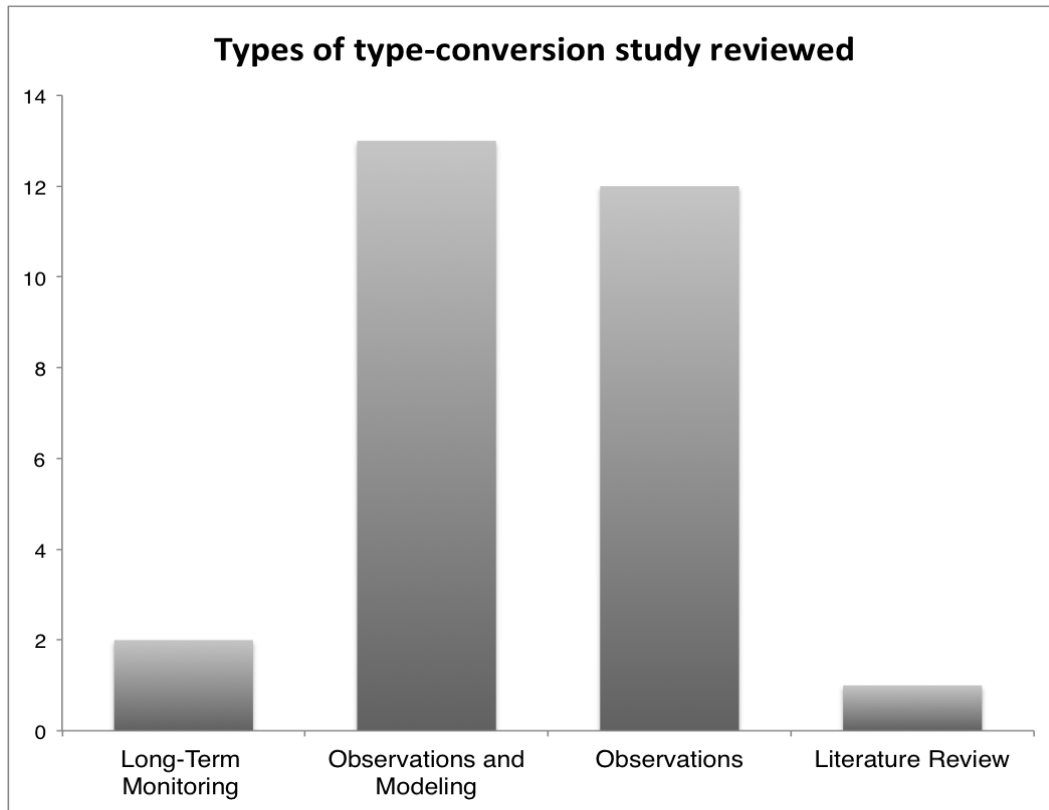


Figure 2-3: The total number of studies using various methods - Observational with modeling was most common approach. Observation alone was nearly as common. Note the lack of experimentation

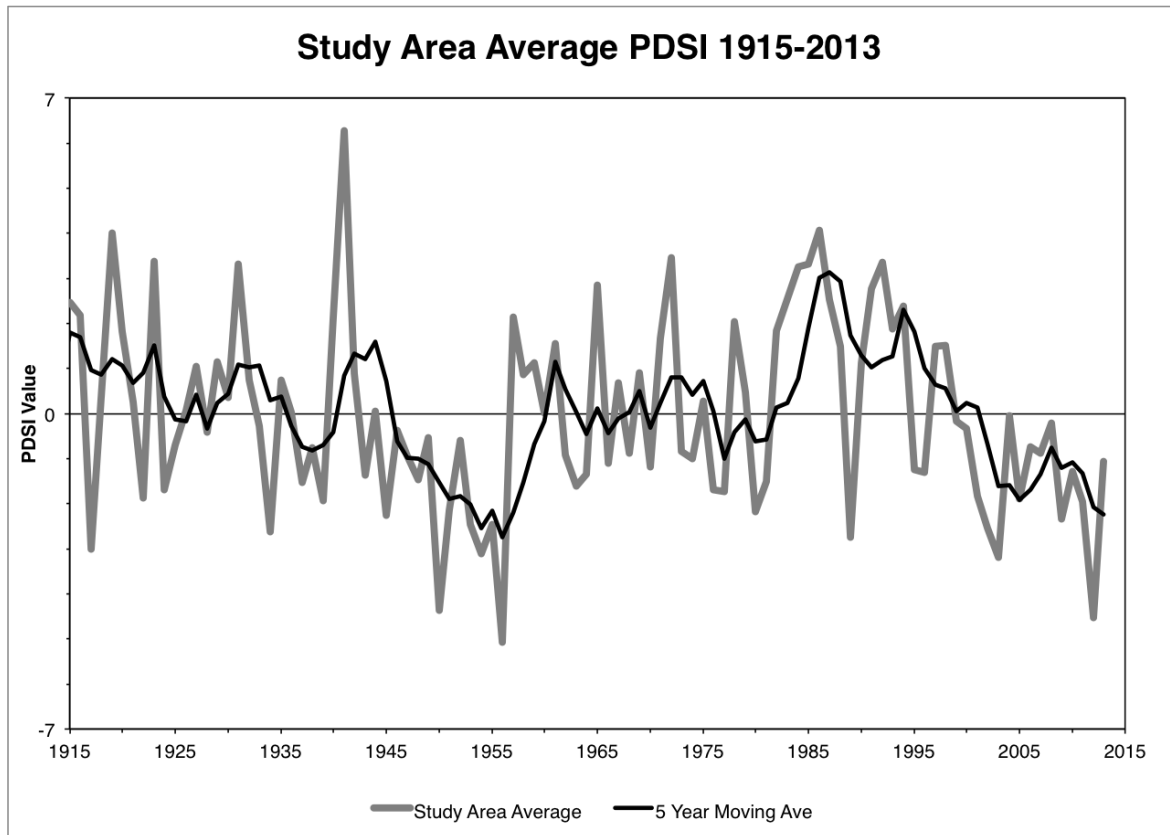


Figure 3-1: Palmer Drought Severity Index average for study area, 1915 to 2013 - data from www.wrcc.dri.edu accessed Jan 2014. The recent period of dry (negative) conditions since 1996 to present is one of the most extreme multi-year windows of persistent drought in the past century (Daly et al. 1994; Schwalm et al. 2012).

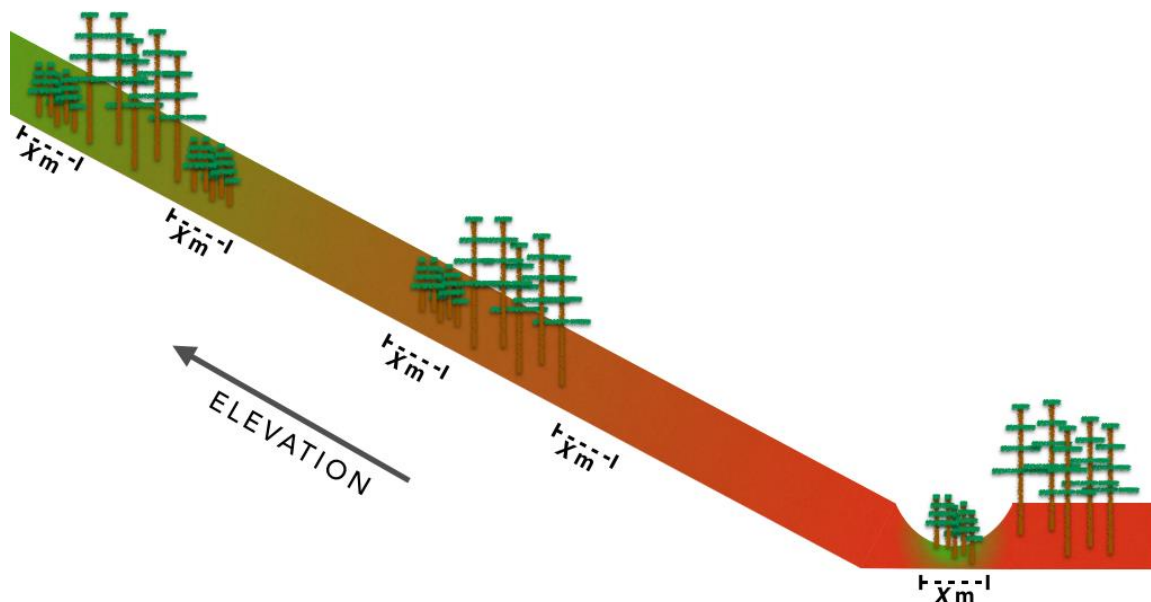


Figure 3-2: Diagram of dry forest type conversion risk - illustrating how post-fire regeneration to pre-fire forest type (small trees) only occurs where nearby tree seed sources (large trees) coincide with landscape locations that are climatically favorable (green shading) along topographic and elevation gradients. Red shading indicates areas that are climatically unfavorable for pine germination. This general “model”, while not spatially explicit, presents the idea in an easily understandable way.

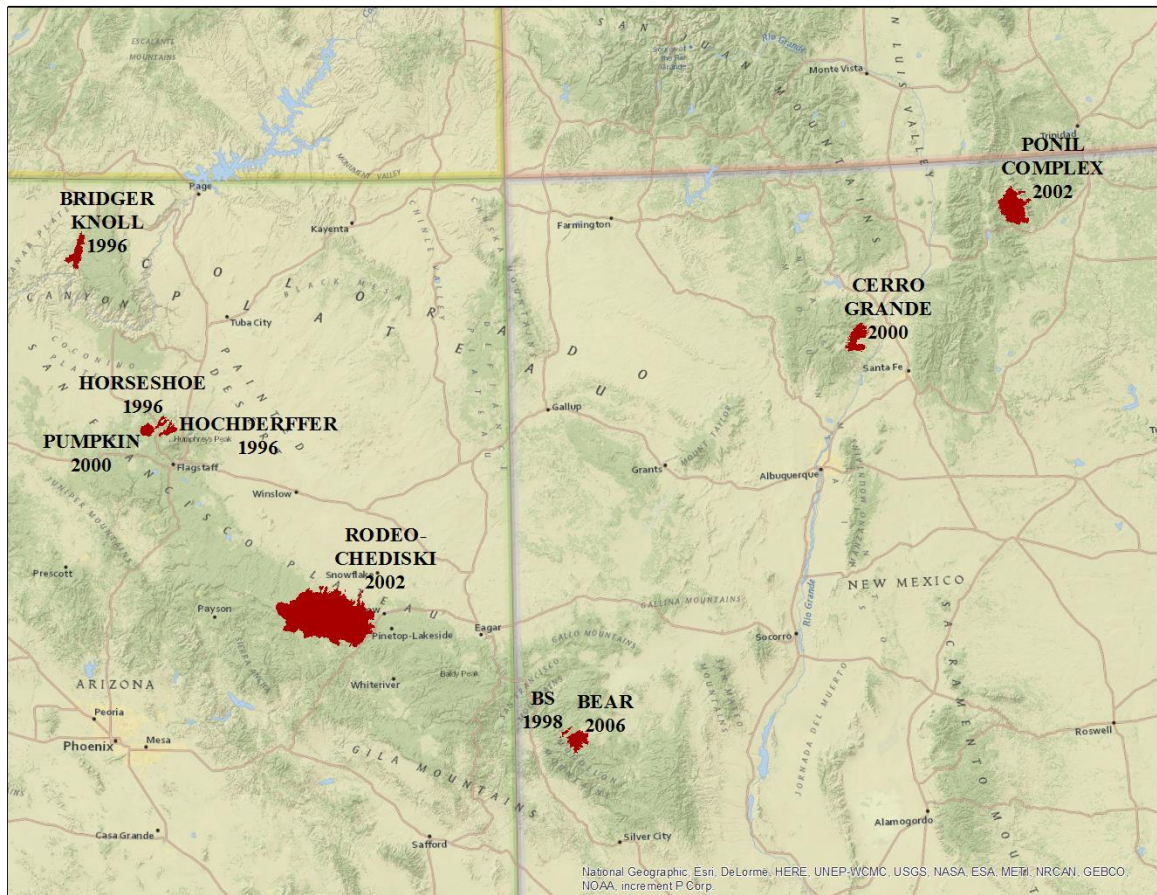


Figure 3-3: Map of the field study region across northern Arizona and New Mexico - Studied fire areas shown in red, with descriptions of each fire in Table 3-1. Study was spread across AZ and NM to capture regional patterns of post-crown-fire landscape response.

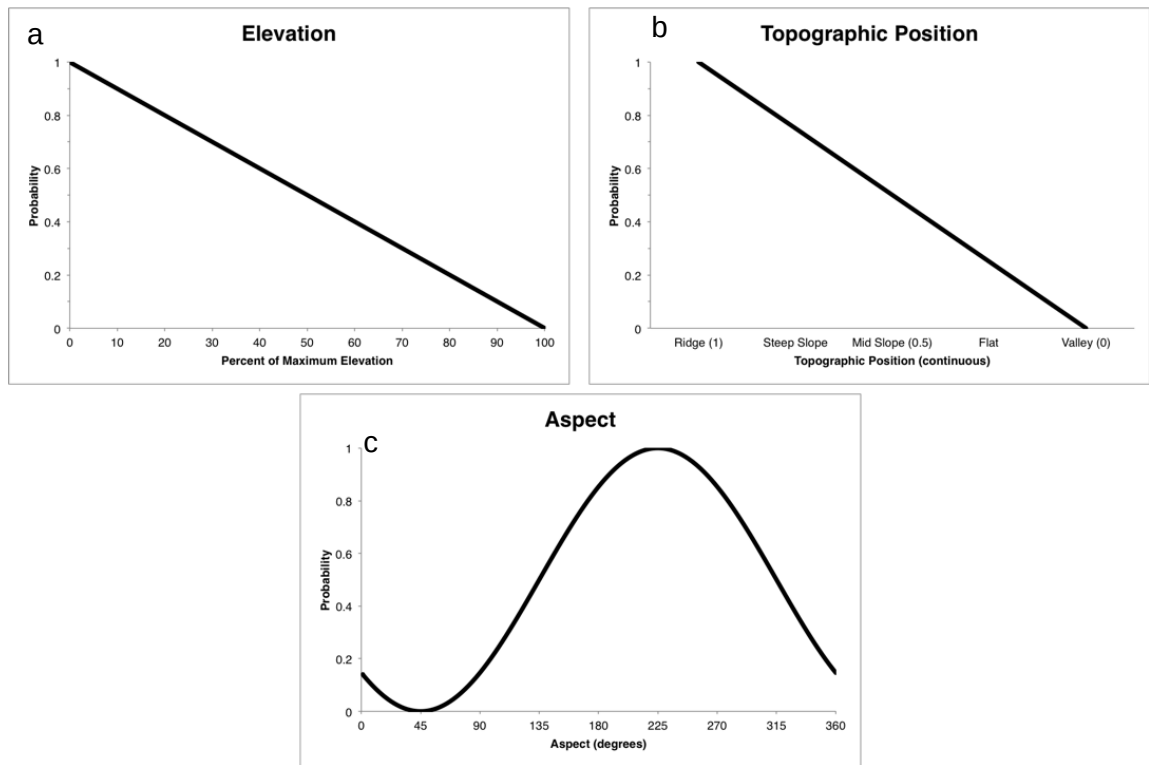


Figure 3-4: Topographic variables and their related hypothetical probabilities - Diagram of relative probabilities of type conversion used in model development and hypothesis testing; a) type conversion probability decreases as the percent of maximum elevation approaches 100%, b) categorized topographic positions (TP) show decreasing probability of type conversion moving from ridges to valleys, for each burned area TP was calculated as a continuous variable and rescaled (0-1), for illustrative purposes the continuous variables on the x-axis have been replaced with TP categories, with the scaled continuous values in parentheses; c) probability of type conversion based on aspect azimuth values, where aspect values represent a deviation from NE (45°), a cosine transformation was then applied to represent the circular value from 0-1, with the highest probability of type conversion being SW (225°).

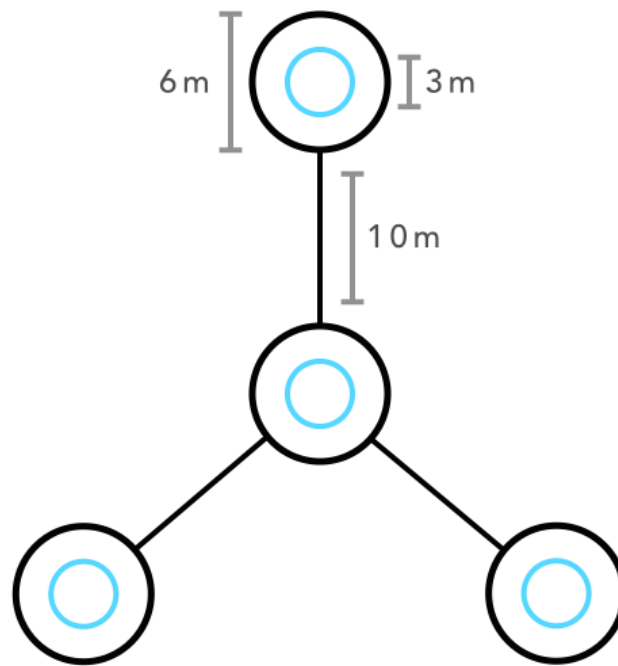
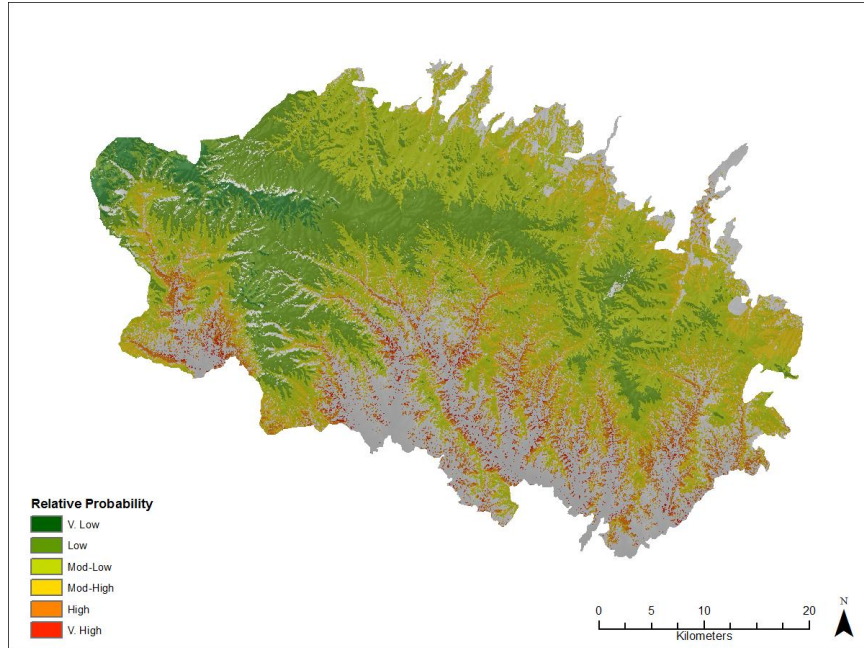


Figure 3-5: Plot layout with nested subplots - Outer subplots separated by 120° from an initial randomly generated azimuth. Inner nested plot is 3m in diameter and used from vegetation cover classification. Larger subplot is 6m in diameter and used for regeneration survey.

a.



b.

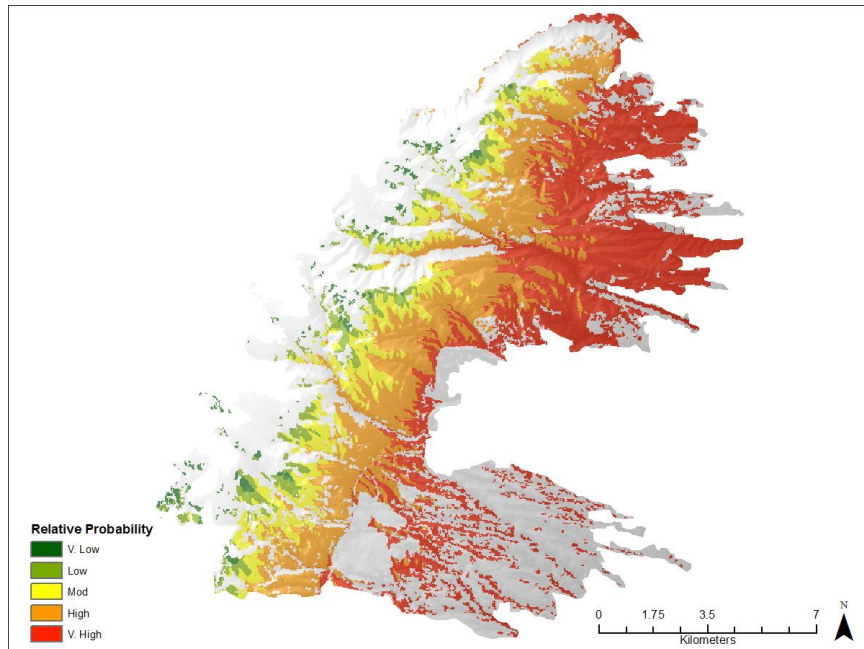


Figure 3-6: Spatial model output, topographic variables only - Spatial representation of weighted model outputs. This representation of the model removes distance to seed source a parameter, essentially creating a vulnerability assessment that can be applied for pre-fire planning. Here I show the Rodeo-Chediski (a) and Cerro Grande (b) fires. Greens and yellows indicated mesic topographic conditions; reds and yellows are more xeric areas. Notice the difference in probabilities between the two fires, the Cerro Grande fire burned through steep elevation and at the lower end of the local elevation range for ponderosa. The Rodeo-Chediski fire burned at higher local elevations and on relatively smooth terrain. Gray areas are areas not covered by ponderosa pre fire, and the area burned by the fire.

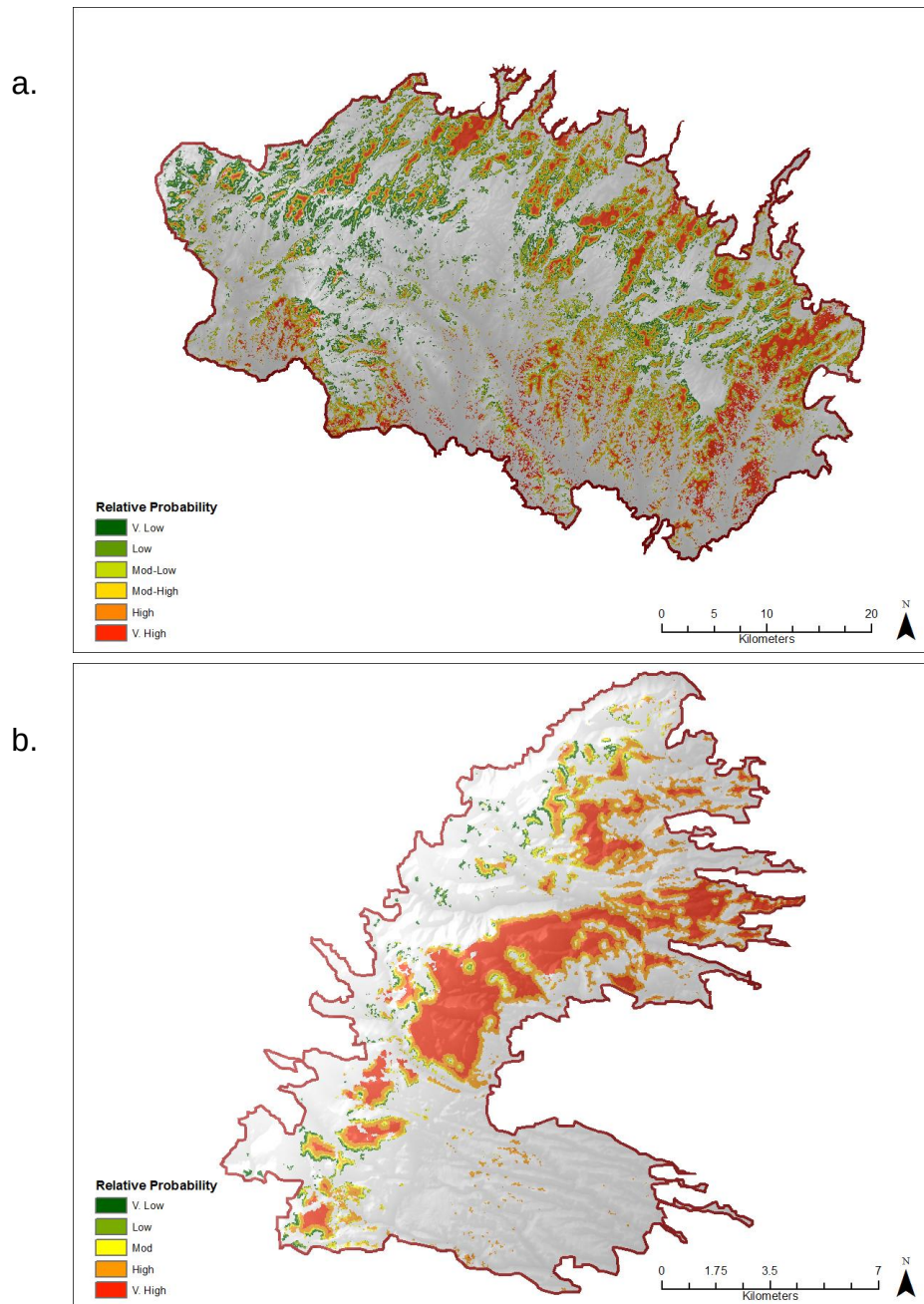


Figure 3-7: Spatial Model output with patches of high severity - Spatial representation of weighted model outputs, this time including distance to seed source for the Rodeo-Chediski (a) and Cerro Grande (b) fires. Greens and yellows indicated low probability of type conversion; reds and yellows are higher relative probability of type conversion. In the Rodeo-Chediski fire, areas that burned in areas with low type conversion probability are now high at high risk for type conversion due to the large patch size and far distance to seed sources. In the case of Cerro Grande the largest high severity patches burned in areas of high or moderate type conversion probability, the large patch size and far distance from seed sources reduces the likelihood of forest regeneration even further. Gray areas are areas not covered by ponderosa pre fire, and red lines show the perimeter of the fire.

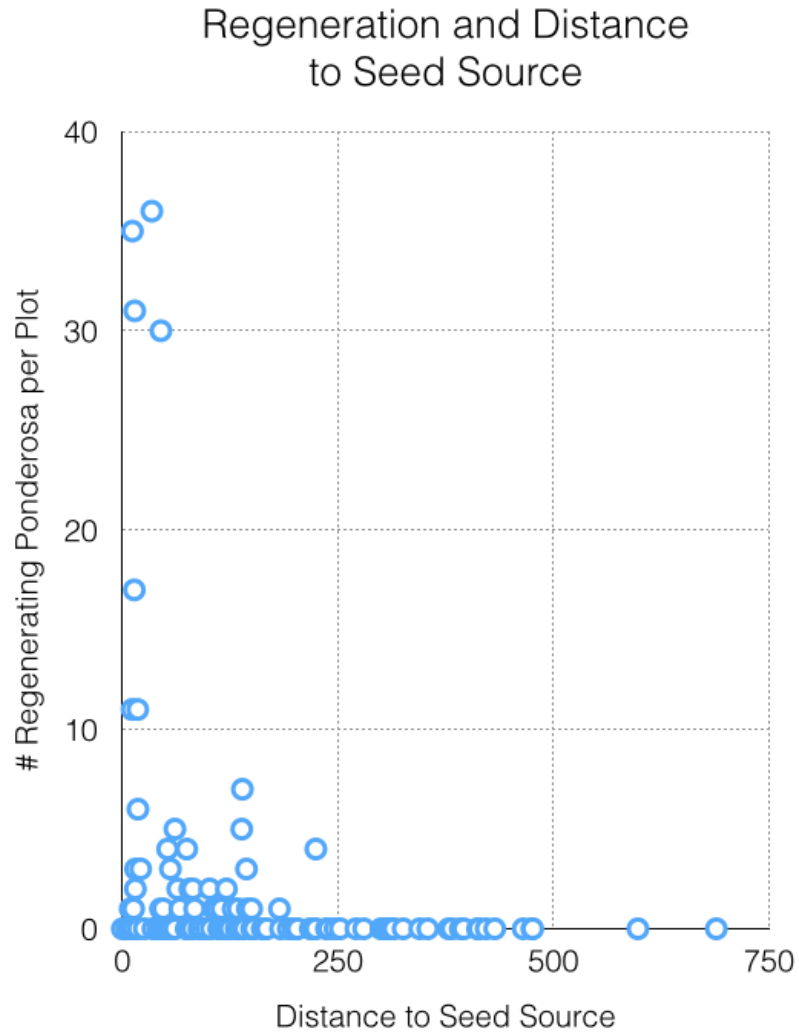


Figure 3-8: Natural ponderosa pine regeneration - Shows regenerating trees per plot relative to distance to the nearest seed source. Seed source defined as a group of reproductive trees, generally 10 or more. No natural regeneration was observed outside of 250m from a viable seed source with most regeneration occurring within 150m of seed source, half of the sampled locations were outside of 150m

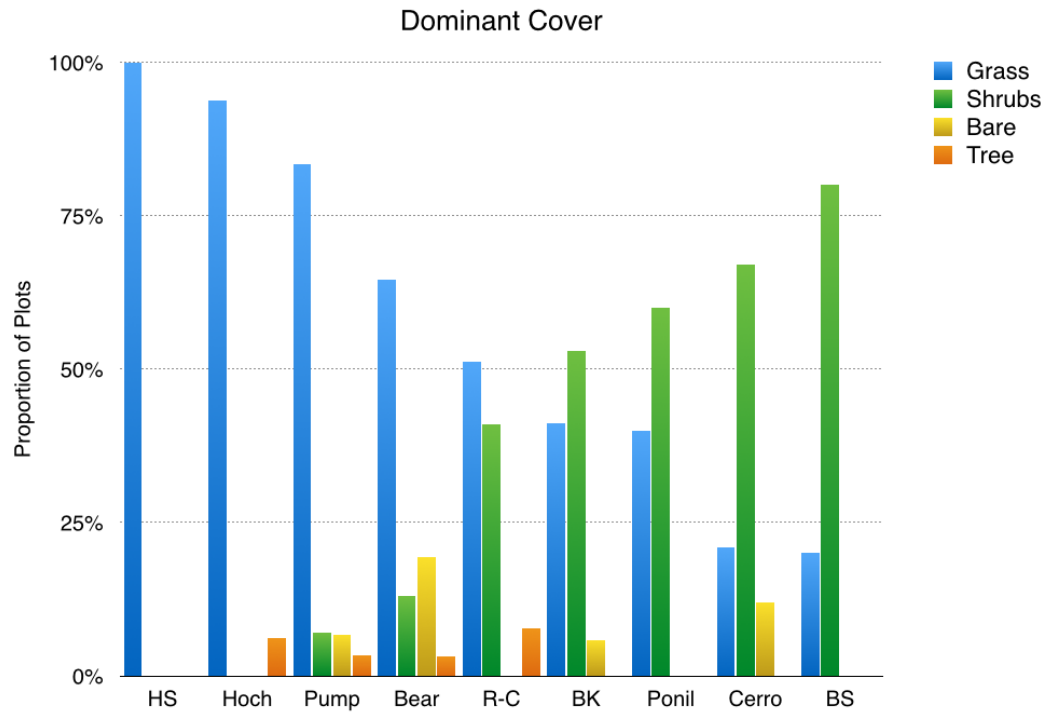


Figure 3-9: Proportion of Dominant Plot Cover per Fire - proportion of plots from each fire dominated by grass, shrubs, bare ground, or tree regeneration. Shrub and grass dominated areas are the most common followed by bare ground and tree regeneration.

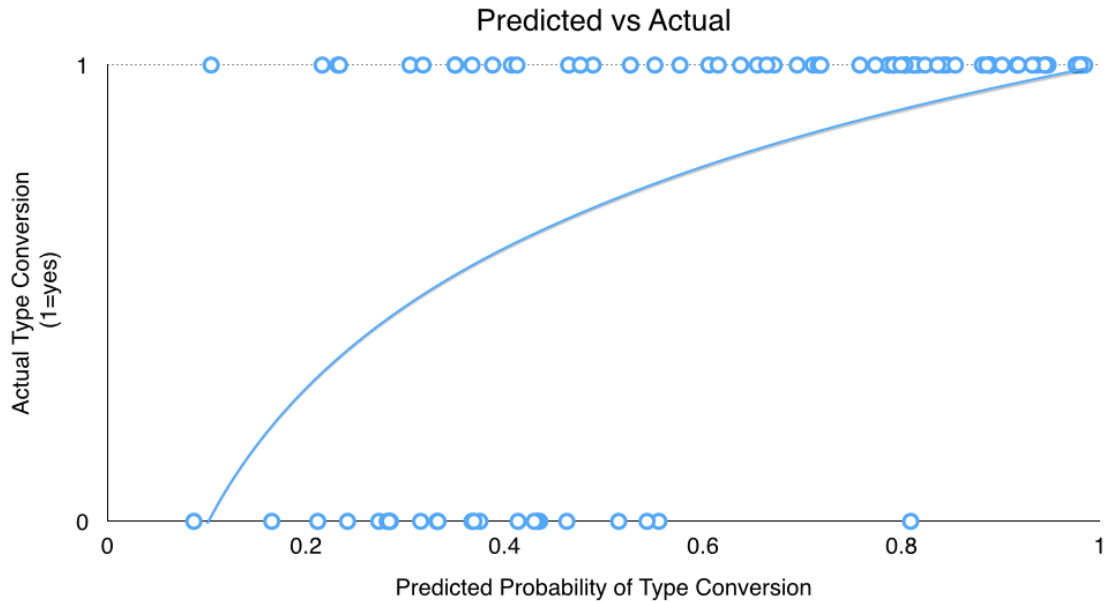


Figure 3-10: Logistic Regression Output - Output from logistic regression (blue line) with sample plots represented as blue dots. On the x-axis values near 0 are the areas predicted to have a low probability of type conversion, with values near 1 being the highest probability. On the y-axis 0 = not type converted (i.e. more than 2 ponderosa pine found at the site) 1 = type converted (i.e. fewer than 2 ponderosa found on a plot). Notice the large amount of sites that type converted despite being at areas with low portability of type conversion, indicating complex dynamics result in type conversion.

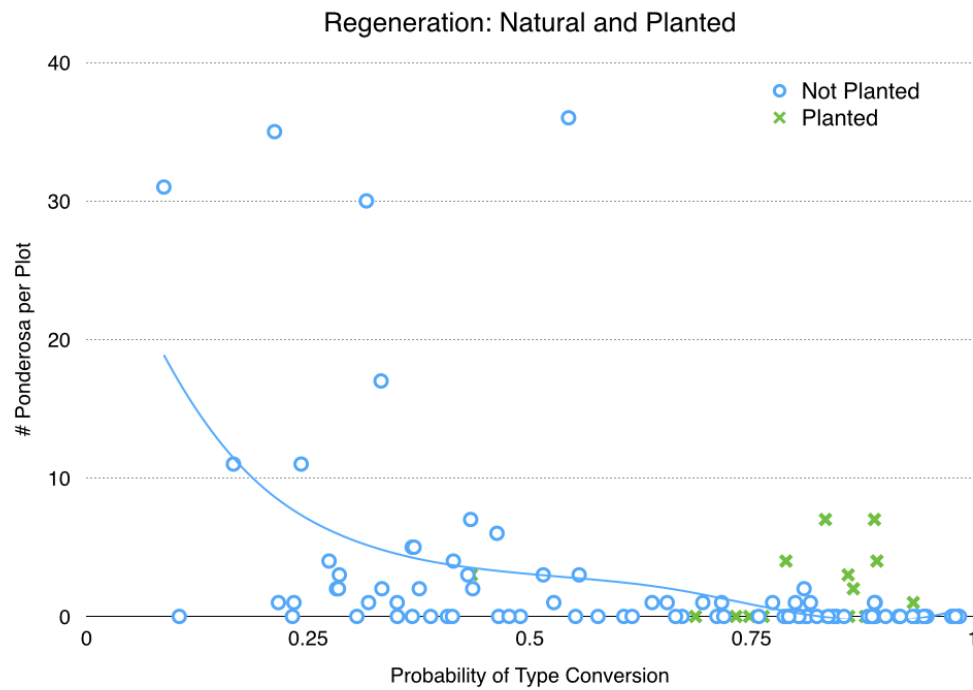


Figure 3-11: Number of regenerating ponderosa per plot along type conversion probability scale - Post fire ponderosa regeneration shown as number of ponderosa per plot. Notice the large amount of regeneration near 0, the more favorable sites. The planted areas (green x's) are near the least favorable (1) end of the probability gradient indicating planting helps cross the germination “hump,” but not always.