Responses of dry forest understory diversity to thinning intensity and burning: the importance of time, space, and analytical approach

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A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2017

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Program Authorized to Offer Degree:
Environmental and Forest Sciences

University of Washington

Abstract

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Mechanical thinning and prescribed burning are commonly used to restore dry, mixed-conifer forests that historically experienced frequent fire. Although these treatments successfully reduce fuel loads, their ability to achieve ecological objectives, such as promoting native plant diversity, is less certain. My thesis research examined how temporal and spatial scales of observation and the approach to analyzing scale-dependent data influence our understanding of understory vegetation responses to thinning intensity and burning. I used long-term data on understory species richness from a restoration experiment in central Washington. I found no effect of thinning intensity alone and scale-dependent responses to burning. For example, annual richness increased over time in burned plots, particularly at small spatial scales, suggesting enhanced recruitment from early-established populations and little perennial expansion. I also found that the analytical approach used to address common challenges of large-scale, long-term

experiments, such as variation in pre-treatment conditions and the loss of sample units over time, can affect the conclusions drawn from these experiments. However, careful specification of research questions and consideration of data limitations can yield insights into these conclusions. This research highlights long-term ecological benefits of prescribed burning and the need for measurements over time and among spatial scales, as well as the careful evaluation of analytical approaches, to clarify whether fuel-reduction treatments meet the ecological objectives of dry forest restoration.

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Acknowledgements

I am very grateful to both of my advisors, Dr. Jon Bakker and Dr. Charlie Halpern, for their tireless support of my work on this thesis. They have provided valuable advice and improved all aspects of this work. I thank Dr. Richy Harrod for his advice and assistance with field season logistics, for sharing data from previous monitoring of the experiment, and for serving on my thesis committee. I thank Dr. Ryan Haugo for also serving on my thesis committee and for his constructive comments that clarified earlier drafts. This study would not have been possible without the members of the 2015 field crew, Kelly Broadlick, Jessica Celis, Chris Parson, Ben Saari, Mari Schramm, and Kaitlyn Schwindt, whose perseverance and positivity overcame the challenges of rugged field work and living in an abandoned building. I also thank all of those who previously assisted with field work. I must acknowledge the incredible Rae Mecka who smoothly managed data, equipment, and all office matters with great attention to detail. Dr. Dave W. Peterson has been a helpful collaborator on this project. I am also grateful to my family and friends who have patiently supported me during my two and half years in graduate school. Finally, the following funders made this work possible: Joint Fire Science Program; University of Washington School of Environmental and Forest Sciences; McIntire-Stennis Cooperative Forestry Research Program; Northwest Scientific Association; and Sigma Xi, The Scientific Research Society.

Introduction

Forty percent of Northwest forests that historically experienced frequent fire are in need of restoration (Haugo et al. 2015). Nearly a century of fire exclusion and a history of grazing and selective logging have altered vegetation patterns and processes and increased the risks of high-severity wildfire and insect outbreak (Agee 1993, Hessburg and Agee 2003). Increases in overstory density and homogeneity in spatial patterning–documented by dendrochronology and historical photos–are suspected to have been accompanied by a shift in understory vegetation from a diverse shrub and herbaceous community to one favoring late-successional species (Hessburg et al. 2000, Allen et al. 2002).

Loss of understory diversity is important for dry forests. Comprising more than 95% of forest vascular plant species in these coniferous forests, understory vegetation plays an important role in ecosystem functions by competing with tree seedlings, facilitating the recycling of plant nutrients, and providing forage and cover for wildlife (Gilliam et al. 2007). High biodiversity has also been shown to increase productivity and ecosystem resilience to disturbance (Zhang et al. 2012, Mellin et al. 2014). Restoring understory diversity may very well have broad benefits for dry forest ecosystems.

To reduce wildfire risk and restore ecological processes and conditions, land managers increasingly use mechanical thinning and controlled burning (Brown et al. 2004, USDA et al. 2004, Agee and Skinner 2005, Martinson and Omi 2013). While fuel reduction using these treatments is typically successful (Stephens et al. 2009,, Stephens et al. 2012, Fulé et al. 2012, Martinson and Omi 2013), restoring ecological attributes, such as understory diversity, has proven to be a more complex goal. Studies to date show considerable variation in the responses of understory diversity to thinning and burning (Bartuszevige and Kennedy 2009, McIver et al. 2013, Schwilk et al. 2014, Abella and Springer 2015, Wills et al. 2017, L. Urgenson, *unpublished data*). In this thesis, I explore three factors that may contribute to this variation: temporal scale, spatial scale, and analytical approach. Many others, such as forest type, physical environment, disturbance history, and treatment implementation, may also play a role.

A fundamental challenge of thinning and burning research is incorporating the long temporal scales and multiple spatial scales over which forests respond to management. Most studies examine responses in the short-term (fewer than five years following treatment) and at a single spatial scale (e.g., 0.1-ha plots; Bartuszevige and Kennedy 2009, Abella and Springer 2015, Wills et al. 2017, L. Urgenson, *unpublished data*), despite evidence that responses vary over longer timeframes (e.g., 5-20 years; Harrod et al. 2008, Webster and Halpern 2010) and among sampling areas (e.g., 1-m^2 to 10 ha; Dodson and Fielder 2006, Dodson and Peterson 2010). Explicitly considering time and space may enhance our understanding of how thinning and burning affect understory diversity. Furthermore, examining these scales in conjunction has the potential to reveal patterns in variation not seen at single measures of either (White et al. 2010).

Another challenge is appropriately analyzing ecological data that is subject to low replication and high pre-existing variation. Researchers make analytical choices regarding, for example, aggregating nested sample units, incorporating variable thinning or burning intensities, and accounting for pre-existing variation among sample units. Decisions regarding these issues vary widely among studies, despite similar research questions and experimental designs (e.g., Metlen et al. 2004, Dodson et al. 2008, Strahan et al. 2015). Examining how and why these decisions affect research conclusions can aid in selecting the most appropriate approach for a data set and perhaps unify studies in the pursuit of answers to similar questions.

To explore these ideas, I used long-term data from a restoration experiment in central Washington designed to test thinning and burning alone and in combination. In Chapter 1, I partitioned variation in understory diversity responses over temporal scales of two and 12 years and spatial scales of 1 m^2 and 0.1 ha. In Chapter 2, I compared outcomes of statistical tests following assorted analytical decisions to determine the most appropriate approach for the study. These chapters serve to examine the effects of temporal scale, spatial scale, and analytical approach on our understanding of outcomes of dry forest restoration.

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Chapter 1

Effects of thinning and burning on dry forest understory richness vary with temporal and spatial scales

Abstract

Despite the widespread use of thinning and burning to reduce fuel loads and restore the structure of dry forests of the western U.S., the ability of these treatments to achieve ecological objectives remains uncertain. In this study, I examined how temporal and spatial scales of observation influence our understanding of the effectiveness of these treatments in promoting understory diversity. I examined the effects of thinning intensity, burning, and pre-treatment species richness on post-treatment richness at differing temporal and spatial scales using data from a long-term experiment in central Washington that is part of the national Fire and Fire Surrogate study. I used linear mixed-effects models to compare responses among different components of the understory (shrub vs. herbaceous species, annuals vs. perennials, natives vs. non-natives) at two points in time (two and 9-12 years after treatment) and at two spatial scales (1-m^2 quadrats and 0.1-ha plots).

Understory diversity generally increased in response to burning but not to thinning intensity, though responses of individual plant groups varied with time since treatment and spatial scale. Both natives and non-natives had a lagged response to burning, suggesting slow colonization via seed or clonal spread. Annuals, however, had an immediate and persistent response, reflecting their adaptations to disturbance and suggesting low levels of competition with perennials. Thinning intensity in the absence of burning had little effect on richness, but in combination with burning, enhanced local species density (i.e., quadrat-scale richness), presumably via effects of increased fuel loads on fire behavior. Post-treatment richness showed a strong and persistent correlation with pre-treatment richness, suggesting that most species survived disturbance. This study demonstrates there are long-term benefits to thinning and burning, but detection relies upon monitoring at sufficient temporal and spatial scales.

1. Introduction

Ecological restoration seeks to restore the species, structures, and ecological processes that defined a system prior to alteration or degradation by humans (Allen et al. 2002, Falk et al. 2005). Across much of the western U.S., decades of fire exclusion, selective logging, and livestock grazing have substantially altered the composition and structure of dry forests with historically low- or mixed-severity fire regimes (Agee 1993, Harrod et al. 1999, Hessl et al. 2004, Wright and Agee 2004, Nacify et al. 2010, Merschel et al. 2014, Odion et al. 2014). Increases in the density of fire-intolerant species and in the amount and continuity of fuels have heightened risk of high-severity wildfire and insect outbreaks—disturbances that can degrade the habitat qualities and ecosystem services of these forests (Everett et al. 1994, Hessburg et al. 1999, Everett et al. 2000). In Oregon and Washington alone, it has been estimated that 40% of dry forests are in need of restoration to reduce these risks (Haugo et al. 2015). Recognizing this need, land managers are using mechanical thinning and prescribed burning to reduce fuel loads and, ultimately, to restore the structure that characterized these forests prior to fire exclusion (Brown et al. 2004, USDA et al. 2004, Agee and Skinner 2005, Martinson and Omi 2013).

A common assumption is that by reducing stand density and reintroducing fire, fuels-reduction treatments will enhance other attributes of the forest that benefit from more open conditions and more frequent fire (Bartuszevige and Kennedy 2009). Although fuels treatments are effective at reducing spread of and increasing resilience to high-severity fire (Stephens et al. 2009, Stephens et al. 2012, Fulé et al. 2012, Martinson and Omi 2013), their ability to achieve other ecological objectives is less certain. For example, studies to date show considerable variation in the responses of understory diversity to thinning and burning across western North America (see reviews and meta-analyses by McIver et al. 2013, Schwilk et al. 2014, Abella and Springer 2015, Willms et al. 2017). Many factors may contribute to this variation: initial structure, disturbance history, intensity of treatment, physical environment, landscape context, and, as I explore in this paper, temporal and spatial scales of observation. For ecological responses that are scale-dependent, explicit consideration of time and space can clarify when and where variation occurs (White et al. 2010). However, recent reviews of the literature (Abella and Springer 2015, L. Urgenson, *unpublished data*) indicate that few studies explicitly consider the joint effects of time and space, and fewer are longitudinal in design (which avoids confounding space for time; Pickett 1989, Johnson and Miyanishi 2008, Walker et al. 2010). In this study, I use long-term (including pre-treatment) data from a large-scale fuels-reduction experiment to demonstrate how temporal and spatial scales of observation influence our understanding of thinning and burning effects on understory diversity in dry forests of central Washington.

Models of community succession and assembly suggest strong dependence of plant diversity on time since disturbance (Noble and Slatyer 1980, Halpern and Spies 1995, Pyke et al. 2010). Mechanical thinning and prescribed burning are disturbances that can reduce diversity by physical damage, burial, or consumption of existing plants, or that can increase it by creating open space, stimulating germination, reducing competition, and enhancing light and soil resources. The magnitude and longevity of these effects depend on the severity of disturbance and on post-disturbance processes that are time dependent, such as litter accumulation, vegetative regrowth, seed dispersal and establishment, and the outcomes of species' interactions. Understory diversity thus integrates biotic and abiotic conditions of the past and present. As such, initial responses to disturbance may differ from those a decade later and be poor predictors of those of the future.

Species richness depends on sampling area (as modeled by species-area curves; Preston 1962, Palmer and White 1994) because mechanisms that regulate diversity vary with spatial scale. At small scales (e.g., meter or sub-meter), resource availability and biotic interactions can either constrain or promote it. At larger scales (e.g., tenths to dozens of hectares), diversity reflects small-scale mechanisms plus the influences of habitat heterogeneity (Williams 1964, Rosenzweig 1995) and chance establishment and extinction events (area *per se* hypothesis; Preston 1962, MacArthur and Wilson 1967). The effects of treatments on diversity among spatial scales depend on the extent to which disturbance alters these mechanisms. For example, strong responses at small scales suggest that thinning or burning increased resource availability or reduced competition, allowing a greater number of species to establish per unit area (i.e., increased species density; Fig. 1.1b). Conversely, strong responses at larger but not smaller scales suggest that thinning or burning enhanced habitat heterogeneity, allowing for the establishment of species with a greater variety of habitat requirements (Fig. 1.1c).

By design, restoration treatments in dry forest landscapes are intended to enhance both resource availability and habitat heterogeneity. Thinning typically removes smaller stems, retaining larger trees in undisturbed patches (Agee and Skinner 2005, Bartuszevige and Kennedy

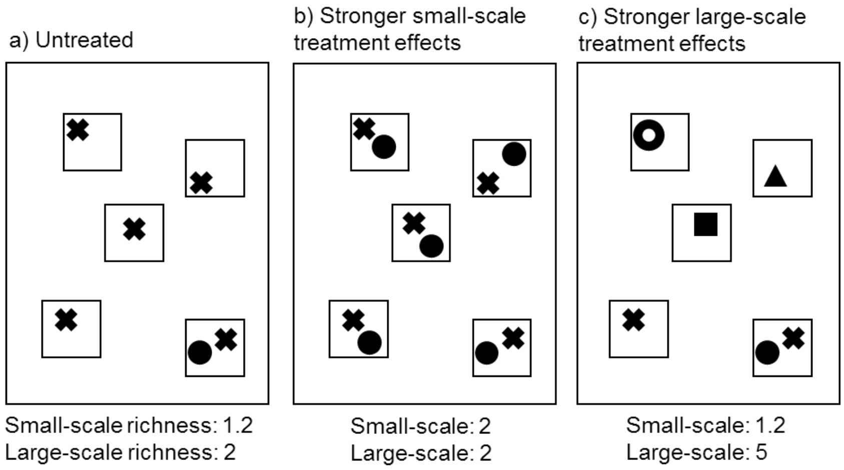

Figure 1.1 Hypothetical diversity responses to restoration treatments at contrasting spatial scales. Symbols represent unique species. Large-scale richness is the number of unique species in each panel; small-scale richness is the mean number of species in each sampling unit (small boxes in each panel). Compared to (a), (b) contains higher small-scale but not large-scale richness, whereas (c) contains higher large-scale but not small-scale richness.

2009) to emulate the structure and spatial patterning of historic forest conditions (Harrod et al. 1999, Larson and Churchill 2012). Thinning thus results in patchy distributions of soil disturbance and residual slash and increased heterogeneity of light and soil resources (Sprugel et al. 2009, Grayson et al. 2012). Prescribed burning, alone or in combination with thinning, is typically conducted at low severity with the goal of consuming fine woody debris while limiting overstory mortality to small trees (Brown et al. 2004, Neary et al. 2005, Bartuszevige and Kennedy 2009, Fule et al. 2012). Depending on the continuity of fuels and the intensity or duration of heating, the effects of fire on microsite quality and resource availability (e.g., exposure of mineral soil or enhancement of available nitrogen) can be highly variable (Wan et al. 2001, Antos et al. 2003, Neary et al. 2005). At what spatial scales thinning and burning affect plant diversity—and how these play out over time—likely depends on the magnitude, spatial heterogeneity, and longevity of disturbance effects, and on the pace at which species respond.

Plant species' responses to disturbance are shaped by their life histories (Noble and Slatyer 1980, Halpern 1989, Kerns et al. 2006, Harrod et al. 2008, Pyke et al. 2010). Persistence through thinning or burning requires that species are able to tolerate damage or burial, high temperature or prolonged heating, and abrupt changes in understory microclimate (Nelson et al. 2007, Pyke et al. 2010). Colonization after disturbance hinges on the availability of propagules in the soil or surrounding landscape (reflecting the proximity, abundance, and fecundity of source populations), the ability of the propagules to disperse, and the suitability of microsites for germination and survival (Kraft et al. 2014). For example, among annuals (and many non-natives), high fecundity, long-distance dispersal, and maintenance of a soil seed bank confer an advantage immediately after disturbance. Gradual loss of germination sites and increasing competition with perennials, however, may limit persistence in the longer term. Partitioning diversity among groups of species, and examining the spatial and temporal scales over which they respond, can help characterize the effects of thinning and burning on the understory plant community as a whole.

In this study, I use pre- and post-treatment data from the Mission Creek (central Washington) site of the national Fire and Fire Surrogate Study to explore plant diversity responses to thinning and burning at two spatial scales (1-m^2 quadrats and 0.1-ha plots) and two times since treatment: early (2 yr) and late (9-12 yr). I expand on early studies that showed positive responses to thinning, but not burning (Dodson et al. 2008) and significant species enrichment at larger (10 ha), but not moderate (0.1 ha) or smaller (1 m^2) spatial scales (Dodson et al. 2010). I also explore the spatial and temporal dependence of post-treatment richness on thinning intensity and pre-treatment richness (both varied markedly among plots) and on their potential interactions with burning. I consider the responses of woody and herbaceous species separately, seeking insight into the latter from the responses of annuals, perennials, natives, and non-natives, groups for which I had differing expectations.

I posed the following hypotheses of trends in species richness:

H1. General responses to thinning and burning. (*H1a*) I expected herbaceous and woody (shrub) species to respond positively to thinning intensity and burning. (*H1b*) Among herbaceous taxa, I expected stronger responses to burning by annuals than perennials and by non-natives than natives (groups that respond positively to exposure of mineral soil by fire). (*H1c*) Among species present prior to treatment, I expected greater losses to burning than to thinning.

H2. Temporal effects. (*H2a*) I expected the positive responses of annuals to decline with time (with loss of germination sites and increasing competition from perennials). (*H2b*) In contrast, I expected perennials to show a temporal lag in response (reflecting greater seed limitation and the slower pace of vegetative spread).

H3. Effects of spatial scale. For all plant groups, I expected stronger responses at the plot than at the subplot/quadrat scale (reflecting greater microsite heterogeneity from patchy thinning and burning).

H4. Roles of pre-treatment richness: (*H4a*) I expected a strong correlation between pre- and post-treatment richness (reflecting the tolerance of most perennial species in this system to disturbance). (*H4b*) I also expected pre-treatment richness to mediate responses to treatments, particularly at smaller spatial scales, by allowing for greater colonization in response to treatment in species-poor plots or quadrats, as well as greater loss of species from species-rich plots or quadrats.

2. Methods

2.1 Study area

The study area is in the eastern Cascade Mountains of central Washington State. It is in the Mission Creek watershed (47’25’ N, 120’32’W) of the Okanogan-Wenatchee National Forest and was selected to represent dry forests of the interior Columbia River basin for the national Fire and Fire Surrogate (FFS) Study (Fig. 1.2; Agee and Lehmkuhl 2009). The experimental units range in elevation from 670 to 1,150 m with slopes averaging 15 to 65%.

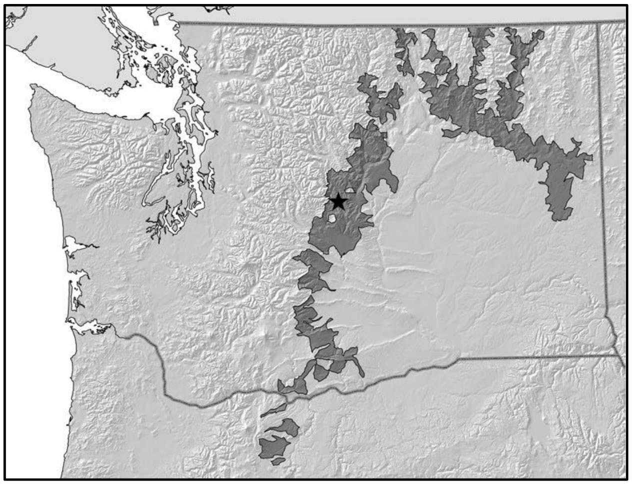

Figure 1.2 Location of the Mission Creek FFS site (star) in Washington State and the ecological subregion that it represents (dark gray). The site is in the eastern Cascade Mountains in the interior Columbia River basin (Ecological Subregion 11). From Agee and Lehmkuhl (2009).

Forests are dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), with small amounts of grand fir (*Abies grandis*) and western larch

(*Larix occidentalis*). The most common shrub species are Saskatoon serviceberry (*Amelanchier alnifolia*), common snowberry (*Symphoricarpos albus*), and rose species and hybrids (*Rosa* spp.). Common species in the herb layer include elk sedge (*Carex geyeri*), pinegrass (*Calamagrostis rubescens*), heartleaf arnica (*Arnica cordifolia*), and sweet-cicely (*Osmorhiza berteroi*).

Prior to Euro-American settlement, the fire return interval for dry forests of the region was approximately 6-7 years; after 1910, it increased to 40 years (Everett et al. 2000). Within the study area, fires have been suppressed since the 1930s and there has been cattle grazing and logging (USDA 1995). Historic forests (mid-1800s) included ~5 trees/ha > 80 cm in diameter (dbh) and ~37 trees/ha of 40-80 cm dbh, whereas current forests contain no trees >80 cm dbh and ~43 trees/ha of 40-80 cm dbh, with even higher densities of stems <40 cm dbh (Harrod et al. 1999). Current overstory structure is also less spatially clumped at all scales (Harrod et al. 1999, Larson and Churchill 2012). Limited commercial thinning was conducted in the 1970s.

The climate is characterized by cool, wet winters and warm, dry summers resulting in frequent drought and long periods of low fuel moisture. Representative weather data from Plain (570 m elevation), 32 km north of the Mission Creek watershed, indicate average (since 1937) low and high temperatures of -2.0 and 2.3°C in the winter and 16.9 and 26°C in the summer. Annual precipitation averages 67 cm, of which three-quarters falls as snow between November and March. (Western Regional Climate Center, Plain, WA, http://www.wrcc.dri.edu). Among the years in which vegetation was sampled, winter precipitation was 54-125% and summer precipitation was 55-131% of the long-term average (Fig. 1.3).

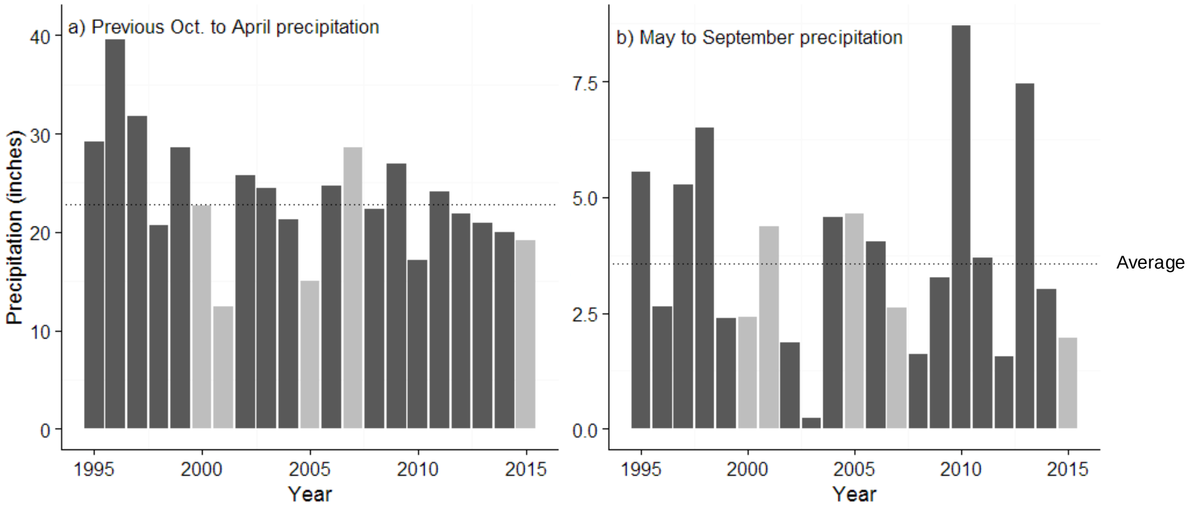

Figure 1.3 a) Winter (October-April) and b) summary (May-September) precipitation prior to and during the study period at the nearest representative weather station (Plain, WA). Gray bars indicate years of vegetation sampling. Dotted lines are the 1937-2016 (79-year) averages.

2.2 Thinning and burning treatments

From a larger set of potential management areas, 12, ~10 ha units were selected in 1999 for inclusion in the study (Fig. 1.4). Two treatments, mechanical thinning and prescribed burning, were applied randomly in a balanced factorial design (three replicates of each treatment combination): (1) thinning, (2) burning, (3) thinning followed by burning, and (4) no treatment (control). In 2012, the Wenatchee Complex wildfire entered four of these units (one thin, one burn, and two control; Fig. 1.4), compromising the treatments; all were dropped from the current analyses.

The silvicultural prescription was thinning from below to a target basal area of 10-14 m^2/ha, allowing 80% of the basal area of dominant or co-dominant trees to survive fire under 80th-percentile weather conditions. Both small commercial and smaller, unmerchantable stems were cut. Merchantable tree boles were yarded by helicopter and branches and tops were left on site. Tree were retained in a clumped fashion, consistent with historical spatial patterning (Harrod et al. 1999). Although the basal area target was not met in more than half of the thinned units, thinned units experienced greater reductions in live basal area and density than did unthinned units (Table 1.1). Thinning was completed in 2003 and burning in four of six units was conducted in the spring of 2004. Due to high fuel moisture, fires charred only 23-51% of the soil surface and failed to meet most fuel reduction objectives (Agee and Lolley 2006). Burning was delayed until 2006 in the remaining two units; they charred 50-65% of the soil surface. Burns were generally patchy and variable in intensity.

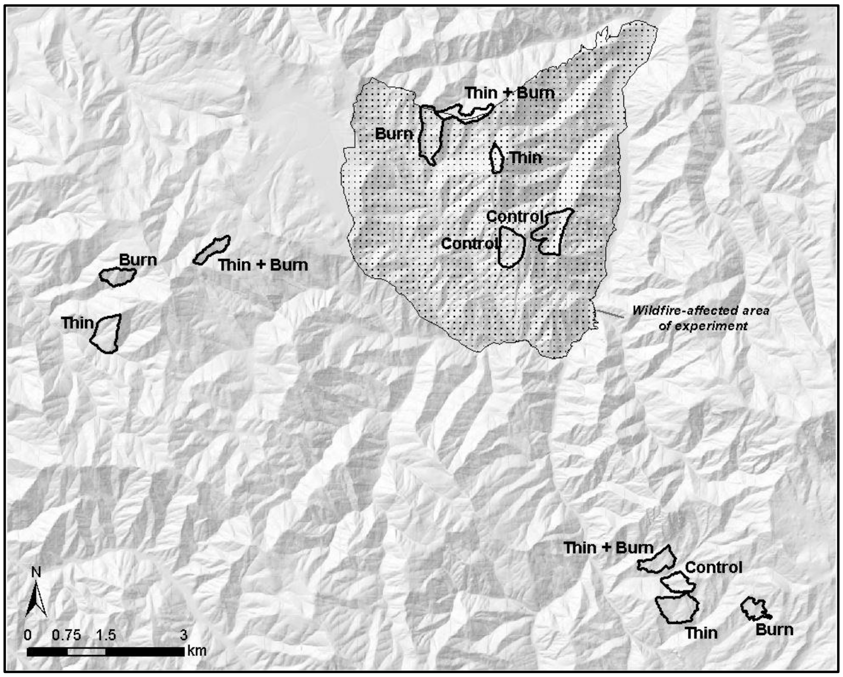

Figure 1.4 Geographical distribution and treatment assignments of the 12 management units selected for the experiment. The dotted polygon is the area affected by a 2012 wildfire; it includes the four units excluded from data analysis.

Table 1.1 Overstory attributes of the eight experimental units at each sampling date. Attributes are mean, plot-level, live density (Den, trees/hectare), basal area (BA, m^2/hectare), stand density index (SDI; √(Den*BA)), and the absolute and percent loss of SDI relative to pre-treatment.

		Pre-treatment			2 years post-treatment				9-12 years post-treatment			
Unit	Treatment	Den.	BA	SDI	Den.	BA	SDI loss	SDI loss (%)	Den.	BA	SDI loss	SDI loss (%)
Crow 3	Control	488	33	126	485	34	-2	-1	415	35	7	6
Crow 1	Thin	492	30	120	127	12	82	67	122	15	79	65
Ruby	Thin	532	39	142	227	25	67	46	242	30	59	41
Spromberg	Burn	493	32	125	485	34	-2	-2	477	38	-9	-7
Pendleton	Burn	352	23	89	322	24	2	0	257	22	15	17
Camas	Thin + Burn	588	34	139	190	18	81	61	170	18	85	61
Tripp	Thin + Burn	937	36	183	423	23	86	46	392	25	83	46
Crow 6	Thin + Burn	488	29	119	95	10	89	74	88	11	87	74

2.3 Sampling of vegetation and ground-surface conditions

Sampling was conducted before treatment and at two post-treatment sampling dates. Wenatchee National Forest staff conducted the sampling before treatment (2000 or 2001) and two growing seasons after treatment was completed (2005 for six units, 2007 for two units burned in 2006). The author led resampling in 2015 (9-12 years after treatment). I refer to these sampling dates as “pre-treatment”, “early post-treatment”, and “late post-treatment”, respectively. Sampling occurred between May and August; sites were visited sequentially from the lowest to the highest elevation.

Each experimental unit was sampled with six permanent 50 m x 20 m modified-Whittaker plots (Fig. 1.5). Plots were established in 2000, randomly located within continuous overstory vegetation and stratified among the dominant plant associations within each unit. In each plot, all coniferous trees >7.6 cm dbh were tagged and measured for diameter. Shrubs (defined as non-coniferous woody plants) were sampled in each of ten, 10 m x 5 m subplots centered on the long axis of the tree plot (Fig. 1.5). Herbaceous species (forbs and graminoids) were sampled within 20 permanent 1-m^2 quadrats distributed in a stratified random fashion throughout the tree plot.

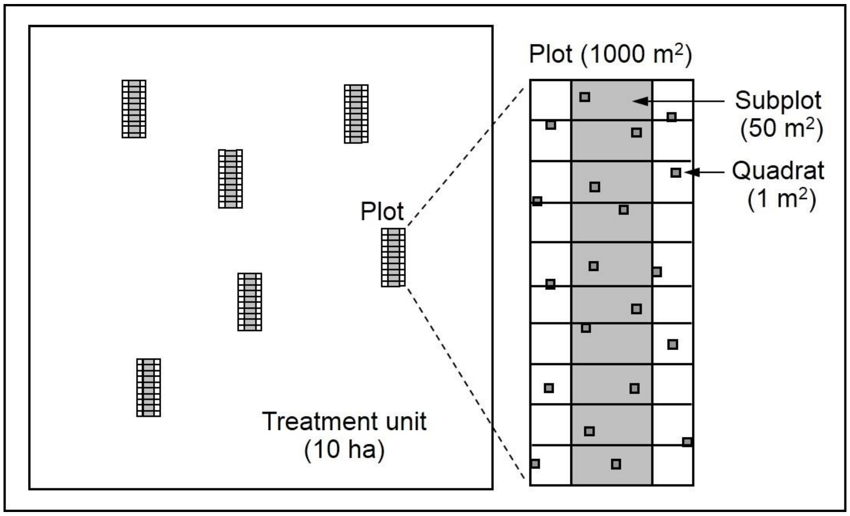

Figure 1.5 The nested sampling design in each experimental unit. Overstory trees were measured in each of the six plots. Cover of individual shrub species was recorded in 10 subplots. Cover of individual herbaceous species was recorded in each of 20 quadrats.

At each measurement date, cover (%) of each vascular plant species was estimated in each quadrat (herbaceous species) or subplot (shrubs). The "raindrop method" was used to estimate cover, discounting spaces between branches and leaves. If two species overlapped, cover was estimated for the taller species (thus the summed cover of species could not exceed 100%). Herb quadrats were also used to estimate the cover (%) of ground-surface conditions, including bare (mineral) soil, rock, duff/litter, and tree boles.

2.4 Species identification and data processing

Plants that could not be identified in the field were collected and identified, if possible, in the lab. Several taxa that could not be reliably identified to species (or consistently identified among sampling dates) were treated as morphospecies or grouped at the genus level. This included two shrubs, seven forbs, and one grass (Appendix). In total, 94 herbaceous records (0.1% of the total) remained unidentified over the course of study; given their low frequency, these records were removed prior to analysis. Vouchers of unknown and difficult-to-identify species in 2015, as well as an informal guide to distinguishing among similar taxa in the study area, are stored in the Halpern lab at the University of Washington, Seattle. Nomenclature follows USDA Plants (USDA and NRCS 2017).

The full set of pre- and post-treatment data were checked for data-entry errors and consistency in coding and identification. I took a conservative approach to the latter. Taxa that are morphologically similar were compared among sampling dates. Identifications from the same plot that differed for one of the three sampling dates were candidates for correction; changes were made if other similar taxa were not present in the plot on the same sampling date. When multiple species from the same genus were present and identities changed over time, all records were reduced to the genus level.

I classified taxa by life form (shrub vs. herbaceous), longevity (annual vs. perennial, and origin (native vs. non-native) using information from the USDA Plants online database (USDA and NRCS 2017) or, for morphospecies, from field observations. Biennial species were treated as annuals. Taxa recorded at the genus level were treated as perennials if the taxon included both annual and perennial species in the study area (three genera in total). Records for the genus *Trifolium*, which could be native or non-native, were treated as native.

2.5 Statistical analysis

To provide abiotic and biotic context for hypothesis testing, I summarized the effects of thinning and burning on exposure of bare ground and on vegetative cover. At each sampling date, I calculated the mean and standard deviation of percent cover of i) bare ground, ii) shrubs, and iii) herbaceous vegetation among the subplots or quadrats in each plot. These data served to evaluate how the availability and heterogeneity of bare space and the local competitive environment (represented by vegetative cover) changed with treatment and over time. I also summarized the total species richness sampled during the study and richness trends over temporal and spatial scales.

Hypotheses were tested using linear mixed-effects models. Response variables were post-treatment richness of each of eight plant groups at each of two sampling dates (early and late) and two spatial scales (plot and quadrat or subplot). Plot-level richness is the total number of unique shrub or herbaceous species sampled among the 10 subplots or 20 quadrats per plot, respectively. Subplot or quadrat richness is the mean number of species per quadrat or subplot in each plot. In addition to the six life form, longevity, and origin groups, I developed two additional plant groups to explore the extent to which species colonization and loss (local extirpation) contributed to net changes in herbaceous richness: herbaceous species that were not present pre-treatment but appeared post-treatment (“colonizers”) and those that were present pre-treatment but disappeared post-treatment (“extirpated”).

Restoration treatments were represented in models by a continuous variable for thinning (thinning intensity) and a categorical variable for burning (yes/no). I used a quantitative variable for thinning because the intensity of thinning conducted in each plot varied a good deal across the experiment. This occurred because thinning was performed to a target basal area but pre-treatment overstory structure varied considerably among plots. Thinning intensity was expressed as the change from pre-treatment to 2 years post-treatment in stand density index (SDI change). SDI was calculated as the square root of the product of live density and basal area in each plot. Although some proportion of SDI change may be attributed to effects of burning or other sources of mortality, only thinned plots (both burned and unburned) showed substantial change (Fig. 1.6). Thinning intensity values were converted to z-scores prior to analysis so that coefficients could be interpreted as effect sizes and compared within models.

Effects of burning also varied substantially within and among experimental units (Agee and Lolley 2006). Because I lacked a sufficient measure of fire severity in the understory (e.g., duff consumption; Webster and Halpern 2010) I treated burning as a categorical variable, assigned at the scale of plots. All plots within an experimental unit were categorized as burned or unburned (per the original treatment designation) except for one plot in a burned unit that inadvertently fell outside the prescribed fire boundary and was classified as unburned.

In each model, pre-treatment richness of the modeled plant group was included as a covariate to account for its influence prior to testing for treatment effects, and to test its hypothesized role in the post-treatment response (*H4a* and *H4b*). For models of species' colonization and loss, I used pre-treatment richness of herbaceous species to test the dependence of these processes on initial richness (hypothesis *4b*). Pre-treatment richness values were converted to z-scores prior to inclusion in models.

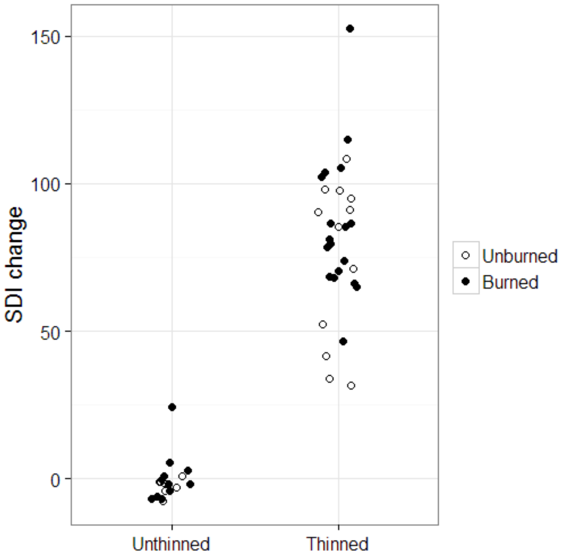

Figure 1.6 Change in stand density index (pre- to 2 years post-treatment) in thinned and unthinned plots. Burning treatment is indicated by symbol fill.

One model was fit for each date, spatial scale, and plant group for a total of 32 models. Each response variable was modeled as a function of pre-treatment richness, thinning intensity, burn treatment (yes/no), and all two- and three-way interactions (a total of seven fixed effects). Experimental unit was included as a random effect influencing the intercept. Interactions with significance levels (p) > 0.1 were iteratively removed from each model to maximize statistical power, beginning with the highest-order term. However, the thinning intensity × burning term was retained to test for the treatment interaction implicit in the original experimental design. Terms lower in order than the highest-order interaction term that was retained (i.e., main effects and, possibly, two-way interactions) were kept in final models no matter their significance level.

Effect sizes of treatments or treatment interactions were represented by parameter estimates (regression coefficients) and were compared within but not among models. Comparisons among plants groups and among spatial or temporal scales within a plant group were based on the significance levels of parameter estimates. An alpha of 0.05 was chosen *a* *priori* as the basis for significance. I did not adjust the alpha level for multiple tests (32 models in total) but took several measures to strengthen the bases for inferences. First, I placed greater emphasis on the consistency of model results among multiple plant groups and scales than on results of individual models. Second, I focused on effects with lower p-values, recognizing the reduced probability of erroneously rejecting the null hypothesis for a least one term at an alpha of 0.05 (30% chance) vs. 0.01 (7% chance). Nevertheless, with 32 models (each initially fit with seven fixed-effect terms) and an alpha of 0.05, it was almost certain that at least one model term showed spurious significance (Gelman et al. 2012). Finally, I used Type III (marginal) sums of squares to calculate test statistics, which is inherently the most conservative distribution of variance among model terms because variance shared among terms is entirely excluded.

Models were developed in R (version 3.3.0; R Core Team 2016) using the nlme package (version 3.1-127; Pinheiro et al. 2016). Final models were parameterized by maximizing the restricted log-likelihood. I tested for collinearity using variance inflation factors; all were below two, suggesting low problematic correlation among main effects. To ensure model assumptions were met, residuals of final models were visually examined for normality and homogeneity across predictor values (Zuur et al. 2009). In the nine models in which residuals were not randomly distributed, outliers (observations with standardized residuals < -2 or > 2) were removed, resulting in residual distributions that met model assumptions. The nine models were late post-treatment plot-level non-natives, early and late plot-level extirpated species, and early and late quadrat-level annuals, non-natives, and extirpated species. Removal of outliers slightly reduced the degrees of the freedom.

3. Results

3.1 Effects of thinning and burning on exposure of bare ground and total plant cover

The mean and variation (SD) in cover of bare ground initially increased in some burned plots, particularly at higher thinning intensity (Fig. 1.7). Effects were short-lived, however. Thinning intensity alone had no effect on cover of bare ground.

Cover of shrub and herbaceous species varied considerably among plots before treatment (Fig. 1.8). Thinning and burning resulted in persistent reductions in both the mean and variation in cover, particularly for herbs. Field observations suggest very little post-treatment tree establishment.

3.2 Total richness among plant groups

In total, 151 taxa were recorded over the course of study among the 480, 50-m^2 shrub subplots and 960, 1-m^2 herbaceous quadrats. Of these, 100 (66%) were observed before treatment, 131 (87%) at the early post-treatment sampling date, and 138 (91%) at the late post-treatment sampling date. Richness of most plant groups, except shrubs, increased over time (Fig. 1.9). Among herbaceous species, there were considerably more perennials than annuals and more natives than non-natives (Fig. 1.9). Twelve taxa (8%) were non-native; all of these were herbaceous and eight were annual or biennial.

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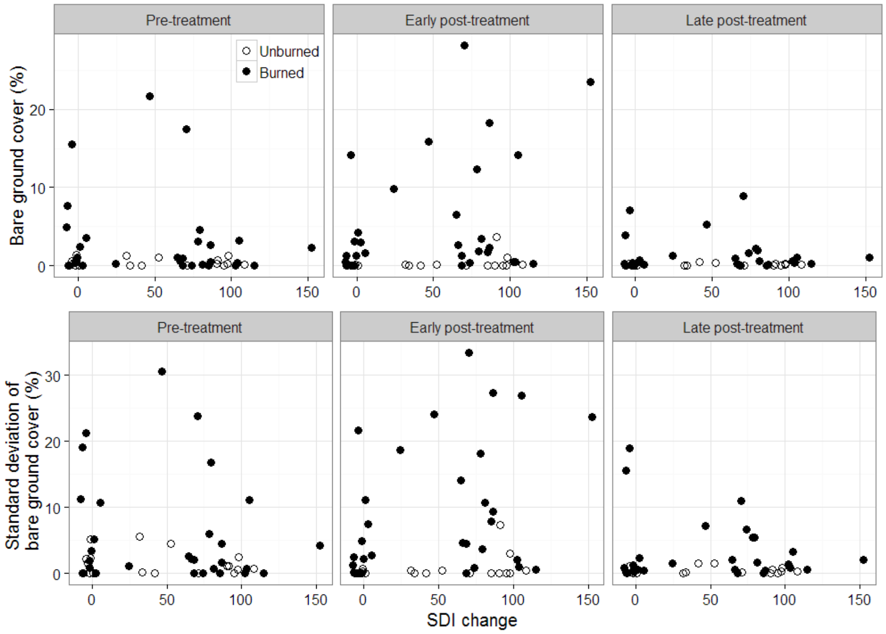

Figure 1.7 Pre-, early post-, and late post-treatment cover (%) of bare ground as a function of thinning intensity (SDI change) and burn treatment (*n* = 48 plots). Points are (a) means and (b) standard deviations of the 20, 1-m^2 quadrats per plot. Filled circles are burned plots; open circles are unburned plots.

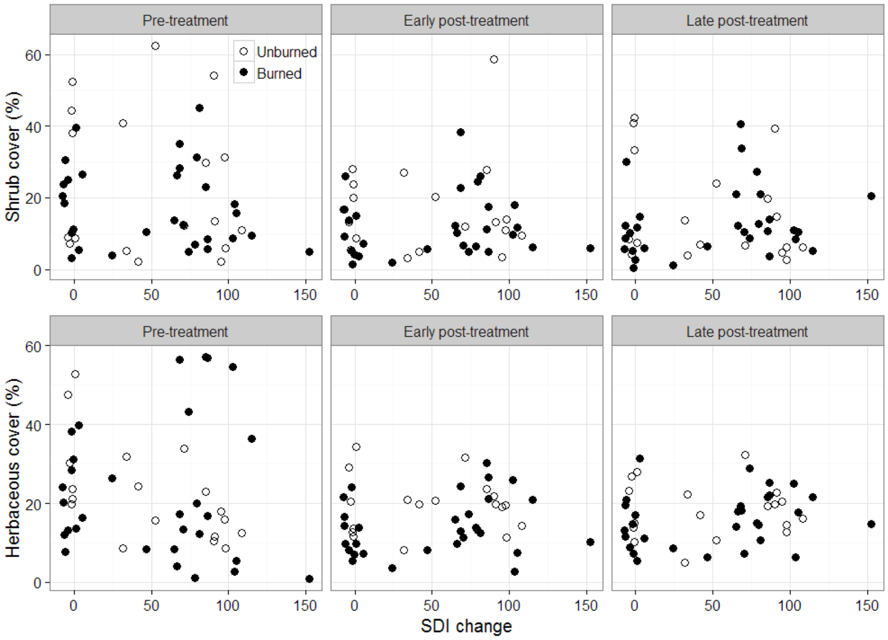

Figure 1.8 Pre-, early post-, and late post-treatment cover (%) of all (a) shrub and (b) herbaceous species as a function of thinning intensity (SDI change) and burn treatment (*n* = 48 plots). Points are the means of the 10 shrub subplots or 20 herbaceous quadrats per plot. Filled circles are burned plots; open circles are unburned plots.

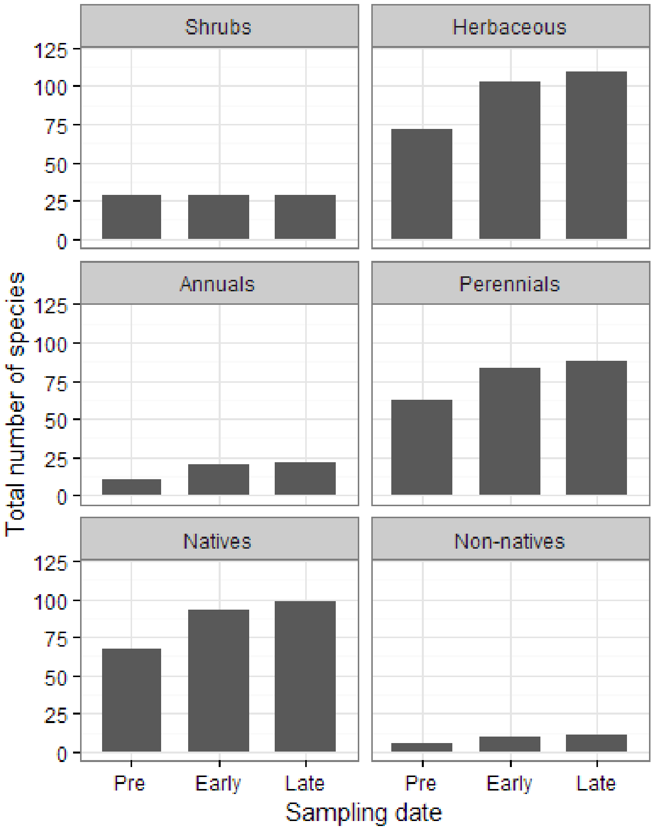

Figure 1.9 Changes over time in the total observed richness of plant groups defined by life form, longevity, and origin. Values are based on 480 subplots (50 m^2) for shrubs and 960 quadrats (1 m^2) for all herbaceous groups.

3.3 General trends in richness of shrub and herbaceous species

Richness of shrub and herbaceous species varied considerably within and among plots both before and after treatment (Fig. 1.10). Relative to the plot scale (i.e., among all 10 subplots or 20 quadrats in each plot), individual subplots supported ~50% of shrub species and individual -quadrats supported ~25% of herbaceous species. Per plot, shrub richness ranged from 3-20 and herbaceous richness range from 6-35. Prior to treatment there was a strong negative correlation between plot-scale herbaceous richness and subsequent thinning intensity (the latter was strongly

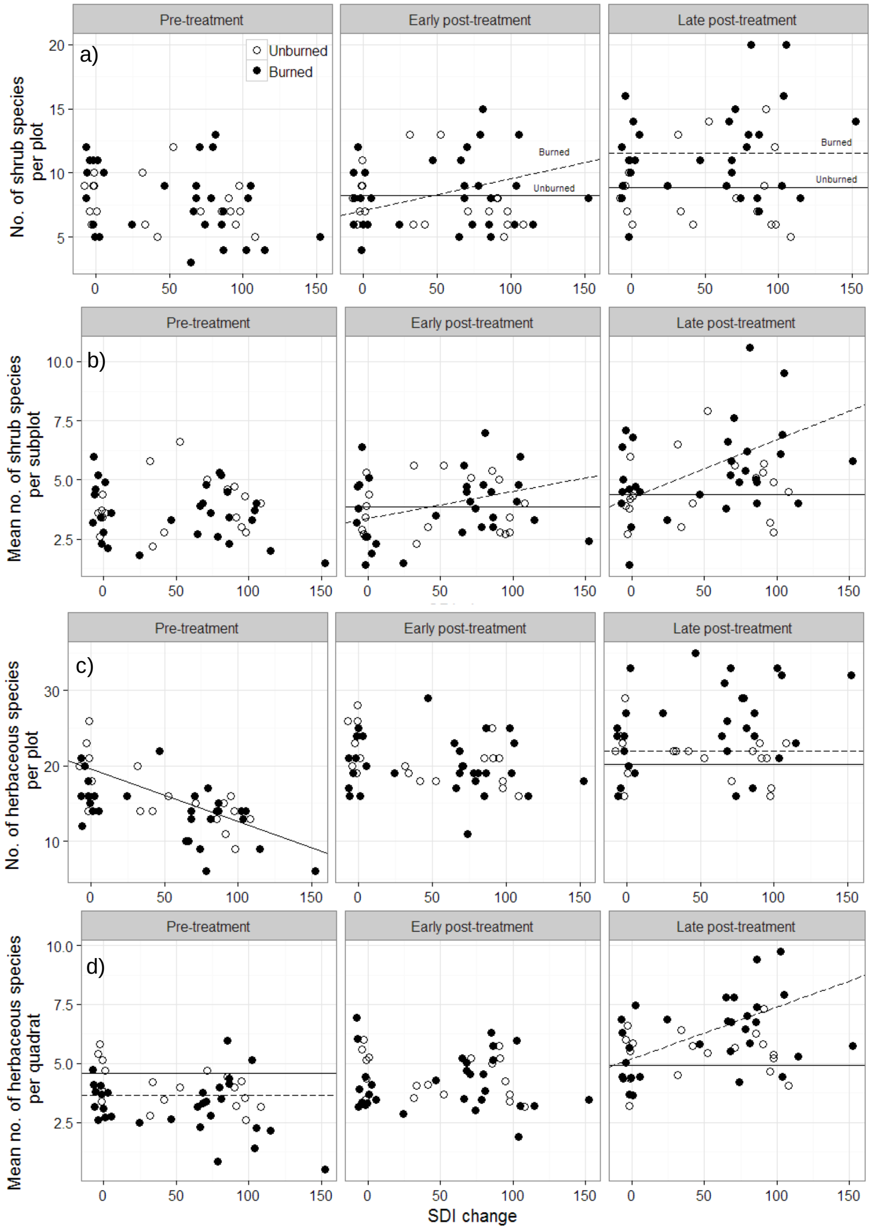

Figure 1.10 Pre-, early post-, and late post-treatment richness of (a, b) shrubs and (c,d) herbaceous species at each of two spatial scales as a function of thinning intensity (SDI change) and burn treatment. Filled circles are burned plots; open circles are unburned plots. Regression lines represent significant relationships between richness and treatment(s), with dashed and solid lines representing those of burned and unburned plots, respectively.

correlated with pre-treatment SDI; Fig. 1.10c). After treatment, plot-scale herbaceous richness was unrelated to thinning intensity (Fig. 1.10c)

3.4 Tests of hypothesized responses to thinning intensity, burning, and pre-treatment richness

H1. General responses to thinning and burning.

H1a. I hypothesized that shrub and herbaceous species richness would increase with thinning intensity and burning. Post-treatment responses were consistent, in part, with this expectation. Burning had a positive effect for most plant groups, but the size and significance of these effects were contingent on time and spatial scale (Figs. 1.11, 1.12, Table 1.2; see details in *H2* and *H3*). In contrast, thinning intensity enhanced richness only when combined with burning and, often, effects were only marginally significant (Table 1.2).

H1b. Among herbaceous taxa, I expected stronger responses to burning by annuals and non-natives than by perennials and natives. Responses were largely consistent with expectations: annuals showed positive responses to burning at both spatial scales and at one or both sampling dates while perennials did not respond to burning (Fig. 1.11, Table 1.2). Both natives and non-natives showed positive responses to burning, but non-natives only at the quadrat scale. For many plant groups, the effects of burning were enhanced by increasing intensity of thinning, particularly at the late post-treatment date and at smaller spatial scales.

H1c. I expected greater loss of herbaceous species to burning than to thinning, but there was little evidence of this effect. At the plot scale, species' loss did not vary with thinning intensity or burn treatment. Instead, loss correlated only with pre-treatment richness: loss was larger in plots with greater initial richness (Fig. 1.12, Table 1.2). At the quadrat scale, the

Table 1.2 Significance of fixed effects in linear mixed models of post-treatment richness at contrasting spatial scales, plot (P) vs. subplot (S) or quadrat (Q); and times since treatment, early (2 yr) vs. late (9-12 yr). Separate models were run for species of differing life forms, longevities, origins, and temporal behaviors. All groups other than shrubs include only herbaceous species. Bold font indicates statistical significance at α = 0.05 and underline indicates marginal significance (0.05 < p < 0.1). Dashes denote interaction terms that were not included in final models. Spatial scales differ for shrubs (10, 50 m^2 subplots per 0.1 ha plot) and herbs (20, 1 m^2 quadrats per 0.1 ha plot). Numerator and denominator degrees of freedom (df) are 1 and 36, except for models with significant interactions with pre-treatment richness or from which outliers were dropped.

Plant group	Pre- richness		Thin intensity		Burn		Thin intensity × Burn		Pre- richness × Thin intensity		Pre- richness × Burn	
(Spatial scale)	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late
Life form												
Shrubs (P)	**<0.001**	**<0.001**	0.44	0.59	0.42	**0.02**	**0.003**	0.12	—	—	—	—
Shrubs (S)	**<0.001**	**<0.001**	0.43	0.97	0.26	**0.02**	**0.005**	**0.01**	—	—	—	—
Herbaceous (P)	**<0.001**	**0.005**	0.68	0.75	0.67	**0.02**	0.57	0.10	—	—	—	—
Herbaceous (Q)	**<0.001**	**<0.001**	0.89	0.60	0.91	0.05	0.22	0.08	—	—	—	—
Longevity												
Annuals (P)	**<0.001**	**<0.001**	0.25	0.97	**0.01**	**<0.001**	0.38	0.21	—	—	—	—
Annuals (Q)*‡	**<0.001**	**<0.001**	0.14	0.15	0.31	**<0.001**	0.20	**0.01**	0.05	—	—	**<0.001**
Perennials (P)	**<0.001**	**0.002**	0.07	0.45	0.23	0.18	0.97	0.26	—	—	—	—
Perennials (Q)	**<0.001**	**<0.001**	0.18	0.11	0.42	0.25	0.62	0.41	—	—	—	—
Origin												
Natives (P)	**<0.001**	**0.003**	0.46	0.86	0.57	**0.02**	0.96	0.12	—	—	—	—
Natives (Q)	**<0.001**	**<0.001**	0.93	0.57	0.72	0.07	0.28	0.09	—	—	—	—
Non-natives (P)‡	0.28	0.098	0.70	0.77	0.06	0.13	0.17	0.08	—	—	—	—
Non-natives (Q)*†‡	0.11	0.92	0.68	0.68	0.14	**<0.001**	0.17	**<0.001**	**0.03**	0.53	—	**<0.001**
Temporal behavior												
Colonizing (P)	0.81	0.85	0.36	0.70	0.48	**0.03**	0.90	0.18	—	—	—	—
Colonizing (Q)	0.56	0.99	0.43	0.90	0.74	**0.04**	0.18	0.09	—	—	—	—
Extirpated (P)‡	**<0.001**	**<0.001**	0.93	0.89	0.80	0.49	0.78	0.77	—	—	—	—
Extirpated (Q)*‡	**<0.001**	**0.004**	0.33	0.12	0.44	0.92	0.36	0.90	**0.005**	—	**0.01**	—

* Inclusion of each pre-treatment richness × treatment interaction term reduced the denominator df by 1.

† The late model included a three-way interaction term (p = 0.003). Inclusion of the pre-treatment richness × burning and three-way interaction terms reduced the denominator df by 2.

‡ Exclusion of outlier(s) reduced denominator df by 1 to 3.

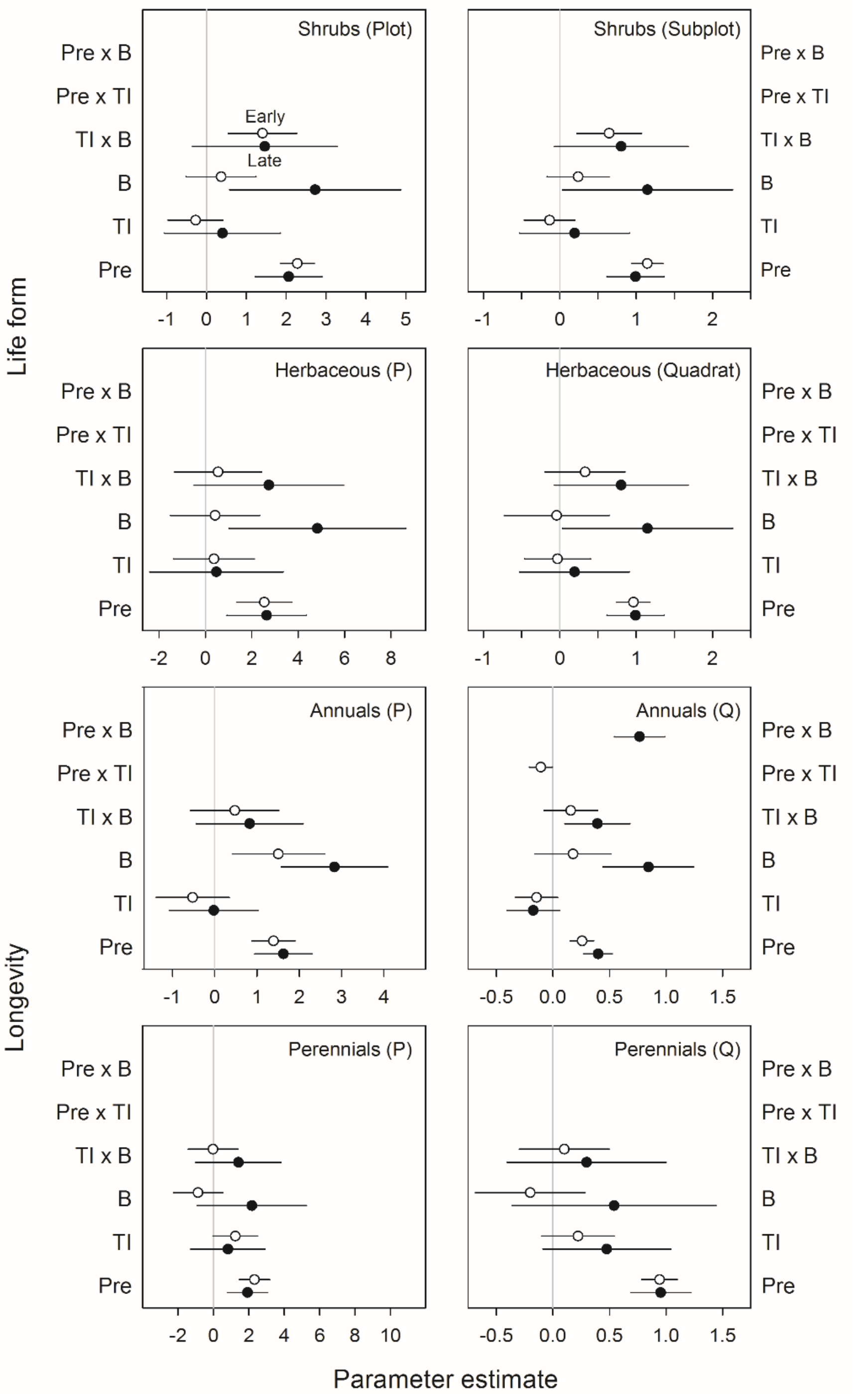

Figure 1.11 Parameter estimates (i.e., regression coefficients) and 95% CI of fixed effects in linear mixed models of post-treatment richness as a function of pre-treatment richness (Pre), thinning intensity (TI), burning (B), and two-way interactions. Estimates are significant (α = 0.05) if error bars do not cross 0 (see *p*-values in Table 1.2). Only terms retained in final models (following iterative elimination of non-significant interactions with pre-treatment richness) are displayed. Each panel contains the results of two models (early and late post-treatment) for a plant group at a single spatial scale, plot (P) or subplot (S)/quadrat (Q). Early post-treatment estimates are open circles; late post-treatment estimates are filled circles.

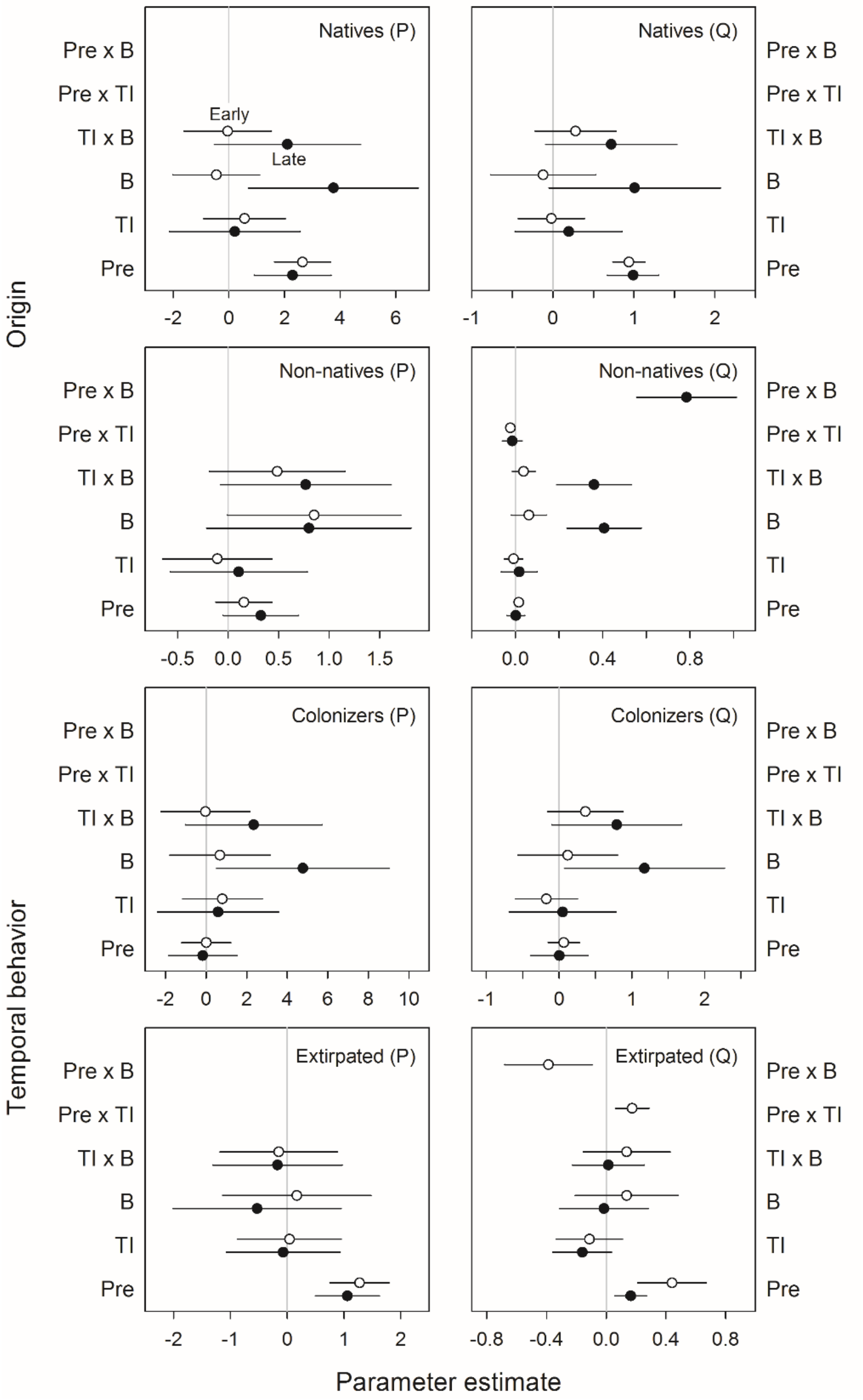

Figure 1.12 Parameter estimates (i.e., regression coefficients) and 95% CI of fixed effects in linear mixed models of post-treatment richness as a function of pre-treatment richness (Pre), thinning intensity (TI), burning (B), and two-way interactions. Estimates are significant (α = 0.05) if error bars do not cross 0 (see *p*-values in Table 1.2). Only terms retained in final models (following iterative elimination of non-significant interactions with pre-treatment richness) are displayed. Each panel contains the results of two models (early and late post-treatment) for a plant group at a single spatial scale, plot (P) or subplot (S)/quadrat (Q). Early post-treatment estimates are open circles; late post-treatment estimates are filled circles.

correlation of loss with thinning and with burning was contingent on pre-treatment richness, although these effects were short-lived (see details in *H4b*).

H2. Temporal effects

H2a. I expected positive responses of annuals to decline with time. Temporal trends ran counter to expectation: at the plot scale, the strength of the burn effect increased with time, and at the quadrat scale, the effect was non-significant at the early post-treatment date but became highly significant at the late date (Fig. 1.11, Table 1.2).

H2b. In contrast to annuals, I expected perennials to show a lagged response to treatments. In fact, responses were limited to marginally significant and transient increase with thinning intensity (Fig. 1.11, Table 1.2).

H3. Effects of spatial scale

I expected stronger responses at the plot than at the subplot/quadrat scale. Support for this hypothesis varied among plant groups and sampling dates. For example, for herbaceous and native species I detected significant responses to burning at the plot (but not the quadrat) scale, though this was limited to the late sampling date (Table 1.2). For annuals and non-natives, I detected significant or marginally significant responses at the plot (but not the quadrat) scale at the early sampling date, but responses became highly significant at the quadrat scale at the late sampling date (Table 1.2). Further, it was more often at smaller spatial scales that thinning enhanced the effects of burning (e.g., shrubs, annuals, and non-natives; Table 1.2).

H4. Relationships to pre-treatment richness

H4a. As I hypothesized, there was a strong correlation between pre- and post-treatment richness in all plant groups (except non-natives). Although pre-treatment richness remained a significant predictor of richness in the late post-treatment period, the effect size declined relative to burning.

H4b. I expected responses to treatments to be mediated by pre-treatment richness such that species-poor plots and quadrats would gain more species and species-rich areas would lose more species. Counter to expectation, treatment responses of most plant groups, including colonizers, were unaffected by initial richness (non-significant interactions with pre-treatment richness; Table 1.2). For annuals and non-natives, the effect sizes of the significant interactions between pre-treatment annual or non-native richness and thinning were very small, and the direction of the significant interactions with burning were opposite of that expected: plots with initially greater local density (quadrat-scale richness) gained more species that did plots with lower density (Fig. 1.11, 1.12). However, species loss from quadrats was contingent on initial conditions: plots with greater local species density lost more species as thinning intensity increased; with burning, however, plots with lower local species density lost more species (Fig. 1.12, Table 1.2). Both of these effects were transient.

4. Discussion

Previous studies have shown positive, negative, and neutral responses of understory vegetation to thinning and burning (e.g., Metlen et al. 2004, Collins et al. 2006, Dodson et al. 2008, Strahan et al. 2015, Willms et al. 2017). Some have documented how responses change over time or with the spatial scale of measurement (e.g., Dodson and Fielder 2006, Harrod et al. 2008, Dodson and Peterson 2010, Webster and Halpern 2010), but none have considered both the spatial and temporal aspects of this variation. The current study, based on longitudinal data from a large-scale restoration experiment, clearly illustrates that the spatial and temporal scales at which observations are made can influence our interpretation of the effectiveness of these treatments. Although species richness was enhanced by burning, there was a temporal lag in the effect, attributable to the gradual colonization and persistence of native annuals. I also found that the timing and strength of burning effects varied with spatial scale, reflecting time-dependent increases in the local density of both native and non-native species. This study demonstrates that there are long-term benefits to thinning and burning, but detection relies upon monitoring at sufficient temporal and spatial scales.

4.1 Overall trends in richness

Understory richness of the study area was dominated by herbaceous rather than woody species, which make up more than 80% of vegetative biodiversity in forests across North America (Gilliam et al. 2007), and even more in conifer forests (Halpern and Spies 1995). Increasing total herbaceous richness over time reflects enhancement of a critical component of local biodiversity. Although some of this increase may be due to improved knowledge of local flora by sampling personnel or to favorable weather, I attribute the majority to colonization by new species as a result of treatment for several reasons. First, richness increased more in treated units than in untreated units. Second, I took measures to ensure consistent identification over time to avoid mistaken additions to species lists. Finally, while annual variation in weather may affect diversity, with wetter weather thought to enhance emergence of annual species, seasonal precipitation of the late sampling year was lower than or comparable to the other sampling years, so that diversity was likely tempered by the weather rather than enhanced.

Conversely, total richness of shrubs did not change over time (while shrub richness in treated units did), perhaps reflecting a smaller regional species pool that was effectively captured at each sampling period by the 10, 50-m^2 subplots used to sample shrubs (compared to the 20, 1-m^2 quadrats used to sample herbaceous plants). This differential sampling effort may also have contributed to the less spatially dynamic diversity responses by shrubs in this study.

4.2 Lagged enhancement of herbaceous richness to burning

Richness of herbaceous species showed a lagged increase with prescribed burning. The mechanisms underlying this response can be inferred from the dynamics of colonization and extirpation. Early (two-year) post-treatment richness represented the net effect of species loss to disturbance and short-term colonization, whereas late post-treatment richness reflected the cumulative establishment (or re-establishment) of species over a considerably longer period of time (7-10 years). The lagged response could thus be due to (i) significant turnover in the short-term and/or (ii) delayed colonization. Evidence of turnover was contingent on spatial scale. Species loss at the plot scale was low and did not differ among treatments (experiment-wide mean of 2.5 or 12% of species). However, at the quadrat scale, losses were contingent on treatment and initial richness. Losses were greater in thinned plots where the local density of species was greater and thinning intensity was higher, but in burned plots where the local density of species was lower. Overall losses among quadrats were low, however, averaging 0.97 or 22%

of species. Thus, although species' turnover was more dynamic at smaller spatial scales, at neither scale was there sufficient extirpation of species to explain the delay in the positive response to burning. The strong correlation between pre- and early post-treatment richness provides further evidence of the relatively high rates of species survival, or rapid recovery, after burning (as observed in other studies of post-fire recovery in western forests; e.g., Halpern 1989, Halpern and Spies 1995, Harrod et al. 2008). Although species vary in their sensitivity to fire (Pyke et al. 2010) and the likelihood of extirpation varies with abundance, the low severity and patchy distribution of burning in this experiment (Agee and Lolley 2006) resulted in minimal species loss.

Consequently, the delayed total herbaceous response to burning reflects the relatively slow rates of species colonization. Results among plant groups indicate that annual species were the primary contributors to the lagged colonization; in fact, seven of the ten most frequent late colonizing species were annuals (Appendix B). This was unexpected. Post-disturbance successional theory predicts a decline in disturbance-adapted species with the expansion of competitive species over time and transient soil nutrient enhancement (Noble and Slatyer 1980, Monleon et al. 1997, Neary et al. 2005). Thus, I expected a decline in annual richness over time as the abundance of suitable germination sites declined and competition with perennial herbs and shrubs increased. Indeed, cover of bare ground decreased during this time period; however, cover of competing species did not show a detectable increase. Following large-scale disturbance in more productive west-side systems, perennials rapidly expand outcompeting annuals (Halpern and Spies 1995). In contrast, perennial expansion in this study may have been limited by higher levels of stress and the variable and often lower-than-average precipitation between the early and sampling dates (Fig. 1.3). Annuals, meanwhile, colonized an increasing number of quadrats and plots. Early colonization after treatment likely enhanced local seed production (propagule pressure), thus promoting the expansion of annual populations within and among plots (Halpern 1989, Halpern et al. 1997), despite the decline in bare ground.

Unlike the lagged response, I expected the immediate response of annuals to burning. Previous studies have shown positive responses to fire among annuals in the short-term (Laughlin et al. 2004, Moore et al. 2006, Webster and Halpern 2010). I predicted that annuals would respond positively to the exposure of mineral soil from burning. Indeed, richness responses were consistent with transient increases in bare ground (Fig. 1.7). However, bare ground exposure was variable, suggesting that the creation of open space by burning did not occur homogeneously within each plot. This likely to only occasional initial colonization within plots and the observed early response at the plot but not the quadrat scale.

In addition to the availability of germination sites, colonization by annuals in the short-term required that propagules survived fire *in situ* or quickly dispersed after treatment. Seed survival through fire depends on the thickness of the seed coat and the soil depth at which the seed located (Pyke et al. 2010). Adaptations among annual species such as seed polymorphism (i.e., variation in seed size and dormancy) or seed-banking (i.e., storing seeds in the soil) enhance the likelihood that seeds will survive fire and subsequently germinate (Syminoides 1988). However, despite findings that seed-banking is common among post-fire colonizers (Donato et al. 2008), including the most frequent colonizer in this study, *Claytonia perfoliata* (Matthews 1993), some studies have not found buried seeds to contribute substantially to post-fire recruitment (Vose and White 1987, Wienk et al. 2004). Nonetheless, the mild and patchy fire behavior in this study likely limited seed exposure to lethal temperatures (Vose and White 1987, Agee and Lolley 2006, Knapp and Keeley 2006), enabling the survival and germination of many annual seeds.

In addition to existing propagules, post-fire colonization could result from seeds dispersed from outside the sampling area. Rapid time to reproduction and long-distance dispersal are important characteristics of many annuals (Syminoides 1988) that contribute to species' abilities to disperse seeds immediately into disturbed areas (Donato et al. 2008). Indeed, *Collomia grandiflora*, a frequent colonizer in this study (Appendix B), produces non-opening, self-pollinating (cleistogamous) flowers that ensure rapid seed production following disturbance (Johnson and Wilken 2017). Seeds of other frequent colonizers were equipped for wind (*Bromus carinatus* and *Epilobium brachycarpum*; Tollefson 2006) or animal dispersal (*Cryptantha torreyana*). Source populations may have been located near or far from sample plots, but earlier work on this study reported that few colonizing species were present in the nearby meadow areas (Dodson et al. 2008). Rainfall events and hydrologic flow play large roles in the dispersal of seed in semi-arid environments (Speight 1980, Teckenberg 2003, Stella et al. 2006, Rhodes et al. 2014), so the rugged landscape setting of this experiment and dry weather patterns may have played a substantial role in local seed distribution, both restricting and facilitating dispersal.

In contrast to the strong responses by annual species, richness of perennials was not enhanced by burning. I hypothesized that perennials would show a positive response to burning that was slow to develop due to the regenerative constraints of species in this group (e.g., low-level seed production, dispersal limitation, and slow or no clonal growth). It appears that these hypothesized limitations remained in effect throughout the sampling period. Others have shown similar insensitivity among perennials for as many as five (Kerns et al. 2006) to 20 years after treatment (Webster and Halpern 2010). These authors suggest that it may not be possible to generalize among perennials due to the diversity of their life histories (including regenerative strategies) and responses to disturbance. Indeed, varying capacities among perennial species in propagule arrival and vegetative spread following disturbance have long been recognized (Noble and Slatyer 1980, Keeley 1981, Halpern 1989, Harrod et al. 2008, Pyke et al. 2010, and references therein). While some perennial species in this study colonized a substantial number of plots (Appendix B), total richness of this diverse group did not respond to burning.

4.3 Limited responses to thinning intensity in the absence of burning

In contrast to expectations, thinning intensity alone did not have a significant effect on richness at any spatial or temporal scale. I expected thinning to increase the availability of light and below-ground resources and, through ground disturbance associated with felling and yarding, to create germination sites for colonization. In fact, bare ground increased little with thinning over pre-treatment levels (Fig. 1.7); indeed, thinning of the treatment units (with yarding by helicopter) was observed to generated little soil disturbance relative to typical thinning activities (Boerner et al. 2009). Further, thinning considerably increased fuelbed depths and 10-hr fuel loads (Agee and Lolley 2006), suggesting that slash buried understory vegetation and covered bare ground. The lack of germination sites may have negated the benefits of increased resource availability. Other experiments have found increased species richness with higher thinning intensity (Thomas et al. 1999, Zenner et al. 2006), but Thomas et al. (1999) observed that understory diversity responses to thinning intensity were not simply reactions to concurrent canopy cover or understory light availability; rather, the slow accumulation of benefits from resource release and the recovery from trampling and burial caused lags in understory responses. Perhaps similar benefits in this study are yet to be realized. Or, benefits were accrued solely by species already present in the sampling areas, with burial and lack of soil exposure limiting colonization by new species.

When accompanied by burning, however, higher thinning intensities led to richness increases for many groups. I suggest this is due to slash created from thinning that increased the amount of fuel available to burn (Agee and Lolley 2006), leading to higher fire intensity and/or duration of burning, exposure of mineral soil, and resource modification within plots. Indeed, exposure of bare ground was highest in burned plots with high thinning intensities. While this enhancement of burning effects by thinning occurred only late post-treatment for herbaceous species, shrub species responded at the early as well as the late post-treatment sampling date. While their above-ground structures may have been consumed by fire, most *in situ* shrubs persisted, as evidenced by little to no decline in subplot frequencies of species (Appendix B). I suggest this response was enabled by the ability of many shrubs to resprout from rhizomes or root crowns, as exhibited by the three most common species in the experiment: *Rosa spp.*, *Symphoricarpos albus,* and *Amelanchier alnifolia* (Reed 1993, Fryer 1997, McWilliams 2000, Hauser 2006). Subsequent seed dispersal or rhizomatous spread into open areas by these species, and the emergence of others from the seed bank (such as common colonizers *Ceanothus sanguineus* and *Sambucus nigra ssp. cerulea*; Appendix B; Crane 1989, Johnson 2000), likely led to the early richness responses of shrubs as compared to herbaceous species.

4.4 Small increases in local species density of non-natives

Non-natives can threaten ecosystems by outcompeting natives, reducing habitat quality, and altering disturbance regimes. Creating conditions favorable to non-natives is a common concern with using fire as a restoration tool (Keeley 2006). Unfortunately, enhancement of non-natives has emerged as a common theme of both restoration thinning and burning (Nelson et al. 2008, Willms et al. 2017). Some studies have observed low-level increases in non-natives with restoration treatments (Abella and Covington 2004, Nelson et al. 2008), while others reported more moderate increases (Dodson and Fielder 2006, Metlen and Fiedler 2006).

In this study, non-native richness responded positively to burning. Significant responses occurred at small scales and the late sampling date. While these responses indicate an increase over time in the density of non-native species, richness increases were small, and the presence of non-native species throughout plots and quadrats was a fraction of that of native species. The most common late post-treatment colonizer was *Bromus tectorum*, which occurred in one-third of all plots by the late sampling date but was present in only 4% of quadrats (Appendix B). The likelihood of this species altering the fire regime in this dry forest, as it has in sagebrush communities across the western U.S., is minimal. *Tragopogon dubius*, the second-most common late colonizer, was extirpated from almost as many plots as it colonized. The presence of this annual/biennial species was temporally and spatially dynamic; its frequent colonization does not indicate an invasion. Furthermore, native species also responded positively to burning, showing that burning did not favor non-natives over natives.

4.5 Little mediation of treatment effects by pre-treatment richness

In addition to statistically accounting for pre-existing variation among plots, I used a pre-treatment richness covariate in models to evaluate hypotheses about the mediation of treatment effects by pre-treatment conditions. I found few instances of treatment mediation by pre-treatment richness. In fact, the nature of the interaction with burning ran counter to expectation: burned plots with initially greater local density of annual and non-native species had greater post-treatment colonization by annuals and non-natives, and burned plots with greater herbaceous density lost fewer herbaceous species. This suggests that these higher diversity plots were favorable locations for annuals and non-natives both before and after burning. It appears that burning did little to diminish habitat quality for these groups nor improve it for perennial colonization, a finding consistent with reports that post-disturbance richness is largely driven by unchanging environmental variables (e.g., slope, aspect; Metlen et al. 2004, Nelson et al. 2008). This result also suggests that a rich local plant community can readily provide propagules following disturbance, perhaps contributing to enhanced long-term resilience.

4.6 Management implications

Results of this study highlight long-term (9-12 year) ecological benefits of restoration burning. I found enhanced native diversity, particularly of annual species, more than a decade following treatment. This result provides evidence that additional burning treatments are not necessary to maintain the diversity benefits provided by first entry burns (for up to 12 years). Furthermore, richness enhancement at small spatial scales indicated that colonization occurred frequently throughout the study area. This local enrichment may ensure greater community resilience to future disturbance (e.g., wildfire) since species are less likely to be locally extirpated if they occur frequently. In comparison, studies in the Black Hills and Sierra Nevada have estimated the longevity of fuels reduction from prescribed burning to be 10-15 years, with the addition of thinning further enhancing treatment longevity (Battaglia et al. 2008, Stephens et al. 2012). This study indicates that the longevity of understory diversity benefits are at least as long.

A common concern with thinning and burning treatments is the potential for limited benefits to be accompanied by adverse effects, such as the enhancement of non-native as well as native diversity. Fire-suppressed plant communities appear to successfully exclude non-natives (Keeley 2006 and references therein), but the re-introduction of fire has been shown to increase their abundance and diversity (Nelson et al. 2008, Willms et al. 2017). This study shows that while diversity trade-offs occur, they are small, and field observations indicate that non-native abundance is low. The continued resistance to non-natives may be a result of the isolation of the study sites from known vectors (e.g., roads, human habitation), helicopter yarding minimized disturbance, and high fuel moisture kept fire severity low so alteration of the soil surface was minimized. While non-native responses to treatments should be closely monitored and controlled (see Nelson et al. 2008), I suggest that the ability of thinning and burning to reduce the risk of high-severity wildfire, and the risk for non-native invasion accompanying it, outweigh the low-level spread of non-natives resulting from these activities.

This study demonstrated that time of observation can affect our understanding of the effectiveness of restoration treatments. We cannot assume that short-term responses represent long-term responses, though additional studies can confirm whether the variation in short-term responses among studies persists, or if responses converge over time. Thus, despite the challenges to conducting long-term experiments, it is crucial that monitoring of them continues so we can fully evaluate the benefits and trade-offs of thinning and burning for dry forest restoration.

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6. Appendix A

Taxa observed over the course of study ordered by life form and longevity group used in analyses. Species grouped at the genus level are listed in footnotes. Asterisk indicates non-native species.

	Latin name	Family	Common name
Shrub taxa			
	Acer glabrum	Aceraceae	Rocky Mountain maple
	Acer macrophyllum	Aceraceae	bigleaf maple
	Amelanchier alnifolia	Rosaceae	Saskatoon serviceberry
	Ceanothus sanguineus	Rhamnaceae	redstem ceanothus
	Ceanothus velutinus	Rhamnaceae	snowbrush ceanothus
	Chimaphila menziesii	Pyrolaceae	little prince's pine
	Chimaphila umbellata	Pyrolaceae	pipsissewa
	Crataegus douglasii	Rosaceae	black hawthorn
	Holodiscus discolor	Rosaceae	oceanspray
	Lonicera ciliosa	Caprifoliaceae	orange honeysuckle
	Mahonia aquifolium	Berberidaceae	hollyleaved barberry
	Mahonia nervosa	Berberidaceae	Cascade barberry
	Paxistima myrsinites	Celastraceae	Oregon boxleaf
	Penstemon fruticosus	Scrophulariaceae	bush penstemon
	Philadelphus lewisii	Hydrangeaceae	Lewis' mock orange
	Populus tremuloides	Salicaceae	quaking aspen
	Prunus emarginata	Rosaceae	bitter cherry
	Prunus virginiana	Rosaceae	chokecherry
	Purshia tridentata	Rosaceae	antelope bitterbrush
	Ribes spp.[1]	Grossulariaceae	currant
	Robinia pseudoacacia	Fabaceae	black locust
	Rosa spp.[2]	Rosaceae	rose
	Rubus leucodermis	Rosaceae	whitebark raspberry
	Rubus parviflorus	Rosaceae	thimbleberry
	Salix scouleriana	Salicaceae	Scouler's willow
	Sambucus nigra ssp. *cerulea*	Caprifoliaceae	blue elder
	Sorbus scopulina	Rosaceae	Greene's mountain ash
	Spiraea betulifolia var. *lucida*	Rosaceae	shinyleaf spirea
	Symphoricarpos albus	Caprifoliaceae	common snowberry
	Symphoricarpos oreophilus	Caprifoliaceae	mountain snowberry
Herbaceous taxa			
Annual			
Forb			
	Clarkia rhomboidea	Onagraceae	diamond clarkia
	Collinsia parviflora	Scrophulariaceae	maiden blue eyed Mary

Latin name	Family	Common name
Collomia grandiflora	Polemoniaceae	grand collomia
Cryptantha affinis	Boraginaceae	quill cryptantha
Cryptantha torreyana	Boraginaceae	Torrey's cryptantha
Epilobium spp.[3]	Onagraceae	annual willowherb spp.
Gayophytum diffusum	Onagraceae	spreading groundsmoke
Madia exigua	Asteraceae	small tarweed
Madia gracilis	Asteraceae	grassy tarweed
Microsteris gracilis	Polemoniaceae	slender phlox
*Mycelis muralis**	Asteraceae	wall-lettuce
Phacelia linearis	Hydrophyllaceae	threadleaf phacelia
Polygonum douglasii	Polygonaceae	Douglas' knotweed
Stellaria nitens	Caryophyllaceae	shiny chickweed
*Cirsium vulgare**	Asteraceae	bull thistle
Conyza canadensis	Asteraceae	Canadian horseweed
*Lactuca serriola**	Asteraceae	prickly lettuce
*Senecio vulgaris**	Asteraceae	old-man-in-the-Spring
*Tragopogon dubius**	Asteraceae	yellow salsify
Claytonia perfoliata	Portulacaceae	miner's lettuce
*Verbascum thapsus**	Scrophulariaceae	common mullein
Arabis holboellii	Brassicaceae	Holboell's rockcress
Senecio integerrimus	Asteraceae	lambstongue ragwort
Graminoid		
*Bromus racemosus**	Poaceae	bald brome
*Bromus tectorum**	Poaceae	cheatgrass
Bromus carinatus	Poaceae	California brome
Perennial		
Forb		
Achillea millefolium	Asteraceae	common yarrow
Achlys triphylla	Berberidaceae	sweet after death
Adenocaulon bicolor	Asteraceae	American trailplant
Agoseris grandiflora	Asteraceae	bigflower agoseris
Agoseris retrorsa	Asteraceae	spearleaf agoseris
Agoseris sp.[4]	Asteraceae	agoseris
Anemone oregana	Ranunculaceae	blue windflower
Angelica arguta	Apiaceae	Lyall's angelica
Antennaria microphylla	Asteraceae	littleleaf pussytoes
Antennaria racemosa	Asteraceae	raceme pussytoes
Apocynum androsaemifolium	Apocynaceae	spreading dogbane
Arnica cordifolia	Asteraceae	heartleaf arnica
Balsamorhiza sagittata	Asteraceae	arrowleaf balsamroot
Cacaliopsis nardosmia	Asteraceae	silvercrown
Calochortus lyallii	Liliaceae	Lyall's mariposa lily
Castilleja hispida	Scrophulariaceae	harsh Indian paintbrush
Castilleja miniata	Scrophulariaceae	giant red Indian paintbrush
Chamerion angustifolium ssp. *angustifolium*	Onagraceae	fireweed
Claytonia lanceolata	Portulacaceae	lanceleaf springbeauty
Clintonia uniflora	Liliaceae	bride's bonnet
Corallorhiza maculata	Orchidaceae	summer coralroot

Latin name	Family	Common name
Crepis atribarba	Asteraceae	slender hawksbeard
Cystopteris fragilis	Dryopteridaceae	brittle bladderfern
Delphinium sp.[5]	Ranunculaceae	larkspur
Epilobium ciliatum ssp. *watsonii*	Onagraceae	fringed willowherb
Erigeron speciosus	Asteraceae	aspen fleabane
Eriogonum elatum	Polygonaceae	tall woolly buckwheat
Eriogonum umbellatum	Polygonaceae	sulphur-flower buckwheat
Erythronium grandiflorum	Liliaceae	yellow avalanche-lily
Eucephalus engelmannii	Asteraceae	Engelmann's aster
Eurybia conspicua	Asteraceae	western showy aster
Galium sp.[6]	Rubiaceae	bedstraw
Geum triflorum	Rosaceae	old man's whiskers
Gnaphalium sp.[5]	Asteraceae	cudweed
Goodyera oblongifolia	Orchidaceae	western rattlesnake plantain
Helianthella uniflora	Asteraceae	oneflower helianthella
Heuchera cylindrica	Saxifragaceae	roundleaf alumroot
Hieracium albiflorum	Asteraceae	white hawkweed
Hieracium scouleri	Asteraceae	Scouler's woollyweed
Hydrophyllum capitatum	Hydrophyllaceae	ballhead waterleaf
Kelloggia galioides	Rubiaceae	milk kelloggia
Lathyrus pauciflorus	Fabaceae	fewflower pea
Lilium columbianum	Liliaceae	Columbian lily
Lithophragma sp.[5]	Saxifragaceae	woodland-star
Lithospermum ruderale	Boraginaceae	western stoneseed
Lomatium nudicaule	Apiaceae	barestem biscuitroot
Lomatium triternatum	Apiaceae	nineleaf biscuitroot
Lupinus sp.[5]	Fabaceae	lupine
Maianthemum racemosum ssp. *amplexicaule*	Liliaceae	feathery false lily of the valley
Maianthemum stellatum	Liliaceae	starry false lily of the valley
Microseris nutans	Asteraceae	nodding microceris
Mitella trifida	Saxifragaceae	threeparted miterwort
Moehringia macrophylla	Caryophyllaceae	largeleaf sandwort
Montia parvifolia	Portulacaceae	littleleaf minerslettuce
Osmorhiza berteroi	Apiaceae	sweetcicely
Osmorhiza occidentalis	Apiaceae	western sweetroot
Penstemon procerus	Scrophulariaceae	littleflower penstemon
Phacelia hastata	Hydrophyllaceae	silverleaf phacelia
Piperia unalascensis	Orchidaceae	slender-spire orchid
Polystichum munitum	Dryopteridaceae	western swordfern
Potentilla glandulosa	Rosaceae	sticky cinquefoil
Pseudostellaria jamesiana	Caryophyllaceae	tuber starwort
Pyrola picta	Pyrolaceae	whiteveined wintergreen
Sedum stenopetalum	Crassulaceae	wormleaf stonecrop
Silene menziesii	Caryophyllaceae	Menzies' campion
Silene scouleri	Caryophyllaceae	simple campion
Stephanomeria minor var. *minor*	Asteraceae	narrowleaf wirelettuce
*Taraxacum officinale**	Asteraceae	common dandelion
Thalictrum occidentale	Ranunculaceae	western meadow-rue

Latin name	Family	Common name
Trifolium sp.[5]	Fabaceae	clover
Trillium ovatum	Liliaceae	Pacific trillium
Triteleia grandiflora var. *grandiflora*	Liliaceae	largeflower triteleia
Vicia americana	Fabaceae	American vetch
Viola glabella	Violaceae	pioneer violet
Zigadenus venenosus	Liliaceae	meadow deathcamas
Graminoid		
Achnatherum occidentale	Poaceae	western needlegrass
*Agropyron cristatum**	Poaceae	crested wheatgrass
Bromus vulgaris	Poaceae	Columbia brome
Calamagrostis rubescens	Poaceae	pinegrass
Carex concinnoides	Cyperaceae	northwestern sedge
Carex geyeri	Cyperaceae	Geyer's sedge
Carex rossii	Cyperaceae	Ross' sedge
Elymus glaucus	Poaceae	blue wildrye
Festuca idahoensis	Poaceae	Idaho fescue
Festuca occidentalis	Poaceae	western fescue
*Festuca ovina**	Poaceae	sheep fescue
Koeleria macrantha	Poaceae	prairie Junegrass
Melica bulbosa	Poaceae	oniongrass
Oryzopsis sp.[5]	Poaceae	ricegrass
Poa nervosa	Poaceae	Wheeler bluegrass
*Poa pratensis**	Poaceae	Kentucky bluegrass
Poa secunda	Poaceae	Sandberg bluegrass
Poa secunda ssp. *juncifolia*	Poaceae	rush bluegrass
Pseudoroegneria spicata ssp. *spicata*	Poaceae	bluebunch wheatgrass
Trisetum canescens	Poaceae	tall trisetum

*Non-native

[1] *Ribes aureum*, *R. cereum*, *R. hudsonianum*, *R. niveum*, and *R. viscosissimum*

[2] *Rosa gymnocarpa*, *R. nutkana*, *R. woodsii*, and their hybrids

[3] *Epilobium brachycarpum* and *E. minutum*

[4] *Agoseris grandiflora* or *A. retrorsa*

[5] Unidentified single species

[6] *Galium aparine* and *G. triflorum*

7. Appendix B

Frequency of occurrence and temporal behavior of taxa at two spatial scales. Only those taxa present in ≥10% of plots and ≥2% of subplots or quadrats for at least one sampling date are listed. Taxa are arranged by life form and ordered by descending rate of colonization of plots at the early sampling date. Numbers are percentage of total plots (*n* = 48), subplots (for shrubs; *n* = 480), or quadrats (for herbaceous species; *n* = 960). Bold font indicates annual or biennial taxa. Asterisk indicates non-native species.

	Frequency of occurrence						Early temporal behavior						Late temporal behavior					
	Plots			Subplots/Quadrats			Plots			Subplots/Quadrats			Plots			Subplots/Quadrats		
Life form/Species	Pre	Early	Late	Pre	Early	Late	Colonized	Lost	Persisted	Colonized	Lost	Persisted	Colonized	Lost	Persisted	Colonized	Lost	Persisted
Shrub taxa																		
Symphoricarpos oreophilus	25	38	52	9	12	23	25	13	13	11	8	1	33	6	19	18	4	5
Ceanothus sanguineus	6	29	50	1	9	19	23	0	6	9	0	1	46	2	4	18	0	0
Sambucus nigra ssp. *cerulea*	10	21	25	1	4	6	15	4	6	4	1	0	17	2	8	5	0	1
Prunus emarginata	29	38	54	9	10	17	13	4	25	5	3	6	27	2	27	10	2	7
Lonicera ciliosa	4	15	19	1	4	7	10	0	4	3	0	1	15	0	4	6	0	1
Symphoricarpos albus	88	94	94	56	60	62	10	4	83	11	7	48	13	6	81	14	8	48
Ribes spp.	13	15	15	2	3	4	8	6	6	2	1	1	8	6	6	3	1	1
Ceanothus velutinus	21	15	38	6	4	16	6	13	8	1	3	2	27	10	10	13	3	3
Chimaphila menziesii	6	8	27	1	1	9	6	4	2	1	1	0	23	2	4	8	1	0
Rubus parviflorus	2	8	21	0	2	5	6	0	2	2	0	0	19	0	2	5	0	0
Acer glabrum	40	33	40	11	10	12	6	13	27	3	4	6	8	8	31	5	4	6
Penstemon fruticosus	0	4	15	0	1	5	4	0	0	1	0	0	15	0	0	5	0	0
Paxistima myrsinites	25	19	33	7	4	13	4	10	15	2	5	2	13	4	21	8	1	5
Holodiscus discolor	54	54	60	20	18	26	4	4	50	3	5	15	6	0	54	8	2	18
Salix scouleriana	15	19	17	2	4	3	4	0	15	2	0	0	4	2	13	5	0	0
Prunus virginiana	29	33	29	13	13	12	4	0	29	3	3	10	2	2	27	1	2	10
Purshia tridentata	27	15	40	8	4	18	2	15	13	1	5	3	13	0	27	11	2	6

	Frequency of occurrence						Early temporal behavior						Late temporal behavior					
	Plots			Subplots/Quadrats			Plots			Subplots/Quadrats			Plots			Subplots/Quadrats		
Life form/Species	Pre	Early	Late	Pre	Early	Late	Colonized	Lost	Persisted	Colonized	Lost	Persisted	Colonized	Lost	Persisted	Colonized	Lost	Persisted
Acer macrophyllum	13	8	21	3	2	5	2	6	6	1	2	1	10	2	10	3	1	2
Mahonia aquifolium	79	79	88	39	41	45	2	2	77	0	0	0	8	0	79	0	0	0
Spiraea betulifolia var. *lucida*	69	65	69	45	51	52	0	4	65	10	4	41	2	2	67	8	1	44
Mahonia nervosa	10	6	13	6	6	6	0	4	6	1	1	4	2	0	10	1	0	5
Amelanchier alnifolia	100	92	98	68	59	73	0	8	92	6	14	54	0	2	98	12	6	61
Rosa spp.	100	98	100	64	63	69	0	2	98	8	9	55	0	0	100	11	5	58
Herbaceous taxa																		
Claytonia perfoliata	17	75	77	3	18	17	60	2	15	16	1	2	63	2	15	16	1	2
Bromus carinatus	17	52	58	2	5	8	40	4	13	4	1	1	42	0	17	7	1	1
Chamerion angustifolium ssp. *angustifolium*	2	29	15	0	5	3	29	2	0	5	0	0	15	2	0	3	0	0
Collomia grandiflora	44	67	92	7	12	24	27	4	40	8	3	4	48	0	44	19	2	5
***Epilobium* spp.**	0	25	33	0	2	5	25	0	0	2	0	0	33	0	0	5	0	0
Hydrophyllum capitatum	27	42	29	3	5	3	25	10	17	4	2	1	17	15	13	2	2	1
Cryptantha torreyana	13	35	31	1	4	3	23	0	13	4	0	1	21	2	10	3	0	1
Calochortus lyallii	29	44	48	4	6	6	23	8	21	5	2	2	25	6	23	4	2	2
Collinsia parviflora	38	46	63	4	11	15	21	13	25	9	2	2	38	13	25	14	2	1
Clarkia rhomboidea	8	29	44	1	4	7	21	0	8	3	0	1	35	0	8	6	0	1
Polygonum douglasii	4	23	17	0	2	2	19	0	4	2	0	0	13	0	4	2	0	0
Pseudoroegneria spicata ssp. *spicata*	44	56	52	7	9	13	19	6	38	6	3	4	17	8	35	8	3	4
Crepis atribarba	21	33	23	2	4	4	19	6	15	3	1	2	13	10	10	2	1	1
Agoseris retrorsa	6	25	31	1	2	3	19	0	6	2	0	0	25	0	6	3	1	0
Lactuca serriola*	0	19	8	0	3	1	19	0	0	3	0	0	8	0	0	1	0	0
Galium spp.	13	27	31	1	5	8	17	2	10	3	0	1	21	2	10	7	0	1
Hieracium scouleri	40	52	52	6	7	9	15	2	38	2	1	5	15	2	38	4	1	5
Elymus glaucus	4	17	46	0	2	8	15	2	2	2	0	0	42	0	4	8	0	0
Vicia americana	0	13	13	0	2	3	13	0	0	2	0	0	13	0	0	3	0	0
Microsteris gracilis	13	17	25	1	2	4	10	6	6	1	0	0	17	4	8	4	1	0
Eurybia conspicua	27	33	35	3	3	4	10	4	23	1	1	2	13	4	23	2	1	2
Phacelia hastata	4	15	10	0	2	1	10	0	4	1	0	0	6	0	4	1	0	0
Tragopogon dubius*	17	15	21	2	1	3	10	13	4	1	2	0	19	15	2	3	2	0
Lupinus sp.	50	54	63	11	13	18	8	4	46	4	3	9	17	4	46	8	2	10

	Frequency of occurrence						Early temporal behavior						Late temporal behavior					
	Plots			Subplots/Quadrats			Plots			Subplots/Quadrats			Plots			Subplots/Quadrats		
Life form/Species	Pre	Early	Late	Pre	Early	Late	Colonized	Lost	Persisted	Colonized	Lost	Persisted	Colonized	Lost	Persisted	Colonized	Lost	Persisted
Eucephalus engelmannii	21	29	33	3	3	5	8	0	21	1	1	2	13	0	21	3	1	2
Adenocaulon bicolor	8	17	10	1	2	3	8	0	8	2	0	1	2	0	8	2	0	1
Heuchera cylindrica	0	8	17	0	1	3	8	0	0	1	0	0	17	0	0	3	0	0
Bromus tectorum*	2	8	33	0	0	4	8	2	0	0	0	0	31	0	2	4	0	0
Angelica arguta	50	54	52	8	12	13	6	2	48	5	2	7	8	6	44	6	2	7
Balsamorhiza sagittata	38	40	44	7	7	9	6	4	33	2	2	4	13	6	31	4	2	5
Lithophragma sp.	8	10	0	1	1	0	6	4	4	0	1	0	0	8	0	0	1	0
Melica bulbosa	0	6	21	0	1	4	6	0	0	1	0	0	21	0	0	4	0	0
*Poa pratensis**	4	10	19	0	1	2	6	0	4	1	0	0	15	0	4	2	0	0
Lathyrus pauciflorus	75	73	77	17	18	21	4	6	69	5	4	13	6	4	71	8	4	13
Moehringia macrophylla	46	46	44	12	14	24	4	4	42	4	3	10	4	6	40	13	1	11
Apocynum androsaemifolium	31	33	35	6	7	9	4	2	29	2	1	5	6	2	29	4	1	5
Hieracium albiflorum	40	29	50	5	4	16	4	15	25	2	3	2	25	15	25	14	3	2
Cacaliopsis nardosmia	27	29	35	4	5	8	4	2	25	2	2	3	10	2	25	5	1	3
Lomatium nudicaule	33	25	29	4	3	4	4	13	21	2	2	2	6	10	23	3	2	2
Poa nervosa	0	4	19	0	1	3	4	0	0	1	0	0	19	0	0	3	0	0
Cryptantha affinis	0	2	15	0	0	2	2	0	0	0	0	0	15	0	0	2	0	0
Calamagrostis rubescens	94	94	94	54	45	48	2	2	92	5	14	40	2	2	92	7	13	41
Osmorhiza berteroi	85	75	90	20	22	32	2	13	73	8	6	14	8	4	81	18	7	14
Trifolium sp.	13	13	10	6	6	6	2	2	10	0	1	5	0	2	10	0	0	6
Pseudostellaria jamesiana	23	21	19	5	4	5	2	4	19	1	2	3	0	4	19	2	2	3
Carex rossii	15	6	25	1	1	4	2	10	4	1	1	1	15	4	10	3	0	1
Goodyera oblongifolia	15	10	29	1	1	3	2	6	8	0	1	0	17	2	13	2	0	1
Festuca occidentalis	8	10	29	1	1	5	2	0	8	1	0	1	21	0	8	4	0	1
Antennaria racemosa	6	8	13	1	1	2	2	0	6	0	1	0	6	0	6	2	0	1
Agoseris grandiflora	0	2	10	0	0	2	2	0	0	0	0	0	10	0	0	2	0	0
Carex geyeri	100	100	100	69	70	81	0	0	100	10	8	60	0	0	100	16	4	65
Arnica cordifolia	71	69	69	21	23	29	0	2	69	5	4	17	0	2	69	9	2	19
Achillea millefolium	60	54	71	17	14	20	0	6	54	2	5	12	13	2	58	7	4	13
Anemone oregana	48	46	46	14	13	16	0	2	46	3	4	10	0	2	46	4	2	12
Mitella trifida	17	17	19	3	2	5	0	0	17	1	2	1	2	0	17	3	1	2

*Non-native

Chapter 2

Choosing among approaches for analyzing understory responses to thinning and burning

Abstract

There are multiple approaches to statistical analysis of the effects of thinning and burning on understory diversity. If the approach is not specified by the research question or the original design is compromised, researchers must decide among options regarding data processing and model terms. I evaluate four considerations relevant to thinning and burning studies: aggregation of nested sample units, categorical versus quantitative treatment predictors, accounting for pre-treatment conditions, and collinearity among predictor variables. I use a case study to demonstrate analytical options. I first conclude that plot-level analysis of treatments has clear advantages and can be accomplished without pseudoreplication. Second, quantitative treatment predictors allow for analysis of thinning or burning intensity that may be more sensitive than categorical representation. Third, accounting for pre-treatment conditions can be accomplished in several ways, but some approaches alter the research question and limit the ability to evaluate hypotheses about pre-treatment conditions. Finally, collinearity should always be examined and the type of sums of squares used should be carefully considered.

1. Introduction

Recent increased interest in ecological restoration objectives that accompany fuel reduction treatments has resulted in a considerable body of literature testing the effects of thinning and/or burning on understory diversity (e.g., Metlen et al. 2004, Metlen and Fielder 2005, Dodson and Feidler 2006, Dodson et al. 2008, Webster and Halpern 2010, Fonda and Binney 2011, Strahan et al. 2015). Multiple reviews have pointed out the variation in conclusions among studies (Schwilk et al. 2009, McIver et al. 2013, Abella and Springer 2015). This variation may be due to many factors, including initial stand structure, seasonality of treatment, landscape context, or, as I explore in Chapter 1, the temporal and spatial scales of observation. However, even when these site and study-specific considerations are controlled, the same data set can be statistically analyzed in multiple ways to answer conceptually similar research questions (that may later be united in a single meta-analysis or literature review). These analytical choices can affect the parameter estimates and significance level of treatment effects, with the result that conclusions may vary even for the same data set.

Ideally, analytical methods are determined by the research question prior to experimentation. However, even when the question is defined, it might not specify details or intentionally leave room for fine-tuning, leaving open the possibility for multiple inquiries. For example, of the same data set, one could ask, how does thinning affect diversity at a given time post-treatment? And, how does thinning affect the change in diversity from prior to treatment? Both questions address the effect of restoration on understory diversity, but the response variables differ. Neither question addresses how to consider variables besides thinning that may also affect diversity. When not specified in the research question, choices such as these may be made implicitly and expressed in the methodological approaches.

The expectation is that these types of methodological choices are relatively unimportant and that answers to similar questions are consistent, supporting a single trend regarding the effects of treatment on understory diversity. But if they are not consistent and only one question is investigated, researchers and decision-makers may make assumptions about answers to similar questions. Thus, it is important to understand the consistency, or lack thereof, of outcomes among statistical choices and make the best choice for each study. The purpose of this study is to discuss several relevant analytical considerations regarding ecological restoration with thinning and burning, test the consistency of approaches using a single data set, and choose the best approach for the data set.

In this study, I examined considerations for analyzing the general question, “How do thinning and burning affect understory herbaceous richness?” I used a case study of data from a fuels-reduction experiment in central Washington to examine consistency in conclusions drawn among approaches and discuss the implications of each choice. In particular, I examined data disaggregation, categorical versus quantitative treatment predictors, accounting for pre-treatment conditions, and examining and remediating collinearity among predictor variables.

1.2. Overview of case study

The case study is a long-term fuels-reduction experiment located in a Douglas fir/ponderosa pine forest in the rugged eastern Cascade Mountains of central Washington. It is part of the nationally-coordinated Fire and Fire Surrogate network. The experiment tested the effects of mechanical thinning and prescribed burning, alone and in combination. Thinning was from below and performed to a target basal area of 10-14 m^2/ha with trees left in clumps, consistent with historic spatial patterning (Harrod et al. 1999). Prescribed burning followed thinning. Fires were ignited in the spring and were generally mild and patchy (Agee and Lolley 2006). Each treatment (control, thin-only, burn-only, and thinned and burned) was implemented in three approximately 10-ha experimental units. Nine years after treatment, a wildfire entirely burned four of the 12 experimental units (two control, one thin-only, and one burn-only unit). Field observations indicated substantial deviations in burn severity and plant composition from units adhering to the original treatment design, so they were excluded from the data set.

Sampling of understory and overstory vegetation occurred 2-3 years prior to treatments and two and 9-12 years post-treatment in a nested spatial design (Fig. 2.1). Experimental units were sampled with six permanent 0.1-ha plots. In each plot, all trees were measured while herbaceous vegetation was sampled with 20 permanent 1-m^2 quadrats. Additional information and references about the study site, treatments, sampling methods, and data processing can be found in Chapter 1 of this thesis.

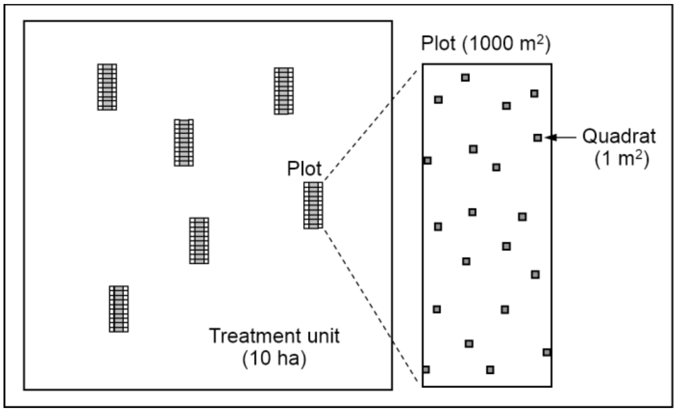

Figure 2.1 Sampling design of the case study. Herbaceous species were sampled in 20 quadrats in each of the six plots of each experimental unit.

In this chapter, I evaluated total herbaceous diversity of each plot from the 9-12 year post-treatment sampling date using a variety of statistical choices. Plot richness values (n = 48) were the total number of unique species sampled among quadrats. Unit-level richness values (n = 8) were the averages of the plot richness values of all treated plots within each unit (n = 5 or 6); plots outside the prescribed burn boundary were not included in unit-level calculations. At the unit level, I modeled richness with a 2-factor analysis of variance with categorical predictors of thinning and burning and Type III (marginal) sums of squares. At the plot level, I modeled richness with mixed-effects models that included fixed effects of thinning, thinning intensity, burning, and/or pre-treatment richness and the random effect of unit identity on the intercept. For these models, the use of Type I (sequential) or Type III (marginal) sums of squares is specified in the text. Modeling was performed in R (version 3.3.0; R Core Team 2016) with the base package and nlme package (version 3.1-127; Pinheiro et al. 2016). I present R^2 values as goodness-of-fit estimates; for mixed-effects models, this was the variance explained by the full model (including both random and fixed effects; Nakagawa and Schielzeth 2012), obtained using the MuMIn packaging (version 1.15.6; Barton 2016). R code used to produce results is provided in an appendix (Appendix A). Prior to testing, a significance level of 0.1 was chosen.

2. Aggregation of spatially nested sample units

Implementation of mechanical thinning and prescribed burning is costly and logistically complex. Typically, experimentation of these treatments involves few replicates, which are implemented at relatively large spatial scales (hectares or tens of hectares). Sampling is often performed in smaller plots within each experimental unit. This nested design creates options for analyses, the most straightforward of which is to aggregate the plot data in each unit (by averaging or summing) and conduct an analysis of variance (ANOVA) of treatment effects.

Analyzing data from the case study in such a way showed no significant effects of treatment on the average herbaceous richness of each unit (Table 2.1; Fig. 2.2a). The model explained 42% of the variation in the data. With eight units to analyze, the residual (i.e., denominator) degrees of freedom were four.

Table 2.1 Linear model results at the unit level. Treatments are categories. The t-statistic is equivalent to the square root of the F-value, and its sign corresponds to the sign of the parameter estimate. Type III (marginal) sums of squares were used.

		Thin		Burn		Thin x Burn	
R^2	Residual degrees of freedom	t	P	t	P	t	P
0.42	4	-0.73	0.51	-0.12	0.91	1.39	0.24

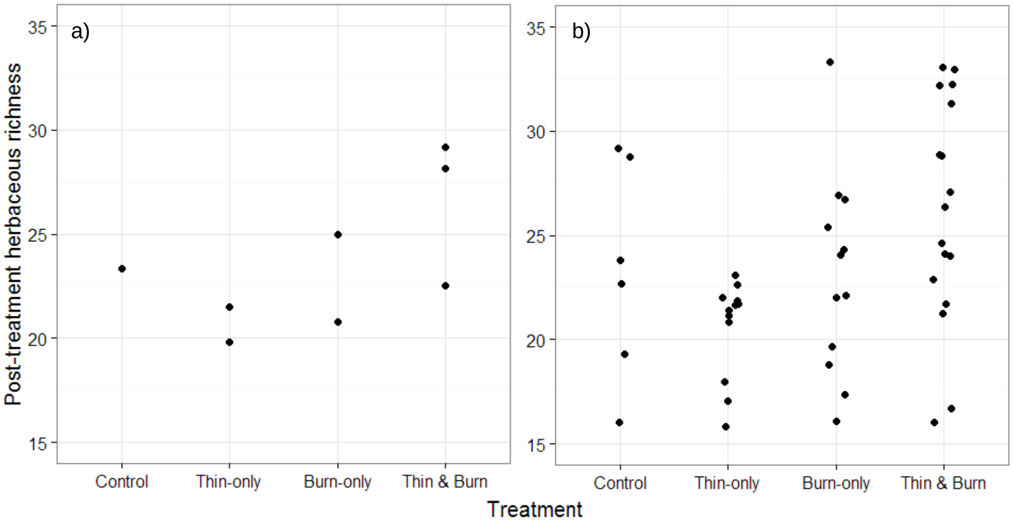

Figure 2.2 Post-treatment herbaceous richness among treatments at the a) unit and b) plot levels.

The unit-level ANOVA approach is effective when the experiment is balanced (equal sample sizes in all units and treatment groups), variation within each unit is small, and treatment design is not compromised by external factors. However, environmental variation, logistical challenges, and unforeseen events can alter a researcher's ability to collect or analyze data as originally conceived.

The case study was subject to several such data challenges. First, the study area was topographically rugged, and experimental units and plots varied noticeably in characteristics such as aspect, slope, hydrology, and soil depth. Perhaps due in part to this environmental variation, thinning and burning intensities varied considerably among plots (Agee and Lolley 2006). Second, during prescribed burning, two plots were unintentionally outside the burn line. Finally, the wildfire nine years after treatment reduced the number of units from 12 to eight and created an unbalanced treatment design. As a result of these characteristics and events, the data set had low replication and considerable variability in pre-treatment conditions and treatment intensities. When one wishes to make such an experiment useful, the ability to adapt statistical techniques to accurately and appropriately analyze the existing data is critical.

One important such adaptation for my data set was analyzing observations of plots not aggregated to the unit level (Fig 2.2b). By using plot-level covariates, I could accommodate variation in the physical environment that occurred within experimental units. Plot-level treatment attributes allowed for inclusion of untreated plots and quantification of treatment intensity, and by modeling variation among plots instead of just among unit means, treatment effects could be better detected, even with low replication. These adjustments resulted in denominator degrees of freedom based upon the number of plots rather than the number of units. To avoid pseudoreplication, I used random effects to account for variation due to unit identity;

further, I believe the spatial variation in treatment implementation (clumpy thinning, patchy burning) merits consideration of treatment effects at the plot level rather than purely at the unit level. It is important to garner useful insights from ecological experiments such as this in which it is infeasible to produce many replicates (Davies and Gray 2015). In sum, plot-level analysis of these data without pseudoreplication was possible and accommodated the challenges of this thinning and burning experimental data set.

3. Categorical versus quantitative treatment variables

Thinning and burning are often experimentally implemented in a categorical fashion (applied or not) but are rarely homogeneous in intensity. Frequently, thinning is intended to leave larger trees in higher-density patches consistent with historical spatial patterning (Bartsusevige and Kennedy 2009, Harrod et al. 2009). Prescribed burning tends to vary greatly in time and space, resulting in heterogeneous severity (Knapp and Keeley 2006). While this variation is often desired for creating environmental heterogeneous habitats at larger scales (Weins 2000, Dodson and Peterson 2010, Gossner et al. 2013), it opens the possibility of analyzing ecological response variables across a range of thinning and burning intensities at smaller scales.

A strict statistical approach dictates that levels of predictor variables should be only those that were intentionally manipulated (University of Washington Biostatistics consultants, *pers. comm.*). Indeed, many studies exclusively use categorical thinning and burning predictor variables when evaluating understory responses to treatment (e.g., Metlen and Fedler 2006, Dodson et al. 2008, Strahan et al. 2015). In addition to adhering to original experimental intentions, using categorical predictors is advantageous if measurements of treatment intensity are not made and/or one wishes to generalize across them, encompassing the variety of intensities in one level.

Loosening this restriction, however, allows researchers to test hypotheses about levels of treatment intensities that were not necessarily experimentally manipulated. Indeed, significant relationships between understory vegetation and levels of thinning or burning intensity have been found (Zenner et al. 2006, Webster and Halpern 2010). Treatment intensity (or severity) can be measured in various ways, such as direct effects of burning on the understory environment (e.g., duff consumption, mineral soil exposure), burning effects on trees (e.g., char height, percent crown scorch), or thinning changes to overstory structure (e.g., change in live or dead basal area and density). Change metrics can be expressed in absolute or relative terms. Using quantifiable metrics such as these allow for hypotheses beyond that of categorical treatment effects, a distinct advantage of this approach.

On the other hand, a researcher must choose which quantified intensity metrics to use in models. This choice may be limited by the feasibility of measurement or what was measured during treatment (if the experiment has already occurred). Metrics may not be direct measurements of thinning or burning intensity and, as such, may represent activities or processes beyond those intended. For example, I chose the pre- to two-years-post-treatment change in live stand density index (SDI; calculated as the square root of the product of density and basal area) to quantify thinning intensity. This metric characterized change in overstory structure during the treatment period, which may have been affected by burning or pathogens as well as thinning. Visualizing that high levels of SDI loss occurred only in thinned but in both burned and unburned plots increased my confidence that it primarily represents thinning intensity (Fig. 2.3).

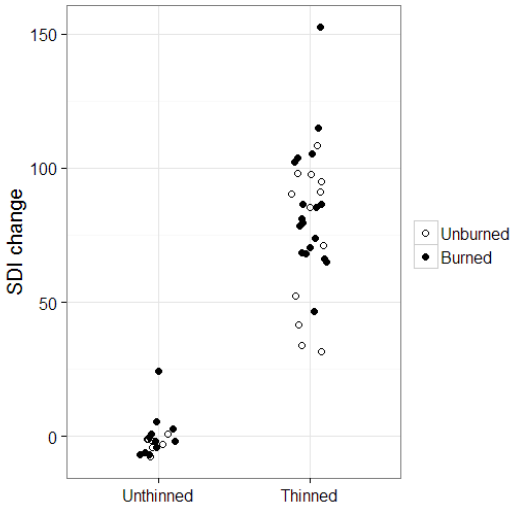

Figure 2.3 Pre- to 2-years-post-treatment change in stand density index of plots by thinning and burning treatments.

I compared outcomes of modeling understory herbaceous richness with categorical versus quantitative thinning intensity variables. The quantified thinning variable was the loss in live stand density index (positive values corresponded to more tree loss). Burning was not represented quantitatively due to insufficient measurement of its intensity or severity; it remained categorical (burned or unburned). I used linear mixed-effects models with Type III (marginal) sums of squares to evaluate both types of variables.

Results using categorical or quantitative treatment variables differed (Table 2.2). With categorical variables, I concluded that thinning and burning had no effect on herbaceous richness. When quantitative variables were used, a significant interaction was found between thinning and burning such that at the mean and 75th percentile of SDI change (plots with mean and high thinning intensities), burned plots had significantly higher herbaceous richness than unburned plots (Fig. 2.4). This result indicates that in plots that experienced relatively high levels of thinning and burning, herbaceous richness was enhanced. This conclusion would not have been drawn from the categorical analysis and shows the additional insights that can be drawn from quantitative forms of treatment variables.

Table 2.2 Model results using categorical ("Thin") or quantitative ("SDI change") forms of the thinning predictor variable. Type III (marginal) sums of squares were used. Bold terms indicate significance at α = 0.1.

		Thin or SDI change		Burn		Thin or SDI change x Burn	
Thinning variable type	R^2	t	P	t	P	t	P
Categorical	0.35	-0.83	0.44	-0.11	0.92	1.59	0.17
Quantitative	0.35	-1.08	0.29	0.02	0.99	**1.87**	**0.07**

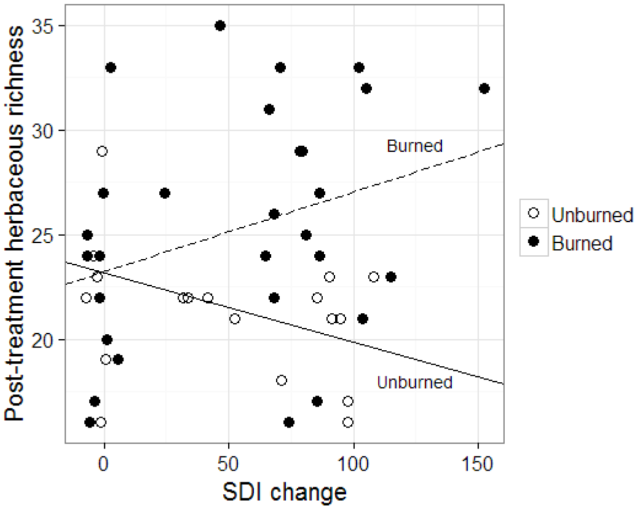

Figure 2.4 Post-treatment herbaceous richness versus SDI change. Unfilled circles and the solid line represent unburned plots. Filled circles and the dashed line represent burned plots. At mean and high SDI change, burned plots had significantly higher richness values than unburned plots.

4. Accounting for pre-treatment conditions

Pre-treatment conditions should be considered when evaluating the effects of treatments on understory diversity. They may be part of hypotheses relating to treatment effects or they may be considered extraneous to the experiment. They can be included as predictors, calculated into the response variable, or excluded from the model (if justified). A variety of approaches are possible; for example:

- Test for differences between treated and control groups in pre-treatment richness. If none are found, excluding pre-treatment richness entirely from models of post-treatment richness may be justified (Strahan et al. 2015).
- Use environmental and biotic variables (e.g., aspect, slope, overstory cover) to describe and account for existing differences among sample units; relevant environmental variables are then included in models of post-treatment diversity and abundance (Metlen et al. 2004).
- Use pre- to post-treatment change in understory metrics as response variables (Dodson and Peterson 2010). Change can be expressed as a raw value or relative to the pre-treatment measure.
- Use pre- to post-treatment change in understory metrics and a pre-treatment covariate in models. Interactions between the covariate and treatment variables are included in full models and then eliminated if not significant (Dodson et al. 2008).
- Conduct repeated measures tests of richness at all time periods with time as a predictor variable (Kerns et al. 2011).

When choosing an approach, I considered i) which pre-treatment variables to include, ii) relationships between pre-treatment conditions and treatments, iii) the response variable tested, and iv) hypotheses (if any) regarding pre-treatment conditions.

i) Pre-treatment conditions can be represented by environmental variables and/or measurements of overstory structure (e.g., Metlen et al. 2004), or by the pre-treatment value of the response variable (e.g., Dodson et al. 2008). The latter may be considered representative of pre-treatment ecological conditions upon which treatments act and/or simply the baseline of the response variable. In the case study, I chose to represent initial conditions with pre-treatment herbaceous richness.

ii) Some data sets may exhibit pre-existing relationships between initial conditions and forthcoming treatments. In relatively environmentally homogenous study sites where environmental differences among experimental units can be kept to a minimum, relying on the comparison of treated to control sites may be appropriate, as Strahan et al. (2015) did in the Southwest. In rugged or diverse sites, such as in the Cascade Mountains of the case study, examining and/or accounting for the impact of pre-treatment conditions is critical. Ideally, variation among units is accommodated with experimental blocking so no relationship exists between treatment and pre-treatment conditions. However, case study model results indicated a pre-existing, negative relationship between richness and SDI change in the case study (Table 2.3). Thus, I was not justified in excluding pre-treatment conditions from the consideration of post-treatment responses.

iii) Pre-treatment richness can be included as part of the response variable by subtracting or dividing it from post-treatment richness (e.g., Dodson et al. 2008, Dodson and Peterson 2010). Doing so, however, changes the question being asked of the data. In the case study, for example, burning was seen to have a positive effect on post-treatment richness (Table 2.3, Fig. 2.5), indicating that burned plots had higher richness than unburned plots at that sampling period. However, its positive effect on richness change (Table 2.3, Fig. 2.5) indicated that burned plots saw a larger increase in richness over the treatment period rather than at a single point in time. The difference may be subtle, but the research question should be considered when making a choice. One can also consider the goodness-of-fit of the model. In the case study, using richness change increased the variance explained by 33% (Table 2.3). Guided by my research question, I chose to use post-treatment richness as the response variable.

Table 2.3 Model results using different approaches to account for pre-treatment conditions. Type I (sequential) sums of squares were used. Dashes indicate non-applicable cells. Bold terms indicate significant results at $\alpha = 0.1$.

				Pre-treatment richness		SDI change		Burn		SDI change x Burn	
Approach	Response	Predictors	R^2	t	P	t	P	t	P	t	P
Exclusion	Pre-treatment richness	SDI change, Burn	0.56	-	-	**-4.59**	**<0.001**	-1.59	0.12	0.71	0.49
Exclusion	Post-treatment richness	SDI change, Burn	0.35	-	-	-0.69	0.50	1.67	0.10	**1.87**	**0.07**
Predictor	Post-treatment richness	Pre-treatment richness, SDI change, Burn	0.49	**1.95**	**0.06**	**2.07**	**0.05**	**2.28**	**0.03**	1.66	0.10
Response	Pre- to post-treatment richness change	SDI change, Burn	0.62	-	-	**3.74**	**<0.001**	**2.59**	**0.02**	1.52	0.14
Predictor & Response	Pre- to post-treatment richness change	Pre-treatment richness, SDI change, Burn	0.63	**-3.87**	**<0.001**	**2.10**	**0.05**	**2.30**	**0.03**	**1.70**	**0.097**

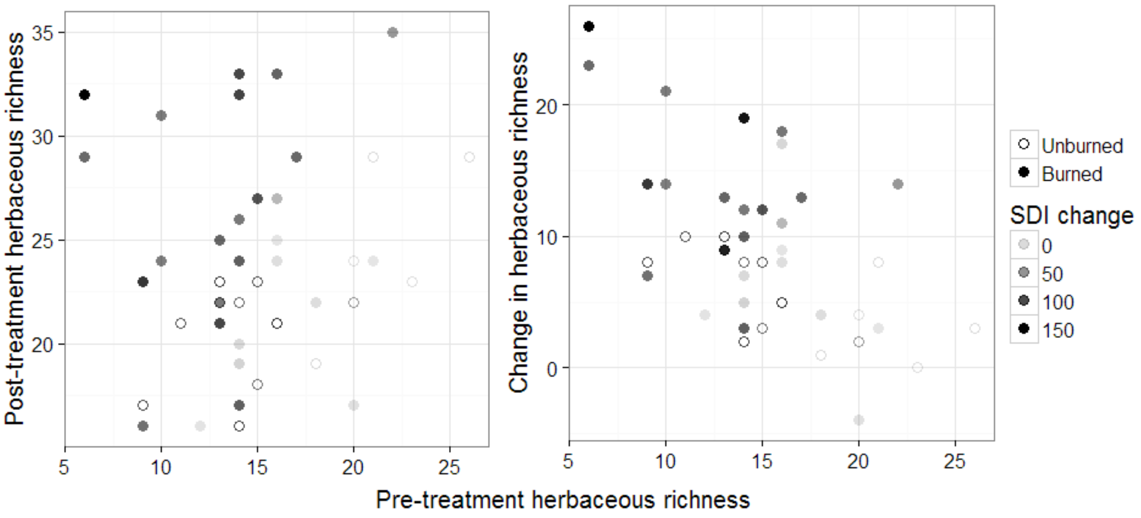

Figure 2.5 Post-treatment herbaceous richness or the pre- to post-treatment change in herbaceous richness versus pre-treatment richness, colored by burn status and SDI change.

iv) Pre-treatment conditions may be considered extraneous or may be part of hypotheses relating to treatment effects. If they are considered extraneous, the goal is to sufficiently account for pre-treatment differences among experimental units so as to not to bias results toward treatment effects (i.e., variable omission bias; Mela and Kopalle 2002). This can be accomplished by any of the approaches discussed here. If they are part of hypotheses, however, including them as predictors or covariates is preferred, as it allows for estimation and significance testing of parameters and the possibility for interactions with treatments.

Because of these advantages, I chose to include pre-treatment richness as a covariate in the case study. I did so by fitting a full model with all possible interactions and then iteratively removing insignificant interactions ($p > 0.1$), starting with the 3-way interaction (the interaction between SDI change and burning was not removed). I used Type I (sequential) sums of squares to ensure that the pre-treatment covariate was accounted for first in each model. I found that higher pre-treatment richness values led to higher post-treatment richness values, suggesting that most species persisted through treatments (Table 2.3). Including the pre-treatment covariate in the model of post-treatment richness had another advantage: it improved the variance explained by 40% (Table 2.3). However, it also dramatically altered the parameter estimate and p-value of SDI change, raising my concerns about collinearity between these predictors.

5. Addressing collinearity among predictors

Collinearity is the correlation of predictors in a multiple regression model. It is a potential issue in all multiple regression-type analyses, particularly if some variables are observed and not experimentally manipulated (Mela and Kopalle 2002, Graham 2003, Dorman et al. 2013). Among thinning and burning studies, which frequently employ multiple regression, I have rarely seen collinearity among predictors addressed (except see Metlen et al. 2004), despite its potential effect on model outcomes. If collinearity is substantial, it increases the standard error of parameter estimates, making estimates unstable among fitted models and reducing the power to detect significant effects (Kutner et al. 2004, Zar 2014). It also makes the effects of the predictors on the response ambiguous, as effects on the response may be due to only one of the correlated predictors or to a true combination of them (Graham et al. 2003, Kutner et al. 2004).

5.1 Diagnosing collinearity

There are several methods for examining data and models for problematic collinearity. First, one can examine the correlation coefficients between pairs of continuous predictors (a common threshold is $|r| \geq 0.8$; Zar 2014). Second, unstable parameter estimates can be examined by adding or deleting correlated predictors from models and looking for substantial changes in parameter estimates and standard errors based on marginal sums of squares (Kutner et al. 2004). Finally, a widely-used diagnostic is the variance inflation factor, which measures the degree to which the standard errors of parameter estimates are inflated by correlation among predictors (Kutner et al. 2004). Common thresholds are 5 or 10, but some authors argue substantial effects on p-values can be seen at values as low as 2 (Graham 2003, O'brien 2007). Despite these available methods, no tests for "significant" effects of collinearity exist; a researcher ultimately must use his/her best judgement to determine if it is problematic to a study.

In my study, I was suspicious of collinearity between SDI change and pre-treatment richness (see section 4). I examined the collinearity in my model via the three methods outlined above. The correlation coefficient between pre-treatment richness and SDI change was -0.63 (Fig. 2.6), the absolute value of which was below the common threshold of 0.8. When I removed the predictors one at a time from a model testing just pre-treatment richness and SDI change[1]

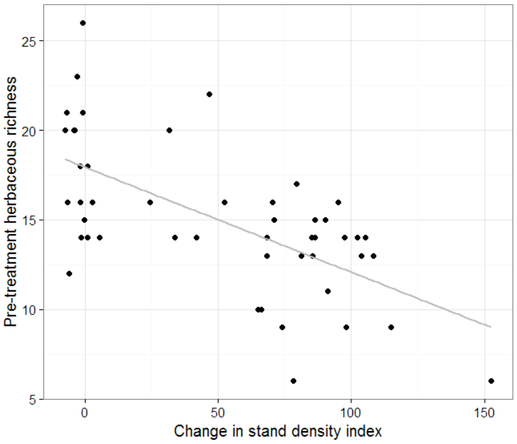

Figure 2.6 Pre-treatment herbaceous richness and SDI change are negatively correlated (r = -0.63, p < 0.001).

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[1] In the linear mixed-effects models of section 5, I scaled SDI change by its standard deviation and normalized pre-treatment richness to attain comparable effect sizes and errors. This standardization did not affect t-statistics or p-values of treatment effects. (Scaling and/or centering predictors is another important consideration in modeling; see Robinson and Schumaker [2009] and references therein.)

(without an interaction), the magnitudes of the parameter estimates decreased and the p-value of SDI change increased substantially (Table 2.4). However, the standard errors of both predictors did not change much, and the amount of variance explained improved 55% when pre-treatment richness was included, indicating that pre-treatment richness explained a substantial amount of variation not also explained by SDI change. The variance inflation factors for a model of pre-treatment richness, SDI change, and burning (no interactions) were 1.51, 1.44, and 1.06, respectively. These are well below the common thresholds of 5 or 10. I interpreted these diagnostics all together as showing a small but insubstantial effect of collinearity between the predictors in the case study. If, on the other hand, I had found major evidence of collinearity, I would consider the remediation measures presented in the following section.

Table 2.4 Parameter estimates (b), their standard errors, and p-values when different sets of correlated predictors are in models of post-treatment richness. Predictors were standardized by their standard deviations. Type III (marginal) sums of squares were used as suggested by Kutner et al. (2004) for this test. Dashes indicate non-applicable cells. Bold terms indicate significance at $\alpha = 0.1$.

		Pre-treatment richness			SDI change		
Predictors in model	R^2	b	SE(b)	P	b	SE(b)	P
Pre-treatment richness, SDI change	0.49	**2.52**	**0.89**	**0.01**	**3.25**	**1.75**	**0.07**
Pre-treatment richness	0.48	**1.70**	**0.78**	**0.04**	-	-	-
SDI change	0.31	-	-	-	0.80	1.51	0.60

5.2 Remediating collinearity

If collinearity is deemed problematic using the diagnostics described above, multiple approaches to reduce its effects are possible (Graham 2003, Kutner et al. 2004, Zar 2014). Using the case study, I illustrate three options.

5.2.1 Remove a correlated predictor

A simple approach to remediating collinearity is to eliminate one of the correlated predictors from the model. In the case study, I eliminated either pre-treatment richness or SDI change from a full model that included the categorical burn predictor and all possible interactions (as in section 4, the insignificant interactions between pre-treatment richness and treatment variables were iteratively removed; as in section 5.1, predictors were standardized by their standard deviations). As we saw when testing for collinearity (section 5.1), removing pre-treatment richness substantially altered the significance of SDI change and the amount of variation explained (R^2; Table 2.5), pointing to the importance of considering the influence of pre-treatment richness in our model. Statistics of burning or the interaction between SDI change and burning were little changed.

There are two major drawbacks to this approach: loss of explanatory power of the removed predictor and difficulty deciding which predictor to remove. I experienced both of these. The model lost 35% of the variance it explained when pre-treatment richness was removed (Table 2.5). I saw elsewhere the large influence pre-treatment richness had on model results, so I did not want to remove it. However, the purpose of the study was to test the effects of thinning and burning, so removing the thinning predictor from the model inhibited our ability to answer the research question. In sum, removing a correlated predictor was a poor choice for this case study. It may be a better choice when modeling a suite of environmental predictors, for example (e.g., Metlen et al. 2004).

Table 2.5 Model results when either or neither pre-treatment richness or SDI change are excluded from full models of post-treatment richness. Predictors were standardized by their standard deviations. Type I (sequential) sums of squares were used to ensure the covariate, pre-treatment richness, was accounted for first. Dashes indicate non-applicable cells. Bold terms indicate significance at α= 0.1.

		Pre-treatment richness		SDI change		Burn		SDI change x Burn	
Predictors in model	R^2	t	P	t	P	t	P	t	P
Pre-treatment richness, Burn	0.43	**1.99**	**0.05**	-	-	**1.81**	**0.08**	-	-
SDI change, Burn	0.35	-	-	-0.69	0.50	1.67	0.10	**1.87**	**0.07**
Pre-treatment richness, SDI change, Burn	0.49	**1.95**	**0.060**	**2.07**	**0.05**	**2.28**	**0.03**	1.67	0.11

5.2.2 Combine correlated predictors

A second approach to remediating collinearity is combining correlated predictors into one or more composite indices. This is often accomplished with Principal Component Analysis (PCA), since the resulting indices are uncorrelated (McCune and Grace 2002, Kutner et al. 2004). Performing a PCA on pre-treatment richness and SDI change in the case study resulted in two orthogonal components explaining 81.7% and 18.3% of the variation in these variables (Fig. 2.7). Loadings on the first component were 0.71 and -0.71 for pre-treatment richness and SDI change, respectively, and -0.71 for both variables on the second component. I used the scores of the first component and the categorical burn predictor in a linear mixed-effects model of post-treatment herbaceous richness (Type I sums of squares). I found no significant effects of any predictor or interaction (Table 2.6). In another model testing the scores of both components and burning, I found positive effects of the second component scores and burning and no significant interactions (Table 2.6).

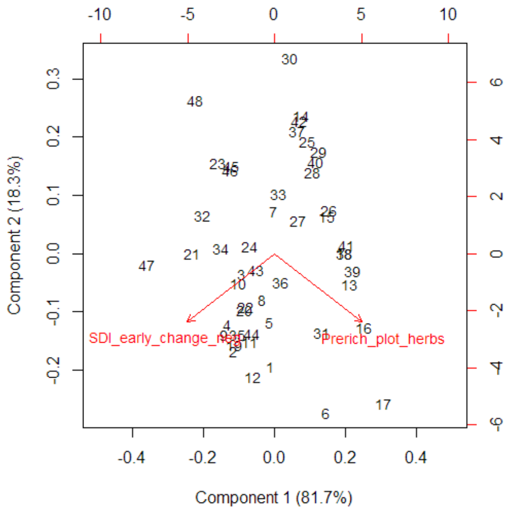

Figure 2.7 PCA biplot of a synthesis of pre-treatment richness and SDI change to ameliorate collinearity in models that use both variables.

Table 2.6 Model results of the PCA approach to remediating collinearity. Either just the first or both components were included in the models. Type I (sequential) sums of squares were used. Insignificant interactions were removed from the models. Dashes indicate non-applicable cells. Bold terms indicate significance at α= 0.1.

		Component 1		Component 2		Burn	
PCA components included in model	R^2	t	P	t	P	t	P
Component 1	0.37	0.89	0.38	-	-	1.52	0.14
Component 1, Component 2	0.42	0.83	0.41	**2.66**	**0.01**	**2.26**	**0.03**

While the composite approach includes all predictors in the model in some fashion, there are two disadvantages. If not all PCA components are included, less variation is explained by the model than when all unmodified predictors are included (in this study, R^2 of 0.37 versus 0.49). Second, the interpretation of the composite index as a function of the predictors may be ambiguous and/or limit the applicability of the results to the original research question. In the case study, higher values of Component 1 corresponded to higher pre-treatment richness and lower SDI change. We might expect, however, for these predictor levels to have opposite effects on post-treatment richness: higher pre-treatment richness should result in higher post-treatment richness whereas lower SDI change (corresponding to lower thinning intensity) should result in lower post-treatment richness. These opposing expectations could be the reason for the lack of significance of the component in the model (especially compared to the highly significant individual variables, Table 2.5). The positive effect of Component 2 in the second model indicates that plots with lower pre-treatment richness as well as lower SDI change had higher post-treatment richness. The effects of the components, while interpretable, do not aid greatly in answering the research question regarding the effects of thinning and burning, rendering this approach not a good choice for the case study, especially since collinearity was deemed a minimal issue. In a different study, where expectations were the same for correlated predictors, combining them via PCA may be a good option.

5.2.3 Prioritizing predictors and using sequential sums of squares

Graham (2003) suggests a third approach to remediate collinearity: instead of using marginal tests of parameter significance (e.g., Type III sums of squares), use sequential regression (e.g., Type I sums of squares) on predictors that have been prioritized. This ensures that shared contributions to the variation of the response variable are attributed to the predictor of higher priority, allowing for clearer interpretation of the effects of correlated predictors.

The challenge of this approach is ensuring that predictor prioritization reflects ecological functionality and/or there is a research-based hierarchy of predictors contributing to variation in the response variable (Graham et al. 2003). In the case study, the inclusion of the pre-treatment covariate aided in determining predictor priority. In fact, I used Type I (sequential) sums of squares throughout this chapter when I desired to account for the effect of pre-treatment richness prior to testing the effects of treatments. However, the hierarchy of SDI change and burning, and their interaction, was less clear. In plots that were both thinned and burned, thinning occurred first. But thinning and burning were also implemented independently, and the temporal relationship of the variables did not dictate that any shared variation should be attributed to thinning instead of burning.

I tested both Type I and Type III sums of squares on the model specified in section 5.2.1. For Type I sums of squares, in which the order of terms matters, pre-treatment richness was always the first term in the model, the interaction was the last, and both orders of the SDI change and burning terms were tested.

The type of sums of squares had a substantial effect on case study model outcomes (Table 2.7), but choosing the best type of sums of squares was not straightforward. Prioritizing predictors and using Type I sums of squares resulted in significant effects of both SDI change and burning (no matter the order of terms), but both effects were very insignificant with Type III sums of squares. Because the only difference for these terms between the types of sums of squares tests was the inclusion of the interaction term in calculating the extra sums of squares

(Kutner et al. 2004), it was clear that the interaction term shared a large amount of explained variance with thinning and burning. The question was, how should that shared variance be attributed? When it was entirely excluded as in Type III, no significant treatment effects were seen. When it was attributed to thinning and/or burning while ignoring that it was shared with the interaction, both thinning and burning were significant. Visualizing post-treatment richness as a function of SDI change and burning does seem to suggest that treatments are affecting richness (Fig. 2.4). Thus, it may be that Type III sums of squares is too conservative an approach and hides real effects of treatments. While arguable, it appeared Type I was the better choice for the case study.

Table 2.7 Model results using Type I (sequential) or Type III (marginal) sums of squares to examine the method of accounting for collinearity by prioritizing predictors. Terms were ordered in the model as presented in the table, except for in the second test when burning was tested prior to SDI change. Dashes indicate non-applicable cells. Bold terms indicate significance at α= 0.1.

			Pre-treatment richness		SDI change		Burn		SDI change x Burn	
Type of sums of squares	First treatment term	R^2	t	P	t	P	t	P	t	P
I (sequential)	SDI change	0.49	**1.95**	**0.06**	**2.07**	**0.05**	**2.28**	**0.03**	1.66	0.10
I (sequential)	Burn	0.49	**1.95**	**0.06**	**2.22**	**0.03**	**2.14**	**0.04**	1.66	0.10
III (marginal)	-	0.49	**3.03**	**0.01**	0.33	0.75	0.70	0.49	1.66	0.10

6. Conclusion

There is no “one-size-fits-all” approach to analyzing thinning and burning studies. A researcher must make conscientious choices about statistical approaches to ensure the research question is being answered and data set challenges are being met. Unfortunately, these choices are not always straightforward, as I saw when evaluating and accounting for collinearity with my case study. Nonetheless, I was able to make informed choices to accommodate for the challenges of this data set (Table 2.8) and formulate a final approach:

Post-treatment richness of plots~
Fixed effects: Pre-treatment richness, SDI change, Burn, interactions
Random effect: Experimental unit identity
Sums of squares: Type I (sequential).

Table 2.8 Analytical considerations, best approaches, and advantages of choices made for the case study presented.

Consideration	Best approach for case study	Advantages of chosen approach
Data aggregation	Plot-level data with mixed-effects model	Include unintentionally untreated plots, model variation among plots, achieve higher statistical power despite low replication
Categorical or quantitative thinning predictor	Quantitative (SDI change)	Account for and detect effects of variation in treatment intensity
Accounting for pre-treatment richness	Covariate predictor	Account for relative pre-treatment variation among plots, hypothesize about pre-treatment effects
Collinearity	Type I (sequential) sums of squares	Collinearity not found to be problematic, attribute shared variation among predictors to main effects rather than exclude entirely

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8. Appendix A

Script of R code to obtain model results and summaries.

```
#Chapter 2 code for model results and summaries ----

#Libraries used

library(nlme) #Run mixed models
library(MuMIn) #Calculated pseudo-R^2
#Also enter vif.mer function https://github.com/aufrank/R-
   hacks/blob/master/mer-utils.R

#Read data file

lmdata48<-read.csv("lmdata48.csv")

#Section 2. Data disaggregation

#Summarize data to unit scale, removing the unburned plot

lmdata47_unit<-ddply(lmdata48[!lmdata48$PlotID=="Spromberg.5",],
                     .variables=.(Unit,Treatment,Thin,Burn), .fun=summarise,
   Earlyrich_unit_herbs=mean(Earlyrich_plot_herbs),
   Laterich_unit_herbs=mean(Laterich_plot_herbs),
   Prerich_unit_herbs=mean(Prerich_plot_herbs))

#Run mixed model on unit and then plot data

summary(lm(Laterich_unit_herbs~Thin*Burn, data=lmdata47_unit)) #Default SS is
   type iii
r.squaredGLMM(lm(Laterich_unit_herbs~Thin*Burn, data=lmdata47_unit))
summary(lme(Laterich_plot_herbs~Thin*Burn, random=~1|Unit, data=lmdata48))
r.squaredGLMM(lme(Laterich_plot_herbs~Thin*Burn, random=~1|Unit,
   data=lmdata48))

#3. Categorical vs continuous treatment variables

#Model using categorical treatment variables

summary(lme(Laterich_plot_herbs~Thin*Burn, random=~1|Unit, data=lmdata48))
r.squaredGLMM(lme(Laterich_plot_herbs~Thin*Burn, random=~1|Unit,
   data=lmdata48))

#Model using continuous thinning variable

summary(lme(Laterich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48))
r.squaredGLMM(lme(Laterich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48))
```

```
# Significant thin x burn interaction; use different levels of variables to
   investigate

summary(lme(Laterich_plot_herbs~SDI_early_change_neg_75quantile + Burn +
   SDI_early_change_neg_75quantile:Burn,
            random=~1|Unit, data=lmdata48)) #effect of burning at high thin
   levels
summary(lme(Laterich_plot_herbs~SDI_early_change_neg_mean + Burn +
   SDI_early_change_neg_mean:Burn,
            random=~1|Unit, data=lmdata48)) #effect of burning at mean thin
   levels
summary(lme(Laterich_plot_herbs~SDI_early_change_neg + Burn_negone +
   SDI_early_change_neg:Burn_negone,
            random=~1|Unit, data=lmdata48)) #effect of thinning in burned
   plots

#4. Pre-trt accounting

#Table 3 Results. Type I SS.

#pre-trt~t,b

summary(lme(Prerich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48))$tTable #signs
   of t-statistics
anova(lme(Prerich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential") #p-values
sqrt(anova(lme(Prerich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential")[,3]) #obtain t-statistics (which are
   sqrt of F-values)
r.squaredGLMM(lme(Prerich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48)) #conditional
   pseudo R2

#post~t,b

summary(lme(Laterich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48))$tTable #signs
   of t-statistics
anova(lme(Laterich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential") #p-values
sqrt(anova(lme(Laterich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential")[,3]) #obtain t-statistics (which are
   sqrt of F-values)
r.squaredGLMM(lme(Laterich_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48)) #conditional
   psuedo R2

#post~pre,t,b
```

```
summary(lme(Laterich_plot_herbs~Prerich_plot_herbs + SDI_early_change_neg +
   Burn + SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48))$tTable
   #signs of t-statistics #final
anova(lme(Laterich_plot_herbs~Prerich_plot_herbs + SDI_early_change_neg +
   Burn + SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential") #p-values
sqrt(anova(lme(Laterich_plot_herbs~Prerich_plot_herbs + SDI_early_change_neg
   + Burn + SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential")[,3]) #t-stats
r.squaredGLMM(lme(Laterich_plot_herbs~Prerich_plot_herbs +
   SDI_early_change_neg + Burn + SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48)) #conditional psuedo R2

#change~t,b

summary(lme(Richchange_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48))$tTable #signs
   of t-statistics
anova(lme(Richchange_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential") #p-values
sqrt(anova(lme(Richchange_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential")[,3]) #obtain t-statistics (which are
   sqrt of F-values)
r.squaredGLMM(lme(Richchange_plot_herbs~SDI_early_change_neg + Burn +
   SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48)) #conditional
   pseudo R2

#change~pre,t,b

summary(lme(Richchange_plot_herbs~Prerich_plot_herbs + SDI_early_change_neg +
   Burn + SDI_early_change_neg:Burn, random=~1|Unit, data=lmdata48))$tTable
   #signs of t-statistics #final
anova(lme(Richchange_plot_herbs~Prerich_plot_herbs + SDI_early_change_neg +
   Burn + SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential") #p-values
sqrt(anova(lme(Richchange_plot_herbs~Prerich_plot_herbs +
   SDI_early_change_neg + Burn + SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48),type="sequential")[,3]) #t-stats
r.squaredGLMM(lme(Richchange_plot_herbs~Prerich_plot_herbs +
   SDI_early_change_neg + Burn + SDI_early_change_neg:Burn, random=~1|Unit,
   data=lmdata48)) #conditional psuedo R2

#5. Collinearity

#5.1 Testing collinearity

#Bivariate correlation coefficient

with(lmdata48,cor.test(Prerich_plot_herbs,SDI_early_change_neg))

#Table 4 model results
```

```
summary(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered, random=~1|Unit, data=lmdata48));
   r.squaredGLMM(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered, random=~1|Unit, data=lmdata48))
summary(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled, random=~1|Unit,
   data=lmdata48));
   r.squaredGLMM(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled,
   random=~1|Unit, data=lmdata48))
summary(lme(Laterich_plot_herbs~SDI_scaled_notcentered, random=~1|Unit,
   data=lmdata48));
   r.squaredGLMM(lme(Laterich_plot_herbs~SDI_scaled_notcentered,
   random=~1|Unit, data=lmdata48))

#Variance inflation factors

vif.mer(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn, random=~1|Unit,data=lmdata48))

#5.2 Remediating collinearity

#5.2.1 Eliminate one predictor from full models

#Table 5. Type I SS.

r.squaredGLMM(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled + Burn,
   random=~1|Unit, data=lmdata48))
summary(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled + Burn,
   random=~1|Unit, data=lmdata48)) #signs of t-stats
anova(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled + Burn,
   random=~1|Unit, data=lmdata48), type="sequential") #p-values
sqrt(anova(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled + Burn,
   random=~1|Unit, data=lmdata48), type="sequential")[,3]) #t-stats

r.squaredGLMM(lme(Laterich_plot_herbs~SDI_scaled_notcentered + Burn +
   SDI_scaled_notcentered:Burn, random=~1|Unit, data=lmdata48)) #R2
summary(lme(Laterich_plot_herbs~SDI_scaled_notcentered + Burn +
   SDI_scaled_notcentered:Burn, random=~1|Unit, data=lmdata48)) #signs of t-
   stats
anova(lme(Laterich_plot_herbs~SDI_scaled_notcentered + Burn +
   SDI_scaled_notcentered:Burn, random=~1|Unit,
   data=lmdata48),type="sequential") #pvals
sqrt(anova(lme(Laterich_plot_herbs~SDI_scaled_notcentered + Burn +
   SDI_scaled_notcentered:Burn, random=~1|Unit,
   data=lmdata48),type="sequential")[,3]) #tstats

r.squaredGLMM(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn + SDI_scaled_notcentered:Burn,
   random=~1|Unit, data=lmdata48)) #R2
summary(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn + SDI_scaled_notcentered:Burn,
   random=~1|Unit, data=lmdata48)) #signs of t-stats
anova(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn + SDI_scaled_notcentered:Burn,
   random=~1|Unit, data=lmdata48), type="sequential") #pvals
```

```
sqrt(anova(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn + SDI_scaled_notcentered:Burn,
   random=~1|Unit, data=lmdata48), type="sequential")[,3])#tstats

#5.2.2 Combine correlated predictors (PCA)

#Create PCA

summary(thinpre.pca3 <- princomp(lmdata48[,
   c("SDI_early_change_neg","Prerich_plot_herbs")],
                                 cor = TRUE))
loadings(thinpre.pca3)

#Add plot scores of PC components to data frame

lmdata48$ThinprePCA3<-thinpre.pca3$scores[,1]
lmdata48$ThinprePCA3_PC2<-thinpre.pca3$scores[,2]

#Table 6

#Model with only PC component 1

r.squaredGLMM(lme(Laterich_plot_herbs~ThinprePCA3 + Burn, random=~1|Unit,
   data=lmdata48))#R2
summary(lme(Laterich_plot_herbs~ThinprePCA3 + Burn, random=~1|Unit,
   data=lmdata48))#signs of t-stats
anova(lme(Laterich_plot_herbs~ThinprePCA3 + Burn, random=~1|Unit,
   data=lmdata48), type="sequential")#pvals
sqrt(anova(lme(Laterich_plot_herbs~ThinprePCA3 + Burn, random=~1|Unit,
   data=lmdata48), type="sequential")[,3])#tstats

#Model with PC components 1 and 2

r.squaredGLMM(lme(Laterich_plot_herbs~ThinprePCA3 + ThinprePCA3_PC2 + Burn,
   random=~1|Unit, data=lmdata48)) #R2
summary(lme(Laterich_plot_herbs~ThinprePCA3 + ThinprePCA3_PC2 + Burn,
   random=~1|Unit, data=lmdata48)) #signs of t-stats
anova(lme(Laterich_plot_herbs~ThinprePCA3 + ThinprePCA3_PC2 + Burn,
   random=~1|Unit, data=lmdata48), type="sequential") #pvals
sqrt(anova(lme(Laterich_plot_herbs~ThinprePCA3 + ThinprePCA3_PC2 + Burn,
   random=~1|Unit, data=lmdata48), type="sequential")[,3]) #t-stats

#5.2.3 Prioritizing predictors

#Table 7

r.squaredGLMM(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn + SDI_scaled_notcentered:Burn,
   random=~1|Unit, data=lmdata48)) #R2 for all types of SS

#Type III (marginal)

summary(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn + SDI_scaled_notcentered:Burn,
```

```
   random=~1|Unit, data=lmdata48)) #type iii (marginal) ss; t-stats and p-
   values

#Type I (sequential). signs of t-stats are same as with original summary
   function (all positive)

#SDI change as first term

anova(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn + SDI_scaled_notcentered:Burn,
   random=~1|Unit, data=lmdata48),type="sequential") #pvals
sqrt(anova(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled +
   SDI_scaled_notcentered + Burn + SDI_scaled_notcentered:Burn,
   random=~1|Unit, data=lmdata48),type="sequential")[,3])#tstats

#Burn as first term

anova(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled + Burn +
   SDI_scaled_notcentered + SDI_scaled_notcentered:Burn, random=~1|Unit,
   data=lmdata48),type="sequential") #pvals
sqrt(anova(lme(Laterich_plot_herbs~Prerich_plot_herbs_scaled + Burn +
   SDI_scaled_notcentered + SDI_scaled_notcentered:Burn, random=~1|Unit,
   data=lmdata48),type="sequential")[,3])#tstats
```

Conclusion

Evaluating ecological restoration of dry forests is a complex task. As I have demonstrated, responses to thinning and burning may be sensitive to temporal and spatial scales of observation and to analytical specifications. Consideration of these sensitivities is essential to the full evaluation of ecological objectives.

In Chapter 1, I found that species diversity generally increased with prescribed burning, but responses varied among temporal and spatial scales. Herbaceous diversity responded only at the later post-treatment sampling date, suggesting that colonization was limited by slow dispersal and clonal growth. Annual species constituted most of this lagged response (in contrast with successional theory; Noble and Slatyer 1980). Both natives and non-natives showed positive responses to burning, with small-scale non-native responses indicating increases in local species density. While enhancement of non-natives has emerged as a theme among thinning and burning studies, short-term effects on natives are typically neutral or negative (Nelson et al. 2008, Willms et al. 2017). By examining responses over longer timeframes, I found that the diversity of natives (and annuals) continued to benefit more than a decade following treatment. This finding points to lasting positive effects of burning without the need for re-entry.

As thinning and burning experiments mature and more long-term, multi-scale studies are conducted, determining approaches to overcome common data challenges will become even more important. Such challenges include low replication, pre-existing variation, and spatially nested sampling plots. In Chapter 2, I presented alternative approaches to several critical considerations: aggregation of nested sample units, categorical or quantified treatment intensities, accounting for pre-treatment conditions, and collinearity among predictors. I found that different approaches often result in different outcomes of statistical models. However, careful specification of research questions can help determine how to handle these challenges and permit use of data that necessitate alternative analytical approaches.

As managers move forward with planning and implementing dry forest restoration, they should be conscientious that ecological outcomes can vary among temporal and spatial scales and analytical approaches. To accommodate this variation, I recommend specifying the scales at which objectives are targeted and identifying solutions to data challenges before initiating experiments. I also recommend bearing in mind that short-term results can obscure long-term benefits. The enhancement of native understory diversity from thinning and burning, an important ecological benefit of these treatments, may only be detected if responses are measured over sufficient time periods. Planning for long-term monitoring that aligns with the temporal scales of ecological responses is key to determining if treatments primarily applied for the reduction of fuels in dry forests also achieve ecological objectives.

Literature Cited

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