University of Nevada, Reno

Vegetation dynamics at the woodland-shrubland interface: Role of climate, disturbance, and species interactions

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by

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ABSTRACT

The boundary between woodlands and shrublands delineates the distribution of the tree biome in many regions across the globe. Woodlands and shrublands interface at multiple spatial scales, and many ecological processes operate at different spatial scales to determine the position of the woodland-shrubland boundary. The overall objective of this dissertation was to examine processes affecting vegetation dynamics at the woodland-shrubland interface in the western United States, at spatial scales ranging from biomes to individual plants. In Chapter 1, I examined broad-scale drivers of the position of lower treeline in the Intermountain West, using vegetation classifications derived from remote sensing imagery. I found that pinyon-juniper woodlands are broadly limited by water balance and will likely be sensitive to climate change, but that lower treelines at more northern latitudes are functionally constrained by permanent landscape features, land use and disturbance. In Chapters 2 and 3, I characterized post-fire plant community trajectories in an experimental network of prescribed fire treatments at the interface between pinyon-juniper woodlands and sagebrush shrublands in the Great Basin. I found that plant community responses to burning were strongly stratified along gradients of elevation and pre-fire tree cover, and that resistance to fire-induced invasion of the annual grass *Bromus tectorum* (cheatgrass) was low on sites that were relatively warm and dry (lower elevations) and on sites that lacked perennial understory species before burning (high pre-fire tree cover). Seeding perennial species after burning decreased invasibility in sites with low resistance, increasing perennial cover while reducing the abundance of invasive plants. In Chapter 4, I used field experiments to examine the interaction between *Artemisia tridentata* (big sagebrush) and *Pinus monophylla* (singleleaf pinyon pine), the dominant species within respective shrubland and woodland types that interface over broad environmental gradients in the Great Basin. I found that the effect of *A. tridentata* on *P. monophylla* shifted from strongly positive (facilitative) toward neutral after the vegetative transition from juvenile to adult foliage in *P. monophylla*. The timing of the ontogenetic shift did not vary across an elevational gradient, suggesting that this shrub-tree interaction may be relatively insensitive to increasing temperatures. Taken together, this research illustrates the dynamic link between woodland and shrubland ecosystems, and suggests that future dynamics at their interface will be complex and scale dependent.

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OVERVIEW

Ecological boundaries have long been of fundamental interest in ecology (Wiens *et al.*, 1985). Boundaries define the distribution of ecosystem components, and as such the dynamics of boundary systems are key drivers of landscape change (Peters *et al.*, 2006). Additionally, vegetation responses to global change processes are expected to be most rapid and extreme at the boundaries between ecosystems (Gosz, 1993; Risser, 1995). In many arid and semiarid regions of the world, boundaries between trees and shrubs delineate the distribution of forests and woodlands. The position of the woodland-shrubland ecotone is therefore an important determinant of the distribution of the global forest biome, with major implications for carbon stocks and other ecosystem services (Ahlström *et al.*, 2015). Prolonged drought events have resulted in sudden shifts in semiarid woodland-shrubland ecotones in recent decades (Breshears *et al.*, 2005), and widespread tree mortality events are expected to increase under future climate conditions (Anderegg *et al.*, 2013). However, ecotones that are controlled by non-climatic processes will be less responsive to climate change than those at or near their ecophysiological limits (Holtmeier & Broll, 2005). Understanding the drivers of dynamics at the woodland-shrubland interface boundary is critical for anticipating future shifts in the distribution of global woodlands and shrublands.

The overall objective of this dissertation was to examine processes affecting vegetation dynamics at the woodland-shrubland interface in the western United States at multiple spatial scales. Ecological boundaries exist across a hierarchy of spatial scales because ecosystem properties are scale-dependent (Naiman & Decamps, 1997). Boundaries that are apparent at fine spatial scales may not be discernable at broader scales, and vice versa (Strayer *et al.*, 2003). In general, boundaries defined with coarse grain sizes are relatively linear and stable through time (Yarrow & Marín, 2007), as spatial and temporal dynamics occurring at finer scales than the grain size will be undetected (Fig. 1a). At finer resolutions, landscape heterogeneity becomes increasingly apparent (Fig. 1b-c).

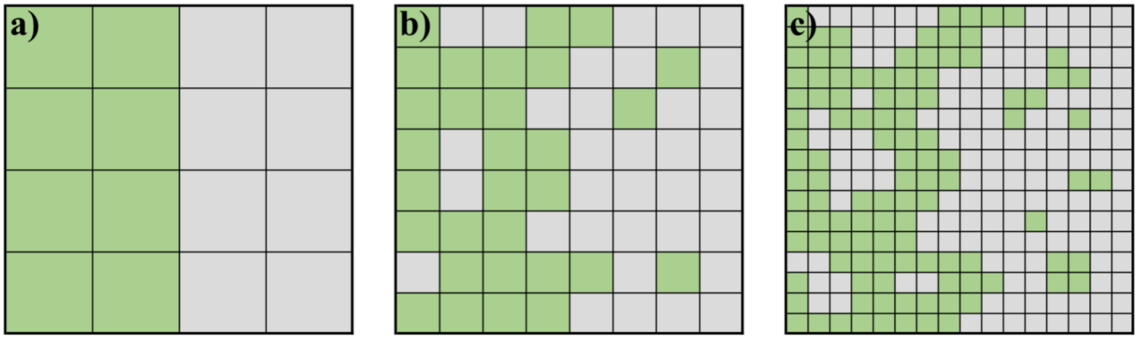

Figure 1. Distribution of two ecosystem components (shown in green and gray). a) Boundary defined using a coarse grain size; b) boundary defined using an intermediate grain size; and c) boundary defined using a fine grain size.

Tree- and shrub-dominated ecosystems interface at multiple spatial scales simultaneously, ranging from biomes to communities, populations, and individual plants. Boundaries defined at a given scale are controlled by processes operating at corresponding scales (Gosz, 1993; Cadenasso *et al.*, 2003). At coarse spatial scales, the position of the boundary separating woodland biomes from shrublands corresponds to broad-scale controls on the distribution of the component species. These controls include characteristics of the abiotic environment such as climate and soils, regional land use patterns, and historical disturbance regimes. At intermediate scales, woodland-shrubland boundaries are the result of individual disturbances, dispersal events or limitations, specific land management decisions, or abiotic drivers that vary over steeper gradients. At very fine scales, tree-shrub boundaries reflect the distribution of individual plants, which are controlled by interactions with other plants and plant-scale variation in microhabitat availability. In this dissertation, I examine processes that control biome boundaries at broad/regional scales (Chapter 1), plant communities at intermediate/patch scales (Chapters 2-3), and individual plant outcomes at fine/microhabitat scales (Chapter 4).

In Chapter 1, I examined the broad-scale drivers of the position of lower treeline in the Intermountain West, a 1.7 million km^2 region of the USA. Lower treelines constitute a major boundary of the forest biome in many mountainous regions, yet they have received little scientific attention compared to other treeline types. I used existing vegetation classifications to map lower treelines, and I used the resulting map to characterize the distribution of forest types at lower treeline and explore latitudinal trends. I then modeled topoclimatic drivers of lower treeline position for each of three dominant forest types. I found that much of lower treeline of the Intermountain West is currently limited by water balance and will likely be sensitive to climate change. Lower treelines in other regions around the globe may also be climate-controlled, although response to climate change will be locally mediated by soils, biotic interactions, disturbance and land use. I developed a functional categorization of lower treelines for anticipating future shifts in global forest distribution in response to environmental change.

In Chapters 2 and 3, I characterized post-fire plant community trajectories in an experimental network of prescribed fire treatments at the interface between pinyon-juniper woodlands and sagebrush shrublands in the Great Basin, USA. I used repeat vegetation surveys, including pre-fire measurements, from replicate pairs of burned and control plots to investigate community assembly processes along gradients of elevation and pre-fire tree cover. In Chapter 2, I characterized natural short-term (4 years post-fire) plant community responses to burning, during which time cattle grazing and other anthropogenic land uses were prohibited. I found that unburned understory communities and their responses to disturbance were strongly stratified along an elevational gradient of productivity. Whereas burning largely eliminated the differences in understory composition among sites at the same elevation, sites with high pre-fire tree cover experienced divergent post-fire community pathways with sparse plant establishment, suggesting that the lost ecological memory of the native understory community had initiated unpredictable community trajectories.

In Chapter 3, I resampled permanent survey plots to examine long-term (14 years post-fire) plant community responses to prescribed fire and post-fire seeding treatments. In the years between the original experimental duration (Ch. 2) and the long-term resampling, cattle grazing, wood harvest, and other anthropogenic disturbances had occurred, and the study area had experienced a severe drought. I found that long-term resistance to fire-induced invasion of the annual grass *Bromus tectorum* (cheatgrass) was highest on relatively cool and moist sites (higher elevation), but that the warmer and drier burned sites had become heavily invaded. Post-fire *B. tectorum* dominance was highest in sites with high pre-fire tree cover, where post-fire establishment of native perennial species was lacking. Seeding perennial species after burning decreased invasibility in sites with low resistance, increasing perennial cover while reducing the abundance of invasive plants.

In Chapter 4, I examined interactions between *Artemisia tridentata* (big sagebrush) and *Pinus monophylla* (singleleaf pinyon pine), the dominant species within respective shrubland and woodland types that interface over broad environmental gradients in the Great Basin. I used a combination of field experiments and environmental measurements to characterize interactions between individual plants, at sites along an elevational gradient and for multiple stages of *P. monophylla* regeneration. *A. tridentata* facilitated *P. monophylla* at multiple ontogenetic stages, but the net outcome of the interaction shifted from strongly positive toward neutral after the vegetative transition from juvenile to adult foliage in *P. monophylla*. The timing of the ontogenetic shift did not vary across the elevational gradient, although results suggest that the mechanism of facilitation may have differed among elevations, with facilitation more strongly related to abiotic stress amelioration at low elevations.

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CHAPTER 1. Identifying controls on lower treeline position for understanding response to environmental change

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ABSTRACT

Aim: Lower and upper treelines delimit the edges of forests in many mountainous regions across the globe. Forest responses to global environmental change depend on the factors controlling forest edges, which remain poorly understood for lower treeline. We examined the drivers of lower treeline position throughout an arid, mountainous region.

Location: Intermountain West, United States.

Methods: We used existing vegetation classifications to map lower treelines. We characterized the distribution of forest types at lower treeline and explored latitudinal trends. For each of three dominant forest types, we modeled topoclimatic drivers of lower treeline position, and we quantified the association of lower treeline with land use and disturbance.

Results: Three forest types comprised more than 65% of lower treeline length: Colorado Plateau pinyon-juniper woodland, Great Basin pinyon-juniper woodland, and Northern Rockies dry mixed conifer forest. The position of lower treeline was limited by a threshold of aridity in pinyon-juniper woodlands of the Colorado Plateau and the Great Basin, and lower treeline extended to drier locations where near-surface soil available water storage was low. In contrast, Northern Rockies dry mixed conifer forests rarely reached their modeled topoclimatic limit, suggesting that non-climatic processes, including disturbance and land use, constrain lower treeline above its ecophysiological limits in this forest type.

Main conclusions: Much of the lower treeline of the Intermountain West is currently limited by water balance, and will likely shift in response to anticipated increases in water deficits. However, for the less arid forests in the northern portion of the Intermountain West, any response to climate change is likely to be mediated by localized drivers, including soil properties, biotic interactions, and natural or anthropogenic disturbances. We present a functional categorization of global lower treelines as a starting point for understanding responses to environmental change.

INTRODUCTION

Lower and upper treelines jointly determine the distribution of forests in many mountainous regions. As climate changes, both treelines are expected to respond by shifting their position (Grace *et al.*, 2002; Clark *et al.*, 2016), directly impacting the distribution of tree cover. Based on mountain geometry, lower treelines typically constitute the lengthier range boundary where both treelines occur. Therefore, minor shifts in the position of the lower treeline ecotone have the potential to disproportionately affect global tree cover and, by extension, carbon stocks and other forest ecosystem services (Anderegg *et al.*, 2012; Ahlström *et al.*, 2015). Forest responses to global change processes depend on the factors controlling range limits (Copenhaver-Parry *et al.*, 2017). In order to anticipate future shifts in the distribution of global forests and woodlands, we must first understand current limitations to lower treelines and how they vary geographically.

Despite its importance to global tree cover, lower treeline has received little scientific attention. In contrast, a comprehensive framework exists for upper treeline, based on a rich conceptual development that has spanned more than a century (reviewed in Harsch *et al.,* 2009). Ultimate limits to upper treeline position correspond to temperature controls on ecophysiological processes (Körner, 1998), though physical barriers, land use, and disturbance can exert secondary constraints, preventing treelines from reaching their climate potential and making them less sensitive to climate changes (Motta & Nola, 2001; Weisberg *et al.*, 2013). We expect that the position of lower treelines is similarly controlled by a combination of ultimate ecophysiological limits and proximate secondary constraints, yet the relative importance of climate, biotic interactions, land use, and disturbance for determining the position of lower treeline is largely undescribed.

Where forests are not bounded by a lower treeline – such as in wet or temperate regions where forest cover extends into the lowest available elevations – the lower range limit of tree species has been found to correlate more strongly with biotic interactions than with climate (Ettinger *et al.*, 2011), consistent with theoretical expectations of biotic range limitations in areas with low abiotic stress (reviewed in Louthan *et al.*, 2015). However, many arid and semi-arid mountainous regions are characterized by lower elevation forest edges, below which the tree growth form is absent. In these regions, aridity is inversely related to elevation, resulting in relatively low water availability – and high levels of abiotic stress – at lower elevations (McDowell *et al.*, 2010; Herrero *et al.*, 2013). At low elevations, unfavorable water balance (precipitation minus evapotranspiration) may impose direct limits to tree demographic processes, creating lower treeline edges defined by the ecophysiological limits of the most drought-tolerant species present (Daubenmire, 1943; Rowlands, 1993).

Soil characteristics may also play a key role in the determination of lower treeline position in arid and semi-arid regions, especially as they relate to water availability. Deep rooting habits allow trees to access water stored deep in the soil profile and in fissures and pores within bedrock (Schwinning, 2010). Rocky soils can facilitate tree expansion into adjacent plant communities (Whitesides & Bekker, 2011), because trees can access deep soil water pools that more shallowly-rooted plants cannot access (Leffler & Ryel, 2012). Deep-rooted, woody plants also dominate in regions where the majority of annual precipitation falls during the winter, because winter precipitation stored in deep soil pools provides water during the dry growing season to those plants that can access it (Lauenroth *et al.*, 2014). More generally, the inverse texture hypothesis (Noy-Meir, 1973) predicts higher plant water stress in fine-textured soils due to higher rates of surface evaporation and runoff, especially in arid systems (Sala *et al.*, 1988). Unsuitably wet or saline soil conditions may directly constrain the distribution of trees by preventing tree establishment on or near features such as wetlands or lake playas (Kozlowski, 1997).

In addition to the limits imposed by abiotic and biotic gradients, natural and anthropogenic disturbances that remove low-elevation trees or hinder tree establishment can directly affect where lower treeline occurs. For example, extensive wood harvest to support settlement-era mining and construction resulted in widespread deforestation in many areas of the western US, particularly in easy-to-access areas near transportation corridors that often coincided with the lower treeline boundary (Young & Budy, 1979; Ko *et al.*, 2011). Periodic wildfire at the grassland-forest ecotone can also push the lower forest edge into higher elevations by reducing opportunities for seedling escape (Bond, 2008), and fire exclusion, often associated with over-grazing of grasslands, can promote downhill tree expansion (Arno & Gruell, 1983; Miller & Wigand, 1994; Mast *et al.*, 1998).

Although lower treelines occur in many regions globally, broad-scale factors determining the position of lower treeline are poorly understood. In this study, we examine the distributional correlates of lower treeline throughout the Intermountain West of the United States. The region contains a large extent of lower treelines, due to arid conditions created by a long north-to-south rain shadow, and a complex, mountainous topography. Our study area spans more than fifteen degrees of latitude and encompasses long gradients of precipitation magnitude and seasonality, temperature, and geology, allowing for the consideration of treeline responses to multiple abiotic gradients simultaneously. We used existing vegetation cover classifications derived from remotely sensed imagery to produce a map of lower treelines for the Intermountain West. First, we characterized lower treelines across the range of our study area, quantifying their distribution by forest type and exploring latitudinal trends in treeline elevation and topoclimate. We expected to find that lower treeline extends to lower elevations at more northerly latitudes where potential evapotranspiration rates are relatively low, and that lower treelines across the study area are characterized by a cline of aridity that is relatively consistent across latitudes. Second, we examined the drivers of lower treeline position for each of three dominant forest types to account for differences in ecophysiological tolerances, regional climate, and disturbance regimes. We modeled abiotic drivers of forest cover across gradients of climate, soils, and topography, and examined the extent to which land use and disturbance are associated with lower treeline position. We hypothesized that a threshold of aridity ultimately limits the presence of trees at the lowest treeline edges, and we evaluated multiple indicators of water balance to determine which were most strongly associated with lower treeline position.

METHODS

Study Area and Treeline Delineation

This study took place in the Intermountain West of the United States, defined here as the area between the Pacific Crest and the Continental Divide. The study area includes portions of 11 US states and covers nearly 1.7 million km^2. We mapped lower treelines across the entire study area using National Land Cover data from the Gap Analysis Program (US Geological Survey, 2011), which provides a 30m-resolution classification of major vegetation types from Landsat imagery. Land cover data were reclassified into a binary forest/non-forest raster, such that “forest” represented all ‘Warm or Cool Temperate Forest’ types (NVC_FORM classification level) and “non-forest” represented all other vegetation types (including urban and riparian areas dominated by trees). Discrete patches of forest or non-forest smaller than 0.9km^2 were merged with their surrounding cover type. The edge between forest and non-forest polygons was then used to represent upper and lower treelines. To differentiate lower treelines from upper treelines, mean elevations of forest and non-forest were calculated within a 4km^2 neighborhood surrounding each treeline vertex, and the mean non-forest elevation was subtracted from the mean forest elevation to produce an elevation contrast for each line segment. Segments with a positive elevation contrast (where forests were at a higher elevation than adjacent non-forested areas) were classified as lower treelines. Treelines occurring within 100m of water bodies or with a mean elevation greater than 2500m a.s.l. were removed. Finally, we visually inspected the resulting map with high-resolution aerial imagery, excluding segments that were not representative of lower treeline (e.g. sections around interior disturbances, lake basins, or meadows, which accounted for <1% of the treelines resulting from the automated process).

Environmental and Disturbance Variables

We used publicly-available data sources to generate spatial variables of interest (Table 1). USGS Digital Elevation Models (US Geological Survey, 2009) were used to map elevation and to generate a topographic heat-load index (‘Heatload’), which represents topographic effects on solar radiation and potential evapotranspiration (McCune & Keon, 2002). We used 30-year-normal gridded PRISM climate data (PRISM Climate Group, 2016) to calculate climatic variables that have previously been shown to be strong predictors of tree performance (Williams *et al.*, 2013; Redmond *et al.*, 2017): winter precipitation (‘WinPPT’), summer vapor pressure deficit (‘SumVPD’), and the proportion of annual precipitation falling during summer (‘Monsoon’). Soil available water storage (‘AWS’), which represents the amount of water that the soil can store in the top 1m, was obtained from the USDA soil survey gridded SSURGO database (Natural Resources Conservation Service, 2013). A Thornthwaite water balance model (Lutz *et al.*, 2010), which incorporates 65-year normals of monthly temperature and precipitation, elevation, and soil water holding capacity, was used to calculate annual climatic water deficit (‘CumlCWD’) and annual actual evapotranspiration (‘CumlAET’). Climatic water deficit represents the amount by which potential evapotranspiration exceeds actual evapotranspiration, and is strongly correlated with vegetation distributions (Dilts *et al.*, 2015). Actual evapotranspiration represents the simultaneous availability of energy and water and is considered a proxy for site net primary productivity (Stephenson, 1990). Fire boundaries from the MTBS database (Monitoring Trends in Burn Severity, 2014) were used to make a binary classification of recently (since 1984) burned or unburned areas (‘Burn’).

Data Analysis

Distribution of lower treeline

We first examined the distribution of lower treeline across forest types and latitude across the study area. To do this, we located one sampling point at every 1km interval along the mapped lower treeline (391,131 sampling points), which we joined with relevant spatial layers (Table 1). We quantified the distribution of lower treelines across forest types (ECOLSYS_LU classification categories) and identified major forest community types to focus on for analyses of lower treeline drivers. We then used simple generalized linear regressions (testing both linear and quadratic terms) to examine patterns of lower treeline along latitudinal gradients. We first examined the relationship between lower treeline elevation and latitude across the study area. We calculated the elevation of lower treeline above nearby valleys, which were mapped using a moving window of minimum elevation within a 22.5km radius, to compare latitudinal trends in absolute versus relative elevation. We then examined latitudinal trends of lower treeline climate (Variables 4-9 in Table 1), using transformations for climatic variables with non-normal distributions.

Drivers of lower treeline position

For each major forest type, we evaluated the effects of topoclimatic predictors on the position of lower treeline. To do this, we randomly generated 7000 points within a 1 km buffer distance of the lower treeline boundary, with a minimum spacing of 1 km, and classified as either forested (above lower treeline) or non-forested (below lower treeline). We used generalized boosted regression trees to model the probability that a point is forested or non-forested (Bernoulli distribution) as a function of topoclimatic variables. Boosted regression trees are a computer-learning approach in which classification and regression trees are iteratively fit to the data and cross-validated on withheld samples (De'ath, 2007; Elith *et al.*, 2008), allowing for the modeling of interactions, thresholds, and other non-linear relationships. We used the gbm.step function in the R package 'dismo' (Hijmans *et al.*, 2017), which uses 10-fold cross-validation to optimize the number of trees in the final model to minimize variance. Learning rate was adjusted so that the final model included at least 1000 trees. Models were fit using a random subset of 80% of the data points, and final models were evaluated against the remaining 20%. Topoclimatic predictor variables (Variables 3-9 in Table 1) were chosen to represent components of plant water balance, based on *a priori* hypotheses of the factors limiting tree growth, survival, and establishment below lower treeline (Piedallu *et al.*, 2013; Williams *et al.*, 2013). For all models, pairwise correlations among predictor variables were less than 0.7. Models were optimized separately for each major forest type. We used simple linear regressions of lower treeline CumlCWD as a function of elevation to describe the elevational gradient of aridity for each major forest type. Finally, we quantified the proportion of lower treelines adjacent to known disturbances, anthropogenic pressures, and other non-forest land cover types (Table A1).

RESULTS

Distribution of Lower Treeline

Our mapping process resulted in 422,429 km of lower treeline across the study area. 57 forest types were present at lower treeline, but most types were uncommon, and only 16 forest types occurred at 1% or more of the total lower treeline length (Appendix A: Fig. A1). We combined forest types that shared tree species and co-occurred in a fine-scale mosaic (Appendix A: Table A1). Three forest community types collectively represented 65.2% of lower treeline (Fig. 1). Colorado Plateau Pinyon-Juniper Woodlands (30.7%) are dominated by *Pinus edulis* and/or *Juniperus osteosperma* and occur on dry mountains and foothills of the Colorado Plateau region. Great Basin Pinyon-Juniper Woodlands (21.5%) are dominated by *Pinus monophylla* and/or *Juniperus osteosperma* and are found on dry mountain ranges of the Great Basin and the eastern foothills of the Sierra Nevada. Northern Rocky Mountain Dry Mixed Conifer Forests (13.0%) are dominated by *Pinus ponderosa* with the occasional presence of *Pseudotsuga menziesii* and are found in foothills of the northern Rocky Mountains, the Columbia and Modoc Plateaus, and the eastern Cascades. We focused on these three forest community types for analyses of lower treeline drivers.

We found several important latitudinal trends in lower treeline distribution. Treeline elevation had a strong quadratic relationship with latitude (adjusted R^2=0.52), such that mean lower treeline elevation was highest at mid-latitudes (Fig. 2a). However, lower treeline elevation above adjacent valley bottoms did not vary by latitude (adjusted R^2=0.02), averaging 350-500m across the study area (Fig. 2b). Lower treeline CumlCWD was strongly negatively correlated with latitude (adjusted R^2=0.53), such that lower treelines were driest at southerly latitudes (Fig. 2c). Lower treeline CumlAET had a negative quadratic relationship with latitude (adjusted R^2=0.31). Latitude was only weakly correlated with lower treeline AWS (adjusted R^2=0.07), WinPPT (adjusted R^2=0.005), SumVPD (adjusted R^2=0.006), and Monsoon (adjusted R^2=0. 05).

Drivers of Lower Treeline Position

For both Colorado Plateau and Great Basin pinyon-juniper woodland types, topoclimate was strongly related to the position of lower treeline. Soil AWS interacted with CumlCWD to predict lower treeline position (Fig. 3a-b), such that the probability of forest cover was highest in areas with shallow or coarse-textured soils (low AWS) and low aridity (low CumlCWD). Partial dependence functions (Fig. 3a-b; Appendix A: Appendix A1) suggest a threshold effect of CumlCWD at 500-600mm for Colorado Plateau pinyon-juniper, and at 400-500mm for Great Basin pinyon-juniper. Much of the lower treeline (24-32%) of both pinyon-juniper woodland types was at or slightly above this threshold of CumlCWD (Fig. 4a-b). CumlCWD was strongly correlated with elevation for both pinyon-juniper woodland types (Fig. 4a, $\beta = -0.40$; Fig. 4b, $\beta = -0.28$), and lower treelines were restricted to relatively high elevations at which aridity was low.

More than 85% of lower treeline in both pinyon-juniper woodland types was adjacent to native shrubland or grassland vegetation, or areas of rock, cliff, or scree (Fig. 5). Fire was more common at lower treeline for Great Basin pinyon-juniper (12%) than for Colorado Plateau pinyon-juniper (3%). Both pinyon-juniper lower treelines rarely bordered known anthropogenic impacts (agriculture or urban/developed areas) or seasonal or perennial wetlands (Fig. 5).

For Northern Rocky Mountain dry mixed conifer forests, topoclimate was weakly related to lower treeline position. CumlCWD showed a threshold effect on forest cover at 300-350 mm, and there was a non-threshold effect of Heatload, such that the probability of forest cover declined with increasing Heatload or CumlCWD (Fig. 3c). Only 5% of the lower treeline was at or above the modeled threshold of CumlCWD (Fig. 4c). For the lower treelines of N. Rocky Mountain dry mixed conifer forests, CumlCWD was not strongly correlated with elevation (Fig. 4c, $\beta = -0.08$), resulting in a shallow elevational gradient of aridity in which the modeled threshold of CumlCWD was rarely exceeded at the lower treeline, even at very low elevations. For this forest type, 53% of lower treeline was adjacent to native shrubland or grassland vegetation, 16% bordered seasonal or perennial wetlands, 14% intersected recent fires, and 17% bordered anthropogenic land uses (Fig. 5).

DISCUSSION

Identifying the factors limiting plant species distributions is a central theme of biogeography and is increasingly important in the current era of rapid global change. With an improved understanding of the drivers of lower treeline formation, more robust projections of future treeline dynamics – and global distributions of the forest biome – can be developed. Currently, many large-scale changes are occurring simultaneously and interacting with each other (Barnosky *et al.*, 2012), including warming climate, land use change, exotic species invasions, and shifts in disturbance regimes. Despite the importance of such interactions among global change agents, many forecasts of future changes rely only on modeled climatic envelopes to predict future range boundaries. Indeed, treelines that are currently limited by water balance are likely to exhibit rapid responses to drought and increased evaporative demand resulting from higher temperatures (Romme & Turner, 1991; Allen & Breshears, 1998). However, lower treelines constrained above their climate potential by other factors will be less responsive to climate change than those at or near their ecophysiological limits (Holtmeier & Broll, 2005).

Our results indicate that much of the lower treeline of the Intermountain West is currently climate-limited, and will thus be sensitive to climate changes. Specifically, we found strong evidence that broad-scale gradients of water balance largely control the position of lower treeline in pinyon-juniper woodlands of the Colorado Plateau and the Great Basin (which together represent more than 50% of lower treelines of the Intermountain West; Fig. 1). Water availability is positively correlated with elevation in arid mountainous regions, and high levels of abiotic stress at low elevations can restrict tree growth and survival (Lajtha & Getz, 1993; Adams & Kolb, 2004). We found that cumulative climatic water deficit, a proxy of overall aridity, was a strong boundary control for all major forest types within the Intermountain West, resulting in forest-specific thresholds of soil water balance beyond which the probability of forest cover was extremely low (Fig. 3). Lower treeline elevation was strongly related to aridity for both pinyon-juniper woodland types, and much of the lower treeline was located at or above the modeled threshold of aridity (Fig. 4a-b), suggesting that future climate changes that reduce water availability will result in widespread treeline shifts to higher elevations or more mesic topographic settings.

Rather than a single threshold value of climatic water deficit beyond which trees are excluded, our results suggest that topoclimatic limits to lower treeline are characterized by a broad ecotone that is marginally suitable for trees. Within these marginal locations, soil properties that ameliorate water stress may increase the probability of tree establishment and survival. Even though deeper, finer textured soils hold more soil moisture than shallow, coarse soils, we found that the probability of forest was highest, and treelines extended to drier, lower elevation locations, where near-surface soil available water storage was low (Fig. 3a-b). Coarse soils allow for rapid infiltration of water, limiting losses to surface evaporation and runoff (Noy-Meir, 1973; Sala *et al.*, 1988) and increasing water storage in deep soil pools and rock fissures to which trees and other deep-rooted plants have access (Schwinning, 2010).

Based on studies of upper treeline, we expected to find widespread evidence that physical barriers, land use, and disturbance constrain the distribution of trees, preventing lower treelines from reaching their climate potential (Motta & Nola, 2001; Weisberg *et al.*, 2013). We found that little of the pinyon-juniper lower treeline bordered or intersected recent natural or anthropogenic disturbance (Fig. 5), suggesting that these factors may not exert strong constraints on lower treeline position. However, our conclusions may be limited by the short record of fire occurrences and poor available records of historic land uses. Because pinyon-juniper woodlands have slow rates of post-disturbance recovery (Bristow *et al.*, 2014), the current position of lower treeline may be impacted by the legacy of past disturbances (Lanner & Frazier, 2011).

For dry mixed conifer forests in the northern portion of the Intermountain West, our results suggest that non-climatic processes, including disturbance and land use, functionally constrain lower treeline above its ecophysiological limits. At upper treeline, temperature controls on ecophysiological processes ultimately limit the presence of trees (Körner, 1998), but physical barriers, land use, and disturbance can exert secondary constraints (Weisberg *et al.*, 2013) that prevent treelines from reaching their climate potential. In some regions of the world, upper treelines are found in mountain ranges where trees are not expected to be limited based on climate alone (Vitali *et al.*, 2017). Our analysis detected a threshold of aridity for northern dry mixed conifer forests (Fig. 3c), yet the lower treeline rarely reached this threshold. The fact that overall aridity was low even at very low elevations (Fig. 2; Fig. 4c) suggests that landscapes in this region may not be dry enough to create extensive topoclimatic lower treelines. Instead, these forests were frequently located adjacent to perennial and seasonal wetlands, recently burned areas, and human land uses, indicating that permanent landscape features and disturbance prevent trees from extending into the lowest available elevations.

To anticipate lower treeline shifts in response to environmental change, we must understand what factors limit its position and how these drivers vary across space and time. Here, we propose a functional categorization of global lower treelines based on the processes that form them (Fig. 6). This typology is neither exhaustive nor definitive, but is meant to serve as a starting framework to inspire future work on lower treeline dynamics. The five lower treeline types, described below, include climatic treelines, topoedaphic treelines, biotic treelines, disturbance-limited treelines, and anthropogenic treelines.

Topoclimatic treelines. These are locations where forest edges reach their ecophysiological limits, beyond which their expansion is limited by unfavorable water balance. Topoclimatic treelines are expected to be more frequent in arid and semi-arid mountainous regions with relatively low levels of human influence. Climate interacts strongly with local soil conditions, other vegetation, and topography to determine site water balance (Herrero *et al.*, 2013). Local variations in parent material and soils create refugia beyond broad-scale limits, such as low-elevation microsites with favorable water balance (e.g. tree stringers along arroyos). By definition, climatic treelines should have high climate sensitivity. They will shift uphill where increased temperatures and associated increases in atmospheric water demand result in widespread tree mortality in combination with regeneration failure (Williams *et al.*, 2010). Indeed, arid regions of the world, where tree species occur in water-stressed conditions, have already seen evidence of lower treeline contraction in response to increasing drought (Allen & Breshears, 1998; Allen *et al.*, 2010). Forecasts of water balance likely to affect lower treeline are challenging and extremely uncertain, but recent studies indicate a future with more severe and frequent droughts (Seager *et al.*, 2007; Dai, 2013) occurring at higher temperatures (Cayan *et al.*, 2010). Water balance may be limiting to one or more demographic stage – regeneration, survival, reproduction, or dispersal – and in-depth studies that identify which stage is limited in specific contexts would help refine projections of climate change responses. Where regeneration or reproduction is most limited, the longevity of trees can create inertia in treeline responses to climate change, and stand-replacing disturbance can catalyze rapid shifts of forest edges (Donato *et al.*, 2016).

Edaphic treelines. In some locations, forest distribution is limited by soil conditions or permanent landscape features in which trees cannot establish. Edaphic treelines occur where soil conditions are unsuitable for trees, such as in saline soils or perennially wet meadows (Kozlowski, 1997). These direct edaphic effects are expected to occur at local spatial scales, yet may constitute broad-scale controls where unsuitable soil features are widespread. True edaphic treelines are expected to be relatively insensitive to climate change, except where the underlying processes are climate-driven (e.g. the drying of wet meadows). In other cases, edaphic effects may be difficult to distinguish from other factors, including biotic interactions. For example, rocky, shallow soils may benefit trees because their deep rooting habits allow access to water stored deep in the soil profile, facilitating tree expansion into adjacent plant communities (Whitesides & Bekker, 2011). Mechanistic studies are needed to disentangle interactions between soil conditions, biotic interactions, and climate.

Disturbance-limited treelines. These treelines occur where forest expansion is inhibited by disturbance. Fire is a common driver of the position of forest-grassland ecotones (Mast *et al.*, 1998; Danz *et al.*, 2011), particularly where high-frequency fire in grass-dominated ecosystems reduces opportunities for seedling escape (Bond, 2008). In woodland types with slow post-fire recovery of tree canopy cover, even infrequent fires can leave long-lasting legacies (Bristow *et al.*, 2014) that can functionally constrain the position of lower treeline. Invasions by highly flammable herbaceous species into historically shrub-dominated systems may amplify the influence of fire on lower treeline (Balch *et al.*, 2013; Board *et al.*, 2018). Although disturbance-limited treelines may not respond directly to changing climatic conditions, associated shifts in disturbance regimes (van Mantgem *et al.*, 2013) would likely have severe and widespread impacts on regional distributions of tree cover.

Anthropogenic treelines. Human land uses can constrain lower treelines where they inhibit tree establishment or remove mature trees. Where forests are adjacent to grass-dominated systems, livestock grazing can select for herbaceous vegetation and impede tree establishment (Sharma *et al.*, 2014). After fire, livestock grazing that removes perennial grasses can promote shrub cover (Chambers *et al.*, 2017), which can in turn facilitate tree establishment through nurse shrub effects (Chambers, 2001; Chapter 4). In other cases, tree harvest at low elevations can directly shift lower treelines to higher elevations (Ko *et al.*, 2011). Anthropogenic treelines would be expected to respond to changing land use patterns rather than to climate changes, and cessation of the constraining disturbance (e.g. agricultural abandonment) can cause downhill expansion of ecotones against uphill trends in favorable climate conditions (Foster & D’Amato, 2015). For example, trees have established beyond historical forest-grassland boundaries in Nepal, where traditional pastoral uses are declining (Sharma *et al.*, 2014). In the western US, where multiple land use practices and management strategies have interacted over the last century, woodland dynamics have been complex, involving simultaneous patterns of expansion and contraction (Romme *et al.*, 2009).

Biotic treelines. In some cases, forest edges may be controlled by widespread interactions with other species, including competition, facilitation, parasitism, herbivory, and mutualism. Competition with herbaceous species and vertebrate herbivory can limit forest expansion into grassland systems where abiotic constraints are absent (Germaine & McPherson, 1999). Where abiotic stress limits tree regeneration, shrubs can facilitate tree establishment by modulating temperatures and increasing resource availability (Chambers, 2001; Sthultz *et al.*, 2007). Interactions with other trees have been found to influence lower-elevation limits of tree species when they do not correspond to a lower treeline (Ettinger & HilleRisLambers, 2017). In other contexts, tree range expansion can be facilitated by escape from negative plant-soil feedbacks (McCarthy-Neumann & Ibáñez, 2012). Where biotic interactions have important influences on range limits of focal species, climate changes will cause complex and unpredictable shifts in species distributions (Wisz *et al.*, 2013; Louthan *et al.*, 2015).

Conclusions

Lower treelines delineate the edge of the forest biome in many mountainous regions across the globe. As lower treeline tends to be much lengthier than upper treeline in regions where both occur, shifts in the lower treeline ecotone result in disproportionately large changes to the distribution of tree cover and associated ecosystem services. Our results suggest that for the Intermountain West of the United States, much of the lower treeline is currently climate-limited, and will thus be sensitive to climate changes. Lower treelines in other arid or semi-arid mountainous regions around the globe may also be strongly linked to climate, though treeline response to climate change will be mediated at the local scale by soil properties, biotic interactions, and natural or anthropogenic disturbances. We recommend a much more intense focus on lower treelines than heretofore, paralleling the development of the extensive body of research concerning upper treeline dynamics.

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TABLES

Table 1. Variable descriptions and sources.

	Variable Name	Definition	Units	Resolution	Date
1	Forest type	Classification of forest cover adjacent to (above) treeline[1]	categorical	30 m	2011
2	Elevation	Elevation above sea level[2]	m	30m	n/a
3	Heatload	Topographic heat-load index[3]	unitless index	500 m	n/a
4	WinPPT	Winter precipitation (November-March)[4]	mm	800 m	1981-2010 (30-yr normal)
5	SumVPD	Summer vapor pressure deficit (May-July)[4]	hPa	800 m	1981-2010 (30-yr normal)
6	Monsoon	Proportion of annual precipitation falling in summer (May-July)[4]	proportion	800 m	1981-2010 (30-yr normal)
7	AWS	Soil available water storage for top 1m of soil[5]	mm	100 m	2013
8	CumlCWD	Cumulative annual climatic water deficit[6]	mm	500 m	1950-2015 (65-yr normal)
9	CumlAET	Cumulative annual actual evapotranspiration[6]	mm	500 m	1950-2015 (65-yr normal)
10	Adjacent land cover	Classification of non-forest cover adjacent to (below) treeline[1]	categorical	30 m	2011
11	Burn	Recent burn status[7]	binary	Vector	1984-2014

[1] Author-generated based on (US Geological Survey, 2011). See Table S1 for merged categories.
[2] (US Geological Survey, 2009)
[3] Author-generated based on (US Geological Survey, 2009)
[4] Author-generated based on (PRISM Climate Group, 2016)
[5] (Natural Resources Conservation Service, 2013)
[6] Author-generated based on (US Geological Survey, 2009; Natural Resources Conservation Service, 2013; PRISM Climate Group, 2016)
[7] (Monitoring Trends in Burn Severity, 2014)

FIGURES

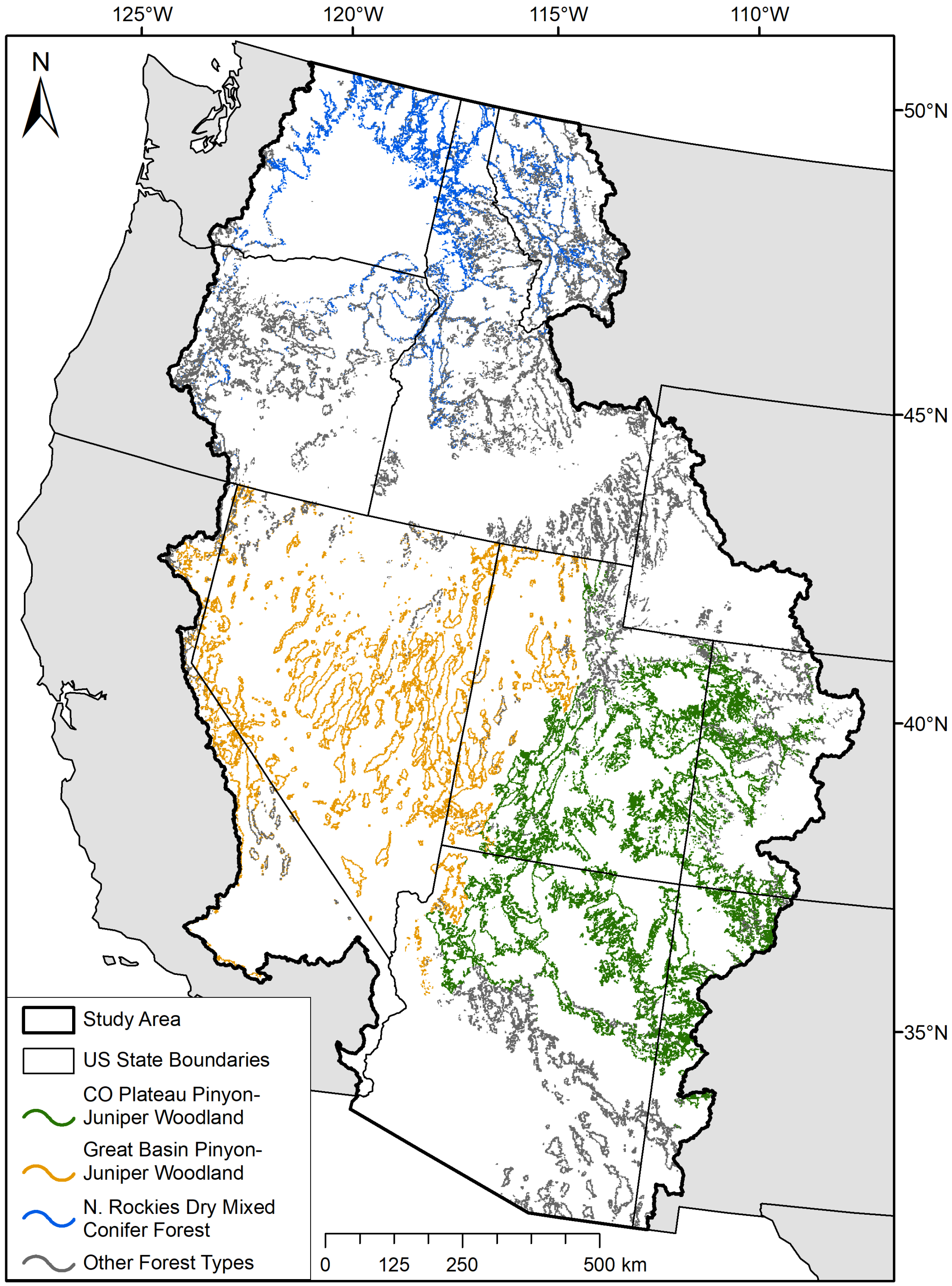

Figure 1. Mapped lower treelines of the Intermountain West, colored by major forest type. Projection: Albers Equal-Area Conic, NAD 1983.

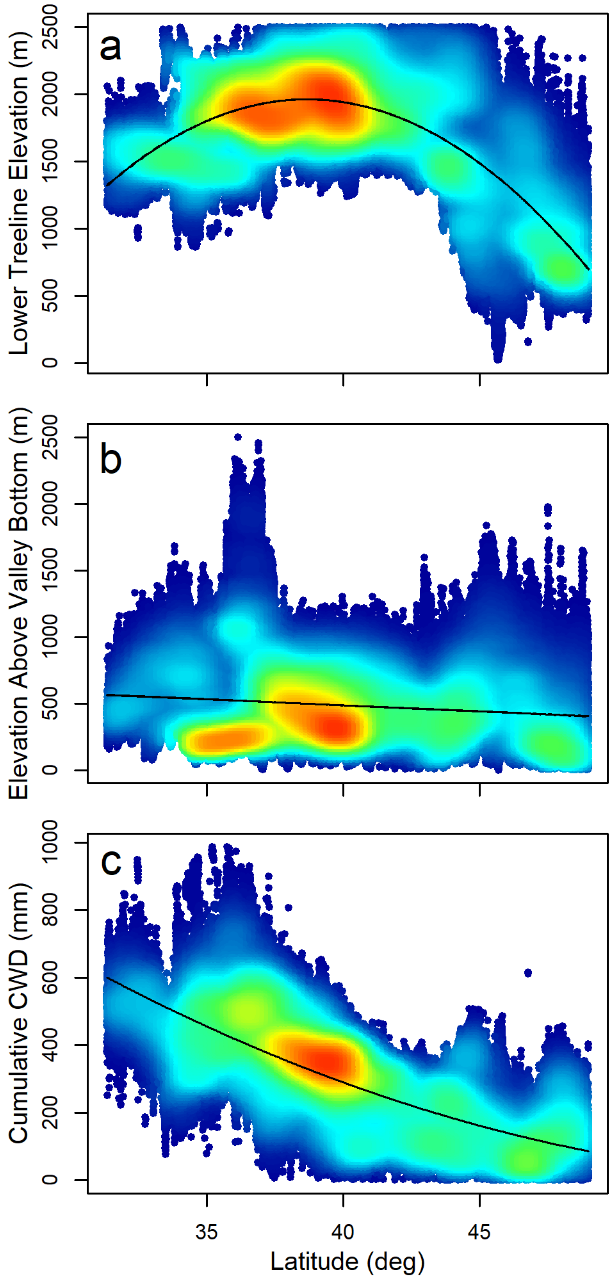

Figure 2. Density scatterplots of lower treeline (a) elevation, (b) elevation above nearby valley bottom, and (c) cumulative annual climatic water deficit (CumlCWD), shown as a function of latitude for the Intermountain West. Warmer colors indicate a higher density of points. Black lines show mean predictions and 95% confidence intervals from simple linear regressions.

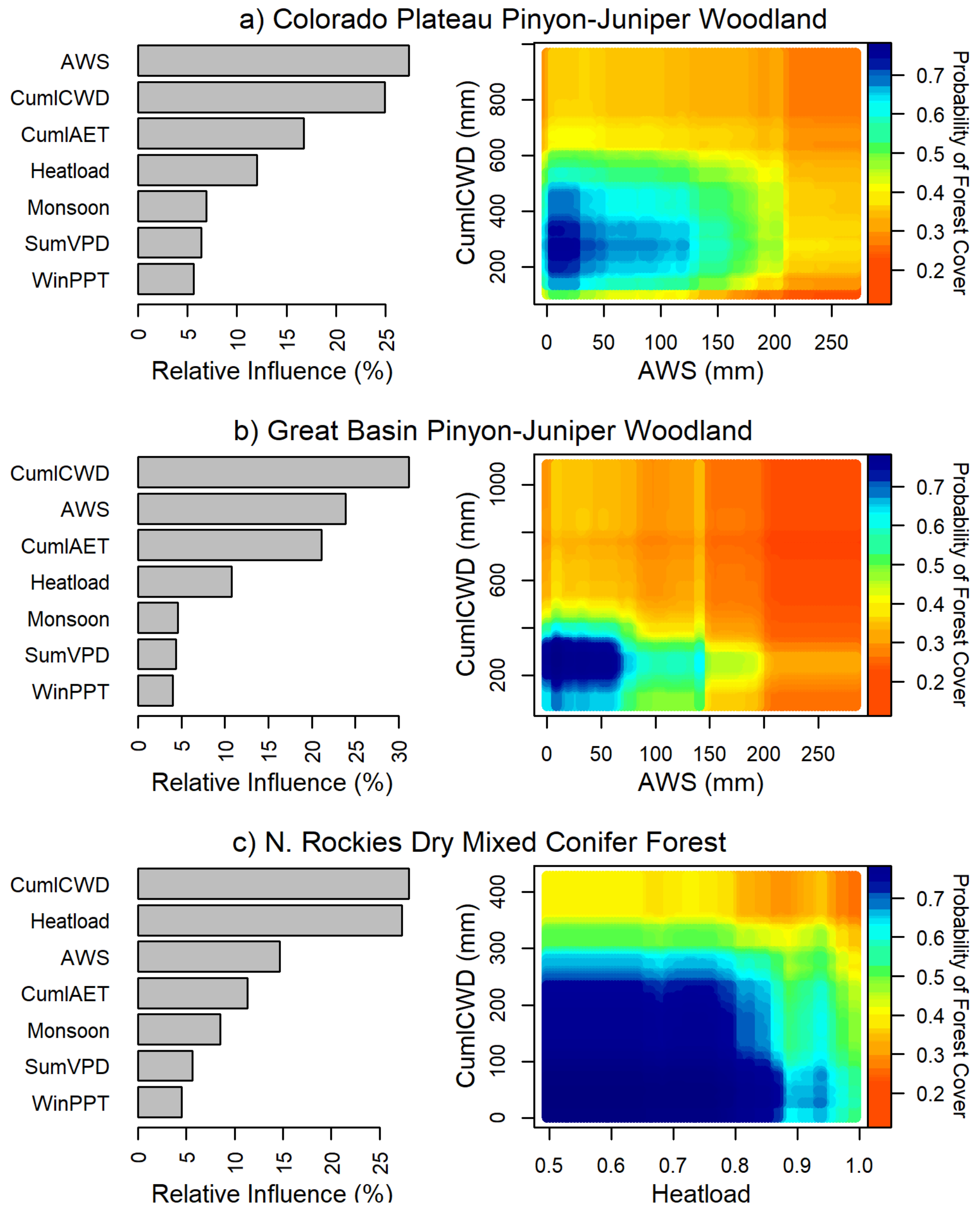

Figure 3. Topoclimatic predictors of forest cover within 1 km of lower treeline for major forest types of the Intermountain West. *Left:* Rank of variable importance. *Right:* Probability of forest cover, expressed as a partial dependence function of the two most important predictors. AWS = soil available water storage; CumlCWD = cumulative climatic water deficit; CumlAET = cumulative actual evapotranspiration; Heatload = heat-load index; Monsoon = summer precipitation / annual precipitation; SumVPD = summer vapor pressure deficit; WinPPT = winter precipitation.

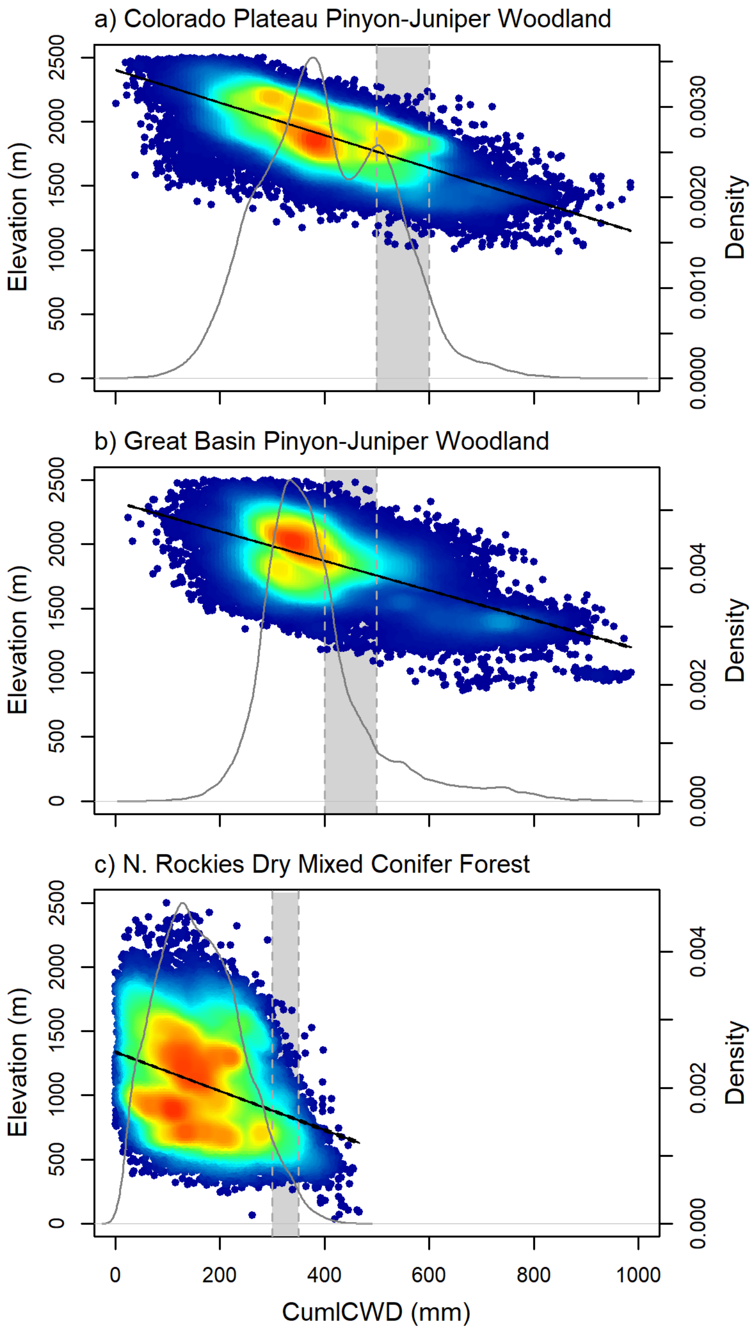

Figure 4. Density scatterplots of lower treeline elevation as a function of cumulative annual climatic water deficit (CumlCWD) for major forest types of the Intermountain West. Warmer colors indicate a higher density of points. Black lines show mean predictions and 95% confidence intervals from simple linear regressions. Vertical gray shading represents the modeled classification threshold of CumlCWD on forest cover, and the gray curve shows the probability density function from kernel density estimation.

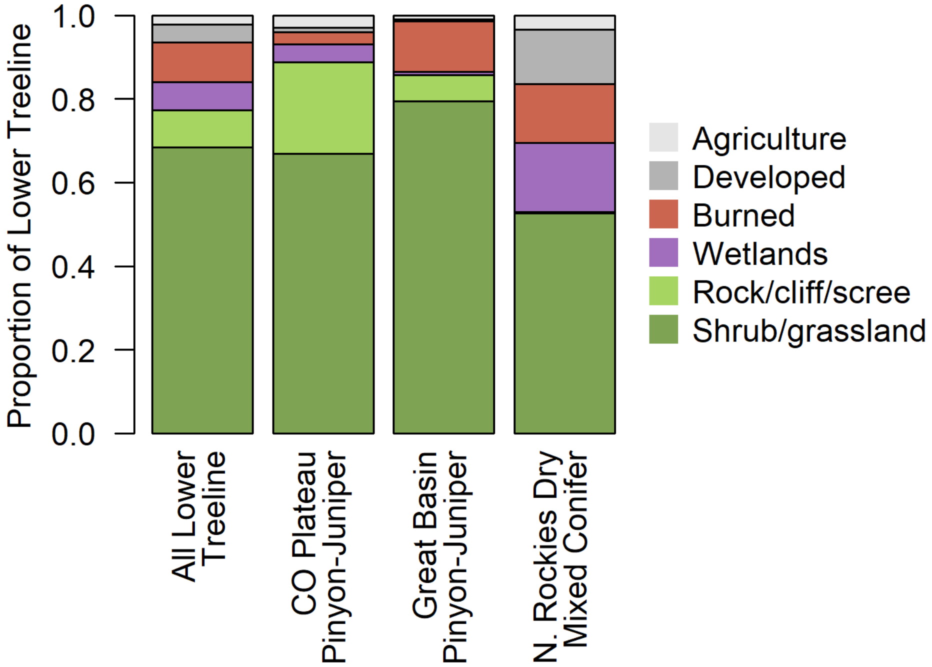

Figure 5. Proportion of lower treeline bordering adjacent land cover types for major forest types of the Intermountain West.

Topoclimatic treelines	
 Lower treeline, Nye County, NV.	Where lower forest edges are limited by unfavorable **water balance**. Primarily occur in **arid and semi-arid mountainous regions** with relatively **low levels of human influence**. Characterized by **high sensitivity to climate change**, and would be expected to shift uphill in response to increased temperatures and associated increases in atmospheric water demand.
Edaphic treelines	
 Wet meadow, Washoe County, NV.	Where **soil conditions are unsuitable for trees**. Direct edaphic effects are expected to occur primarily at **local spatial scales**, yet may constitute broad-scale controls where unsuitable soil features are widespread. True edaphic treelines are expected to be relatively **insensitive to climate change**, except where the underlying processes are climate-driven.
Disturbance-limited treelines	
 Fire edge, White Pine County, NV.	Where **forest expansion is inhibited by disturbance**. Frequent disturbances reduce opportunities for seedling escape, and single disturbance events can leave long-lasting legacies in arid woodland types with slow dynamics. **Shifts in disturbance regimes** associated with **climate change** and/or **exotic plant invasions** are expected to affect tree distributions.
Anthropogenic treelines	
 Tree removal, Eureka County, NV.	Where **human land uses inhibit tree establishment** or **remove mature trees**. Effects can include direct removal of trees or land use practices that promote other vegetation types. Anthropogenic treelines are expected to respond to **changing land use patterns**, which may promote forest dynamics that are **out of sync with climate**.
Biotic treelines	
 Tree under shrub, Nye County, NV.	Where lower forest edges are controlled by **interactions with other species**, including competition, facilitation, parasitism, herbivory, dispersal, and mutualism. Biotic interactions can result in **species ranges that are non-independent**, in which case climate change will cause **complex and unpredictable** patterns of range dynamics.

Figure 6. Hypothesized drivers of lower treeline.

CHAPTER 2. Post-fire vegetation response at the woodland-shrubland interface is mediated by the pre-fire community

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ABSTRACT

Understanding the drivers of ecosystem responses to disturbance is essential for management aimed at maintaining or restoring ecosystem processes and services, especially where invasive species respond strongly to disturbance. In this study, we used repeat vegetation surveys from a network of prescribed fire treatments at the woodland-shrubland interface in the Shoshone Mountains, Nevada, USA to investigate post-fire responses of the understory plant community. First, we characterized post-fire community trajectories for sites located along an elevational gradient, hypothesizing a positive relationship between elevation and resistance to invasion. Unburned understory communities and their responses to disturbance differed along the gradient. As hypothesized, lower elevations experienced greater species turnover and higher invasive annual grass (*Bromus tectorum*) cover after fire. Second, we characterized post-fire plant community trajectories for sites with varying levels of pre-fire pinyon and juniper cover, hypothesizing that pre-fire tree dominance and associated reductions in perennial understory species lead to less predictable post-fire trajectories. Among sites with low to moderate tree cover, burning largely eliminated differences in understory composition, suggesting that biotic legacies were sufficient to result in predictable trajectories. In contrast, sites with high pre-fire tree cover transitioned into an annual forb-dominated community with sparse vegetation cover, suggesting that the loss of the understory community initiated unpredictable and divergent post-fire trajectories. Because plant communities were still changing four years after fire, it is unclear whether the alternate trajectories in sites with high tree cover will result in the formation of alternate states, or whether community composition will eventually converge with other sites at the same elevation. Results indicate that careful evaluation of site characteristics can be used to predict treatment outcomes at the woodland-shrubland interface, and to guide the appropriate use of prescribed fire or other management practices.

INTRODUCTION

Understanding the drivers of ecosystem responses to disturbance is essential for management aimed at maintaining or restoring ecosystem processes and services (Seastedt et al. 2008), particularly when disturbances are used as a management tool (Wisdom and Chambers 2009). The memory of past ecological states often interacts with abiotic filters to shape plant community responses to disturbance (Padisak 1992, Johnstone et al. 2016). Abiotic conditions constrain post-disturbance plant community assembly by imposing filters on resource availability and species pools (Pickett et al.

2009), and topographic gradients of moisture and temperature have been shown to drive post-disturbance vegetation trajectories in deserts (Shryock et al. 2015), savannas (Smit et al. 2010), coastal heathlands (Vandvik et al. 2005), bogs (Benscoter and Vitt 2008), and subalpine and montane forests (Dynesius et al. 2009, Coop et al. 2010). However, differences in pre-disturbance biotic conditions can imprint long-lasting legacies of post-disturbance structure and function (Franklin 2000), initiating alternate and non-convergent trajectories even among communities with identical abiotic environments (Gunderson 2000).

Biotic legacies that persist within a disturbed area, such as surviving organisms, propagules and residual structures, promote the stability of the pre-disturbance plant community (Franklin et al. 2000, Johnstone et al. 2016) and influence initial successional patterns (Turner et al. 1998, Bengtsson et al. 2003). Conversely, a weak ecological memory is generated where few biotic legacies persist through a disturbance, increasing the importance of stochastic dispersal-assembly processes (Myers and Harms 2009) and leading to alternate trajectories of community composition (Gunderson 2000). While biotic legacies comprising ecological memory (or lack thereof) have been credited with driving post-disturbance trajectories in many temperate forest (Seidl et al. 2014, Kemp et al. 2016, Urza and Sibold 2017) and wetland (Matthews and Endress 2010) plant communities, these concepts have been rarely applied to dryland ecosystems.

Plant invasions can influence the loss of biotic legacy and weaken ecological memory. Invasives that alter the composition of the pre-disturbance plant community may limit post-disturbance recovery of native communities (Schaefer 2011) and enhance their own persistence through reinforcing feedback processes. For example, invaders can alter disturbance regimes to favor their own persistence at the expense of native competitors (Brooks et al. 2004, Gaertner et al. 2014), such as through annual grass-fire cycles (D'Antonio and Vitousek 1992).

In sagebrush ecosystems of the Intermountain West, fire is the dominant broad-scale disturbance, although the effects of fire vary greatly across landscapes and among species. Many herbaceous plant species native to sagebrush ecosystems exhibit adaptations to fire, such as root sprouting or seed banking (Everett and Ward 1984, Koniak 1985, Miller et al. 2013). However, the dominant shrub species (*Artemisia* species, or sagebrush) lack re-sprouting capabilities, have poor dispersal ability (Young and Evans 1989), and often recover slowly after fire (Baker 2006, Lesica et al. 2007, Miller et al. 2013). *Bromus tectorum* (cheatgrass), a fire-adapted exotic annual grass species, has invaded vast portions of the Intermountain West, resulting in transformations of entire landscapes to annual grass dominance and altering the ecology of sagebrush ecosystems and their responses to fire (Balch et al. 2013, Germino et al. 2016). While many land use practices facilitate *B. tectorum* invasion, it is mainly fire disturbance that ultimately leads to *B. tectorum* dominance (Pyke et al. 2016). In sagebrush ecosystems, elevational gradients of soil temperature and moisture directly affect the pre- and post-fire environment, influencing plant community trajectories (Davies et al. 2012) and the probability of annual grass invasion (Chambers et al. 2014a, 2014b, 2016). After fire, warm and dry (low elevation) sites have lower resistance to invasion by *B. tectorum* (Chambers et al. 2007, Condon et al. 2011, Taylor et al. 2014), slower recovery of sagebrush (Baker 2006), and lower rates of perennial herbaceous recruitment (Chambers et al. 2014b, 2016). Consequently, low elevation sites are less resilient to fire (Chambers et al. 2014a).

In sagebrush ecosystems, native perennial herbaceous vegetation that persists after fire represents an important biotic legacy that promotes ecosystem resilience to disturbance (Chambers et al. 2014a, 2014b). The progressive loss of fire-adapted, perennial herbaceous vegetation has been pervasive and is widely attributed to two, often interrelated processes: poor livestock management, and expansion or infilling of woodlands. Pinyon-juniper woodland expansion and infilling in the western US results from multiple interacting causes (Romme et al. 2009), including climate change (Miller and Wigand 1994), recovery from settlement-era tree harvesting that was associated with regional-scale production of charcoal for the mining industry (Young and Budy 1979, Ko et al. 2011, Lanner and Frazier 2011), slow reforestation following extensive 19th Century wildfires (e.g. Bauer and Weisberg 2009), poor livestock management (Cottam and Stewart 1940, Miller and Wigand 1994), and fire exclusion (Miller and Rose 1999). Regardless of the underlying causes, increased tree cover often results in the loss of both sagebrush and associated native perennial herbaceous species from the understory (Roundy et al. 2014a), reducing regeneration from residual plants (Chambers et al. 2014b, Roundy et al. 2014a) and altering the composition of the soil seed bank (Allen and Nowak 2008, Bates et al. 2014b).

Cumulatively, these effects can reduce the ecological memory of native understory plant communities after fire. Sites with depleted understories, such as those with high pre-fire tree dominance, are expected to have post-fire trajectories that differ from sites previously dominated by shrubs and grasses. The result is often delayed recovery of native perennial understory vegetation (Condon et al. 2011, Roundy et al. 2014a), but the implications of delayed recovery are unclear. The empty ecological niche produced by the absence of perennial herbaceous vegetation, coupled with a release of soil resources (Rau et al. 2007, 2014, Roundy et al. 2014b), can facilitate post-fire invasion of annual grasses and forbs in climatically suitable areas (Bates et al. 2014a, 2014b, Chambers et al. 2014b, Roundy et al. 2014a). Some have suggested that there is a threshold of pre-fire tree dominance beyond which the pre-fire plant community is unlikely to recover, and will instead enter an alternate state dominated by opportunistic natives or annual plants (Miller et al. 2005, 2013, Bates et al. 2014b, Roundy et al. 2014a).

Here, we used an experimental network of prescribed fire treatments in a Great Basin ecosystem co-dominated by sagebrush and pinyon and juniper to characterize understory community responses to fire for four years post-fire. Management efforts in the region are targeted at reducing tree cover to maintain shrub- and grass-dominated habitats and conserve sagebrush obligate species (Miller et al. 2013). Prescribed fire is one tool to achieve tree reduction objectives. The experimental design included replicate pairs of burned and control plots arranged along gradients of elevation and pre-fire tree cover, while controlling for potentially confounding factors such as topography, soil type, time period, and post-fire management. We used repeated measures of species composition and aerial cover to describe multivariate plant community trajectories and trends for key species and functional groups across abiotic and biotic gradients. We had two primary objectives. First, we characterized post-fire plant community trajectories for sites distributed along an elevational gradient to assess whether community responses to fire varied among ecological site types. We hypothesized that community trajectories would be similar among sites with similar abiotic conditions, and that the low elevation sites would exhibit the greatest turnover in species composition after burning. Second, we characterized post-fire plant community trajectories for mid-elevation sites with varying levels of pre-fire pinyon and juniper cover to assess whether pre-fire tree dominance influenced post-fire community structure. We hypothesized that sites with high pre-fire tree cover would experience greater compositional changes and higher variability among post-fire communities, due to heightened stochasticity where ecological memory was weakened by a reduced presence of perennial understory species before burning.

METHODS

Study Area

The study was located in Underdown Canyon, in the Shoshone Mountains in Nye and Lander Counties, Nevada, USA. The climate of Underdown Canyon is typical of the Great Basin high desert, and is characterized by cold winters and warm summers. Average annual precipitation in Underdown Canyon is 23 cm at the lower elevations and 50 cm at the upper elevations (Board et al. 2011) and typically experiences two peaks: one in January, in the form of snow, and another in May, in the form of rain (PRISM Climate Group 2016). The geology is dominated by welded and non-welded volcanic tuff, and soils are classified as coarse loamy mixed frigid typic haploxerolls (Rau et al. 2005). Tree assemblages in unburned portions of Underdown Canyon are dominated by single-leaf pinyon (*Pinus monophylla*), with lower abundances of Utah juniper (*Juniperus osteosperma*).

Study Design and Sampling

Underdown Canyon is a Joint Fire Sciences Program Demonstration Area and contains a network of experimental prescribed fire treatments. The study utilized a Before/After Control/Impact (BACI) design, with three pairs of adjacent alluvial fans arranged along an elevational gradient (2073m, 2225m, and 2347m) on a north-facing slope within the same watershed. One fan within each pair was burned (impact) by the USDA Forest Service in the spring of 2002, and the other remained unburned (control). Prior to burning, the mid-elevation fans were stratified into polygons representing tree cover categories: low (12% mean cover), moderate (38% mean cover), and high (74% mean cover) (Reiner 2004). Only the mid-elevation alluvial fans contained sufficient variability in tree cover to include all three categories, and the low- and high-elevation fans included only the moderate tree-cover category. Livestock were excluded for the duration of the study. Weather was variable over the study period, with years of drought and years of above-average precipitation.

Three sampling plots approximately 0.1 ha in size were located in each combination of control/burned, elevation group and tree-cover category, for a total of 30 plots (Appendix B: Fig. B1). Data on understory species composition and cover were collected before burning in 2001 and after burning in 2003, 2004, and 2006 in quadrats systematically located along transect lines that were randomly stratified within plots. The 2001 data collection measured two diameters for all herbaceous species and shrubs within 50, 2m^2 quadrats in each plot, which were then converted to percentage of area sampled to obtain aerial cover (Reiner 2004). In 2003, 2004, and 2006, 25 to 30, 0.25m^2 quadrats were used to measure herbaceous cover in each plot; aerial cover was estimated by species using 13 cover categories (Daubenmire 1959), and the mid-point of each cover category was chosen to represent percent cover in each quadrat (Appendix B: Table B1). In 2003, 2004, and 2006, shrub diameters (longest and perpendicular) and height were measured for all individuals in 15 to 30, $2m^2$ quadrats in each plot, and aerial cover was derived by converting to percentage of area sampled. No shrub data were collected on control plots in 2006.

Data Analyses

Community Types

We identified distinct understory plant community types through a cluster analysis of species cover data for all plots across all years. We used the Bray-Curtis distance measure with Ward's hierarchical agglomerative method with the *vegdist* function in the 'vegan' package (version 1.7.5) and the *hclust* function in the R base package version 3.1.2 (R Core Team 2015). Community types were characterized with an indicator species analysis using the 'vegan' package, where the appropriate number of groups was identified by maximizing the number of statistically significant indicator species (Dufrene and Legendre 1997).

Community Trajectories

To compare multivariate patterns of community composition between plots, we performed non-metric multidimensional scaling (NMS) ordinations of species cover data for all plots across all years. NMS is an unconstrained ordination technique that uses rank order correlations to iteratively model observed ecological distances from a site dissimilarity matrix. NMS allows for non-parametric relationships, avoiding the assumption of linear or unimodal responses to environmental gradients, and so is well-suited to non-normal or discontinuous species cover data (McCune and Grace 2002).

Percent cover was averaged by species within each plot. Unknown species and rare species (observed only once) were removed to reduce spurious influences on the ordination, and similar species with identification uncertainty were grouped by genus. For example, although multiple *Artemisia* species are known to exist at this site, they are difficult to distinguish in the seedling stage, so we combined these species for analysis. Wisconsin double standardization, which standardizes across both species and sites, was applied prior to ordination (Bray and Curtis 1957). We used Bray-Curtis distance metrics in the *metaMDS* function in the 'vegan' package version 2.3-1 (Oksanen et al. 2015), which runs the NMS multiple times with random starting configurations to avoid convergence at local minima. In the ordination figures, interannual variability within all unburned (control) plots was shown using ellipses. Fire-induced shifts in species composition within burned plots were represented using arrows connecting each plot through time, as the Bray-Curtis distance metric is representative of beta diversity, or species turnover between sites (Ellingsen 2001).

Variability in Community Composition

To assess the variability of community composition in burned plots over time, we calculated Bray-Curtis dissimilarity metrics among plots within site groupings. We calculated dissimilarity among plots for each elevation and tree cover group for each year of the study. Additionally, we calculated dissimilarity for each of the community types identified from the cluster analysis.

Functional Group Cover

Species were aggregated into six functional groups, which represented >99% of the total cover observed: perennial graminoids, annual graminoids, perennial forbs, annual forbs, non-sprouting perennial shrubs, and sprouting perennial shrubs. Percent cover was summed by functional group within each sampling quadrat, then averaged within each plot. We used the 'lm' function in R to model functional group and total cover (log-transformed). Because the gradients of elevation and tree cover were not fully crossed in the experiment (i.e. only mid-elevation plots span a gradient of tree cover, and vice versa; Appendix B: Fig. B1), we analyzed the effects of elevation and tree cover in separate models: only moderate tree cover plots were used to analyze the effect of elevation, and only mid-elevation plots were used to analyze the effect of tree cover. Control/burned ('Burn'), year, and treatment group (either elevation or tree cover), and all possible interactions were included as predictors in both models. As interactions between factors resulted in a large number of effect size estimates, we report only type-2 ANOVA statistics. We used a standard Bonferroni correction to adjust for multiple comparisons: based on 14 hypothesis tests and a desired significance level of 0.05, our critical alpha-level was 0.004.

RESULTS

Understory Plant Community Types

Eight major plant community types were identified from the cluster analysis, using species composition data from all plots (Table 1; Appendix B: Fig. B2). Four community types were comprised of unburned plots (pre-fire or controls), and four were comprised of burned plots (Appendix B: Table B2). The four unburned community types were (with abbreviated names): big sagebrush/fescue shrubland (sagebrush/fescue), big sagebrush/bluegrass shrubland (sagebrush/bluegrass), sparse perennial understory (sparse perennials), and big sagebrush-dominated (big sagebrush). The four burned community types were: diverse mountain shrubland (diverse shrubland), native perennial forbs & grasses (native perennials), invaded forbs & grasses (invaded), and sparse annual forbs (sparse annuals). Plots with the same combination of site conditions (burned/unburned, elevation, and pre-fire tree cover) generally pertained to a single plant community type, suggesting low variability in species composition among replicate plots.

The eight identified plant community types corresponded to different regions in the NMS ordination of species composition for all plots (Fig. 1). The NMS analysis showed that variation in species composition was best explained along two axes (105 sites, 92 species; final stress = 0.24; Appendix B: Table B3). Axis 1 separated unburned from burned community types along a gradient of disturbance. Plots at the high end of Axis 1 had high annual forb cover ($r = 0.98$, $p=0.001$), low non-sprouting shrub (*Artemisia*) cover ($r = -0.87$, $p=0.001$), and low perennial graminoid cover ($r = -0.78$, $p=0.001$). Axis 2 was related to a gradient of total vegetation cover. All functional groups were negatively correlated with Axis 2, and plots at the high end of the axis had low sprouting shrub cover (r = -0.98, p=0.001), low perennial forb cover (r = -0.98, p=0.001), and relatively sparse cover in all other functional groups.

Understory Plant Community Composition along an Elevational Gradient

Unburned Plots

Species composition within the unburned plots (with moderate pre-fire tree cover) was well-stratified by elevation, with each elevation group corresponding to a different plant community type (Table 1; Appendix B: Table B4). The low-elevation plots corresponded to the 'big sagebrush / bluegrass shrubland' community type, characterized by high cover of *Poa secunda*, *Artemisia*, and *Lupinus argenteus*. Mid-elevation plots were classified as 'big sagebrush-dominated' understory communities, with *Artemisia* comprising the majority of vegetation cover with a minor component of sprouting shrubs. High-elevation plots were characterized as 'big sagebrush / fescue shrubland' communities, with high cover of *Artemisia* and *Festuca idahoensis*, and an abundance of sprouting mountain shrubs such as *Chrysothamnus viscidiflorus* and *Symphoricarpos oreophilus*. All unburned plots shared several common species: *Artemisia, C. viscidiflorus, Elymus elymoides, P. secunda, L. argenteus, Phlox hoodii,* and *Arabis holboellii.* Among unburned plots at different elevations, the composition of the low-elevation plots was most distinctive, while the mid- and high-elevation plots had some overlap in NMS ordination space (ellipses in Fig. 2). Among-plot dissimilarity (Fig. 3a) and total understory cover (Appendix B: Fig. B3) were positively related to elevation, and both were substantially greater at the highest elevation.

Community Trajectories after Burning

After the burn treatment, all plots showed substantial turnover in species composition (trajectory arrows in Fig. 2). All elevation groups lost virtually all *Artemisia* cover as a result of burning, driving similar trajectories towards more positive values along Axis 1 (Fig. 2). All elevations showed slight increases in among-plot dissimilarity after burning (Fig. 3a), which persisted through 2006. This increase was most marked for low- and middle-elevation plots, where plots were less similar before burning.

Low- and mid-elevation plots transitioned first to the ‘native perennial forbs & grasses’ community type, with high cover of *L. argenteus* and several other perennial forbs and grasses as indicator species (Table 1). After two years post-burning, these plots transitioned to the ‘invaded forbs & grasses’ community type, driven by the increase of *Bromus tectorum* and sprouting shrubs (Table 1; Appendix B: Table B4). Both low- and mid-elevation plots had slightly decreased total cover of all functional groups combined in 2003 (one year after burning), followed by increases in subsequent years (Appendix B: Fig. B3). By 2006, burned plots had regained pre-burn cover levels at the mid elevation and exceeded pre-burn levels at the low elevation.

High-elevation plots transitioned into the ‘diverse mountain shrubland’ community type after burning, characterized by high cover and richness of perennial grasses, forbs, and sprouting shrubs (Table 1; Appendix B: Table B4). Total cover was reduced after burning (Appendix S1: Table S4), and control and burned plots showed small but persistent differences in all years (Appendix B: Fig. B3). Overall, the high-elevation plots experienced the least turnover in species composition after burning, as seen in the relatively short trajectory arrows in Fig. 2.

Functional Group Responses to Burning

Perennial graminoid cover was not significantly affected by burning (Year*Burn: p=0.022; Table 2), and was instead driven by high interannual variability in both control and burned plots (Fig. 4a). Perennial grass cover in burn and control plots differed among elevations and was greatest at high elevation (Year*Elevation: p=0.001; Table 2), although there was not a consistent relationship between cover and elevation groups. Perennial grass cover was significantly lower for the burned plots (Burn: p<0.001; Table 2), but this was the case both before and after treatment (Fig. 4a), suggesting that the difference was not due to burning.

Annual graminoid cover showed a distinctive burn response (Year*Burn: p<0.001; Table 2), and the trajectories of control and burned sites diverged sharply after fire (Fig. 4b). Burned sites had large (though highly variable) increases in annual graminoid cover that were apparent in the final year of sampling, whereas control sites had no more than trace amounts in all years. Cover was inversely related to elevation (Elevation: p<0.001; Table 2), as the greatest increases occurred at low elevation, and no annual graminoid cover was recorded at high elevation. *B. tectorum* was the only annual graminoid species recorded.

Perennial forb cover was also increased by burning (Year*Burn: p=0.002; Table 2). Control and burned plots had similar perennial forb cover before burning in 2001, but cover increased on the burned plots through time and was greater than on control plots at all elevations by 2006 (Fig. 4c). This response varied by elevation, and the low-elevation burned plots had the largest apparent increase (Burn*Elevation: p=0.002; Table 2).

Annual forb cover had a short-term positive response to burning (Year*Burn: p<0.001; Table 2). At all elevations, annual forb cover peaked in 2004, though the magnitude of the peak, and the rate of decline to pre-burn levels, varied by elevation (Year*Elevation: p<0.001; Table 2). At low and mid elevations, annual forb cover began to increase in 2003 and was still elevated above pre-burn levels in 2006 (Fig. 4d). The high elevation showed a more short-lived flush of annual forbs, with increased cover only in 2004.

Non-sprouting perennial shrub cover was strongly negatively affected by burning (Year*Burn: p<0.001; Table 2). At all elevations, cover was reduced to trace amounts immediately after burning, and minimal signs of recovery were evident by 2006 (Fig. 4e). Among control plots, there was a positive relationship between non-sprouting shrub cover and elevation, but this relationship was not reflected in burned plots. *Artemisia* (sagebrush) species were the only recorded non-sprouting shrubs.

Sprouting perennial shrub cover was positively affected by burning (Year*Burn: p=0.001; Table 2), particularly at low elevation (Burn*Elevation: p<0.001; Table 2). Low-elevation burned plots had sprouting shrub cover comparable to that of high elevation by 2006, despite a strongly positive relationship between cover and elevation for the control sites (Fig. 4f). Post-fire sprouting shrub cover was dominated by *C. viscidiflorus* at low and mid elevations, and by *S. oreophilus* (with lower amounts of *C. viscidiflorus*) at high elevation.

Understory Responses to Burning along a Gradient of Pre-Burn Tree Cover

Unburned Plots

Mid-elevation unburned plots were arranged along NMS Axis 2 based on tree cover (ellipses in Fig. 5), and each tree cover group corresponded to a different plant community type (Table 1; Appendix B: Table B4). Low tree cover plots were characterized as 'big sagebrush / fescue shrubland' communities, with high cover of *Artemisia* and *F. idahoensis*, as well as sprouting mountain shrubs such as *C. viscidiflorus* and *S. oreophilus*. Moderate tree cover plots were classified as 'big sagebrush-dominated' understory communities, with *Artemisia* comprising the majority of vegetation cover with a minor component of sprouting shrubs. The high tree cover plots corresponded to the 'sparse perennial understory' community type, characterized by lower total cover (Appendix B: Fig. B4), a negligible shrub component (Appendix B: Table B4), and a more diverse and variable assembly of uncommon annual forb species. The unburned 'sparse perennial understory' community type clustered with the burned communities, rather than with the other unburned community types (Appendix B: Fig. B2).

Among unburned plots with different levels of pre-fire tree cover, the high tree cover plots were the most distinct, while there was substantial overlap between low and moderate tree covers in NMS ordination space (ellipses in Fig. 5). High tree cover plots were distinguished from low and moderate plots by the absence of common perennial forb species such as *Eriogonum elatum* and *Eriogonum umbellatum,* and by the relative scarcity of *Artemisia, Agoseris glauca,* and *Crepis acuminata.* All unburned plots shared several common species, including *C. viscidiflorus, E. elymoides, P. secunda, L.*

argenteus, and *P. hoodii.* Among-plot dissimilarity (Fig. 3b) was negatively related to tree cover, and was substantially greater among unburned plots with high tree cover.

Community Trajectories

After the burn treatment, all plots experienced major changes in species composition (trajectory arrows in Fig. 5), and the changes were most pronounced in high tree cover plots. *Artemisia* cover was largely eliminated after burning in all plots, driving all trajectories towards more positive values along Axis 1.

The post-fire trajectories of low and moderate tree cover plots were overlapping and indistinguishable (Fig. 5), and both transitioned to the 'native perennial forbs & grasses' community type immediately after burning, with high cover of *L. argenteus* and several other perennial forbs and grasses as indicator species (Table 1). At two years post-burning, these plots transitioned to the 'invaded forbs & grasses' community type, driven by the arrival of *B. tectorum* (2.3% mean cover) and the increased presence of sprouting shrubs (8.2% mean cover; Table 1; Appendix B: Table B4). A single low tree cover plot transitioned directly to the 'invaded forbs & grasses' community type after burning. Both low and moderate tree cover plots had decreased total cover one year after burning (Appendix B: Fig. B4). Whereas moderate tree cover plots regained pre-burn cover levels by 2006, total cover remained depressed at low tree cover plots. Low and moderate tree cover plots maintained similar among-plot dissimilarity in all post-burn years (Fig. 3b).

High tree cover sites, in contrast, occupied their own area in ordination space (Fig. 5), indicating a distinct vegetation response with much greater species turnover (i.e.

longer trajectory arrows) after burning. Burned high tree cover plots corresponded to the 'sparse annual forbs' community type, a ruderal understory assemblage characterized by consistently low total cover (Appendix B: Fig. B4) and a dominant presence of annual forbs such as *Collinsia parviflora*, *Microsteris gracilis*, and *Mentzelia albicaulis* (Table 1). Among-plot dissimilarity increased for high tree cover plots after burning, and was continuing to increase at the time of last sampling (Fig. 3b).

Functional Group Responses to Burning

Perennial graminoid cover was inversely related to pre-burn tree cover (Tree Cover: $p<0.001$; Table 3), particularly among the control plots. Perennial graminoid cover was not strongly affected by burning (Year*Burn: $p=0.028$; Table 3), and control and burned plots had parallel trajectories over time (Fig. 6a). Perennial graminoid cover showed a strong signal of interannual variability (Year: $p<0.001$; Table 3), with reduced cover in 2003, increased cover in 2004, and little to no change in 2006 (Fig. 6a). Statistically significant differences between control and burned plots (Burn: $p<0.001$; Table 3) were present both before and after treatment and thus cannot be inferred to result from burning.

Annual graminoid cover had a strongly positive response to burning (Year*Burn: $p<0.001$; Table 3), and showed a pattern of gradual increase in burned plots in all tree cover categories (Fig. 6b). This pattern was especially evident in the low tree cover plots (Burn*Tree: $p<0.001$; Table 3), where mean annual graminoid cover doubled at each measurement. Control plots recorded no more than trace amounts of annual graminoid cover in all years. *B. tectorum* was the only annual graminoid species.

There was a strong inverse relationship between perennial forb cover and pre-burn tree cover (Tree cover: p<0.001; Table 3; Fig. 6c). Perennial forb cover was positively affected by burning, and the nature of the response varied by pre-burn tree cover (Burn*Year*Tree: p<0.001; Table 3). Burned plots had similar (or slightly lower) cover than the controls before burning. After burning, perennial forb cover was higher than in the controls (Fig. 6c). Immediate post-fire response was most pronounced at low tree cover, where perennial forb cover in burned plots was double that of the controls two years after fire.

Annual forb cover had a short-term positive response to burning (Year*Burn: p<0.001; Table 3). Cover was low in all control plots, increased dramatically for two years after burning and declined toward pre-burn levels after four years (Fig. 6d).

Non-sprouting shrub cover was negatively affected by burning (Year*Burn: p<0.001; Table 3), and was reduced to trace amounts after burning at all levels of pre-burn tree cover (Fig. 6e). At low and mid tree cover plots, non-sprouting shrubs had only begun to recover by 2006 (2% and 5% of pre-burn cover, respectively), and no recovery was detected in high tree cover plots. Among unburned plots, non-sprouting shrub cover (i.e., *Artemisia* species) was inversely related to pre-burn tree cover (Burn*Tree: p<0.001; Table 3), and ranged from nearly zero for high tree cover to approximately 25% at low tree cover (Fig. 6e).

In our analysis, sprouting shrub cover was not significantly affected by burning (Year*Burn: p=0.845; Table 3). However, our graph of cover indicates an increase over time in burned plots (Fig. 6f). Missing data for control plots in 2006 and high variability may have made the effect of burning difficult to detect statistically. Sprouting shrub cover varied by pre-burn tree cover (Tree cover: $p<0.001$; Table 3), and high tree cover plots had substantially lower cover than low or moderate tree cover plots.

DISCUSSION

The results of our study show that abiotic and biotic gradients interact to influence short-term plant community responses to fire and, under some conditions, initiate alternate successional trajectories. In particular, pre-fire vegetation structure had a pronounced effect on post-fire plant responses, and sites with high tree cover had a profoundly different community trajectory after disturbance. Community composition was still changing rapidly four years after fire, and it remains unclear whether divergent trajectories will result in the formation of alternate states, or whether community composition will eventually converge among site groupings. In dryland landscapes where successional processes are typically slow (Pickett 1980), long-term studies are needed to ascertain the existence of alternate stable states.

The widespread use of prescribed fire as a management tool requires a thorough understanding of potential successional trajectories, particularly where invasive species respond to disturbance and can initiate nonlinear and divergent pathways of plant community change (Brooks et al. 2004, Gaertner et al. 2014). Rather than examining vegetation responses to fire in the context of specific functional groups or species of interest (Young and Evans 1978, Lesica et al. 2007, Pyke et al. 2014, Roundy et al. 2014a), our multivariate approach considered all species within the plant community simultaneously. Post-fire compositional trajectories were similar within specific ranges along biotic and abiotic gradients, suggesting that, at the scale of this study, plant community responses to fire are more predictable than stochastic.

Post-Fire Community Trajectories Differ along Elevational Gradient

Unburned sites in Underdown Canyon with similar ecological conditions (i.e. tree cover) had understory communities stratified along an elevational gradient, clustering into common ecological site types. At the low elevation, the pinyon and juniper understory community was typical of a Wyoming big sagebrush site, characterized by high cover of the non-sprouting shrub *Artemisia tridentata* spp. *wyomingensis* and common perennial native grass *Poa secunda.* The mid-elevation understory community resembled a mountain big sagebrush assemblage, dominated by the non-sprouting shrub *Artemisia tridentata* spp. *vaseyana* and common native perennial species. The high-elevation community had a diverse mountain brush understory, with high total cover dominated by *Artemisia tridentata* spp. *vaseyana* and a varied assemblage of sprouting shrubs, perennial grasses, and perennial forbs.

After fire, sites at all elevations experienced substantial change in species composition and increased among-plot dissimilarity. Spatial heterogeneity of pre-fire vegetation and fire behavior creates mosaics of surviving individuals, propagules, and available resources (Pausas et al. 2004, Johnstone and Chapin 2006, Hollingsworth et al. 2013), and stochastic processes largely determine seed arrival (Egler 1954). All elevation groups lost sagebrush, gained cover of perennial forbs and sprouting shrubs, and experienced a pulse of annual forbs. At the highest elevation, burning led to the formation of a mountain shrub community, with rapid recovery of sprouting shrubs and a diverse collection of native perennial grasses and forbs. Burning resulted in convergent pathways of understory composition at low- and mid-elevations, where these sites transitioned first into an early-seral community of perennial forbs and grasses, then to an invaded community type with clear increases in *Bromus tectorum* and sprouting shrub cover. Sagebrush cover was eliminated in all plots by burning and began to recover four years after fire only in the high elevation site. Post-fire sagebrush establishment rates are often higher on moister ecological sites with greater winter precipitation, where favorable weather for recruitment is more likely to coincide with the ephemeral period during which banked seeds are still viable (Baker 2006, Ziegenhagen and Miller 2009, Nelson et al. 2014).

As predicted, low-elevation sites experienced the greatest species turnover after burning, which was driven by major changes in several functional groups, including the increase in *B. tectorum*. The presence of *B. tectorum* is consistent with previous studies from the Intermountain West, which have shown that resistance to invasion is lower on warm, dry sites where establishment, growth, and reproduction are favored (Chambers et al. 2007, Condon et al. 2011, Leffler et al. 2013). Long-term trajectories are often uncertain for sites with post-fire *B. tectorum* invasion (Chambers et al. 2014b, Morris and Leger 2016). However, multiple studies show that *B. tectorum* cover is negatively related to native perennial grass cover (Anderson and Inouye 2001, Reisner et al. 2013, 2015, Chambers et al. 2014b). Although *B. tectorum* will likely always be a component of these communities, its relative abundance over time will likely depend on the capacity to maintain or increase native perennial herbaceous species (Reisner et al. 2013, Chambers et al. 2014b).

Disturbances provide opportunities for community reorganization by removing species and altering the availability of light, water, and nutrients (Tilman 2004), but the underlying abiotic environmental context constrains the species pool that is available for colonization (Pickett et al. 2009). We saw distinct post-fire trajectories at each elevation (i.e. no overlap of trajectory arrows in Fig. 2), illustrating the importance of the abiotic environment on successional trajectories in pinyon and juniper woodlands. However, the existence of an invaded post-fire community type at the lower elevations suggests that, where resistance to invasion is limited, these ecosystems are susceptible to crossing ecological thresholds to alternative community states. Because the fine fuels produced by *B. tectorum* promote fire spread (Balch et al. 2013, Gaertner et al. 2014), invasion may result in grass-fire cycles that promote its continued dominance (D'Antonio and Vitousek 1992, Brooks et al. 2004).

Ecological Memory of Pre-Burn Tree Cover Affects Post-Fire Community Trajectory

At middle elevations, unburned sites had varying levels of pinyon and juniper cover, and as such contained a mosaic of understory plant communities. Mid-elevation sites with low tree cover belonged to the same community type as high-elevation sites with moderate tree cover (diverse mountain brush community). This is likely due partly to overlap in climatic suitability for dominant species but also demonstrates how overstory vegetation structure interacts with topoclimatic context to determine the resources available to understory vegetation (Tilman 1994). The understories of sites with moderate tree cover were compositionally similar to those with low tree cover, but had lower total cover and a greater dominance of sagebrush. Sites with high tree cover had understory communities with little resemblance to other plots of the same elevation group, and were characterized by much lower vegetation cover, a negligible shrub component, and a more prominent presence of annual forbs (Miller et al. 2000).

After burning, the pre-fire effects of tree cover on the understory species persisted, creating biotic legacies that shaped post-fire trajectories of community assembly (Padisak 1992). Sites with low and moderate tree cover were compositionally similar before burning and converged into the same community types after burning (Fig. 7). These sites transitioned into a native early-seral community of perennial forbs and grasses immediately after burning, and within two years *B. tectorum* and sprouting shrub cover began to increase. Low tree cover sites experienced a stronger short-term pulse of perennial forbs, a weaker pulse of annual forbs, and a greater increase in *B. tectorum* cover than those with moderate tree cover. Overall, burning largely eliminated differences in understory vegetation for sites with low-to-moderate tree cover, suggesting that differences in the biotic legacies from the pre-fire community were insufficient to result in different successional trajectories.

Sites with high pre-fire tree cover, in contrast, had divergent trajectories after fire, transitioning into a community type dominated by annual forbs with persistently sparse vegetation cover. The delayed recovery of perennial species suggests that the pre-fire reduction of common understory species reduced the biotic legacy of the native understory community. The decrease in understory species, combined with the likelihood of increased perennial mortality near heavy fuels, indicates that propagule dispersal from adjacent areas is important for establishment in high tree cover sites (Bengtsson et al.

2003). Relatively low perennial cover may reduce future resistance to *B. tectorum* invasion in the high tree cover sites as the lack of native perennial species and a post-fire pulse of resources can create an empty niche that facilitates establishment and spread of invasive species (Shea and Chesson 2002, Schaefer 2011). However, four years after the burn treatment, *B. tectorum* was nearly absent in sites with higher pre-burn tree cover, perhaps due to limited dispersal to these areas at the time of sampling.

The combination of sharply diverging post-fire trajectories and persistently low perennial vegetation cover suggests that a recovery threshold may have been crossed for sites with high pre-fire tree cover (Beisner et al. 2003). Nonetheless, the possible threshold that we observed between pre-fire tree covers of 38% and 74% should be interpreted with caution and within the specific context of our study area. In our study, the effects of pre-fire tree cover were only tested for mid-elevation sites, and it is logical to assume an interaction between tree cover and elevation effects. We would expect that the recovery threshold would occur at higher levels of tree cover as elevation increases, resources become more abundant, and the species pool contains more species adapted to fire (Johnson and Miller 2006). Additionally, it is possible that the relationship between tree cover and post-fire recovery does not exhibit a distinct threshold (Roundy et al. 2014a), and that a more continuous effect was missed by the discrete tree cover categories in our study design. Although the results of our study show that high tree cover sites can remain in an unproductive state with low vegetation cover for at least four years after burning, vegetation recovery in dryland ecosystems is a slow process (Koniak 1985, Baker 2006, Morris and Leger 2016). Long-term observations of plant community trajectories, gathered from continued monitoring efforts within controlled experiments, are necessary for fully understanding the effects of prescribed fire in dryland landscapes.

Management Implications

The prescribed burning treatment resulted in a mixture of desired and undesired outcomes. Post-fire recovery varied by functional group, suggesting that the outcomes of prescribed fire interventions are highly dependent on the abiotic environment and pre-fire biotic legacies, specifically the residual vegetation and seed sources. In our study area, burning generally resulted in increased perennial forb cover, but did not have a strong effect on perennial grass cover. Burning also reduced shrub cover, especially non-sprouting sagebrush species. As post-fire reductions in sagebrush cover can persist for years to decades (Nelson et al. 2014), mechanical treatments may be a preferred management alternative where tree-reduction objectives coincide with preserving sagebrush habitat (Arkle et al. 2014).

Importantly, the effects of burning were not homogenous across the landscape. Consistent with previous research (Chambers et al. 2007, 2014b, Davies et al. 2012), warm and dry low-elevation sites were less resistant to *B. tectorum* invasion after fire. To reduce the risk of invasion, the use of prescribed fire should be avoided in the drier portions of the landscape, and only more resilient higher elevation sites with sufficient perennial herbaceous species to promote recovery should be considered for prescribed fire treatments (Chambers et al. 2014a, Miller et al. 2014). The increase in *B. tectorum* cover following prescribed fire or mechanical treatment is negatively related to native perennial grass cover, indicating that pre-treatment cover of perennial grass is a strong predictor of site resistance to invasion (Chambers et al. 2014b).

Post-fire plant community responses were also greatly dependent on pre-fire tree cover, and sites with high tree cover followed a post-fire trajectory that was independent of the other sites. Although high tree cover sites at mid elevation did not show increased rates of *B. tectorum* invasion within four years of fire, the delayed recovery of perennial cover suggests prolonged exposure to erosional processes and an increased risk of future invasion, especially in a warming environment. High tree cover sites are generally low priority for meeting tree reduction objectives (Miller et al. 2013, 2014). If the decision is made to treat these sites, mechanical treatments are preferred over burning and biomass removal and seeding may be required to meet management objectives.

These results indicate that careful evaluation of site characteristics, including temperature and moisture regimes and pre-treatment vegetation composition, and potential treatment severity, as indicated by pinyon and juniper cover, can be used to predict treatment outcomes (Miller et al. 2014). Post-treatment monitoring can be used to evaluate successional trajectories and adapt management over time to maintain or increase landscape resilience.

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TABLES

Table 1. Indicator species and dominant species for each community type. Only significant indicator species (p<0.05) are listed (up to 8 per group). Top 6 dominant understory species are listed (based on mean % cover).

Community type	**Indicator understory species (indicator score)**	**Dominant understory species (mean % cover)**
Big sagebrush / fescue shrubland	*Festuca idahoensis* (77), *Artemisia* (75), *Eriogonum umbellatum* (53), *Koeleria macrantha* (51)	*Artemisia* (21), *Festuca idahoensis* (6), *Chrysothamnus viscidiflorus* (2), *Lupinus argenteus* (2), *Symphoricarpos oreophilus* (2), *Elymus elymoides* (1)
Big sagebrush / bluegrass shrubland	*Poa secunda* (71)	*Poa secunda* (6), *Artemisia* (4), *Lupinus argenteus* (2), *Eriogonum microthecum* (<1), *Chrysothamnus viscidiflorus* (<1), *Arenaria aculeata* (<1)
Sparse perennial understory	*Ephedra viridis* (58)	*Poa secunda* (1), *Elymus elymoides* (1), *Artemisia* (1), *Ephedra viridis* (<1), *Lupinus argenteus* (<1), *Symphoricarpos oreophilus* (<1)
Big sagebrush-dominated	*Astragalus purshii* (59)	*Artemisia* (10), *Poa secunda* (1), *Lupinus argenteus* (1), *Chrysothamnus viscidiflorus* (1), *Eriogonum elatum* (1), *Elymus elymoides* (1)
Diverse mountain shrubland	*Penstemon watsonii* (90), *Symphoricarpos oreophilus* (85), *Phlox hoodii* (71), *Silene douglasii* (67), *Achnatherum hymenoides* (66), *Mentzelia albicaulis* (65), *Antennaria rosea* (63), *Carex* (60)	*Symphoricarpos oreophilus* (11), *Lupinus argenteus* (6), *Festuca idahoensis* (3), *Chrysothamnus viscidiflorus* (3), *Phlox hoodii* (2), *Leymus cinereus* (1)
Native perennial forbs & grasses	*Agoseris glauca* (69), *Arenaria aculeata* (60), *Pseudoroegneria spicata* (57), *Gayophytum racemosum* (45)	*Lupinus argenteus* (4), *Chrysothamnus viscidiflorus* (1), *Collinsia parviflora* (1), *Poa secunda* (1), *Eriogonum elatum* (1), *Eriogonum microthecum* (1)
Invaded forbs & grasses	*Bromus tectorum* (95), *Arenaria kingii* (85), *Arabis sparsiflora* (81), *Phlox longifolia* (80), *Chrysothamnus viscidiflorus* (69), *Eriastrum wilcoxii* (69), *Eriogonum elatum* (66), *Lappula occidentalis* (63)	*Chrysothamnus viscidiflorus* (7), *Lupinus argenteus* (3), *Bromus tectorum* (2), *Eriogonum elatum* (2), *Elymus elymoides* (1), *Poa secunda* (1)
Sparse annual forbs	*Microsteris gracilis* (82), *Collinsia parviflora* (66), *Astragalus oophorus* (66), *Lactuca serriola* (59), *Descurainia pinnata* (58)	*Collinsia parviflora* (1), *Symphoricarpos oreophilus* (1), *Microsteris gracilis* (1), *Elymus elymoides* (1), *Mentzelia albicaulis* (<1), *Eriogonum elatum* (<1)

Table 2. Elevation effect on understory cover by functional group. Only moderate tree cover plots were included in the analysis. F-value and p-value calculated from type-2 Anova for a linear model predicting percent cover (log) for each functional group. All predictors are factors. Bolded where $p<0.004$ (based on a Bonferroni correction for 14 tests at a desired significance value of 0.05). Burn=control (unburned) or burned.

Response:	Perennial graminoid cover	Annual graminoid cover	Perennial forb cover	Annual forb cover	Non-sprouting shrub cover	Sprouting shrub cover	Total cover
Predictor:	F (p)						
Year	19.22 **(<0.001)**	9.67 **(<0.001)**	1.70 (0.179)	29.52 **(<0.001)**	14.39 **(<0.001)**	15.26 **(<0.001)**	21.96 **(<0.001)**
Burn	19.18 **(<0.001)**	17.86 **(<0.001)**	44.30 **(<0.001)**	199.14 **(<0.001)**	94.42 **(<0.001)**	77.60 **(<0.001)**	3.22 (0.080)
Elevation	41.31 **(<0.001)**	17.78 **(<0.001)**	10.86 **(<0.001)**	3.41 (0.041)	2.68 (0.080)	102.80 **(<0.001)**	59.41 **(<0.001)**
Year*Burn	3.53 (0.022)	11.42 **(<0.001)**	5.95 **(0.002)**	29.22 **(<0.001)**	20.55 **(<0.001)**	8.13 **(0.001)**	9.98 **(<0.001)**
Year*Elev	4.81 **(0.001)**	2.65 (0.027)	2.89 (0.018)	5.93 **(<0.001)**	0.27 (0.946)	0.59 (0.738)	3.85 (0.004)
Burn*Elev	0.39 (0.681)	5.58 (0.007)	6.91 **(0.002)**	0.81 (0.450)	0.85 (0.434)	54.75 **(<0.001)**	7.17 **(0.0021)**
Burn*Year *Elev	0.29 (0.944)	3.60 (0.005)	1.91 (0.098)	1.77 (0.125)	0.39 (0.814)	3.32 (0.019)	1.62 (0.187)
Adjusted R^2	0.7153	0.6671	0.6179	0.852	0.7498	0.8963	0.7964

Table 3. Tree cover effect on understory cover by functional group. Only mid-elevation plots were included in the analysis. F-value and p-value calculated from type-2 Anova for a linear model predicting percent cover (log) for each functional group. All predictors are factors. Bolded where $p<0.004$ (based on a Bonferroni correction for 14 tests at a desired significance value of 0.05). Burn=control (unburned) or burned.

Response:	Perennial graminoid cover	Annual graminoid cover	Perennial forb cover	Annual forb cover	Non-sprouting shrub cover	Sprouting shrub cover	Total cover
Predictor:	F (p)						
Year	10.05 **(<0.001)**	9.72 **(<0.001)**	22.23 **(<0.001)**	63.48 (**<0.001**)	19.93 (**<0.001**)	0.44 (0.727)	17.89 (**<0.001**)
Burn	14.94 **(<0.001)**	50.63 **(<0.001)**	1.00 (0.322)	310.25 (**<0.001**)	63.63 (**<0.001**)	0.34 (0.566)	3.34 (0.075)
Tree cover	15.44 **(<0.001)**	8.70 **(<0.001)**	274.69 **(<0.001)**	3.74 (0.031)	65.17 (**<0.001**)	26.48 (**<0.001**)	173.40 (**<0.001**)
Year*Burn	3.31 (0.028)	12.93 **(<0.001)**	13.87 **(<0.001)**	43.44 (**<0.001**)	28.85 (**<0.001**)	0.17 (0.845)	13.46 (**<0.001**)
Year*Tree	1.05 (0.408)	1.29 (0.281)	10.11 **(<0.001)**	1.63 (0.159)	0.99 (0.445)	0.79 (0.581)	3.02 (0.015)
Burn*Tree	1.33 (0.275)	8.95 **(<0.001)**	14.98 **(<0.001)**	1.04 (0.360)	13.26 (**<0.001**)	0.16 (0.854)	3.28 (0.047)
Burn*Year *Tree	0.95 (0.466)	1.37 (0.248)	11.38 **(<0.001)**	1.85 (0.109)	0.98 (0.431)	0.27 (0.898)	5.30 (**0.001**)
Adjusted R^2	0.5221	0.6740	0.9180	0.8999	0.8461	0.404	0.8814

FIGURES

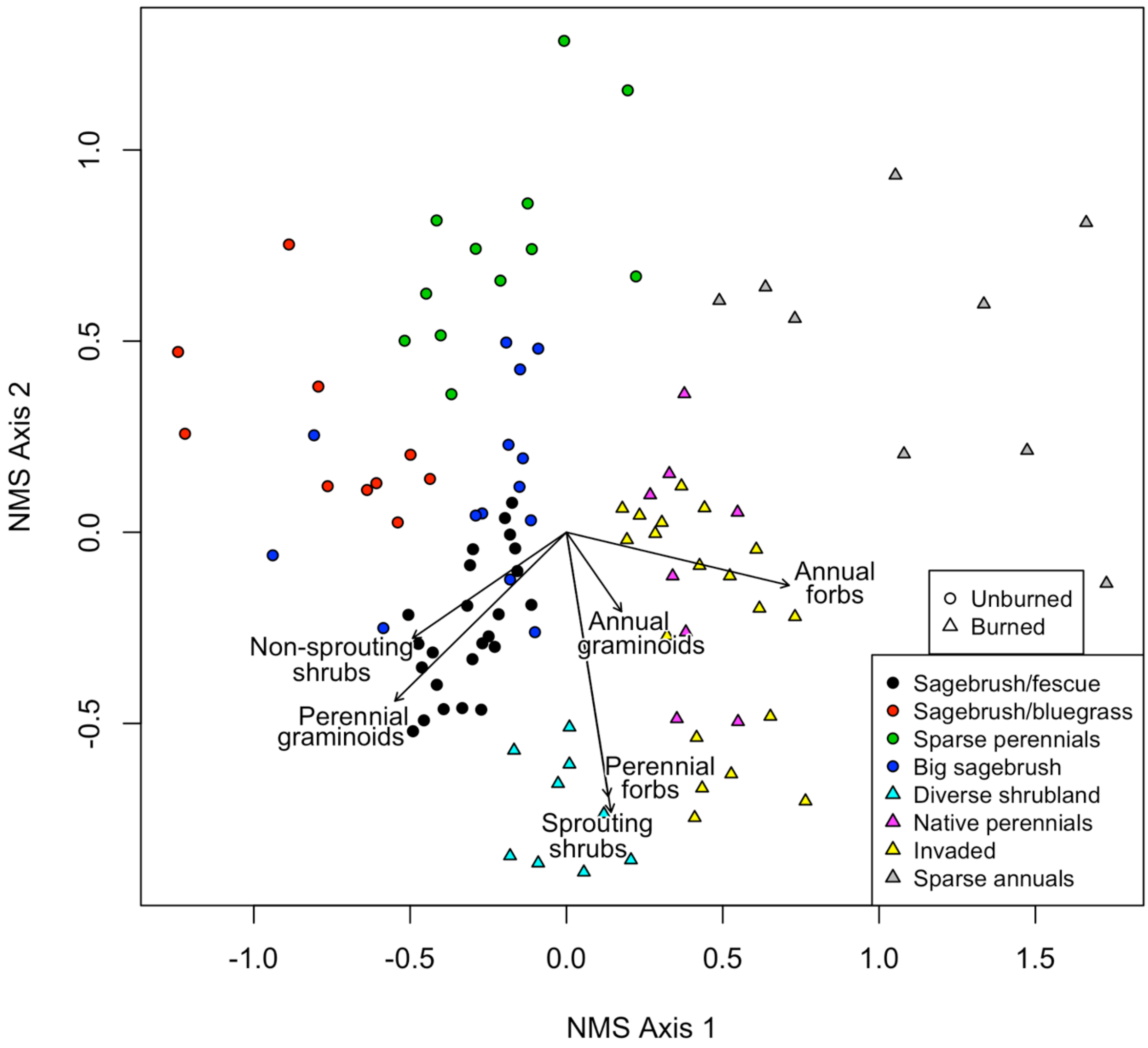

Figure 1. Understory plant community composition for burned (triangles) and unburned (circles) plots, based on NMS (non-metric multidimensional scaling) ordination. Arrows indicate correlations between functional group cover and site NMS scores. Arrow length is proportional to the magnitude of the correlation. Point colors represent plant community types identified from hierarchical cluster analysis.

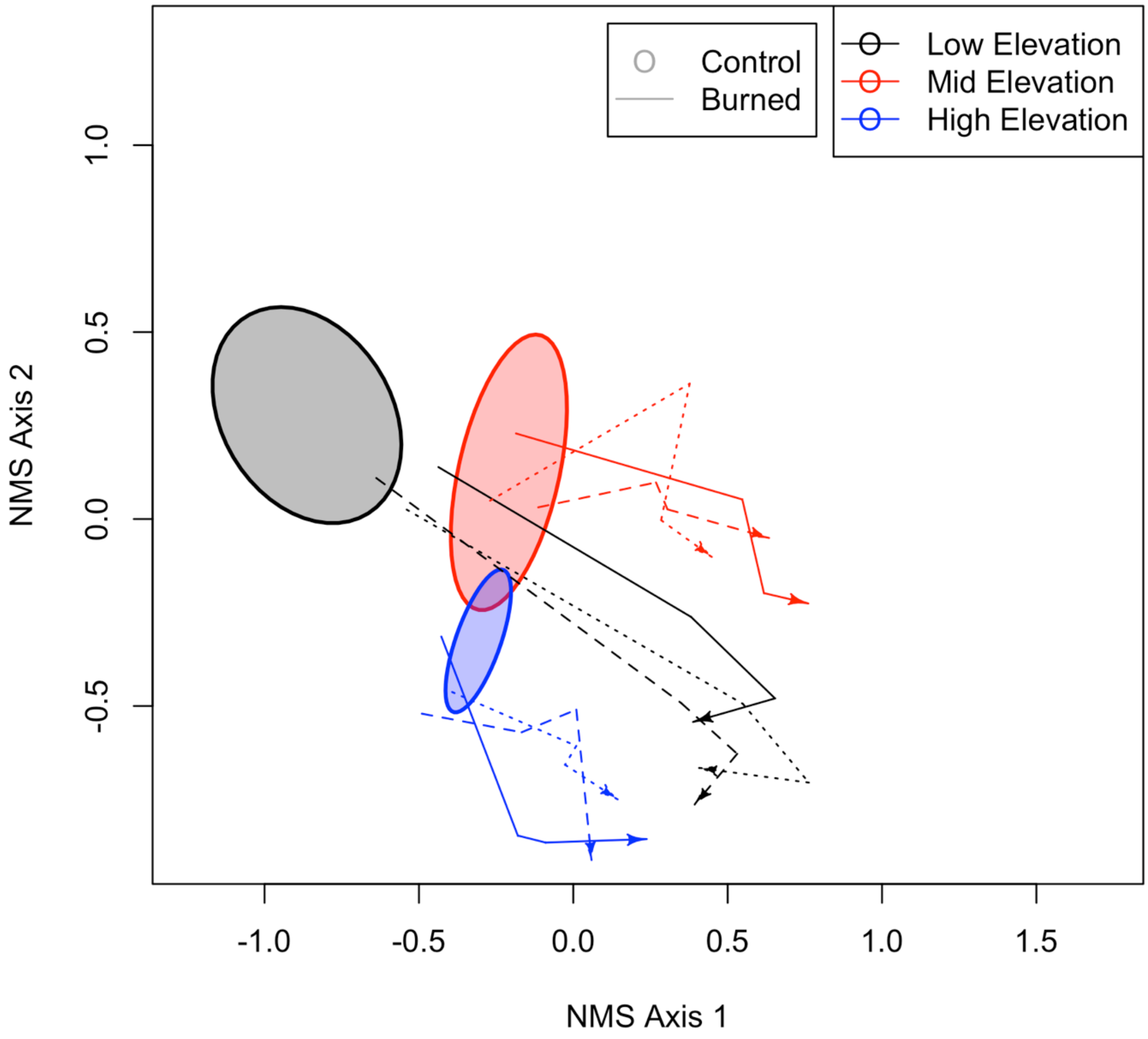

Figure 2. Understory plant community composition of moderate tree cover plots for burned (arrows) and control (ellipses) plots along an elevational gradient, based on NMS (non-metric multidimensional scaling) ordination. Ellipses show the interquartile range for all control plots in 2001, 2003, and 2004 (N=9). Arrows show the community trajectory of each burned plot through time, with a distinct line type for each plot (short-dash, long-dash, solids); arrowheads show plots in 2006, tails show plots in 2001 (pre-burn), and inflection points show plots in 2003 and 2004.

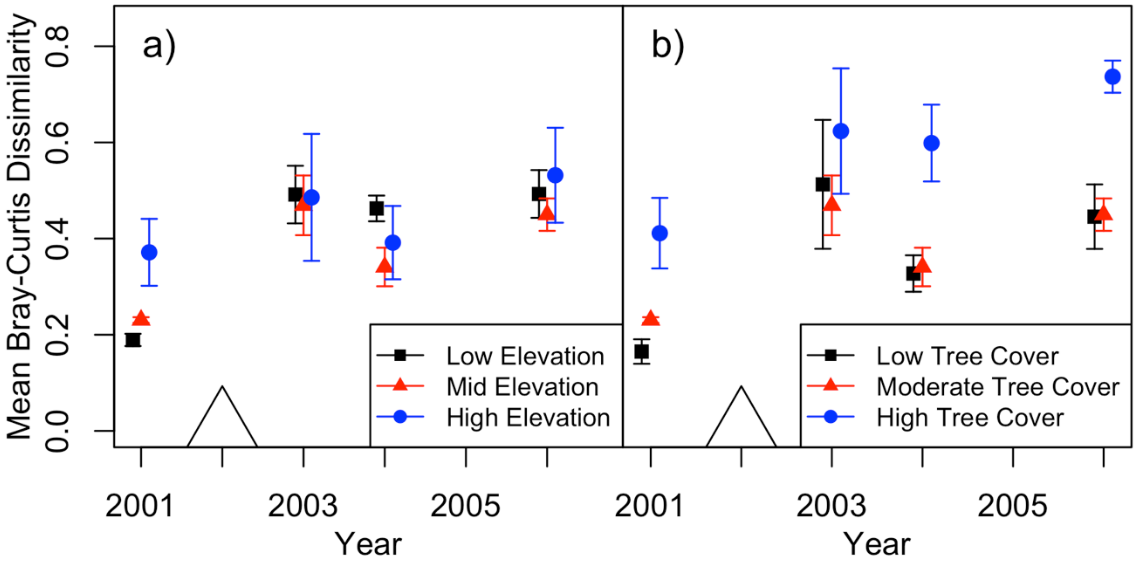

Figure 3. Bray-Curtis dissimilarity among plots within elevation (a) and tree cover (b) groups. Only burned plots are included in the analysis. Data shown as mean +/- 1SE. Large triangle shows year of burn treatment.

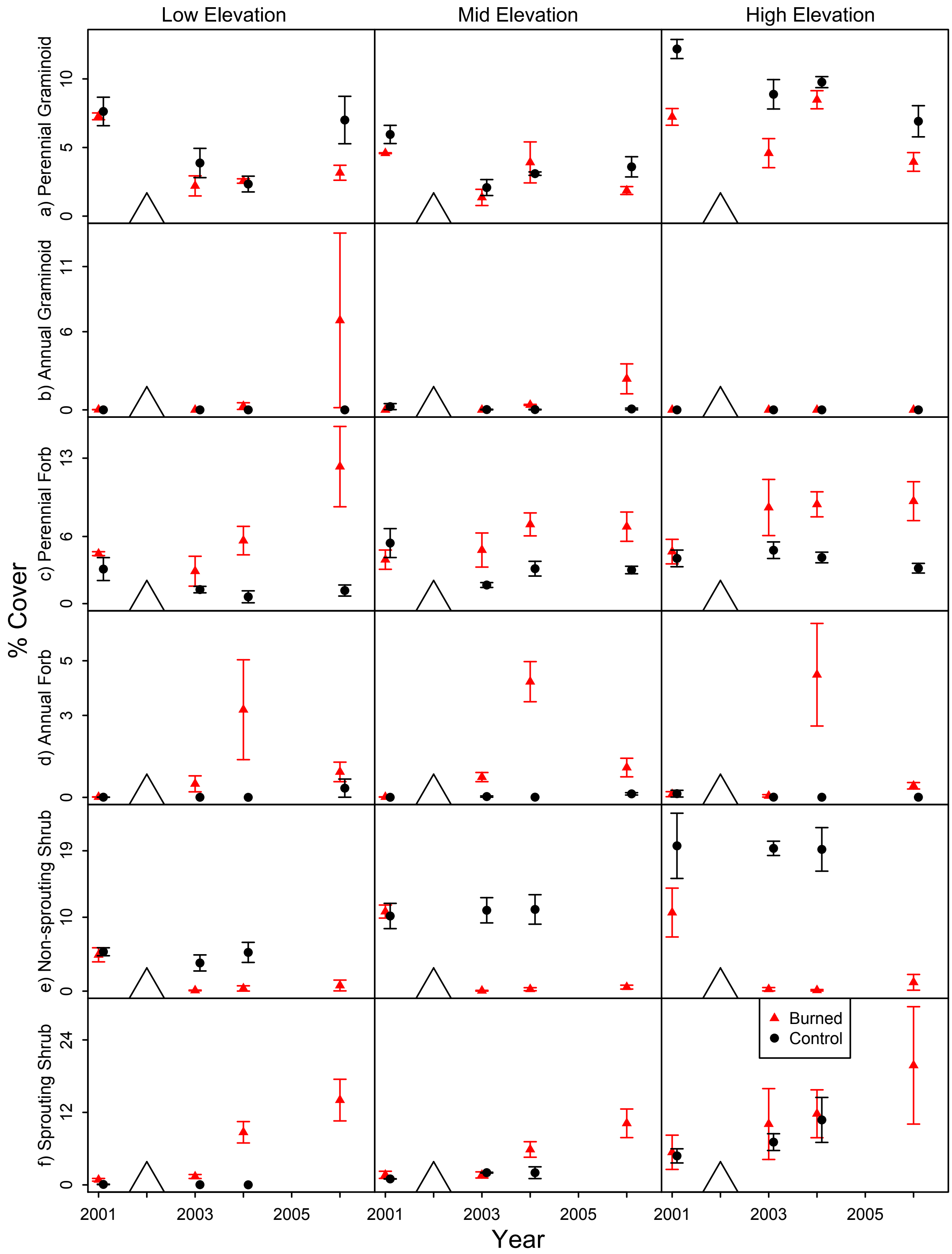

Figure 4. Functional group cover for burned (red) and control (black) plots along an elevational gradient. Only moderate tree cover plots are shown. Data are shown as mean +/- 1SE. No shrub control data collected in 2006. Triangle shows year of burn treatment.

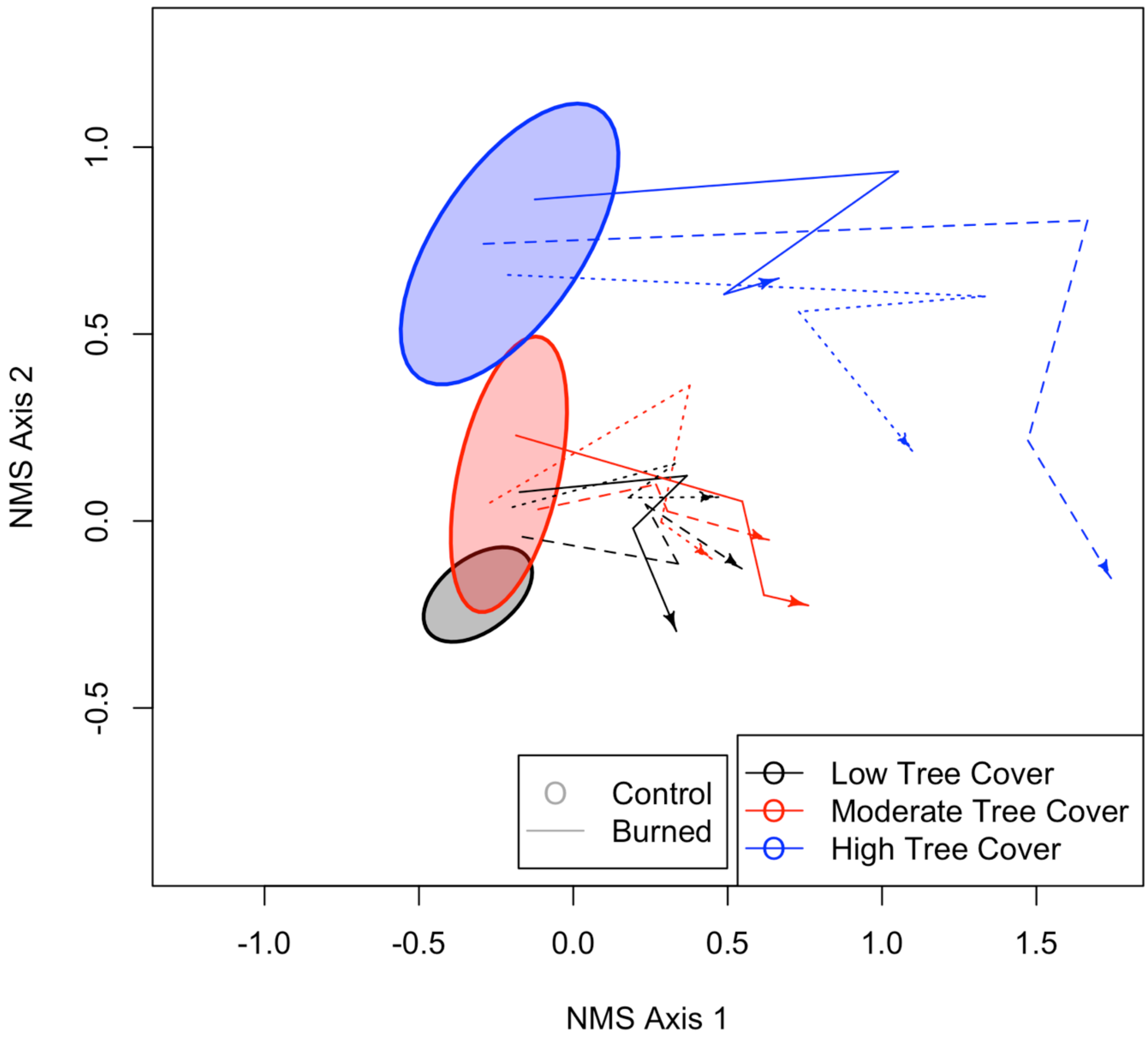

Figure 5. Mid-elevation understory plant community composition for burned (arrows) and control (ellipses) plots along a gradient of pre-burn tree cover, based on NMS (non-metric multidimensional scaling) ordination. Ellipses show the interquartile range for all control plots in 2001, 2003, and 2004 (N=9). Arrows show the community trajectory of each burned plot through time, with a distinct line type for each plot (short-dash, long-dash, solids); arrowheads show plots in 2006, tails show plots in 2001 (pre-burn), and inflection points show plots in 2003 and 2004.

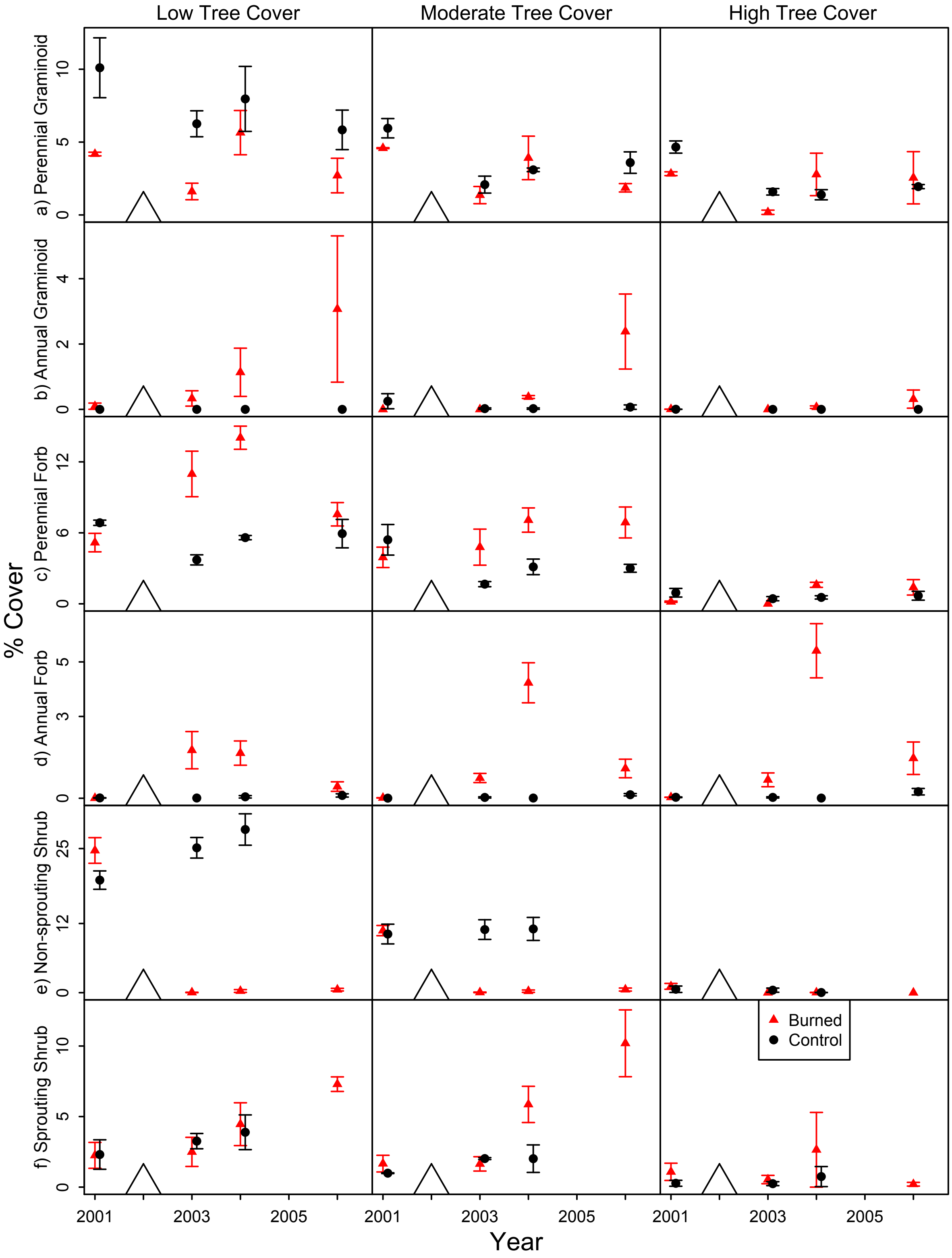

Figure 6. Functional group cover for burned (red) and control (black) plots along a gradient of pre-burn tree cover. Only mid-elevation plots are shown. Data shown as mean +/- 1SE. No shrub control data collected in 2006. Triangle shows year of burn treatment.

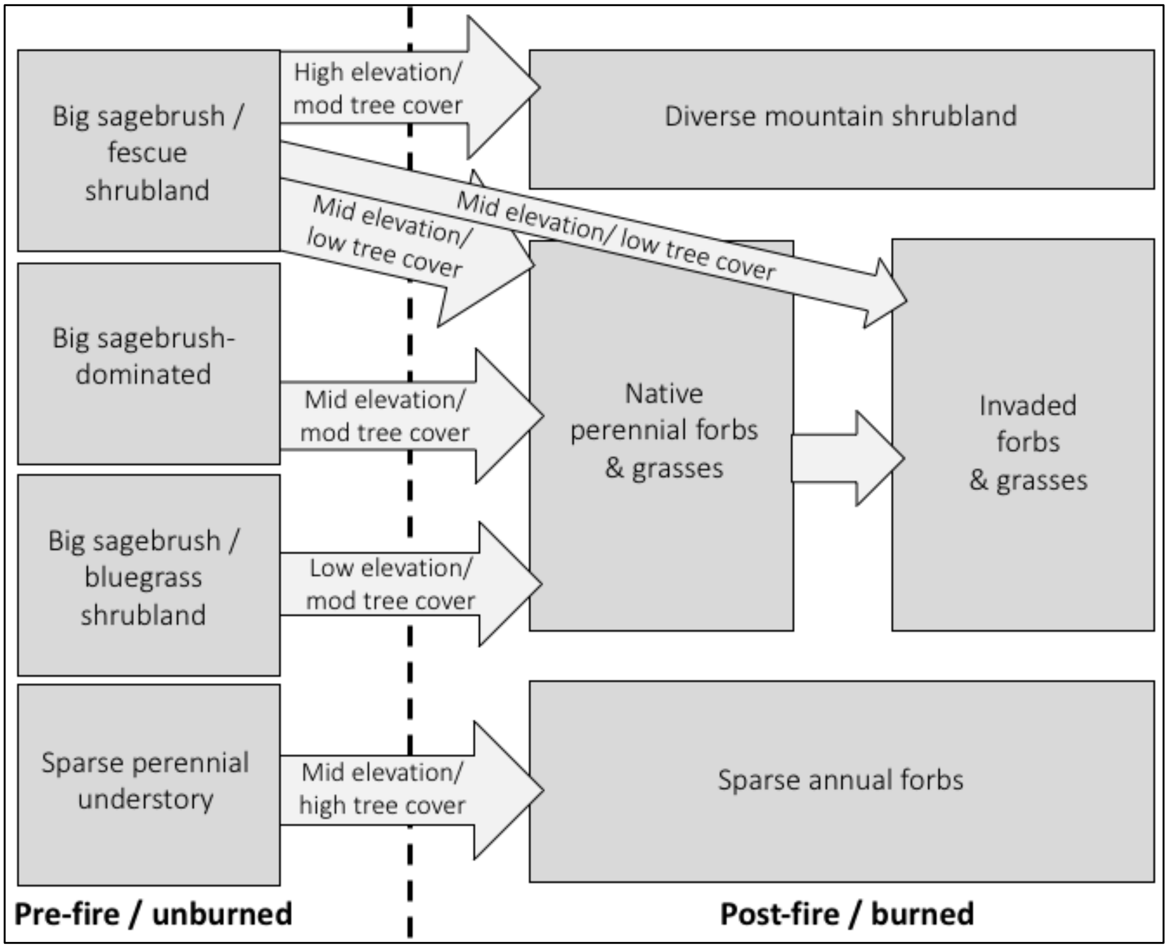

Figure 7. Diagram of community trajectories resulting from burning. Distinct plant community types, identified from cluster and indicator species analysis, are shown in dark gray boxes. Site types transitioning among community types are shown in light gray arrows.

CHAPTER 3. Seeding native species increases resistance to annual grass invasion following prescribed burning of pinyon-juniper woodlands

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ABSTRACT

Alien grass invasions are often facilitated by disturbance, which provides an opportunity for invasion by releasing a pulse of available resources. There is a pressing need to identify ecosystem attributes associated with susceptibility to disturbance-induced invasion, especially where disturbances are used as a management tool, such as prescribed fire. In the Great Basin of the western United States, expansion of the invasive annual grass *Bromus tectorum* is transforming native ecosystems. In this study, we examined long-term understory plant community responses to experimental prescribed fire and post-fire seeding treatments in Great Basin pinyon-juniper woodlands. We asked (1) how long-term ecosystem resistance to *B. tectorum* invasion varies along major abiotic and biotic gradients, and (2) whether post-fire seeding of perennial species promotes perennial plant establishment and increases resistance to invasion. Fourteen years after burning, we found that resistance to fire-induced *B. tectorum* invasion was highest on relatively cool and moist sites (higher elevation), but that the warmer and drier (low- to mid-elevation) burned sites had become heavily invaded by *B. tectorum*. Post-fire *B. tectorum* dominance was highest in sites with high pre-fire tree cover, where native perennial establishment following fire was sparse. We found that seeding perennial species after burning decreased invasibility in sites with low resistance, increasing perennial cover while reducing the abundance of *B. tectorum*. Seeding a mix of native perennial shrubs, forbs, and grasses was more effective at increasing perennial cover and inhibiting *B. tectorum* invasion than seeding a mix of non-native perennial grasses, which is common in post-fire rehabilitation. Our results highlight the need for long-term studies to evaluate plant community responses to prescribed fire, as a shorter (3-4 year) post-fire monitoring period would not have captured important treatment differences including long-term *B. tectorum* dominance that was amplified on sites with high levels of tree cover prior to burning.

INTRODUCTION

Alien grass invasions are transforming structure and function of arid and semi-arid ecosystems worldwide (D’Antonio and Vitousek 1992). Initial invasion is often facilitated by disturbances (Lodge 1993), which increase the quantity of unused resources (Davis et al. 2000) and thus provide niche opportunities for invaders (Shea and Chesson 2002). Ecosystem resistance to invasion varies spatially and temporally, and is dependent on the interactions among underlying resource dynamics, the post-disturbance response of resident species, and traits of the invaders (Lonsdale 1999). To facilitate development of effective management strategies in the current context of climate-change-related shifts in disturbance regimes (Turner 2010), there is a pressing need to identify ecosystem attributes associated with resistance to invasion (Bradley et al. 2010).

Expansion and increasing dominance of the highly flammable invasive annual grass, *Bromus tectorum* L., is transforming native ecosystems in the Great Basin region of the western United States, resulting in increased fire risk (Brooks et al. 2004, Balch et al. 2013) and altering ecosystem processes such as nutrient cycling and soil water flux and storage (Wilcox et al. 2012, Germino et al. 2016). Where Great Basin pinyon-juniper (*Pinus monophylla* and *Juniperus* spp.) woodlands and sagebrush (*Artemisia* spp.) semi-desert overlap, prescribed fire and other tree-reduction measures are often used to maintain native shrub- and grass-dominated habitats and conserve sagebrush obligate animal species (Chambers and Wisdom 2009, Miller et al. 2014). Post-fire management objectives typically prioritize the recovery of perennial herbaceous species that can increase resistance to invasion by exotic annual grasses such as *B. tectorum*. However, fires often accelerate *B. tectorum* invasion (Knapp 1996), and some prescribed fires have unintentionally resulted in increased dominance of *B. tectorum*. Although many understory species are adapted to surviving and reproducing following fire, the dominant shrub and tree species of this region are fire-intolerant and typically killed by fire. Early phenology, rapid growth, and high rates of resource acquisition (Knapp 1996, James 2008, Leffler et al. 2013) allow *B. tectorum* to effectively compete with seedlings of native perennial species for available post-fire resources (Booth et al. 2003, Humphrey and Schupp 2004, Chambers et al. 2016).

Resistance to fire-related *B. tectorum* invasion varies spatially, and landscapes characterized by low resistance to invasion tend to be those in which post-fire establishment of native perennial species is limited or slow (Chambers et al. 2014a). On drier sites, resource-related constraints on seed production limit post-fire seed availability (Chambers et al. 2007). Similarly, landscapes in which perennial understory vegetation is competitively suppressed by trees are less likely to have seeds available for post-fire establishment of perennial understory species (Allen and Nowak 2008).

Where the post-fire response of native perennial species is constrained by seed availability, seeding treatments can theoretically augment the establishment of perennial species and thus inhibit *B. tectorum* invasion through competition (Pyke et al. 2013). However, seeding treatments are often unsuccessful at establishing the seeded species (Arkle et al. 2014), especially on drier sites where unfavorable abiotic conditions can limit plant establishment regardless of seed availability (Knutson et al. 2014). In other words, seeding treatments are often the least successful in those parts of the landscape with lowest resistance to invasion, where they would have the greatest potential to increase invasion resistance if seeding were successful.

We examined understory plant community responses to landscape-scale experimental burning and seeding treatments in the Shoshone Mountains, Nevada. Study sites included replicate pairs of control and burned plots arranged along major abiotic (elevation) and biotic (pre-fire tree cover) gradients. Post-fire seeding treatments of native and non-native species were nested within burned plots. Short-term plant community responses four years after burning indicated that resistance to fire-induced *B. tectorum* invasion increased with elevation along a productivity gradient, although post-fire cover of *B. tectorum* was relatively low at all elevations (Urza *et al.*, 2017). Sites with high pre-fire tree cover contained very little *B. tectorum* after burning, but native perennial species were also scarce, resulting in sparsely vegetated sites four years after fire. In this study, we revisited permanent sampling plots 14 years after burning to investigate long-term plant community responses to fire and resistance to *B. tectorum* invasion. We asked two questions: 1) How does long-term ecosystem resistance to fire-induced *B. tectorum* invasion vary along gradients of elevation and pre-fire tree cover? and 2) Does post-fire seeding of perennial species promote perennial plant establishment and increase resistance to invasion?

MATERIALS AND METHODS

Study Area

Experimental treatments took place in Underdown Canyon, a west-to-east-draining watershed located on the Humboldt-Toiyabe National Forest in the Shoshone Mountains of central Nevada, USA. Climate is characterized by cold winters, during which precipitation falls as snow, and warm summers with precipitation falling as rain (Fig. 1a; Western Regional Climate Center, 2018). Average annual precipitation increases with elevation, ranging from 23 cm to 50 cm (Board et al. 2011). Weather was variable during the study period, including wetter-than-average years and periods of drought (Fig. 1b). Underlying geology is welded and non-welded volcanic tuff, and soils on alluvial fans are classified as coarse loamy mixed frigid typic haploxerolls (Rau et al. 2005). Woodlands of variable density occur in unburned areas throughout Underdown Canyon and are dominated by single-leaf pinyon (*Pinus monophylla*) with lesser amounts of Utah juniper (*Juniperus osteosperma*).

Experimental Design and Data Collection

Underdown Canyon was established as a Joint Fire Sciences Program Demonstration Area to study the ecological effects of landscape-scale prescribed fire treatments. The study used three pairs of adjacent alluvial fans (six fans total, ranging from approx. 1-5 ha) on the north-facing slope of Underdown Canyon. Fan pairs are distributed along an elevational gradient: low (2073m), mid (2225m), and high (2347m). One fan within each pair was burned by the USDA Forest Service in May of 2002, and the other remained unburned (control). Relatively cool and moist conditions during the burns (air temperature < 32°C, relative humidity > 15%, wind speed < 9 $m \cdot s^{-1}$, and gravimetric fuel moisture < 40%) resulted in patchy consumption of vegetation and duff (Rau *et al.*, 2007). Prior to burning, the mid-elevation fans were stratified based on three tree cover categories: low (12% mean cover), moderate (38% mean cover), and high (74% mean cover) (Reiner 2004). The low- and high-elevation fans included only the moderate tree-cover category. Three permanent sampling plots approximately 0.1 ha in size were established in each combination of control/burned, elevation group and tree-cover category, for a total of 30 permanent plots.

Post-fire seeding treatments were nested within the burned plots. Two $100m^2$ seeding subplots were established within each permanent plot for the burned treatments (n=15). For each pair of seeding subplots, one was seeded with a mix of ten native species, and the other was seeded with a mix of five non-native species. The native seed mix contained perennial grasses, forbs, and shrubs and varied in composition among elevations, whereas the non-native seed mix contained commonly used perennial grass species and did not differ among elevations (seeding mixes shown in Table 1). Seeds were applied at a rate of 60 seeds per species per m^2 in both seeding types. Seed mixes were broadcast evenly across the seeding subplots, and the soil surface was raked to ensure seed-soil contact in the fall after the burns. This design resulted in four burn/seeding treatments: unburned (control), burned and unseeded, burned and seeded with native species, and burned and seeded with non-native species. Livestock were excluded from the study initiation until 2006, after which permitted grazing was allowed.

We evaluated the response of the vegetation community in 2016, 14 years after burning. Within each permanent plot, $0.25m^2$ quadrats were systematically located along transect lines that were randomly stratified within each 0.1 ha plot. 15 quadrats were used in the unburned and burned unseeded plots, and 7-8 quadrats were used in the seeded native and seeded non-native subplots. In each quadrat, aerial cover was estimated for each species using 13 cover categories (Daubenmire 1959), and the mid-point of each cover category was chosen to represent percent cover in each quadrat. Plant cover data were also collected in 2001 (pre-fire), 2003, 2004, and 2006 (for more details see Urza *et al.*, 2017). Only the 2016 data were included in analyses in this paper, but the full time series is shown for visual comparisons where relevant.

Data Analyses

To quantify changes in vegetation functional types, species cover data were aggregated into six functional groups: annual forbs, annual grasses, perennial forbs, perennial graminoids, sprouting perennial shrubs, and non-sprouting perennial shrubs. Percent cover was summed by functional group within each sampling quadrat, then averaged within each plot. We used linear regressions to model functional group cover (square-root-transformed) as a function of burn/seeding treatment (unburned, burned unseeded, burned seeded native, and burned seeded non-native), plot type (elevation: low, mid, high; tree cover: low, moderate, high), and their interaction. We estimated the effect of elevation and tree cover in separate models because these factors were only partially crossed in the study design. Only moderate tree cover plots were used to analyze the effect of elevation, and only mid-elevation plots were used to analyze the effect of tree cover. We used a standard Bonferroni correction to determine a critical alpha-level of 0.004, based on 12 hypothesis tests and a desired significance level of 0.05. We used Tukey post hoc comparisons to compare among factor levels for significant predictor variables. All analyses were performed in R version 3.3.3 (R Core Team 2015).

RESULTS

Burning and seeding effects along an elevational gradient

All herbaceous plant functional groups differed across the elevational gradient (Table 2). For perennial graminoids, perennial forbs, and annual forbs, cover was positively related to elevation, but did not differ among burn/seeding treatments. Cover of both perennial graminoids ($p=0.001$; Fig. 2a) and perennial forbs ($p<0.001$; Fig. 2c) was significantly higher at the high elevation compared to the mid and low elevations. Annual forb cover (Fig. 2d) was significantly lower at the low elevation than at the mid or high elevation ($p=0.001$).

Annual grass cover differed among burn/seeding treatment, and the treatment effect varied among elevations (elevation*treatment; $p=0.003$; Fig. 2b). At the low elevation, the burned unseeded plots had significantly higher annual grass cover than the unburned plots, but plots seeded with either native or non-native species did not differ significantly from either the unburned or the burned unseeded plots. At the mid elevation, burned plots that were either unseeded or seeded with non-native species had significantly higher annual grass cover than the unburned plots and burned plots seeded with native species. At the high elevation, annual grasses were effectively absent in all plots, and did not differ among burning or seeding treatments. *Bromus tectorum* was the only annual grass found in any of the study plots.

Sprouting shrub cover did not vary among elevations (p=0.117). For all elevations, burning resulted in increased sprouting shrub cover (p=0.002), regardless of post-fire seeding treatment (Fig. 2f). Burned plots had 7-24% sprouting shrub cover, compared to 0-5% in the unburned plots. *Chrysothamnus viscidiflorus* was the most common sprouting shrub species found in burned plots at all elevations. *Symphoricarpos oreophilus* was also found in burned plots at the mid and high elevation, and burned plots at the low elevation contained *Ericameria nauseosa*, *Tetradymia canescens*, and *Sambucus nigra.*

Non-sprouting shrub cover did not differ significantly among elevations, burn/seeding treatment, or their interaction. At the low and mid elevations, burned plots seeded with native species had the highest *Artemisia* cover (Fig. 2e), but the differences were not statistically significant (Table 2).

Collectively, these differences resulted in substantial long-term differences in plant community composition across the elevational gradient (Fig. 3, center row of panels). At the low and mid elevations, burning increased total understory plant cover, including both native species and invasive annual grasses, but seeding after burning was associated with a smaller increase in invasive annual grasses. At the high elevation, the composition of burned plots closely resembled that of unburned plots, regardless of seeding treatment.

Burning and seeding effects along a gradient of pre-fire tree cover

For some plant functional groups, pre-fire differences in plant community composition, presumably driven by variable levels of pre-fire tree cover, persisted as long-term legacies (Table 2). Perennial forb ($p<0.001$; Fig. 4c) and sprouting shrub cover ($p<0.001$; Fig. 4f) were negatively related to pre-fire tree cover, with significantly lower cover in plots with high pre-fire tree cover.

Burning and seeding treatments had long-term effects on the covers of non-sprouting shrubs (Fig. 4e; $p=0.004$). Non-sprouting shrub cover was significantly higher in burned plots that were seeded with native species (15-22%) than in the other treatment groups (0-16%). Sprouting shrub cover was negatively related to tree cover, but the differences were not statistically significant at the Bonferroni-corrected critical alpha level ($p=0.029$). Non-sprouting shrubs consisted of *Artemisia tridentata* ssp. *wyomingensis* at the low elevation, and *A. tridentata* ssp. *vaseyana* and *A. arbuscula* at the mid and high elevations.

Annual grass (*B. tectorum*) cover differed among all combinations of burn/seeding treatments ($p<0.001$; Fig. 4b, but did not differ across tree cover groups ($p=0.480$). Unburned plots had the lowest cover (0-1%), followed by burned plots seeded with native species (2-7%), burned plots seeded with non-native species (7-11%), and burned plots that were unseeded (9-22%; rank: unburned < burned seeded native <

burned seeded non-native < burned unseeded). Perennial graminoid and annual forb cover did not differ among tree cover groups, burn/seeding treatment, or their interaction (Table 2; Fig. 4a,d).

Taken together, differences in functional group responses resulted in important long-term differences in plant community composition across the gradient of pre-fire tree cover (Fig. 3, center column of panels). Burning resulted in increased cover of non-native annual grasses at all levels of tree cover. All other plant functional groups were negatively related to pre-fire tree cover, however, so burned plots with high pre-fire tree cover were dominated by annual grasses. Burned plots that were seeded after fire had lower annual grass dominance than unseeded burned plots, due to a smaller increase in annual grasses and higher perennial cover.

DISCUSSION

Abiotic and biotic context drives long-term resistance to invasion after burning

Our results show that prescribed burning facilitated the long-term invasion of *Bromus tectorum*, a fire-adapted annual grass (Fig. 3). Disturbance increases susceptibility to invasion by creating niche opportunities (Shea and Chesson 2002). Fire removes resident trees and shrubs (Figs. 2 and 4), reducing resource uptake and thus providing a pulse of available resources (Davis et al. 2000). *B. tectorum* is a highly plastic winter annual, and its early phenology, rapid growth rate, and high reproductive capacity allow it to take advantage of fire-induced resource pulses and undergo rapid population growth as long as the underlying physical environment is suitable (James 2008, Chambers et al. 2016). Site resistance to invasion depends on the ability of resident species to compete with the invader for resources (Davis et al. 2000), which varies based on the abiotic and biotic context.

Our results are consistent with many other studies that have found that resistance to fire-induced *B. tectorum* invasion increases with elevation (Chambers et al. 2007, 2016, Taylor et al. 2014). *B. tectorum* arrived at the drier (low- to mid-elevation) sites shortly after burning (Urza et al. 2017) and gradually increased in abundance over time, demonstrating that these site types are less resistant to invasion (Fig. 2b). In contrast, the high elevation site showed no invasion after burning and a robust response from a diverse suite of native plant species, indicating high resilience to burning and resistance to invasion. The relationship between resistance to invasion and elevation can be explained by two linked mechanisms. First, cold soil temperatures at the high elevation are likely outside the range of suitable climate for *B. tectorum* (Chambers et al. 2007), directly limiting its ability to establish and reproduce. In contrast, the low elevation is highly climatically suitable for *B. tectorum* and the mid elevation site suitable during most years (Chambers et al. 2007). Second, lower resource availability at lower elevations results in lower productivity of the native community (West 1983). As a result, the native community may lack the capacity to take advantage of pulses of resources, like those that become available after fire, providing an opportunity for invasion by *B. tectorum* (Rejmanek 1989).

We found that for the mid elevation, post-fire *B. tectorum* dominance was highest in sites with high pre-fire tree cover. In sites with high pre-fire tree cover, the pre-fire absence of understory vegetation results in a weak ecological memory after burning, and post-fire recovery of native understory species is unlikely if seed dispersal is limited

(Condon et al. 2011, Roundy et al. 2014a). Although burning released abundant soil nutrient resources through the removal of trees and residual *Artemisia* spp. (Rau et al. 2007, 2014, Roundy et al. 2014b), sites with high pre-fire tree cover were sparsely vegetated four years after burning (Urza et al. 2017), providing ample opportunity for invasion. Once *B. tectorum* dispersed to the site, and, in the presence of abundant resources and an ecological void given the absence of native species, the invader was able to dominate the plant community (Fig. 3). Our results are consistent with other studies showing that pinyon-juniper woodland sites with high pre-fire tree cover are less resistant to *B. tectorum* invasion (Bates et al. 2014, Roundy et al. 2014a, Reed-Dustin et al. 2016). It is unclear why *B. tectorum* invasion was delayed in our study compared to other examples from the literature, but it is possible that its initial arrival was dispersal-limited (Simberloff 2009). Cattle grazing and wood harvest were prohibited in Underdown Canyon for four years after burning, but these and other anthropogenic disturbances resumed at high intensity once restrictions were eased and may have dispersed *B. tectorum* into the burns.

Post-fire seeding increased resistance to invasion

We found that seeding perennial species after burning decreased invasibility in sites with low resistance and greatly inhibited *B. tectorum* invasion (Fig. 3). After disturbance, rapid plant establishment or regrowth moderates the pulse of resources that are available, thus limiting opportunities for invasion (Davis et al. 2000, Shea and Chesson 2002). For low- and mid-elevation sites, especially those dominated by trees before fire, burned plots that were seeded had higher perennial cover and a fraction of the

B. tectorum cover seen in unseeded plots. We found that seeding a mix of native shrubs, grasses, and forbs more effectively inhibited invasion than seeding non-native grass species commonly used in restoration. Many studies have found a strong association between perennial graminoid cover and resistance to *B. tectorum* invasion (Chambers et al. 2007, 2014b, James et al. 2008, Condon et al. 2011, Davies et al. 2012, Bates et al. 2014, Roundy et al. 2014a), and there has been recent evidence that competition with native annual forbs may directly suppress *B. tectorum* performance (Leger et al. 2014). In our study, many sites in which the native seeding treatment inhibited *B. tectorum* had increased *A. tridentata* (non-sprouting shrub) cover (Table 1; Fig. 3). Our data do not allow us to determine causality in this relationship, but these results suggest that there may be a direct relationship between *A. tridentata* establishment and *B. tectorum* invasion. Although *A. tridentata* has a much deeper rooting depth than *B. tectorum*, both species use near-surface soil water during the spring and early summer (Ryel et al. 2010), though more research is needed to know whether they are in direct competition for soil water and nutrients during the *B. tectorum* growth period.

Although the link between perennial herbaceous vegetation cover and resistance to *B. tectorum* invasion is well established, successful inhibition of invasion from post-fire seeding has not often been observed. Instead, other studies have shown that management-scale seeding treatments are often unsuccessful at establishing the seeded species (Pyke et al. 2013, Arkle et al. 2014), particularly if the seeded species are natives (Knutson et al. 2014, Davies et al. 2015). The success of our seeding treatments was likely a result of several factors. First, a heavy seed rate combined with our method of seed application – broadcast seeding and surface mixing with minimal soil disturbance –

likely contributed to high rates of establishment of seeded species. Minimizing surface disturbance reduces the loss of residual bunchgrasses that survived burning (Ott et al. 2016), and using heavy seed rates with a minimum-till imprinter – a mechanized analogy to our application method – has been found to be the most successful approach for seeding *A. tridentata* (Ott et al. 2017). Second, the weather conditions following the burn may have been particularly favorable for plant establishment at lower elevations, where the effectiveness of post-fire seeding tends to be unpredictable (Knutson et al. 2014, Ott et al. 2016). Precipitation was above average in both the winter and summer following the burn (Fig. 1b), which likely promoted successful establishment of seeded species. Even when seeds are available, post-fire *A. tridentata* establishment requires favorable weather conditions immediately following fire (Ziegenhagen and Miller 2009, Nelson et al. 2014), so the relatively wet post-fire conditions likely enhanced the success of the seeding treatment.

Finally, the effect of seeding was likely strengthened by prolonged protection from post-fire cattle grazing. Cattle grazing was excluded from Underdown Canyon for four years after burning, compared with the typical management prescription of two years of post-fire grazing deferment (Miller et al. 2014). Grazing reduces growth rates of perennial grasses (Ferraro and Oesterheld 2002), and perennial grasses compete with *B. tectorum* more effectively as adults than as seedlings (Booth et al. 2003, Humphrey and Schupp 2004, Chambers et al. 2007), so protection from herbivory likely increases the ability of seeded species to outcompete invaders (Reisner et al. 2013). Cattle are often seed dispersal agents (Schiffman 1997), so cattle exclusion may also slow the arrival of *B. tectorum* to a burned site if it was not present before fire, giving seeded species further opportunity to establish before interacting with an invader. Our data do not allow us to isolate the effect of cattle as a dispersal agent for invaders or the effect of trampling and herbivory on the establishment and growth of native competitors (Reisner et al. 2013, Chambers et al. 2017), but our results suggest that the role of grazing on fire-facilitated invasions should be explored further.

Management implications

The results of our study contribute to the growing consensus that susceptibility to fire-induced *B. tectorum* invasion is greatest at lower elevations and where native perennial species are lacking in the understory (Davies et al. 2012, Chambers et al. 2014a, 2016, Taylor et al. 2014). However, our results also highlight the need for long-term studies to evaluate plant community responses to prescribed fire, as a shorter (3-4 year) post-fire monitoring period would not have captured important treatment differences including long-term *B. tectorum* dominance that was amplified on sites with high levels of pre-fire tree cover. Four years after burning, annual grass cover was lowest on sites with high pre-fire tree cover, where only trace amounts of *B. tectorum* were observed (Urza et al. 2017).

To reduce the risk of invasion, fire should be avoided in the drier portions of the landscape, especially where tree dominance or inappropriate grazing practices have resulted in depauperate understory vegetation (Chambers et al. 2014a, Miller et al. 2014). When fire cannot be avoided in these low-resistance site types, seeding native perennial shrubs and grasses after burning may speed recovery and reduce the risk of *B. tectorum* invasion. However, post-fire seeding treatments are often unsuccessful in increasing establishment of native species or in preventing invasion of *B. tectorum* (Pyke et al. 2013, Knutson et al. 2014), suggesting that the positive results from our seeding treatments could be challenging to reproduce at typical management scales. Post-fire seeding success tends to be higher on moister sites (Knutson et al. 2014), and on drier sites, repeated seeding may be needed to achieve management objectives.

We recommend that post-fire seeding be used to restore targeted, high-priority areas with inherently low resistance to invasion. Success is more likely with a heavy seeding rate (Ott et al. 2017), and although some surface soil disturbance is required to gain sufficient seed-to-soil contact, minimizing the severity of soil disturbance with low-impact drill seeders reduces the loss of important residual bunchgrasses and shrubs whose roots survive the fire and can resprout (Ott et al. 2016). Native-only seed mixes should be used if restoring native vegetation is a management goal, because non-natives tend to outcompete native species when they are seeded together (Knutson et al. 2014). Where available, locally-adapted seeds or varieties with traits that improve field performance should be used (Brabec et al. 2017, Leger and Goergen 2017). Finally, our results suggest that prolonged protection from post-fire grazing may improve the effectiveness of seeding treatments, especially in drier sites characterized by low resilience to fire and resistance to invasion.

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TABLES

Table 1. Effect of seeding treatment on post-fire cover of seeded species. For each species seeded at each elevation, results of paired t-tests are shown (mean difference = burned seeded plots – burned unseeded plots). For both mixes, seeds were applied at a rate of 60 seeds per species per m^2.

Seeded species	**Functional group**	**Low elevation**	**Mid elevation**	**High elevation**
		Mean difference (p-value)		
Native seed mix ---				
Elymus elymoides	Perennial graminoid	-0.12 (0.78)	-0.85 (0.09)	-0.82 (0.04)
Festuca idahoensis	Perennial graminoid	--	0*	2.58 (0.24)
Poa secunda	Perennial graminoid	-0.37 (0.89)	1.22 (0.09)	0.43 (0.51)
Pseudoroegneria spicata	Perennial graminoid	2.57 (0.40)	1.33 (0.09)	0*
Hesperostipa comata	Perennial graminoid	-0.49 (0.42)	0.32 (0.38)	0*
Eriogonum heracleoides	Perennial forb	0*	0*	0*
Eriogonum umbellatum	Perennial forb	1.50 (0.38)	0.28 (0.75)	0.61 (0.56)
Lupinus alpestris	Perennial forb	0.25 (0.91)	1.89 (0.04)	2.98 (0.28)
Penstemon palmeri	Perennial forb	0*	--	--
Sphaeralcea munroana	Perennial forb	0*	--	--
Linum lewisii	Perennial forb	--	0.00 (0.35)	0*
Artemisia tridentata wyomingensis	Non-sprouting shrub	3.43 (0.55)	--	--
Artemisia tridentata vaseyana	Non-sprouting shrub	--	14.33 (0.01)	1.35 (0.66)
Non-native seed mix ---				
Agropyron cristatum	Perennial graminoid	0.95 (0.42)	2.54 (0.03)	0.17 (0.42)
Bromus inermis	Perennial graminoid	4.48 (0.32)	1.78 (0.08)	0.25 (0.22)
Dactylis glomerata	Perennial graminoid	0*	0*	0*
Phleum pratense	Perennial graminoid	0*	0*	0*
Thinopyrum intermedium	Perennial graminoid	0*	0*	0*

-- Species not included in seed mix

* Species included in seed mix, but not observed during vegetation surveys.

Table 2. Results from linear models predicting plant functional group cover (square-root transformed). Shown are F (p) values for each predictor, using type-2 ANOVA statistics. Only moderate tree cover plots were included in the ‘Elevation model’, and only mid-elevation plots were included in the ‘Tree cover model’. All predictors are categorical factors. Burn-seed treatment levels: unburned, burned unseeded, burned seeded native, and burned seeded non-native. P-values are bolded where < 0.004 (based on a Bonferroni correction for 12 tests at a desired significance value of 0.05).

	Perennial graminoid cover	Annual grass cover	Perennial forb cover	Annual forb cover	Non-sprouting shrub cover	Sprouting shrub cover
Elevation model						
Elevation	9.18 (**0.001**)	39.40 (**<0.001**)	10.12 (**<0.001**)	9.11 (**0.001**)	2.19 (0.134)	2.35 (0.117)
Burn-Seed Treatment	1.31 (0.295)	14.53 (**<0.001**)	4.38 (0.014)	1.08 (0.377)	2.53 (0.081)	6.79 (**0.002**)
Elevation * Burn-Seed Treatment	1.85 (0.131)	4.57 (**0.003**)	3.27 (0.017)	1.59 (0.192)	0.79 (0.590)	0.53 (0.782)
Adjusted R^2	0.39	0.80	0.55	0.36	0.14	0.33
Tree cover model						
Tree cover	2.35 (0.117)	0.76 (0.480)	19.43 (**<0.001**)	2.36 (0.116)	4.10 (0.029)	11.53 (**<0.001**)
Burn-Seed Treatment	2.67 (0.070)	30.51 (**<0.001**)	1.96 (0.147)	3.55 (0.029)	5.76 (**0.004**)	2.95 (0.053)
Tree cover * Burn-Seed Treatment	4.11 (0.005)	1.94 (0.115)	1.39 (0.259)	0.79 (0.586)	1.77 (0.147)	1.33 (0.283)
Adjusted R^2	0.43	0.73	0.55	0.21	0.42	0.45

FIGURES

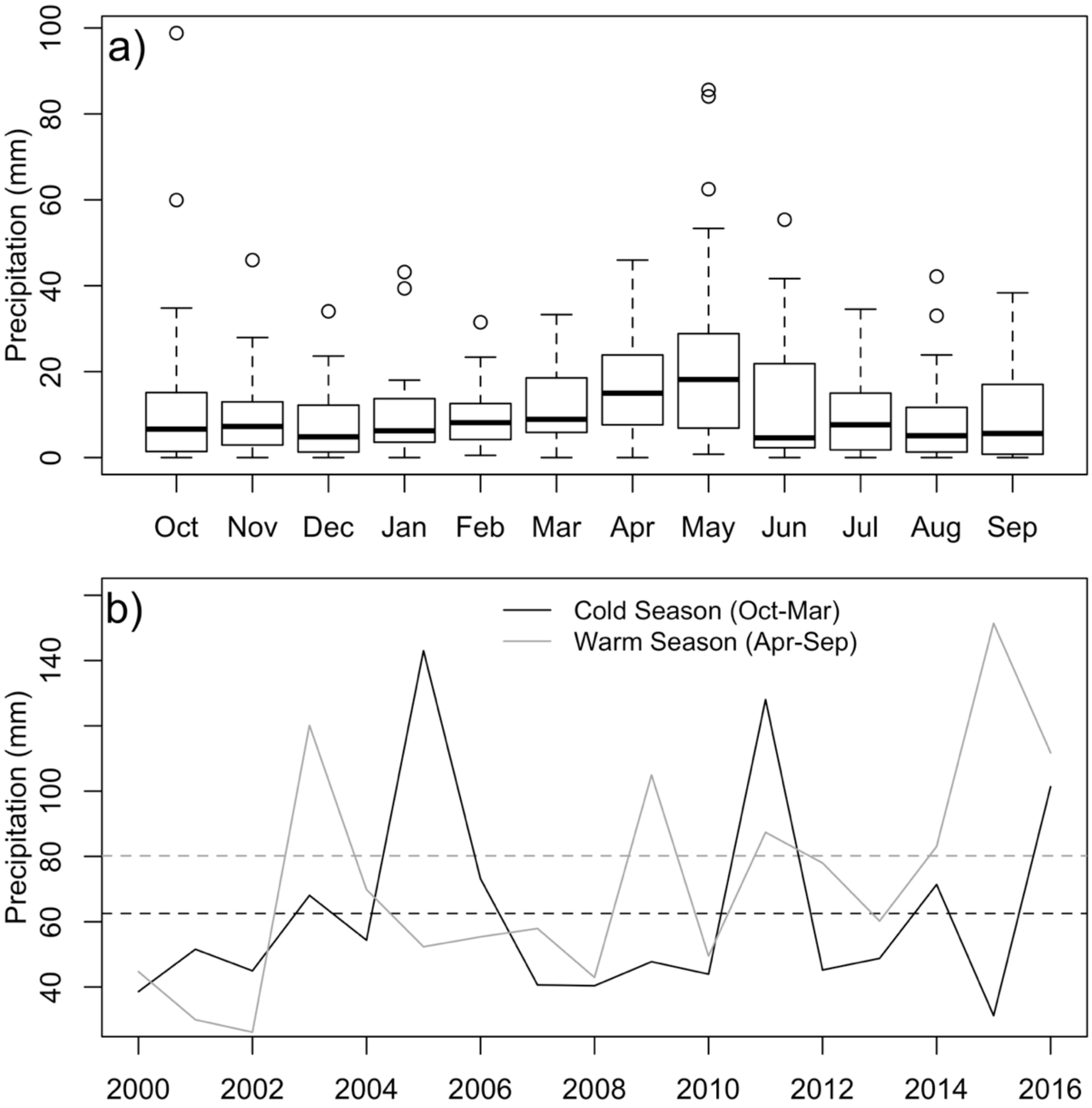

Figure 1. Monthly and annual precipitation patterns for the study area. a) Monthly precipitation for the weather record (1987-2018). Bold line is the median, box margins show the interquartile range, whiskers are the farthest points within 1.5 interquartile range and points are outliers. b) Annual cold (October to March) and warm season (April to September) precipitation totals over the study period. Dashed lines show the long-term means (1987-2018). Climate data are from the Desatoya Mountain RAWS Weather Station (Western Regional Climate Center, 2018) which is located at 1890m elevation approximately 19km to the northwest of the study area.

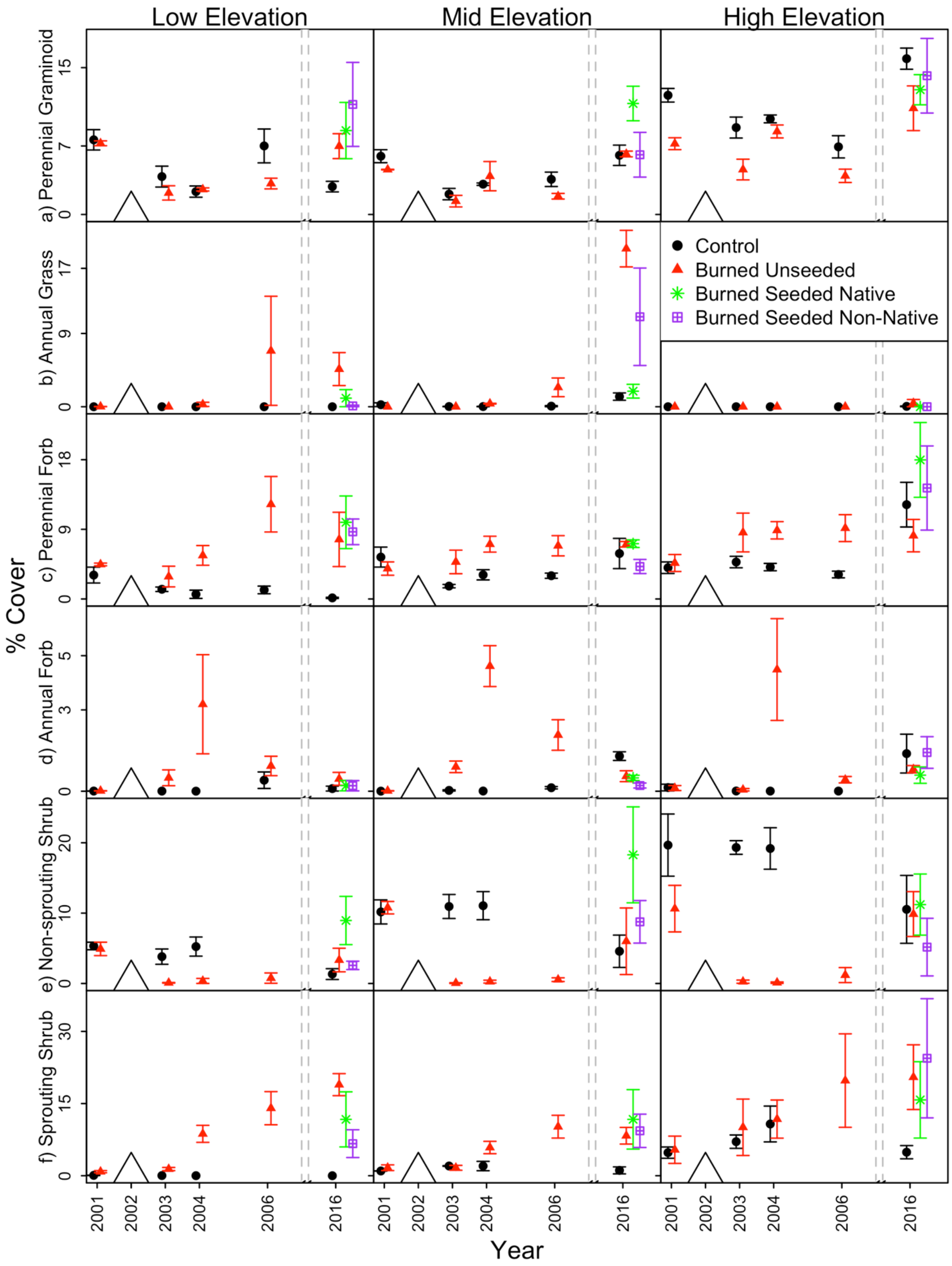

Figure 2. Time series of functional group cover along the elevational gradient. Only plots with moderate tree cover are shown. Data shown as mean ± 1 SE. Large triangle shows year of burn treatment.

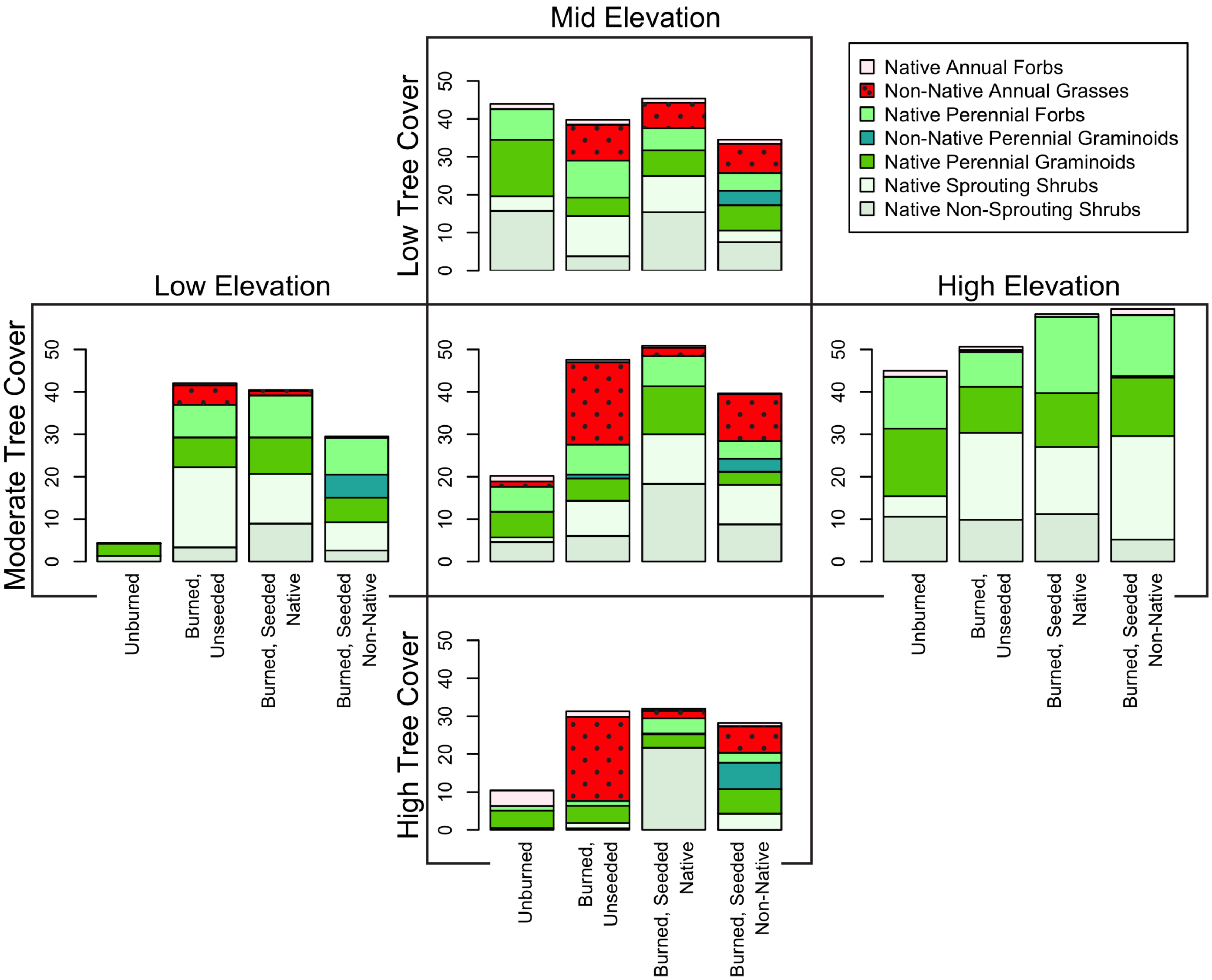
Mid Elevation
Low Elevation
High Elevation
Low Tree Cover
Moderate Tree Cover
High Tree Cover
0
10
20
30
40
50
Unburned
Burned, Unseeded
Burned, Seeded Native
Burned, Seeded Non-Native
Native Annual Forbs
Non-Native Annual Grasses
Native Perennial Forbs
Non-Native Perennial Graminoids
Native Perennial Graminoids
Native Sprouting Shrubs
Native Non-Sprouting Shrubs

Figure 3.

Figure 3 (previous page). Plant community composition by functional group from 2016. Each panel represents mean cover (%) for burn/seeding treatments within all combinations of elevation and pre-fire tree cover. The center row of panels represents the elevational gradient (for sites with moderate pre-fire tree cover) and the center column of panels represents the gradient of pre-fire tree cover (for sites at the mid elevation).

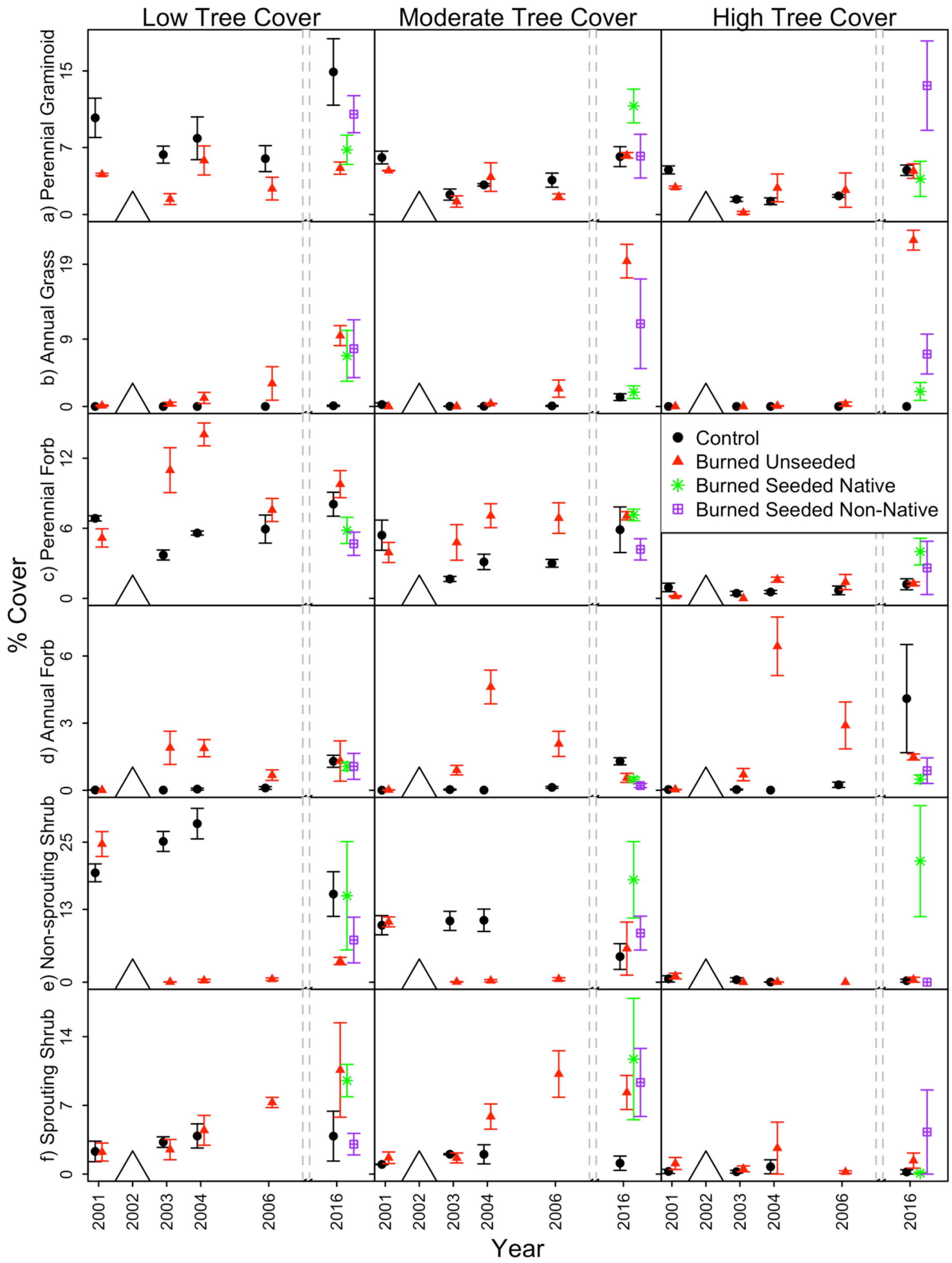

Figure 4. Time series of functional group cover along a gradient of pre-fire tree cover. Only mid-elevation plots are shown. Data shown as mean ± 1 SE. Large triangle shows year of burn treatment.

CHAPTER 4. Shrub (*Artemisia tridentata*) facilitation of tree establishment (*Pinus monophylla*): ontogenetic shifts along stress gradients

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ABSTRACT

- Plant ontogeny and environmental conditions interact to determine the outcome of plant-plant interactions, yet their combined effects are poorly understood.
- We used a combination of field experiments and environmental measurements to examine interactions between *Artemisia tridentata* (big sagebrush) and *Pinus monophylla* (singleleaf pinyon pine), the dominant species within two vegetation communities that interface over broad environmental gradients in the semiarid Great Basin of the USA.
- *A. tridentata* facilitated *P. monophylla* at multiple stages of ontogeny, but the net outcome of the interaction shifted from strongly positive toward neutral after the *P. monophylla* vegetative transition from juvenile to adult foliage. *A. tridentata* microsites ameliorated harsh abiotic conditions to allow *P. monophylla* to overcome an early population bottleneck and successfully establish in areas without tree cover. The timing of the ontogenetic shift did not vary across an

elevational gradient, although results suggest that the mechanisms of facilitation differed among elevations.

- These results contribute to accumulating evidence that plant-plant interactions are major drivers of plant community dynamics, and will likely become more important in the context of increasing frequency and severity of disturbance events. However, the presence of multiple gradients of stress in dry, mountainous regions leads to complex spatial and temporal patterns of interactions.

INTRODUCTION

Interactions among plant species are important for the structure and functioning of plant communities (Brooker *et al.*, 2008; Soliveres *et al.*, 2015). The net outcome of interactions depends on the balance among the underlying abiotic environment (Bertness & Callaway, 1994), plant modification of that environment (Schöb *et al.*, 2013), and plant traits related to resource requirements or physiological tolerances (Liancourt *et al.*, 2005). However, these factors are not constant in time or space, even for a specific pair of interacting species. Both plant ontogeny and spatial variation in the environment may strongly drive plant interactions (Callaway & Walker, 1997), yet few studies have examined their combined effect. Interactions that alter plant seedling establishment and survivorship have important implications for population structure (Le Roux *et al.*, 2013). Knowledge of how plant-plant interactions vary in relation to ontogeny and environmental gradients may provide insight on how plant communities and associated taxa will respond to environmental change (Redmond & Barger, 2013).

Spatial variability in the abiotic environment is a strong driver of plant-plant interactions, and likely interacts with ontogenetic changes in plant tolerances and resource needs to determine the outcome of plant interactions. Several generalized relationships between interaction strength and environmental stress have been proposed (Bertness & Callaway, 1994; Michalet *et al.*, 2006), but cumulative evidence from experimental, observational, and modeling studies is far from conclusive (Brooker *et al.*, 2008). Many studies have found that interactions tend to be more positive in high stress environments and more negative in low stress environments, commonly referred to as the stress-gradient hypothesis (Bertness & Callaway, 1994; He *et al.*, 2013).

Several syntheses have highlighted the importance of studying plant-plant interactions across multiple life stages because the balance between the positive and negative components of interactions often shifts as plants age (i.e. ontogenetic shift) (Callaway & Walker, 1997; Brooker *et al.*, 2008). Many studies show that the effect of neighboring plants transitions from net positive (i.e. facilitative) to neutral or net negative (i.e. competitive) as a plant progresses through life-history stages (Miriti, 2006; Reisman-Berman, 2007; Valiente-Banuet & Verdú, 2008; Armas & Pugnaire, 2009; Paterno *et al.*, 2016). This pattern likely reflects the fact that larger plants typically have greater resource requirements and lower sensitivity to abiotic extremes (Grubb, 1977), increasing their sensitivity to competition while reducing the benefits of environmental stress amelioration by neighboring plants.

Although the effect of environmental stress on interaction outcomes is likely constrained by age-dependent expression of plant traits, few studies have tested whether ontogenetic shifts are modulated by abiotic factors. Two recent studies (Schiffers & Tielbörger, 2006; Le Roux *et al.*, 2013) have shown that the net outcome of interactions remained positive for longer under more stressful conditions, demonstrating that ontogenetic shifts from facilitation to competition can be delayed under greater environmental stress, whereas another study (Soliveres *et al.*, 2010) found unpredictable shifts in interaction intensity in relation to ontogeny and environmental conditions.

In dryland ecosystems, shrub facilitation of tree establishment is a widespread example of plant-plant interactions with major implications for community dynamics. Large, long-lived perennials such as trees experience profound changes in environmental tolerance and resource needs with age, and the requirements for regeneration are much narrower than the range of conditions in which an adult can persist (Grubb, 1977). Therefore, tree recruitment in dry forests is often limited to favorable microsites, where abiotic stress is reduced (Redmond & Barger, 2013). Shrub modification of the under-canopy environment can provide favorable conditions for tree establishment, and shrub facilitation of tree seedlings has been observed in drylands across the globe (McAuliffe, 1986; Kitzberger *et al.*, 2000; Chambers, 2001; Gómez-Aparicio *et al.*, 2005; Smit *et al.*, 2007; Sthultz *et al.*, 2007; Ziffer-Berger *et al.*, 2017). Shrubs ameliorate non-resource abiotic stress by reducing solar radiation, wind velocity, plant transpiration loss, soil temperatures, and soil water loss through evaporation (Kitzberger *et al.*, 2000; Lortie & Cushman, 2007; Holmgren *et al.*, 2012). Shrubs have both positive and negative effects on under-canopy resources, with litter-associated increases in soil fertility and moisture retention (Walker *et al.*, 2001) offset by the shrub's resource use (Maestre *et al.*, 2003). Additionally, shrubs can indirectly facilitate tree seedlings through protection from herbivory (Gómez-Aparicio *et al.*, 2008). In arid and semi-arid environments, some previous studies have found that competitive interactions increase with elevation

(Pugnaire & Luque, 2001; Sthultz *et al.*, 2007), while others have found complex spatial patterns of plant-plant interactions due to opposing water and stress gradients (Tielbörger & Kadmon, 2000; Callaway *et al.*, 2002; Maestre & Cortina, 2004).

In this study, we examined the interactions between big sagebrush (*Artemisia tridentata*) and singleleaf pinyon pine (*Pinus monophylla*) seedlings and juveniles, along a gradient of elevation in a semiarid environment. These species interact across broad environmental gradients, both within and at the edges of pinyon-juniper woodlands. Pinyon-juniper woodlands and sagebrush semi-desert are spatially heterogeneous (West, 1983), resulting in high variability among the microhabitats available for seedling establishment. Under-shrub microhabitats have been observed to have higher nutrient availability, a narrower range of daily temperatures, and more near-surface soil water than shrub interspaces (Burkhardt & Tisdale, 1976; Chambers, 2001). Experimental studies have found that *P. monophylla* seedling survival is higher under *A. tridentata* than in interspaces in the first two years after germination (Callaway *et al.*, 1996; Chambers, 2001). *P. monophylla* individuals that reach maturity eventually outsize and outlive their *A. tridentata* nurse plants. However, it is not known whether *A. tridentata* facilitates *P. monophylla* in ontogenetic stages beyond the seedling stage, or whether the timing of shifts in their interaction varies based on differences in the abiotic environment. Here, we used controlled seeding and shrub removal experiments, coupled with microhabitat environmental data, to test the following hypotheses: 1) the effect of *A. tridentata* cover on *P. monophylla* shifts from facilitative to competitive with *P. monophylla* ontogeny; and 2) the ontogenetic shift in interaction outcomes is delayed at lower elevations, where greater environmental stress increases the importance of habitat amelioration by *A.*

tridentata.

MATERIALS AND METHODS

Study area and experimental design

This study took place in Barrett Canyon (39°05’37” N, 117°29’38” W), an east-to-west oriented drainage on the eastern slope of the Shoshone Mountains in Nye County, Nevada, USA. The study canyon was chosen for its uniformity in relation to potentially confounding factors – aspect orientation, canyon bottom width, and the density and composition of woody plant communities. Lithology of the Shoshone Mountains consists of welded and non-welded silica ash flow tuff, and alluvial fan soils are classified as coarse loamy mixed frigid Typic Haploxerolls (Rau *et al.*, 2005). Average annual precipitation on the eastern slope of the Shoshone Mountains ranges from 23cm at the valley bottom to 50cm at the tops of drainages and arrives mostly as winter snow and spring rains (Board *et al.*, 2011). A weather station from the adjacent Desatoya mountain range (Western Regional Climate Center, 2018) recorded a drought in recent years (2012-2013) but above-average precipitation for the study period (2016-2017; Fig. 1). Woodlands of varying density within Barrett Canyon are dominated by *Pinus monophylla* (singleleaf pinyon pine), with lesser cover of *Juniperus osteosperma* (Utah juniper). *P. monophylla* foliage is dimorphic, transitioning from juvenile to adult (needle) foliage with plant growth stage. Pinyon-juniper woodlands within the study canyon are dissected by several large alluvial fans, which are dominated by *Artemisia tridentata* (big sagebrush), a non-sprouting shrub. *A. tridentata* is also present in tree interspaces within the woodland belt and in areas above and below the current extent of pinyon-juniper woodlands. Subspecies *A. tridentata* ssp. *wyomingensis* occurs at the lower end of the canyon, *A. tridentata* ssp. *vaseyana* occurs at the upper end, and the two subspecies overlap (and likely hybridize) in the middle portions of the canyon.

We located three study sites on *A. tridentata*-dominated alluvial fans within the study canyon, which are regularly spaced along an elevational gradient (2100, 2250, and 2450m) and encompass the range of *P. monophylla* in the watershed. At each site, we established experiments to examine *A. tridentata* effects on three ontogenetic stages of *P. monophylla* establishment: (1) first-year seedlings, (2) early juveniles (with juvenile foliage only), and (3) late juveniles (with adult foliage in at least one previous year). To examine the effect of *A. tridentata* cover on *P. monophylla* first-year seedlings, we planted *P. monophylla* seeds into three microhabitat treatments: under the canopy of a representative adult *A. tridentata* plant ('under-shrub'), in the sparsely vegetated areas between shrubs ('interspace'), and next to the stem of a removed *A. tridentata* plant that was cut at the ground surface ('shrub-removal'). To examine the effect of *A. tridentata* cover on *P. monophylla* early and late juveniles, naturally-occurring associations between adult *A. tridentata* and juvenile *P. monophylla* were randomly assigned to one of two microhabitat treatments: no alteration of *A. tridentata* - *P. monophylla* association ('under-shrub') and full removal of the associated *A. tridentata* plant ('shrub-removal'). The number of replicates within each microhabitat treatment depended on the ontogenetic stage. Abiotic measurements were collected from a central location at each study site, but from microhabitat locations that were not used for the above *P. monophylla* experiments.

P. monophylla **seedling emergence and first-year survival: seeding experiment**

At each of the three sites, five replicate blocks of three microhabitat treatments were established: under-shrub, interspace, and shrub-removal. Two representative *A. tridentata* plants were chosen with a canopy diameter of >50cm for under-shrub and shrub-removal treatments, and the interspace treatment was located centrally between them. Nine seeds were planted in gridded arrays with 7cm spacing within each microhabitat treatment location (3 sites x 5 blocks x 3 microhabitat treatments x 9 seeds = 405 seeds total).

Seeds were collected in September 2016 from a nearby mountain range at approximately the same elevation as our middle-elevation study site. All seeds were visually inspected, and only seeds that were both structurally sound and filled were used. In November 2016, microhabitat treatments were implemented and seeds were planted 3cm deep (Chambers, 2001). To minimize rodent predation, the seed arrays were covered with hardware cloth cages that were 30cm x 30cm wide and 10cm high. The cage walls were buried by 1-2cm and staked down with U-pins. In the under-shrub and shrub-removal microhabitats, surface litter was removed prior to planting and then evenly applied on top of the planted seed array. No litter was present in the interspace microhabitats. Planting locations were monitored for seedling emergence and survival at 1-2 week intervals from April to July 2017, and then monthly until October 2017.

P. monophylla **juvenile survival and growth: nurse shrub removal experiment**

To examine the effect of *A. tridentata* cover on *P. monophylla* juveniles, we experimentally manipulated naturally-occurring associations between adult *A. tridentata* and young *P. monophylla*. In May of 2016, we surveyed the 4-17 ha alluvial fans that comprised the three study sites for *P. monophylla* juveniles shorter than 1.5m in height. Few *P. monophylla* juveniles were found in shrub interspaces, and all of these had evidence that they had once grown in association with a now-deceased *A. tridentata* plant (e.g. wood remnants near their base), so we were not able to include an 'interspace' group. For our experimental treatments, we only used clear associations between *P. monophylla* juveniles and healthy adult *A. tridentata* plants, which were randomly assigned to under-shrub or shrub-removal treatments. Our final sample included 30-32 early juveniles and 50-56 late juveniles at each site (93 total early juveniles; 156 total late juveniles). We used high-precision GPS to map the locations of the study plants so that they could be reliably relocated. For each *A. tridentata* - *P. monophylla* association, and prior to implementing experimental treatments, we measured: *A. tridentata* height and canopy area, *P. monophylla* total height, and the distance and cardinal direction from the *A. tridentata* stem to the *P. monophylla* juvenile. For late juvenile *P. monophylla*, we used bud scars to measure annual terminal leader growth for the five years prior to treatment (2011-2015) and for two years after treatment (2016-2017). All study plants were monitored for survival every 2-4 weeks during the 2016 growing season and every 4-8 weeks during the 2017 growing season.

Environmental measurements

We measured abiotic factors to characterize environmental conditions from three microhabitat treatments: under-shrub, interspace, and shrub-removal. We measured soil temperature and soil moisture from May to October of 2017. At each site, three sensor arrays were installed in each microhabitat treatment. Treatments were implemented in April 2017. For under-shrub and shrub-removal microhabitats, the sensor arrays were located 15cm to the north of the *A. tridentata* stem, which corresponded to an average of 41cm inside the drip line. Soil temperatures were recorded every two hours by five Maxim Thermochron iButton temperature data loggers in each sensor array: two were placed just under the soil surface, two were buried 3cm deep, and one was buried 10cm deep. For each sensor, we calculated temperature minimum, maximum, and range for each day, which were then summarized over the May-to-October measurement period. We also derived frost days (total days for which minimum soil surface temperature was < 0°C) and growing season length (total days between latest spring frost and earliest fall frost) for each sensor. We assigned a maximum growing season length of 132 days for sensors that did not record a frost event during the May-October study period (n=6).

Volumetric water content was measured in each sensor array with one EC-5 soil moisture sensor (METER, Pullman, WA, USA). The sensor measured integrated soil moisture in the top 10-cm of the mineral soil for a 0.2L measurement volume. EM50 data loggers (METER) were programmed to read sensors every minute and to store hourly averages. We used a 5-cm by 15-cm slide hammer (AMS, American Falls, ID, USA) to collect soil samples from three shrub interspaces at each site, which were dried at 105°C until constant mass, sieved to 2mm, and weighed to derive soil rock fraction and fine-soil bulk density. We estimated soil water release curves for each site, using a WP4C water potential meter (METER) to measure soil matric potential for at least ten fine soil (<2mm) subsamples with a range of known gravimetric water contents. Recorded volumetric water content was converted to gravimetric water content using fine-soil bulk density, and gravimetric water content was converted to soil water potential using the soil water release curves derived for each site. We derived total growing season wet days for each sensor, defined as the number of growing season days (using the growing season derived for each sensor, as described above) with soil water content above the permanent wilting point (total hours · 24 h^{-1} when hourly soil water matric potential was > -1.5 MPa). We measured soil depth in nine shrub interspace locations in each site by driving a metal rod into the soil using a sledgehammer until the rod was either stopped by rock or clay hardpan, or the entire 90cm length of rod was driven into the soil.

We measured photosynthetically active radiation (PAR) at noon on June 26, 2017. For each microhabitat treatment at each site, we measured PAR once a minute for 20 minutes. There was no cloud cover during our measurement period. PAR was measured using a QSO-S PAR photon flux sensor (METER), and raw data were converted to photosynthetic photon flux ($\mu mol \cdot m^{-2} s^{-1}$) using the manufacturer-provided conversion.

We measured plant-available pools of soil inorganic nitrogen (ammonium and nitrate) seasonally at four locations in each microhabitat treatment at each site. Treatments were implemented in May 2016, and soil samples were collected in May 2016, August 2016, October 2016, and May 2017. We used a 2-cm diameter soil probe to collect soil samples to 10-cm mineral soil depth. For under-shrub and shrub-removal treatment microhabitats, soil samples were collected from the eastern *A. tridentata* drip line. Soil ammonium and nitrate were extracted from 8-g soil samples with 40 mL of 1 M potassium chloride. After shaking for 1 hr the slurry was filtered through Whatman no. 1 paper and the elutant was analyzed on a flow injection analyzer (Lachat QuickChem 8500, Hach Company, Loveland CO, USA).

Statistical Analyses

Regression models were used to analyze *P. monophylla* outcomes as a function of microhabitat treatment, elevation, and their interaction for each ontogenetic stage (seedling, early juvenile, late juvenile). Linear regressions with Type-2 ANOVA statistics were used for models with a normally-distributed response variable (emergence, growth), and logistic regressions with Chi-squared ANOVA statistics were used for models with a categorical response (survival). For all models, both microhabitat treatment ('under-shrub', 'shrub-removal', and 'interspace' [emergence and seedling survival only]) and elevation (low, mid, and high) were categorical variables. *P. monophylla* emergence was represented by the percent of seeds in each array that emerged during one growing season. Seedling survival was calculated at the end of the first growing season, late juvenile survival was calculated at the end of the second growing season, and early juvenile survival was calculated at three time periods: the end of the first growing season, the end of the first winter, and the end of the second growing season. Some models were unable to estimate the microhabitat-elevation interaction effect due to fitted probabilities of exactly 0 or 1 (either 0% or 100% survival in some treatment-elevation combinations). In these cases, we modeled the effect of elevation on survival within specific treatment types: seedling survival in 'under-shrub' treatment only, and early juvenile survival in 'shrub-removal' treatment only. To test whether shrub removal effects were dependent on plant size, we also modeled final survival of early juveniles from the 'shrub removal' treatment as a function of the interaction of elevation and early juvenile height at the start of the study.

To directly compare interaction strength among *P. monophylla* ontogenetic stages, we used the relative interaction index (RII; Armas *et al.*, 2004). RII is bounded between -1 and 1, with positive values indicating net facilitation, negative values indicating competition, and larger absolute values indicating stronger interaction intensity. RII was calculated for each site and *P. monophylla* life stage by comparing outcomes for nearby pairs of under-shrub and shrub-removal individuals (except for emergence, which was compared between pairs of nearby seed arrays to account for spatial clustering of seeds).

Elevational differences in pre-treatment plant characteristics and general abiotic environmental characteristics were analyzed using simple linear models. Plant characteristic variables included *A. tridentata* height and canopy cross-sectional area, *P. monophylla* 5-yr average late juvenile stem growth, and *P. monophylla* juvenile direction from *A. tridentata* associate [transformed into a northeastness index ranging from -1 to +1]. General abiotic characteristics included soil depth, soil rock fraction, soil bulk density. To test how treatments affected the abiotic environment across elevations, we used linear models of abiotic variables (mean daily temperature minimum, maximum, and range; frost days; growing season length; growing season wet days; and photosynthetically active radiation) as a function of microhabitat, elevation, and their interaction. We used linear mixed models of total available nitrogen as a three-way interaction between microhabitat, elevation, and sampling date (factor), with a random intercept for sample ID to account for temporal dynamics with repeated measures of soil nitrogen. All analyses were performed in R version 3.3.3 (R Core Team, 2015).

RESULTS

A. tridentata microhabitat effects on environmental characteristics across a gradient of elevation

Photosynthetically active radiation (PAR) differed among treatments ($p<0.001$) and elevations ($p<0.001$), but there was no interaction ($p=0.38$) between treatment and elevation. Among treatment types, PAR varied by more than an order of magnitude. In the under-shrub treatments, PAR averaged 160 $\mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$, compared to an average of 3738 $\mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$ in the shrub-removal and interspace treatments (Fig. 2a). Higher elevations had lower PAR in all treatment types, and the highest elevation had 3-30% lower PAR than the lowest elevation.

At all measured depths (0, 3, and 10 cm), soil temperature was strongly related to both microhabitat treatment ($p<0.001$) and elevation ($p<0.01$), but we again found no interaction between treatment and elevation ($p>0.06$). For all soil depths and at all elevations, maximum and mean daily temperature were lower, and minimum daily temperature was higher, in the under-shrub treatment compared to the shrub removal or interspace treatments (Fig. 2b), resulting in much smaller daily soil temperature ranges under *A. tridentata*. Mean, minimum, and maximum daily soil temperatures at all depths were lowest at the high elevation site (Fig. 2b). However, elevation was more strongly related to maximum daily temperature than to minimum daily temperature (Appendix C: Fig. C1a), such that the high elevation had narrower daily temperature ranges than the low elevation. Frost days were more frequent at the middle and high elevation ($p=0.002$), and were, on average, twice as frequent in the interspace or shrub removal microhabitats than under shrubs ($p<0.001$; Appendix C: Fig. C1b). Growing season was shorter at the middle and high elevations than at the low elevation (p=0.012), and was 4-5 days longer in the under-shrub treatment compared to interspaces or shrub removals (p=0.002; Appendix C: Fig. C1c).

Higher elevation soils were rockier, with nearly double the fraction of rock fragments than the lowest elevation, and thus had lower fine-soil bulk density (Table 1). Soil depth was highly variable and did not differ significantly among elevations (p=0.43; Table 1). Total wet days (number of growing season days for which soil matric potential was above wilting point) was not related to treatment (p=0.50), elevation (p=0.74), or their interaction (p=0.42; Fig. 2c). Plant-available inorganic nitrogen did not differ across elevations (p=0.06) but varied non-linearly through time, and all treatments showed a pulse of available N after the growing season had ended (date; p<0.001; Fig. 2d). At all elevations, the late-season pulse of N was nearly three times higher in the shrub removal treatment than in the interspace or under shrub treatments (treatment*date; p<0.001).

A. tridentata **microhabitat effects on** ***P. monophylla*** **at multiple stages of regeneration and across a gradient of elevation**

From 405 planted *P. monophylla* seeds, a total of 77 (19%) emerged (Fig. 3a). Emergence varied by elevation of the study site (p=0.003): 20% at the low elevation, 26% at the mid elevation, and 11% at the high elevation. Emergence did not differ among *A. tridentata* microhabitat treatments (p=0.58), nor by the interaction between microhabitat treatment and elevation (p=0.40).

P. monophylla seedling survival during the first growing season was strongly dependent on *A. tridentata* microhabitat treatment (p<0.001). Half of all seedlings located under *A. tridentata* survived the first growing season, whereas all seedlings located in the interspace or shrub-removal habitats died (Fig. 3b). Among seedlings in the under-shrub treatment, percentage survival was positively related to elevation (p=0.04). However, given elevational differences in emergence, the total number of live seedlings at the end of the first growing season was similar across elevations (Fig. 3c). Of 45 seeds planted under shrubs at each elevation, three seedlings were alive after one growing season at the low elevation, five were alive at the mid elevation, and four were alive at the high elevation.

Prior to treatment implementation, nurse shrub characteristics varied across the elevational gradient. *A. tridentata* size had a non-linear relationship with elevation, and plants were both tallest (p<0.001) and had the largest canopy cross-sectional area (p=0.003) at the middle elevation (Table 1). At low and mid elevations, *P. monophylla* juveniles (both early and late) tended to be located to the northeast of their *A. tridentata* associate, whereas *P. monophylla* juveniles at the high elevation varied in their position within the *A. tridentata* canopy (p=0.01; Table 1; Appendix C: Fig. C2).

P. monophylla early juvenile survival was greatly reduced by removal of *A. tridentata* (p<0.001 for all time intervals). At the end of the second growing season, only 35% of all early juveniles in the shrub-removal treatment were still alive, compared to 90% in the under-shrub treatment. However, the interaction between *A. tridentata* microhabitat treatments and elevation shifted through time (Fig. 4a). At the low elevation, shrub removal induced a rapid mortality response, and at the end of the first growing season, survival in the shrub-removal treatment was lowest at the low elevation site (p=0.02). At mid and high elevations, the response to shrub removal was more delayed, and there was no difference in survival among elevations after the first winter (p=0.41) or at the end of the second growing season (p=0.71). Taller early juveniles were more likely to survive shrub removal (p<0.001), and there was an interaction with elevation (p=0.002) such that there was a threshold relationship between height and survival at the low elevation and a more continuous relationship at the high elevation site (Fig. 4b).

The survival of late juvenile *P. monophylla* did not differ by *A. tridentata* microhabitat treatment, elevation, or their interaction, and only two (1%) late juveniles died over the course of our study (Fig. 5a). For the five-year period prior to treatment, *P. monophylla* late juvenile terminal leader growth was positively related to elevation (p=0.02), and annual growth at the high elevation site averaged 125% of growth at the low elevation (Table 1). This relationship persisted after treatment, and leader growth varied by elevation in both the first (p=0.002) and second (p=0.01) years after treatment (Fig. 5b-c). In the first year after treatment (Fig. 5a), late juvenile terminal leader growth was not affected by treatment (p=0.87). However, shrub removal decreased late juvenile growth in the year following treatment (p=0.02; Fig. 5b) consistently for all elevations (treatment*elevation; p=0.79).

Interaction intensity (RII) varied by *P. monophylla* ontogenetic stage (p<0.0001), with the strongest facilitative effects on seedling survival and early juvenile survival (Fig. 6). Interaction intensity did not differ among elevations (p=0.92), and there was not a significant interaction between elevation and ontogenetic stage (p=0.08), indicating that elevation did not have a strong effect on the temporal progression of interaction intensity.

DISCUSSION

Ontogenetic shift in plant-plant interactions

Our study contributes to growing evidence that the net outcome of plant-plant interactions often shifts with life stage of the focal species. In many ecosystems, facilitation has been shown to be strongest in the early life stages of the beneficiary (McAuliffe, 1986; Miriti, 2006; Reisman-Berman, 2007; Paterno *et al.*, 2016). Species traits have important effects on plant-plant interactions (Callaway, 1998), and ontogenetic shifts in physiology related to stress tolerance or resource acquisition can regulate the interactions between neighboring plants (Armas & Pugnaire, 2009; Soliveres *et al.*, 2010; Le Roux *et al.*, 2013). We found clear evidence that *A. tridentata* directly facilitates *P. monophylla* at multiple stages of regeneration, but that the effect of *A. tridentata* on *P. monophylla* shifted from positive toward neutral with *P. monophylla* ontogeny (Fig. 6).

In arid systems, shrubs modify abiotic factors associated with both non-resource stress (e.g. heat, cold, or salinity) and resource availability (e.g. soil water or nutrients), resulting in complex effects on associated plants (Michalet, 2006; Maestre *et al.*, 2009; Graff & Aguiar, 2017). In our study, *A. tridentata* greatly reduced non-resource stress for *P. monophylla* juveniles growing under its canopy. Consistent with previous studies (Chambers, 2001), the shading structure provided by *A. tridentata* cover reduced irradiance and was associated with lower maximum daily temperatures (Fig. 2a-b), which likely benefits *P. monophylla* juveniles by reducing cumulative atmospheric water demand (Kitzberger *et al.*, 2000; Lortie & Cushman, 2007; Holmgren *et al.*, 2012). Under-shrub environments also had longer growing seasons and higher minimum temperatures, suggesting that *P. monophylla* juveniles growing in association with *A.*

tridentata are less exposed to frost damage from cold conditions early and late in the growing season (Carlsson & Callaghan, 1991; Callaway *et al.*, 2002). In a previous study, Chambers (2001) found that *A. tridentata* cover reduced overwinter mortality of *P. monophylla* seedlings that survived the first growing season. Other studies have found that shrubs indirectly reduce biotic stress by providing protection from predation and herbivory (Callaway *et al.*, 1996; Chambers, 2001; Barbosa *et al.*, 2009), but our experimental design did not allow us to explicitly test for this effect.

In contrast to the strong effects of *A. tridentata* cover on non-resource stress, we found that net effects on resource availability were weak. Previous results have been mixed regarding the effect of *A. tridentata* on growing season soil water availability (Callaway *et al.*, 1996; Chambers, 2001). We found no net effects of *A. tridentata* cover on near-surface soil water potential (Fig. 2c), suggesting that the positive effects of shading (Holmgren *et al.*, 2012), increased litter and organic matter (Pugnaire *et al.*, 2004), and hydraulic redistribution (Prieto *et al.*, 2011) on surface soil water availability are outweighed by shrub water uptake (Armas & Pugnaire, 2009) and canopy interception (Dunkerley, 2000). Simulation models (Butterfield *et al.*, 2016) have shown that shrub cover effects on shallow soil moisture are the most positive in wet years, and our study took place during a relatively wet period (Fig. 1). Overall, the neutral effects of *A. tridentata* cover on soil moisture indicate that facilitation of *P. monophylla* is not likely due to increased water availability. Additionally, soil inorganic nitrogen did not differ between the interspace and under-shrub microhabitats as has been reported elsewhere (Charley & West, 1975; Chambers, 2001). However, net available nitrogen represents the balance between gross nitrogen mineralization and gross nitrogen uptake, and a substantial increase in soil nitrogen immediately after shrub removal (Fig. 2d; i.e. eliminating plant uptake while maintaining litter inputs) may suggest that soils under *A. tridentata* have larger pools of organic nitrogen with higher gross fluxes of nitrogen mineralization and uptake, thereby providing increased opportunities for nitrogen acquisition by shrub-associated plants.

A. tridentata modification of the abiotic environment was most beneficial for *P. monophylla* seedlings and early juveniles (Fig. 6). Our results suggest that first-year survival of *P. monophylla* seedlings represents a population bottleneck, as all seedlings in interspace microhabitats died before the end of their first growing season (Fig. 3). The relatively high seedling survival under *A. tridentata* suggests that *A. tridentata* cover is a major factor allowing *P. monophylla* to overcome this bottleneck, as has been reported previously (Callaway *et al.*, 1996; Chambers, 2001). Survival under *A. tridentata* was also higher for *P. monophylla* early juveniles with juvenile foliage (Fig. 4), though the importance of *A. tridentata* cover declined with *P. monophylla* early juvenile height. For *P. monophylla* late juveniles with adult (needle) foliage, survival was high in all microsites and was no longer affected by *A. tridentata* cover (Fig. 5). However, late juveniles grew faster in association with *A. tridentata* (Fig. 5c), contrary to a previous study that found that *A. tridentata* cover imposed a cost on associated *P. monophylla* juveniles by reducing growth rates (Callaway *et al.*, 1996).

Net interaction strength represents the balance between simultaneous facilitative and competitive interactions (Michalet *et al.*, 2014), and even though we did not observe net negative effects of *A. tridentata* on any tested stage of *P. monophylla* regeneration, our finding that the interaction shifted from strongly positive toward neutral with *P.*

monophylla ontogeny indicates the sum of weaker positive effects and/or stronger negative effects over time (Armas *et al.*, 2013). Specifically, we found that *P. monophylla* plants with only juvenile foliage (seedlings and early juveniles) benefitted more from *A. tridentata* cover than plants with adult foliage (late juveniles). The physiological importance of the shift from juvenile to adult foliage has not been investigated for *P. monophylla*. For other dryland conifer species, the transition from juvenile to adult foliage is associated with a reduction in maximum daily carbon assimilation and stomatal conductance, and a corresponding reduction in water lost to transpiration (Miller, 1995; Nowak *et al.*, 1999). Water potential of juvenile foliage thus tends to be lower than that of adult foliage for most of the growing season, which may explain why stress amelioration associated with *A. tridentata* shading was less important once juveniles developed adult foliage. Additionally, resource requirements increase with plant size, so *P. monophylla* ontogeny also likely corresponds to an increase in competitive interactions with *A. tridentata* over limited resources (Miriti, 2006). *P. monophylla* adults are orders of magnitude larger than adult *A. tridentata*, so eventually, the effects of their competition for resources become more limiting for *A. tridentata* (Connell & Slatyer, 1977). It is unclear at what point the interaction becomes bidirectional, or if the facilitation of *P. monophylla* establishment comes a cost to *A. tridentata* at all stages of *P. monophylla* development (Schöb *et al.*, 2014).

Timing of ontogenetic shift did not vary with elevation

Prior studies have hypothesized that ontogenetic shifts from facilitation to competition are delayed in more stressful locations (Schiffers & Tielbörger, 2006), where positive interactions are expected to be important for longer in a species life history. The elevational gradient across which our sites were distributed represents a gradient of primary productivity (West, 1983). We found that growth rates for both of our focal species were strongly correlated with elevation (Table 1), indicating higher stress at low elevations under common definitions of stress (Grime, 1979; Callaway & Walker, 1997). Contrary to other studies, however, we did not find evidence that facilitation was stronger at less productive sites (Pugnaire & Luque, 2001; Sthultz *et al.*, 2007), nor that the timing of the ontogenetic shift in the *A. tridentata* - *P. monophylla* interaction differed along the elevational gradient (Fig. 6; Le Roux *et al.*, 2013). Our results are also in disagreement with an observational study of these species (Ziffer-Berger *et al.*, 2014), which found that *P. monophylla* early juveniles were as likely to be found in interspaces as under *A. tridentata* in the wettest portions of the *P. monophylla* range, suggesting that facilitation strength may vary with abiotic stress at broader spatial scales.

What accounts for the lack of elevational differences in the timing of the ontogenetic shift? One potential explanation is that elevation integrates multiple gradients of stress, which may be oriented differently in relation to the gradient of elevation (Grime, 1977). Other studies in dry, mountainous environments have found complex spatial patterns of plant-plant interactions (Tielbörger & Kadmon, 2000; Callaway *et al.*, 2002; Maestre & Cortina, 2004; Cavieres *et al.*, 2006). Environmental data from our study suggest the presence of multiple stress gradients that varied in relation to elevation. The low elevation site had higher mean and maximum temperatures and higher levels of irradiance than the high elevation site (Fig. 2a-b), exposing *P. monophylla* juveniles to greater stress from increased atmospheric water demand and the potential for direct damage from high temperatures and incident radiation. However, the higher elevation sites had lower minimum temperatures and more frost events, potentially exposing early stages of *P. monophylla* to cold damage in the absence of shrub cover. Surprisingly, we did not find a clear relationship between growing season wet days and elevation (Fig. 2c), even though precipitation amounts tend to be positively related to elevation in our study area (West, 1983). Instead, orographic precipitation patterns may be offset by variation in soil texture, as surface soils at the high elevation were rockier and thus had lower water storage capacity. Additionally, unmeasured sources of biotic stress, including herbivory from insects and mammals (Callaway *et al.*, 1996; Chambers, 2001), also likely varied across the elevational gradient.

We found that *A. tridentata* facilitated *P. monophylla* at multiple stages of regeneration and at all elevations (Fig. 6), but our results suggest that the mechanisms of facilitation may differ by elevation, which may also be true in other regions with complex patterns of environmental stress (Armas *et al.*, 2013). At the low elevation site, shrub removal induced rapid *P. monophylla* mortality that was strongly linked to early juvenile size (Fig. 4) and naturally-occurring *P. monophylla* juveniles tended to be the northeast canopy of their *A. tridentata* associate (Table 1), suggesting that *A. tridentata* amelioration of environmental stress associated with solar radiation is a primary mechanism of facilitation for small, physiologically sensitive *P. monophylla*. In contrast, at the high elevation site, delayed mortality after shrub removal, a weak relationship between *P. monophylla* survival and early juvenile size (Fig. 4), and a random distribution within the *A. tridentata* canopy (Table 1), all suggest that mechanisms of facilitation may be less related to *P. monophylla* physiological tolerances, and may also involve indirect pathways such as protection from herbivory or other biotic mortality agents (McAuliffe, 1986; Smit *et al.*, 2007; Gómez-Aparicio *et al.*, 2008). Ultimately, disentangling the effects of multiple stress gradients in dry, mountainous regions will require more mechanistic studies that explicitly incorporate spatial and temporal variation to define stress in ways that are functional for the focal species.

Conclusions

P. monophylla and *A. tridentata* are dominant components of some of the most widespread vegetation types of the western US (US Geological Survey, 2011). The interaction between these two species is particularly important in the context of rapid global environmental change. In the western US, climate change is expected to increase the frequency and severity of disturbance events, including fire (van Mantgem *et al.*, 2013) and drought-induced tree mortality (van Mantgem *et al.*, 2009). Because *P. monophylla* is limited in its ability to establish in open areas, favorable microsites provided by *A. tridentata* cover are crucial in *P. monophylla* recovery after stand-replacing disturbance. In consequence, *P. monophylla* responses to disturbance are tightly linked to those of *A. tridentata*, which is itself highly variable and dependent on seed availability and favorable weather conditions (Ziegenhagen & Miller, 2009; Nelson *et al.*, 2014). Other shrub species may also facilitate *P. monophylla* establishment, but the spatial association of *P. monophylla* with other shrub species is much weaker than with *A. tridentata* (Urza, unpublished data). Other studies have hypothesized that with increasing aridity, tree regeneration may become increasingly dependent on the availability of cooler, wetter microsites for successful seedling establishment (Sthultz *et* *al.*, 2007; Redmond & Barger, 2013). However, the fact that we did not observe consistent differences in interaction outcomes across broad spatial gradients of climate suggests that this shrub-tree interaction may be relatively insensitive to increasing temperatures (Metz & Tielbörger, 2016). Our study contributes to the growing body of evidence that species interactions are important drivers of plant community dynamics (Brown *et al.*, 2001) and should be incorporated into models of vegetation responses to global change (Araújo & Luoto, 2007; Malanson *et al.*, 2017).

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TABLES

Table 1. Abiotic and biotic conditions for three study sites distributed along an elevational gradient. Data are given as mean ± 1 SE, with p-values shown for differences among elevations.

	Low elevation	Mid elevation	High elevation	p-value
Soil depth (cm; n=27)	28.7 ± 3.7	32.8 ± 4.6	40.0 ± 8.8	0.43
Soil rock fraction (prop; n=9)	0.37 ± 0.06	0.56 ± 0.02	0.62 ± 0.03	0.01
Fine-soil bulk density (g/cm^3; n=9)	0.95 ± 0.03	0.65 ± 0.02	0.48 ± 0.04	<0.001
Total bulk density (g/cm^3; n=9)	1.53 ± 0.11	1.48 ± 0.03	1.25 ± 0.03	0.04
Pinyon juvenile direction from sagebrush (northeastness index [-1 to 1]; n=241)	0.36 ± 0.07	0.36 ± 0.07	0.08 ± 0.09	0.01
Pinyon late juvenile 5-yr average stem growth (cm; n=156)	3.2 ± 0.16	3.8 ± 0.25	4.0 ± 0.18	0.02
Sagebrush height (cm; n=248)	51.3 ± 1.7	86.4 ± 2.5	73.7 ± 2.5	<0.001
Sagebrush canopy area (m^2; n=248)	0.64 ± 0.04	0.93 ± 0.07	0.78 ± 0.06	0.003

FIGURES

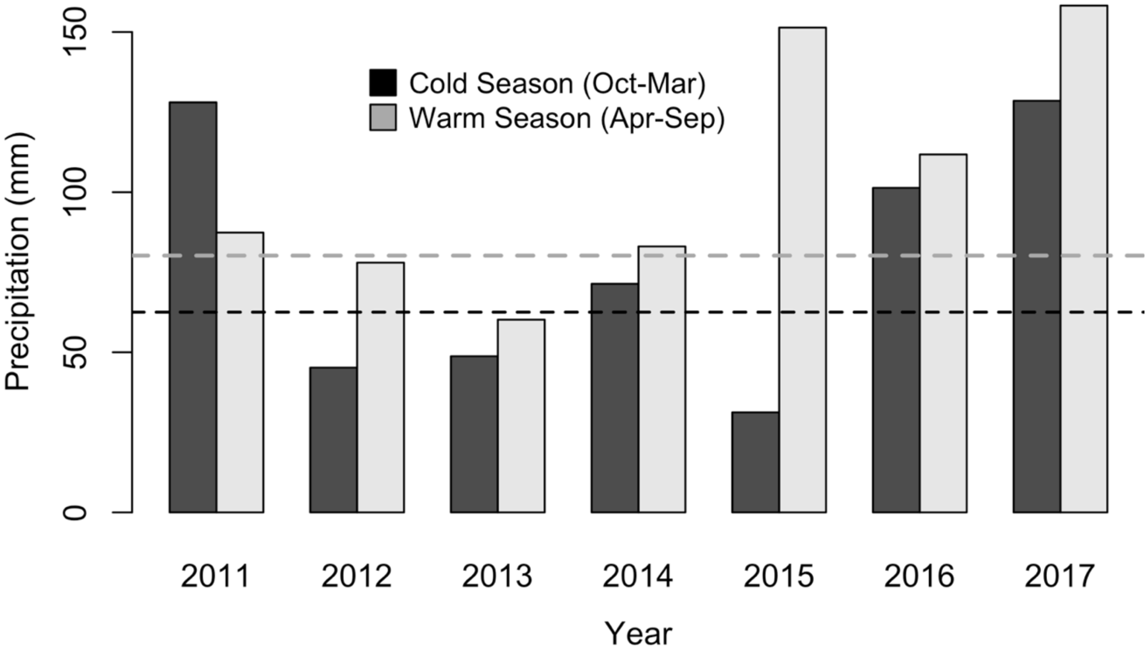


Figure 1. Annual precipitation totals for the cold (October to March) and warm season (April to September) prior to and during the study period. Dashed lines show the long-term means (1987-2018). Climate data are from the Desatoya Mountain RAWS Weather Station (Western Regional Climate Center, 2018) which is located at 1890m elevation approximately 23km to the north of the study area.

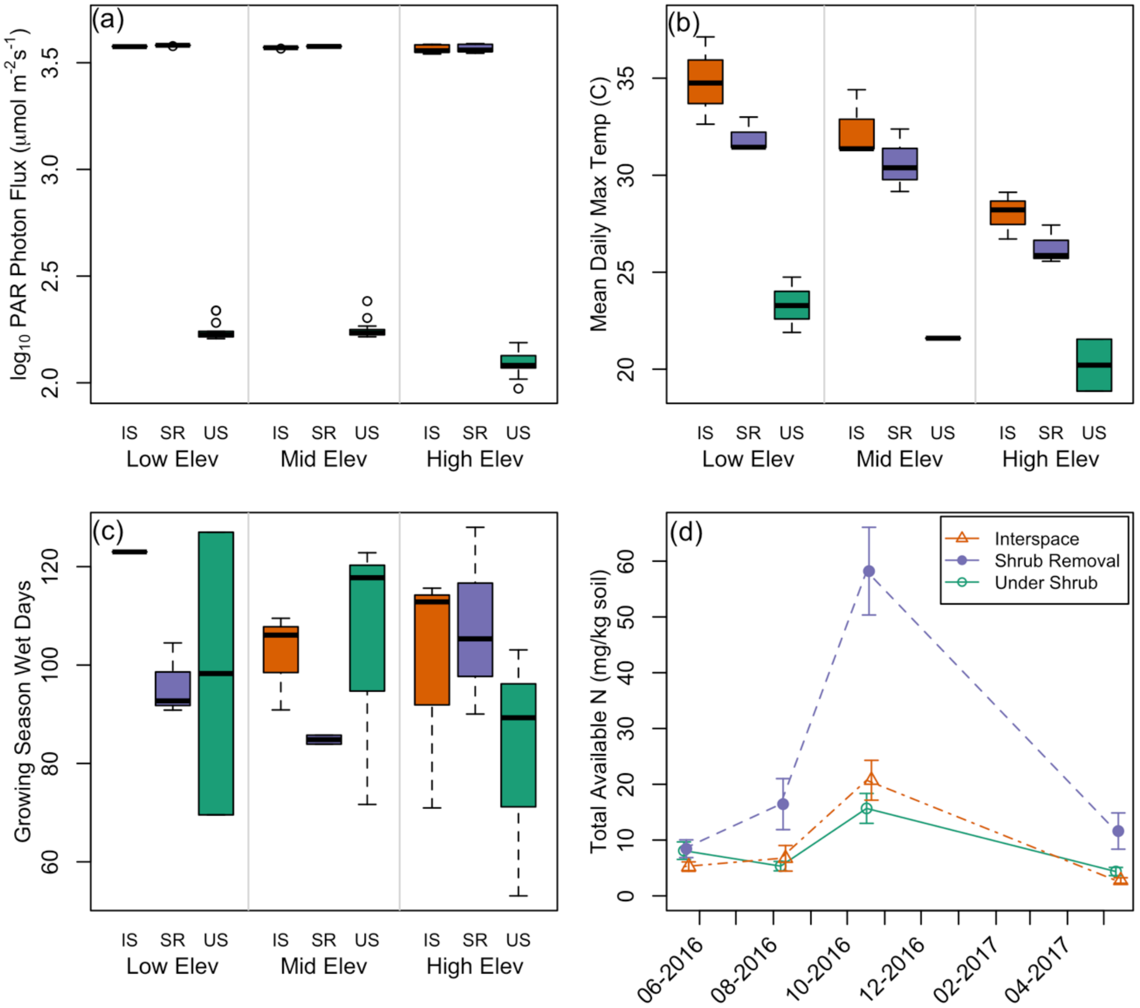


Figure 2. Abiotic environmental measurements from three shrub microhabitat treatments at three sites along an elevational gradient. (a) Midday photosynthetically active radiation near the summer solstice of June 2017 (n=135; shown in $\log_{10}$ scale). (b) Daily maximum soil temperature (10cm depth), averaged for May-October 2017 (n=27). (c) Total 2017 growing season wet days (total hours · 24 h^{-1} when hourly average soil water matric potential was > -1.5 MPa; n=24). (d) Total inorganic nitrogen from four sampling dates in 2016 and 2017 (n=48). There was no relationship between total inorganic nitrogen and elevation, so samples from all elevations (sites) are pooled for each microhabitat treatment. IS = interspace, SR = shrub-removal, US = under-shrub.

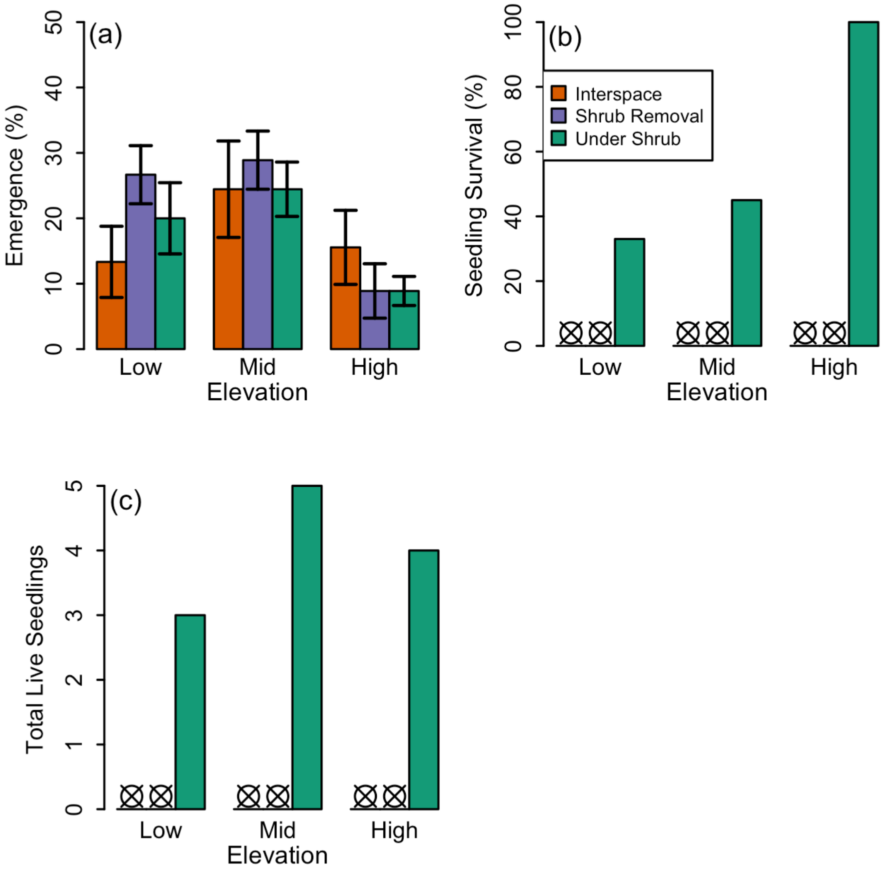


Figure 3. Fate of pinyon pine seeds planted in three shrub microhabitat treatments at three study sites along an elevational gradient. Seeds were planted in fall of 2016. (a) Percent of seeds (n=405) that emerged in 2016 (mean ± 1SE). (b) Percent of total seedlings (n=77) that survived the first growing season. (c) Total number of seedlings alive at the end of the first growing season (n=12).

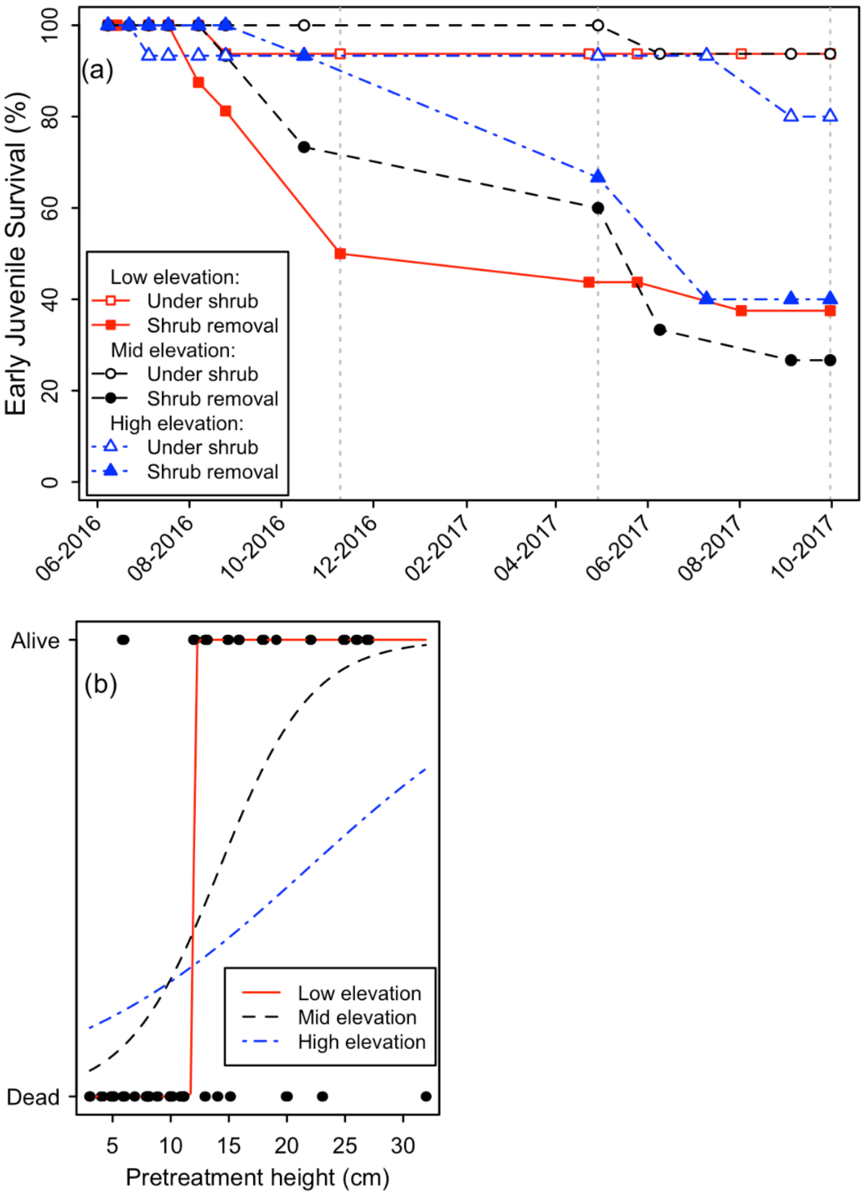


Figure 4. *P. monophylla* early juvenile survival in two shrub microhabitat treatments at three sites along an elevational gradient. Treatment occurred in early June 2016. (a) Early juvenile survival (%) over the 2016 and 2017 growing season, for 'under shrub' (open symbols) and 'shrub removal' (closed symbols) treatments (n=93). Temporal differences in of pinyon early juvenile mortality were tested on three dates represented by vertical dotted lines. (b) Status at the end of the 2017 growing season for all early juveniles in the shrub removal treatment (n=46) as a function of pretreatment height, overlaid with logistic regression prediction curves for each elevation.

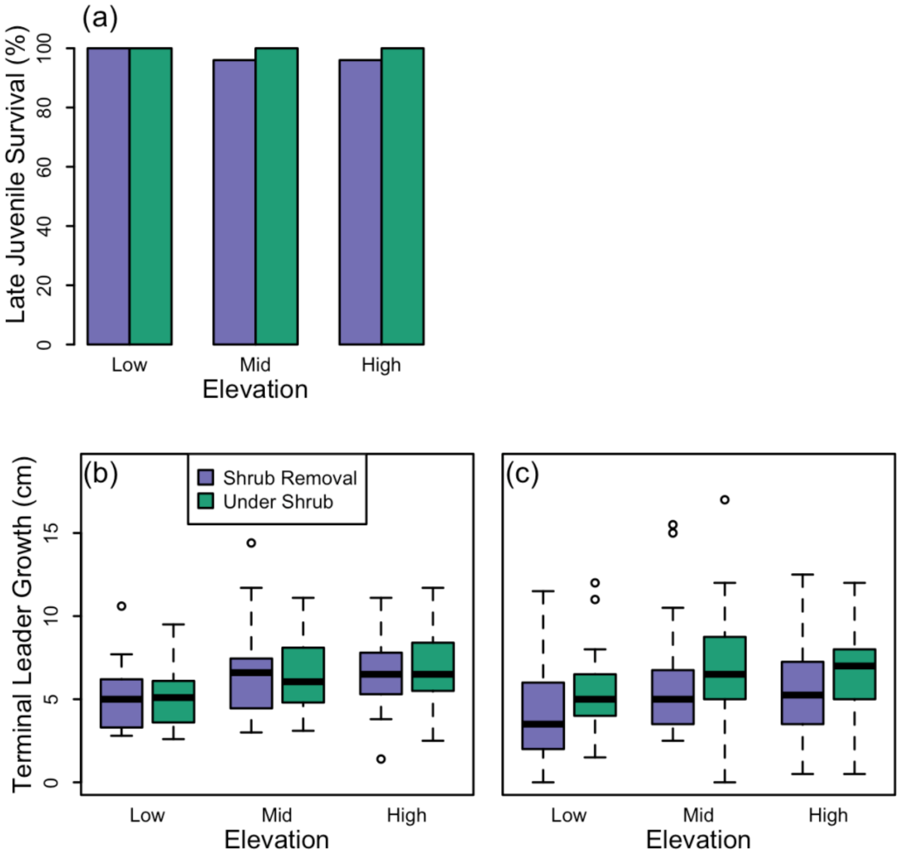


Figure 5. *P. monophylla* late juvenile survival and growth in two shrub microhabitat treatments at three sites along an elevational gradient (n=156). (a) Percent of late juveniles that were alive in October 2017. Terminal leader growth at the end of (b) the first year after treatment (2016) and (c) the second year after treatment (2017).

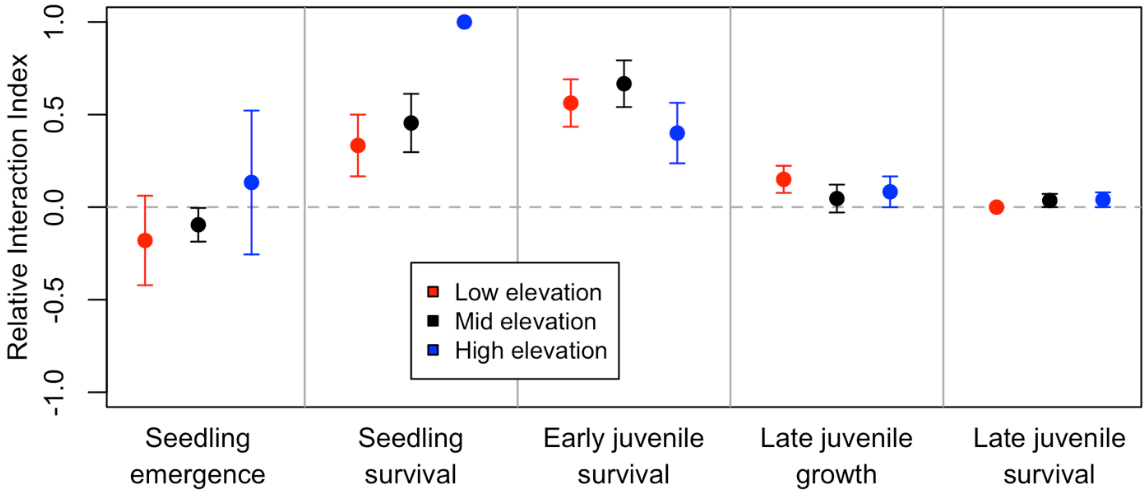


Figure 6. Ontogenetic shifts in interaction intensity between *A. tridentata* and *P. monophylla* for three sites along an elevational gradient. Relative interaction index (RII; shown as mean ± 1SE), a measure of interaction intensity, where positive values indicate facilitation and negative values indicate competition, is shown for each life stage of *P. monophylla*. Seedling emergence and survival were quantified at the end of the first growing season after treatment, and early and late juvenile survival and growth were quantified at the end of the second growing season.

APPENDIX A. Supporting information for Chapter 1

Identifying controls on lower treeline position for understanding response to environmental change

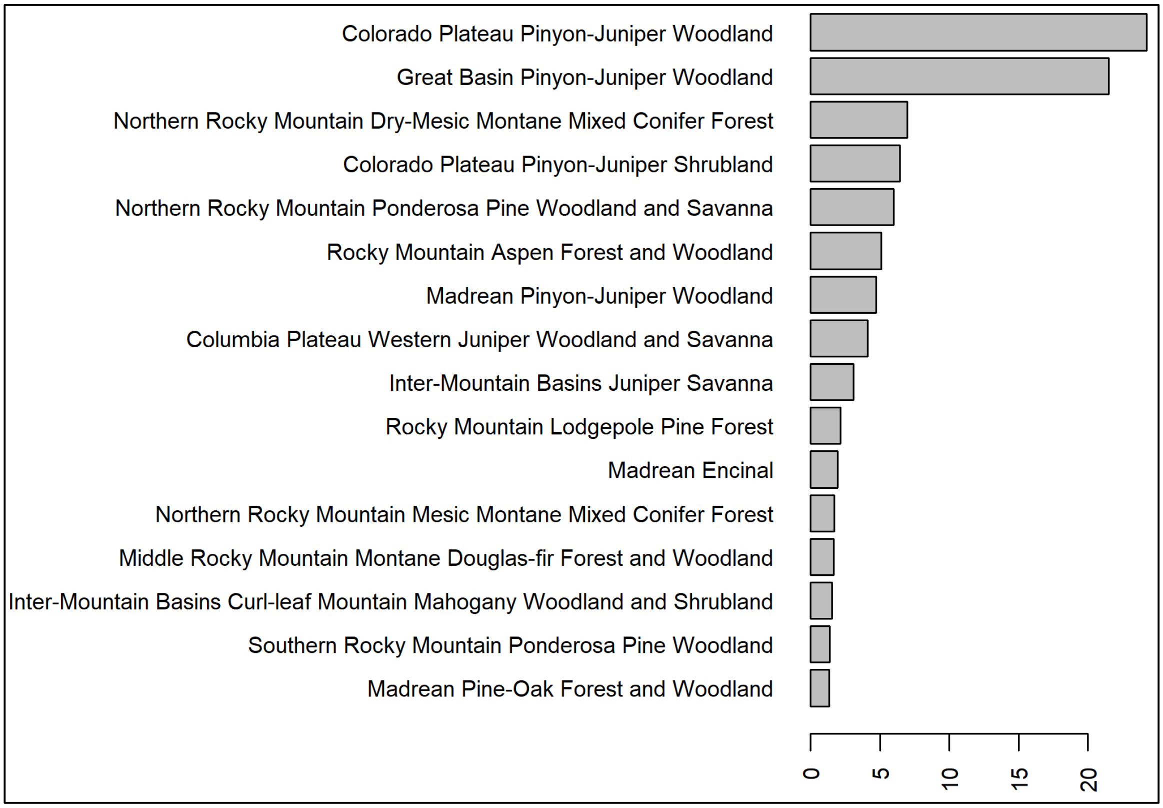
Table A1. Merged land cover categories.

Merged category	NVC_MACRO classification categories[1]
Colorado Plateau Pinyon-Juniper Woodland	• Colorado Plateau Pinyon-Juniper Woodland • Colorado Plateau Pinyon-Juniper Shrubland
Northern Rockies Dry Mixed Conifer Forest	• Northern Rocky Mountain Ponderosa Pine Woodland and Savanna • Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest
Shrubland or Grassland	• Great Basin & Intermountain Tall Sagebrush Shrubland & Steppe • Great Basin & Intermountain Dwarf Sage Shrubland & Steppe • Great Basin & Intermountain Dry Shrubland & Grassland • Southern Vancouverian Lowland Grassland & Shrubland • Mojave-Sonoran Semi-Desert Scrub • North American Warm-Desert Xero-Riparian • Great Basin & Intermountain Xero-Riparian Scrub • Northern Rocky Mountain – Vancouverian Montane & Foothill Grassland & Shrubland • Rocky Mountain – Vancouverian Subalpine & High Montane Mesic Grass & Forb Meadow • Southern Rocky Mountain Montane Grassland & Shrubland • Rocky Mountain Alpine Scrub, Forb Meadow & Grassland • Vancouverian Alpine Scrub, Forb Meadow & Grassland • Great Basin Saltbrush Scrub • North American Warm Desert Alkaline-Saline Semi-Desert Scrub • Warm Interior Chaparral • Cool Interior Chaparral • California Chaparral • California Coastal Scrub • Great Plains Mixedgrass Prairie & Shrubland • California Annual & Perennial Grassland • Apacherian-Chihuahuan Semi-Desert Grassland & Steppe
Rock, Cliff, or Scree	• Barren • Great Plains Badlands Vegetation • Great Plains Cliff, Scree & Rock Vegetation • Intermountain Basin Cliff, Scree & Rock Vegetation • North American Warm Semi-Desert Cliff, Scree & Rock Vegetation • Rocky Mountain Alpine Cliff, Scree & Rock Vegetation • Rocky Mountain Cliff, Scree & Rock Vegetation • Vancouverian Alpine Cliff, Scree & Rock Vegetation

	• Vancouverian Cliff, Scree & Rock Vegetation • Warm Pacific Coastal Beach, Dune & Bluff Vegetation
Urban or Developed	• Developed & Urban • Quarries, Mines, Gravel Pits and Oil Wells • Recently Disturbed or Modified
Agriculture	• Herbaceous Agricultural Vegetation • Introduced & Semi Natural Vegetation
Seasonal or Perennial Wetlands	• Cool Semi-Desert Alkali-Saline Wetland • Great Plains Brackish Marsh & Saline Wet Meadow • Great Plains Floodplain Forest • Great Plains Wet Meadow, Wet Prairie & Marsh • North Pacific Bog & Fen • Open Water • Rocky Mountain and Great Basin Flooded & Swamp Forest • Rocky Mountain Subalpine & Montane Fen • Vancouverian Flooded & Swamp Forest • Warm Desert Freshwater Shrubland, Meadow & Marsh • Warm Mediterranean & Desert Riparian, Flooded & Swamp Forest • Warm Semi-Desert & Mediterranean Alkaline-Saline Wetland • Western North American Vernal Pool • Western North American Montane Wet Meadow & Low Shrubland • Western North American Lowland Freshwater Wet Meadow, Marsh & Shrubland

[1] (US Geological Survey, 2011)

Figure A1. Percent (%) of lower treeline length by forest type (NVC_MACRO classification categories; US Geological Survey, 2011). Only forest types representing >1% of lower treeline are shown (all other categories combined represented 6.2%).



Appendix A1. Additional outputs from boosted regression tree models.

Colorado Plateau Pinyon-Juniper Woodland

Model parameters and performance.

Model parameters:

Number of trees = 1250

Bag fraction = 0.5

Model complexity = 5

Learning rate = 0.005

Family = “bernoulli”

Model performance:

Mean total deviance = 1.386

Mean residual deviance = 1.244

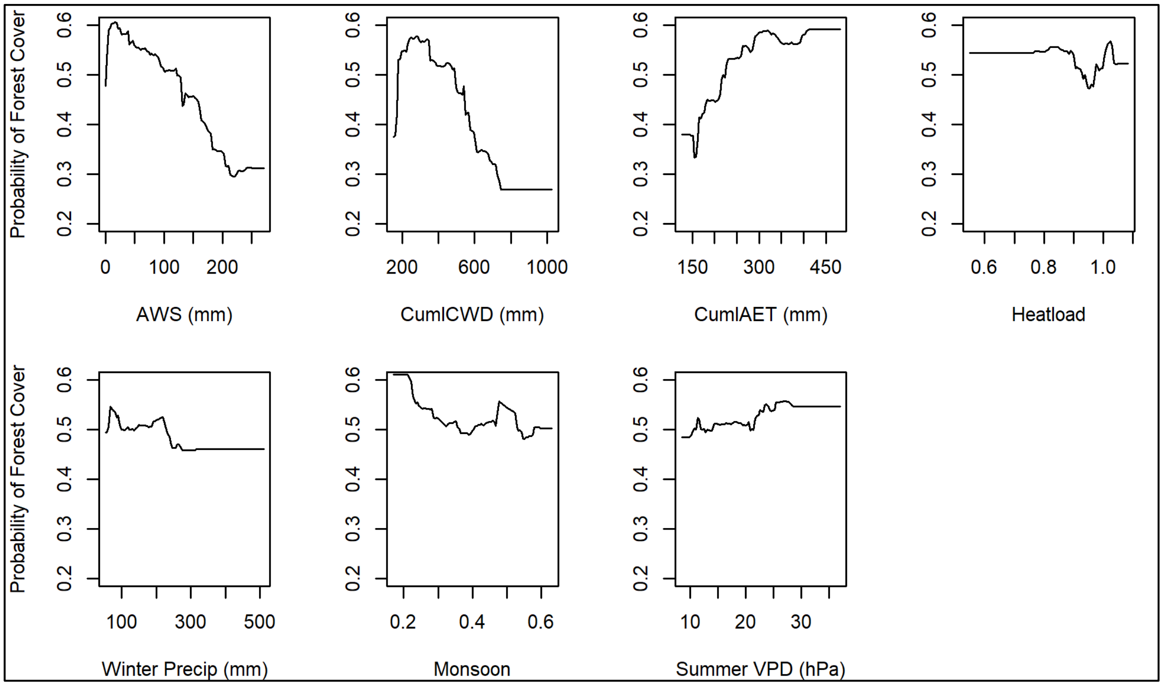
Estimated cross-validated deviance = 1.313 ; SE = 0.007

AUC (training data set) = 0.72

Cross-validated AUC = 0.652 ; se = 0.006

AUC (test data set) = 0.638

Partial dependence functions for all predictor variables after accounting for the mean effect of other predictors (displayed in order of variable importance rank). Predicted response is shown as the probability that a point is forested.



Interaction scores for all combinations of predictor variables.

	CumlCWD	CumlAET	Heatload	Winter_ppt	Monsoon	Summer_vpd
AWS	14.77	4.17	14.08	0.69	0.45	0.14
CumlCWD		6.86	2.11	1.78	0.63	0.19
CumlAET			0.65	0.10	0.36	0.18
Heatload				0.33	0.25	1.70
Winter_ppt					0.46	0.11
Monsoon						0.30

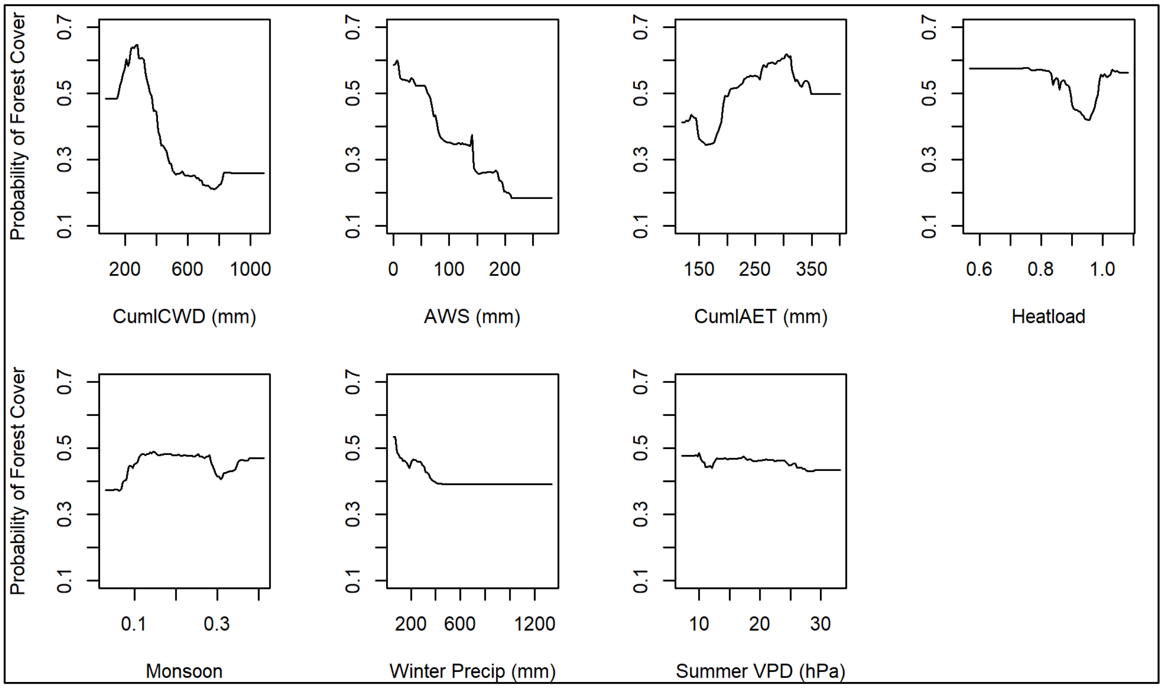
Great Basin Pinyon-Juniper Woodland

Model parameters and performance.

Model parameters:
Number of trees = 1450
Bag fraction = 0.5
Model complexity = 5
Learning rate = 0.005
Family = “bernoulli”

Model performance:
Mean total deviance = 1.383
Mean residual deviance = 1.158
Estimated cross-validated deviance = 1.233; SE = 0.005
AUC (training data set) = 0.769
Cross-validated AUC = 0.716; se = 0.004
AUC (test data set) = 0.670

Partial dependence functions for all predictor variables after accounting for the mean effect of other predictors (displayed in order of variable importance rank). Predicted response is shown as the probability that a point is forested.



Interaction scores for all combinations of predictor variables.

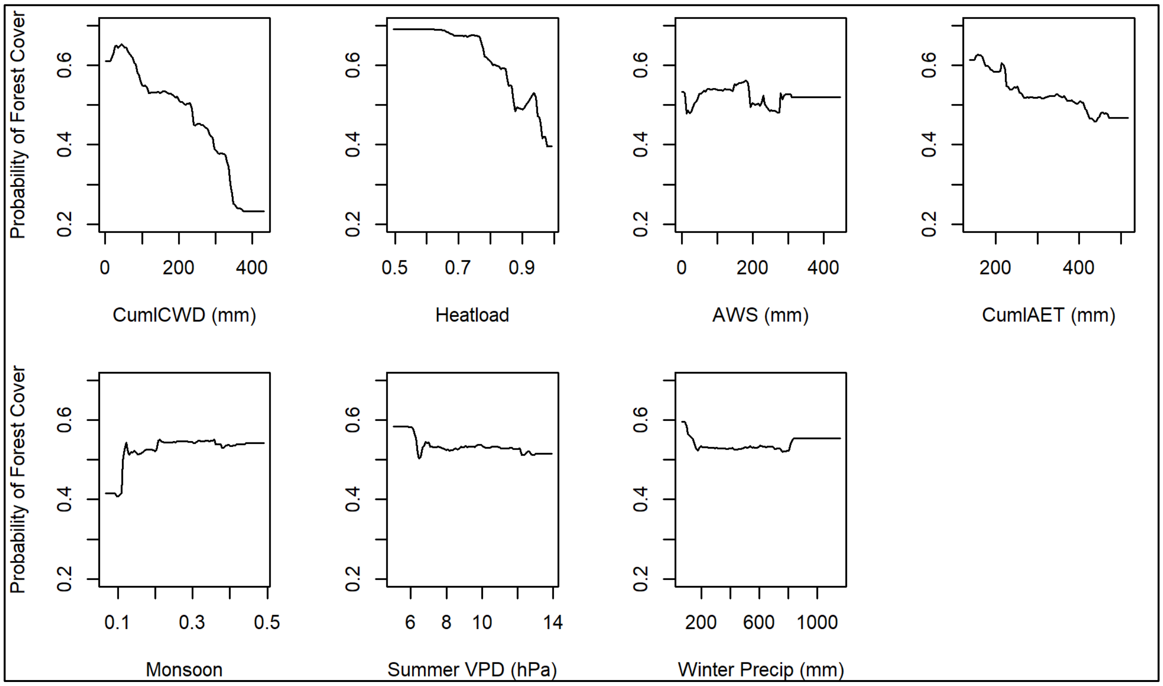
	CumlCWD	CumlAET	Heatload	Winter_ppt	Monsoon	Summer_vpd
AWS	65.95	8.50	4.34	0.23	0.60	0.29
CumlCWD		106.09	5.31	0.07	0.88	0.92
CumlAET			2.33	0.11	0.68	0.33
Heatload				0.46	1.66	0.65
Winter_ppt					0.52	0.33
Monsoon						0.38

Northern Rocky Mountain Dry Mixed Conifer Forest

Model parameters and performance.

Model parameters:	**Model performance:**
Number of trees = 1000	Mean total deviance = 1.383
Bag fraction = 0.5	Mean residual deviance = 1.28
Model complexity = 5	Estimated cross-validated deviance = 1.335; SE = 0.005
Learning rate = 0.005	AUC (training data set) = 0.697
Family = "bernoulli"	Cross-validated AUC = 0.622; SE = 0.007
	AUC (test data set) = 0.636

Partial dependence functions for all predictor variables after accounting for the mean effect of other predictors (displayed in order of variable importance rank). Predicted response is shown as the probability that a point is forested.



Interaction scores for all combinations of predictor variables.

	CumlCWD	CumlAET	Heatload	Winter_ppt	Monsoon	Summer_vpd
AWS	2.33	1.00	10.43	0.16	0.76	0.18
CumlCWD		4.01	10.60	0.41	1.21	0.34
CumlAET			3.40	0.09	0.17	0.63
Heatload				0.11	1.18	0.31
Winter_ppt					0.06	0.07
Monsoon						0.12

APPENDIX B. Supporting information for Chapter 2

Post-fire vegetation response at the woodland-shrubland interface is mediated by the pre-fire community

Table B1. Cover categories used for estimating aerial vegetation cover in 2003, 2004, and 2006.

Category	**Range of aerial cover (%)**	**Value used for analyses (% cover)**
trace	< 1	0.01
1	1 – 3	2.0
2	3.1 – 5	4.0
3	5.1 – 15	10.0
4	15.1 – 25	20.0
5	25.1 – 35	30.0
6	35.1 – 45	40.0
7	45.1 – 55	50.0
8	55.1 – 65	60.0
9	65.1 – 75	70.0
10	75.1 – 85	80.0
11	85.1 – 95	90.0
12	95.1 – 100	97.0

Table B2. Site types represented by each community type identified through cluster analysis.

Community type	Represented site types (number)	No. of sites
Big sagebrush / fescue shrubland	Unburned high-elevation, moderate tree cover (12) Unburned mid-elevation, low tree cover (12)	24
Big sagebrush / bluegrass shrubland	Unburned low-elevation, moderate tree cover (10)	10
Sparse perennial understory	Unburned mid-elevation, high tree cover (12)	12
Big sagebrush-dominated	Unburned mid-elevation, moderate tree cover (12) Unburned low-elevation, moderate tree cover (2)	14
Diverse mountain shrubland	Burned high-elevation, moderate tree cover: all years (9)	9
Native perennial forbs & grasses	Burned low-elevation, moderate tree cover: 1 yr post-fire (3) Burned mid-elevation, moderate tree cover: 1 yr post-fire (3) Burned mid-elevation, low tree cover: 1 yr post-fire (2)	8
Invaded forbs & grasses	Burned low-elevation, moderate tree cover: 2-4 yrs post-fire (6) Burned mid-elevation, moderate tree cover: 2-4 yrs post-fire (6) Burned mid-elevation, low tree cover: 1 yr post-fire (1); 2-4 yrs post-fire (6)	19
Sparse annual forbs	Burned mid-elevation, high tree cover: all years (9)	9

Table B3. Species information and corresponding NMS axis scores.

Genus	**Species**	**Common Name**	**Functional Group**	**NMS Axis 1**	**NMS Axis 2**
Achnatherum	*hymenoides*	Indian ricegrass	Perennial Graminoid	0.265	-0.786
Achnatherum	*nevadense*	Nevada needlegrass	Perennial Graminoid	0.390	-1.021
Achnatherum	*pinetorum*	Pine needlegrass	Perennial Graminoid	0.457	-0.424
Achnatherum	*thurberianum*	Thurber's needlegrass	Perennial Graminoid	-0.063	0.415
Agoseris	*glauca*	Pale agoseris	Perennial Forb	0.493	-0.012
Antennaria	*dimorpha*	Low pussytoes	Perennial Forb	0.078	-0.397
Antennaria	*rosea*	Rosy pussytoes	Perennial Forb	-0.386	-0.681
Arabis	*holboellii*	Holboell's rockcress	Perennial Forb	-0.303	0.321
Arabis	*sparsiflora*	Sicklepod rockcress	Perennial Forb	0.565	-0.803
Arenaria	*aculeata*	Prickly sandwort	Perennial Forb	-0.226	0.039
Arenaria	*kingii*	King's sandwort	Perennial Forb	0.160	-0.206
Artemisia		Sagebrush	Perennial Shrub Non-Sprouting	-0.541	-0.094
Astragalus	*atratus*	Mourning milkvetch	Perennial Forb	-0.460	-0.473
Astragalus	*calycosus*	Torrey's milkvetch	Perennial Forb	-0.450	-0.726
Astragalus	*oophorus*	Egg milkvetch	Perennial Forb	1.265	0.310
Astragalus	*purshii*	Woollypod milkvetch	Perennial Forb	-0.368	0.075
Bromus	*tectorum*	Cheatgrass	Annual Graminoid	0.589	-0.484
Calochortus		Mariposa lily	Perennial Forb	-0.694	0.289
Carex		Sedge	Perennial Graminoid	-0.086	-0.442
Castilleja	*linariifolia*	Wyoming Indian paintbrush	Perennial Forb	-0.555	-0.557
Caulanthus	*crassicaulis*	Thickstem wild cabbage	Perennial Forb	2.392	-0.213
Chaenactis	*douglasii*	Douglas' dustymaiden	Perennial Forb	0.577	0.274
Chenopodium	*album*	Lambsquarters	Annual Forb	0.092	-0.897
Chenopodium	*desiccatum*	Aridland goosefoot	Annual Forb	1.311	-0.369

Chenopodium	*leptophyllum*	Narrowleaf goosefoot	Annual Forb	0.641	-0.255
Chrysothamnus	*viscidiflorus*	Yellow Rabbitbrush	Perennial Shrub Sprouting	0.196	-0.414
Claytonia	*perfoliata*	Miners lettuce	Annual Forb	0.447	1.104
Collinsia	*parviflora*	Maiden blue eyed Mary	Annual Forb	1.250	0.538
Cordylanthus	*ramosus*	Bushy bird's beak	Annual Forb	-0.657	-0.788
Crepis	*acuminata*	Tapertip hawksbeard	Perennial Forb	-0.158	-0.144
Cryptantha	*circumscissa*	Cushion Cryptantha	Annual Forb	1.506	0.305
Cryptantha	*flavoculata*	Roughseed cryptantha	Perennial Forb	0.046	0.603
Cryptantha	*watsonii*	Watson's cryptantha	Annual Forb	0.947	-0.442
Dactylis	*glomerata*	Orchardgrass	Perennial Graminoid	0.127	-1.278
Descurainia	*pinnata*	Western tansymustard	Annual Forb	0.745	0.215
Elymus	*elymoides*	Squirreltail	Perennial Graminoid	-0.099	0.377
Ephedra	*viridis*	Mormon tea	Perennial Shrub Sprouting	-0.180	0.877
Epilobium	*ciliatum*	Fringed willowherb	Perennial Forb	1.146	-0.153
Eriastrum	*sparsiflorum*	Great Basin woollystar	Annual Forb	0.119	0.679
Eriastrum	*wilcoxii*	Wilcox's woollystar	Annual Forb	0.906	-0.273
Ericameria	*nauseosa*	Rubber rabbitbrush	Perennial Shrub Sprouting	0.106	-0.427
Erigeron	*aphanactis*	Rayless shaggy fleabane	Perennial Forb	0.024	-0.282
Eriogonum	*baileyi*	Bailey's buckwheat	Annual Forb	1.141	-0.553
Eriogonum	*elatum*	Tall woolly buckwheat	Perennial Forb	0.214	-0.067
Eriogonum	*esmeraldense*	Esmeralda buckwheat	Annual Forb	0.614	-0.322
Eriogonum	*microthecum*	Slender Buckwheat	Perennial Forb	0.015	-0.225
Eriogonum	*ovalifolium*	Cushion Buckwheat	Perennial Forb	-0.018	-0.146
Eriogonum	*umbellatum*	Sulphur-flower buckwheat	Perennial Forb	-0.105	-0.175
Festuca	*idahoensis*	Idaho fescue	Perennial Graminoid	-0.399	-0.458
Galium	*bifolium*	Twinleaf bedstraw	Annual Forb	-0.102	-1.126
Gayophytum	*diffusum*	Spreading groundsmoke	Annual Forb	0.600	-0.852

Gayophytum	*racemosum*	Blackfoot groundsmoke	Annual Forb	0.193	0.595
Gayophytum	*ramosissimum*	Pinyon groundsmoke	Annual Forb	0.927	-0.313
Gilia	*inconspicua*	Shy Gilia	Annual Forb	-0.128	0.227
Hesperostipa	*comata*	Needle and thread	Perennial Graminoid	0.320	0.743
Koeleria	*macrantha*	Prairie junegrass	Perennial Graminoid	-0.200	-0.317
Lactuca	*serriola*	Prickly lettuce	Annual Forb	1.388	-0.161
Lappula	*occidentalis*	Flatspine stickseed	Annual Forb	0.630	-0.289
Leptosiphon	*septentrionalis*	Northern linanthus	Annual Forb	-1.566	0.359
Lesquerella	*kingii*	King bladderpod	Perennial Forb	-0.822	-0.402
Leymus	*cinereus*	Basin wildrye	Perennial Graminoid	0.113	-0.562
Linanthus	*pungens*	Granite prickly phlox	Perennial Forb	-0.379	-0.150
Lupinus	*argenteus*	Silvery lupine	Perennial Forb	-0.078	-0.305
Machaeranthera	*canescens*	Hoary tansyaster	Perennial Forb	0.508	-0.827
Mentzelia	*albicaulis*	Whitestem blazingstar	Annual Forb	0.841	-0.310
Microsteris	*gracilis*	Slender phlox	Annual Forb	1.307	0.272
Mimulus	*densus*	Yellow and purple monkeyflower	Annual Forb	0.863	-0.474
Mimulus	*suksdorfii*	Suksdorf's monkeyflower	Annual Forb	0.918	-0.759
Opuntia		Pricklypear	Perennial Succulent	-0.387	0.812
Packera	*multilobata*	Basin butterweed	Perennial Forb	0.225	1.014
Pascopyrum	*smithii*	Western wheatgrass	Perennial Graminoid	0.118	0.243
Penstemon	*speciosus*	Royal penstemon	Perennial Forb	-0.361	-0.720
Penstemon	*watsonii*	Watson's penstemon	Perennial Forb	-0.236	-1.052
Phlox	*hoodii*	Spiny phlox	Perennial Forb	-0.154	-0.201
Phlox	*longifolia*	Longleaf phlox	Perennial Forb	0.232	-0.048
Phoenicaulis	*cheiranthoides*	Wallflower phoenicaulis	Perennial Forb	0.143	-0.758
Pleiacanthus	*spinosus*	Thorn skeletonweed	Perennial Forb	-0.622	-0.462
Poa	*fendleriana*	Muttongrass	Perennial Graminoid	-0.299	0.118

Poa	*secunda*	Sandberg Bluegrass	Perennial Graminoid	-0.705	0.347
Polygonum	*douglasii*	Douglas' knotweed	Annual Forb	-0.334	1.031
Polygonum	*ramosissimum*	Bushy knotweed	Annual Forb	1.246	0.514
Pseudoroegneria	*spicata*	Bluebunch wheatgrass	Perennial Graminoid	0.322	-0.534
Ribes	*aureum*	Golden currant	Perennial Shrub Sprouting	-0.990	0.490
Ribes	*cereum*	Wax currant	Perennial Shrub Sprouting	0.662	-1.132
Sambucus	*nigra*	Black elderberry	Perennial Shrub Sprouting	0.689	-0.972
Silene	*douglasii*	Douglas's catchfly	Perennial Forb	0.089	-1.158
Stenotus	*acaulis*	Stemless mock goldenweed	Perennial Forb	0.803	-0.921
Stipa		Stipa	Perennial Graminoid	-0.275	-0.391
Symphoricarpos	*oreophilus*	Mountain snowberry	Perennial Shrub Sprouting	0.074	-0.554
Tetradymia	*canescens*	Spineless horsebrush	Perennial Shrub Sprouting	0.027	-0.889
Vicia		Vetch	Annual Forb	-0.663	0.348
Viola	*purpurea*	Goosefoot violet	Perennial Forb	0.202	-1.225

Table B4. Cover and species richness by plant functional group, and Bray-Curtis dissimilarity, for each community type identified through cluster analysis.

Community Type	Perennial grasses	Annual grasses	Perennial forb	Annual forb	Sprouting shrubs	Non-sprouting shrubs	Total	Bray-Curtis dissimilarity
	Mean % cover (mean richness)							*Mean (SE)*
Big sagebrush / fescue shrubland	8.3 (6.7)	0.0 (0.3)	4.8 (12.8)	0.0 (1.6)	5.0 (2.4)	20.8 (1.0)	38.9 (24.8)	0.31 (0.006)
Big sagebrush / bluegrass shrubland	5.9 (3.4)	0.0 (0.6)	2.5 (13.2)	0.0 (1.9)	0.3 (1.4)	4.4 (1.0)	13.1 (21.9)	0.33 (0.018)
Sparse perennial understory	2.6 (5.3)	0.0 (0.5)	0.5 (10.4)	0.0 (3.0)	0.6 (1.9)	0.5 (0.8)	4.3 (22.1)	0.59 (0.016)
Big sagebrush-dominated	3.6 (6.2)	0.1 (0.6)	3.2 (13.1)	0.0 (3.0)	1.4 (2.1)	10.2 (1.0)	18.6 (26.3)	0.34 (0.009)
Diverse mountain shrubland	5.6 (7.8)	0.0 (0)	8.9 (12.2)	1.3 (5.2)	13.9 (2.7)	0.5 (1.0)	30.2 (28.9)	0.46 (0.026)
Native perennial forbs & grasses	1.8 (5.0)	0.0 (1.0)	6.0 (11.4)	1.1 (5.3)	1.5 (2.6)	0.1 (0.8)	10.6 (26.1)	0.55 (0.022)
Invaded forbs & grasses	3.2 (5.1)	2.3 (1.0)	8.8 (12.3)	2.1 (8.1)	8.2 (2.3)	0.4 (0.9)	25.1 (29.6)	0.51 (0.008)
Sparse annual forbs	1.8 (5.4)	0.1 (0.9)	1.0 (7.9)	3.3 (9.0)	1.1 (1.2)	0.0 (0.1)	7.4 (24.9)	0.82 (0.023)

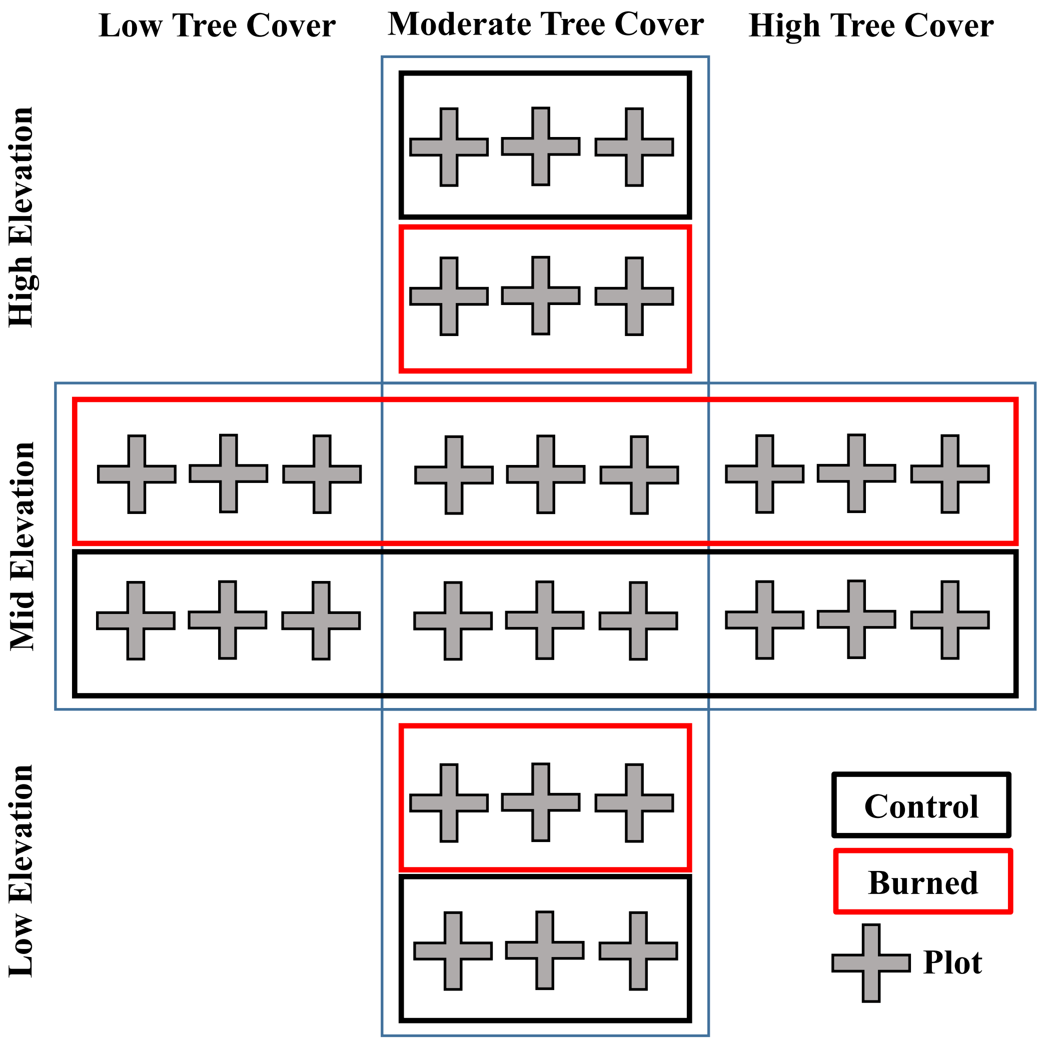


Figure B1. Conceptual schematic of the study design in Underdown Canyon, Shoshone Mountains, Nevada. A total of thirty plots were distributed across three elevations and three tree cover classes in a partially-crossed design. Mid-elevation plots were used to examine the tree cover gradient, and moderate tree cover plots were used to examine the elevational gradient.

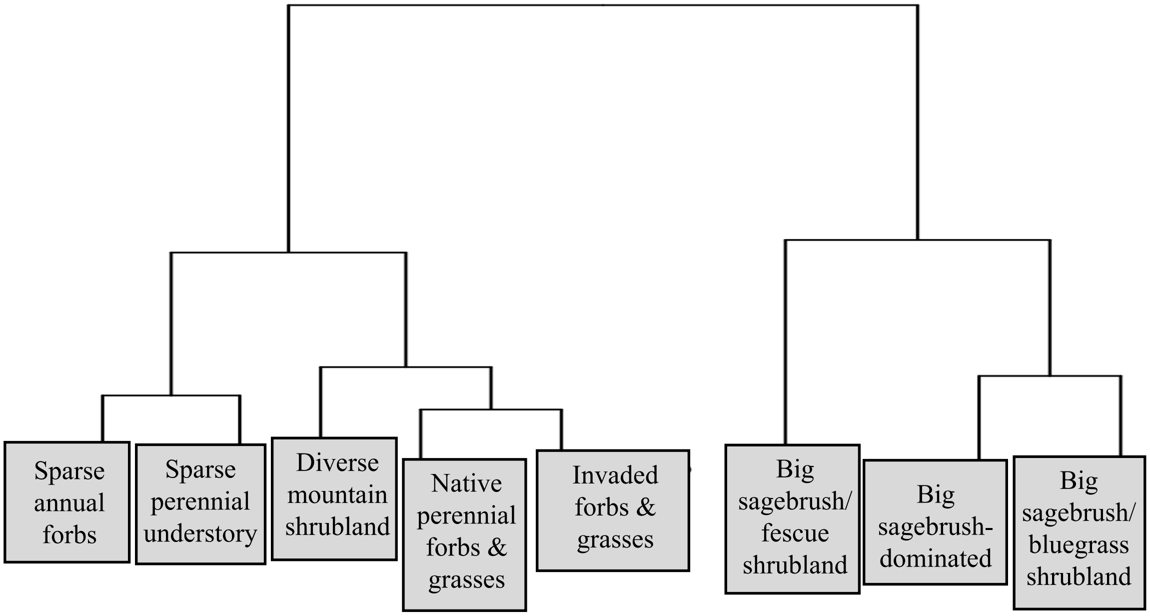


Figure B2. Dendrogram of community types identified from hierarchical cluster analysis.

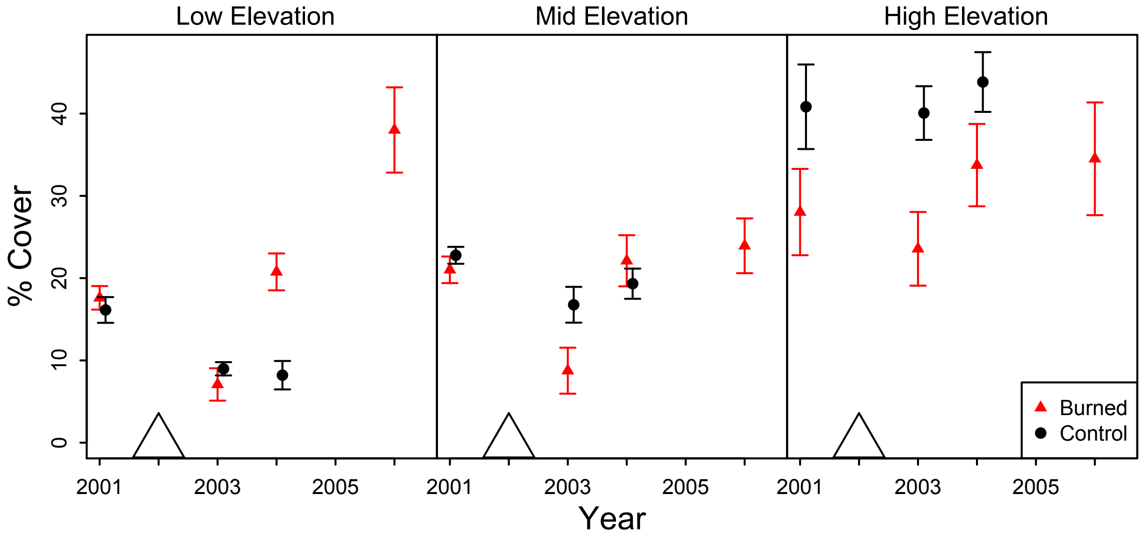


Figure B3. Total understory cover for burned (red triangles) and control (black circles) plots along an elevational gradient. Only moderate tree cover plots are shown. Data are shown as mean +/- 1SE. No shrub control data were collected in 2006, so total cover is not shown for 2006 control plots. Large triangle shows the year of burn treatment (2002).

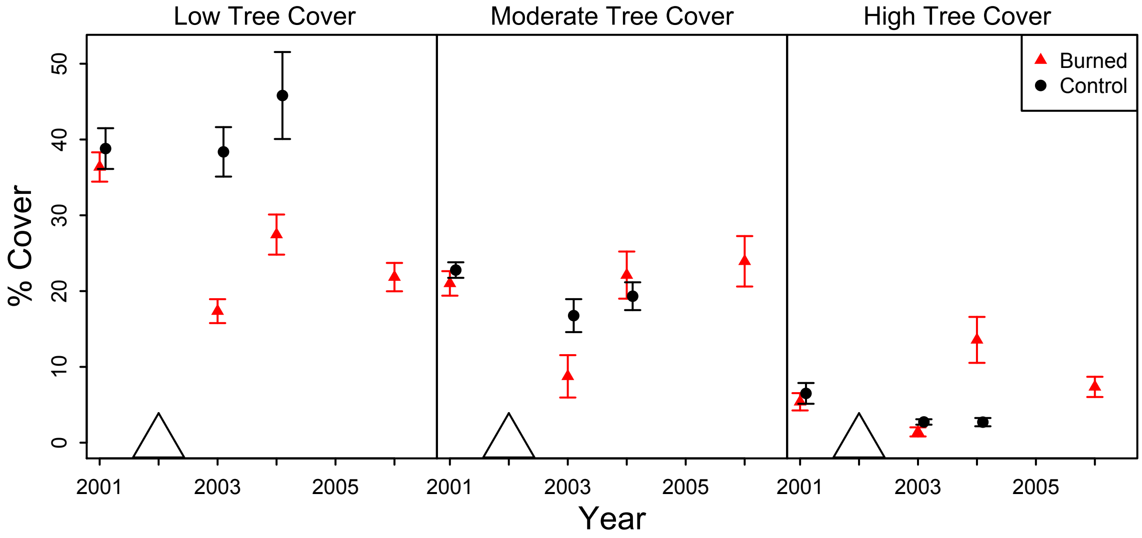


Figure B4. Total understory cover for burned (red triangles) and control (black circles) plots along a gradient of pre-burn tree cover. Only mid-elevation plots are shown. Data are shown as mean +/- 1SE. No shrub control data were collected in 2006, so total cover is not shown for 2006 control plots. Large triangle shows the year of burn treatment (2002).

APPENDIX C. Supporting information for Chapter 4

Shrub (*Artemisia tridentata*) facilitation of tree establishment (*Pinus monophylla*): ontogenetic shifts along stress gradients

Figure C1. Additional abiotic environmental measurements from three shrub microhabitat treatments at three sites along an elevational gradient. (a) Daily minimum surface soil temperature, averaged for May-October 2017 (n=54). (b) Number of frost events (daily minimum temperature < 0°C) between May and October 2017 (n=54). (c) Growing season length (total days between last spring frost and first fall frost) for 2017 (n=54).

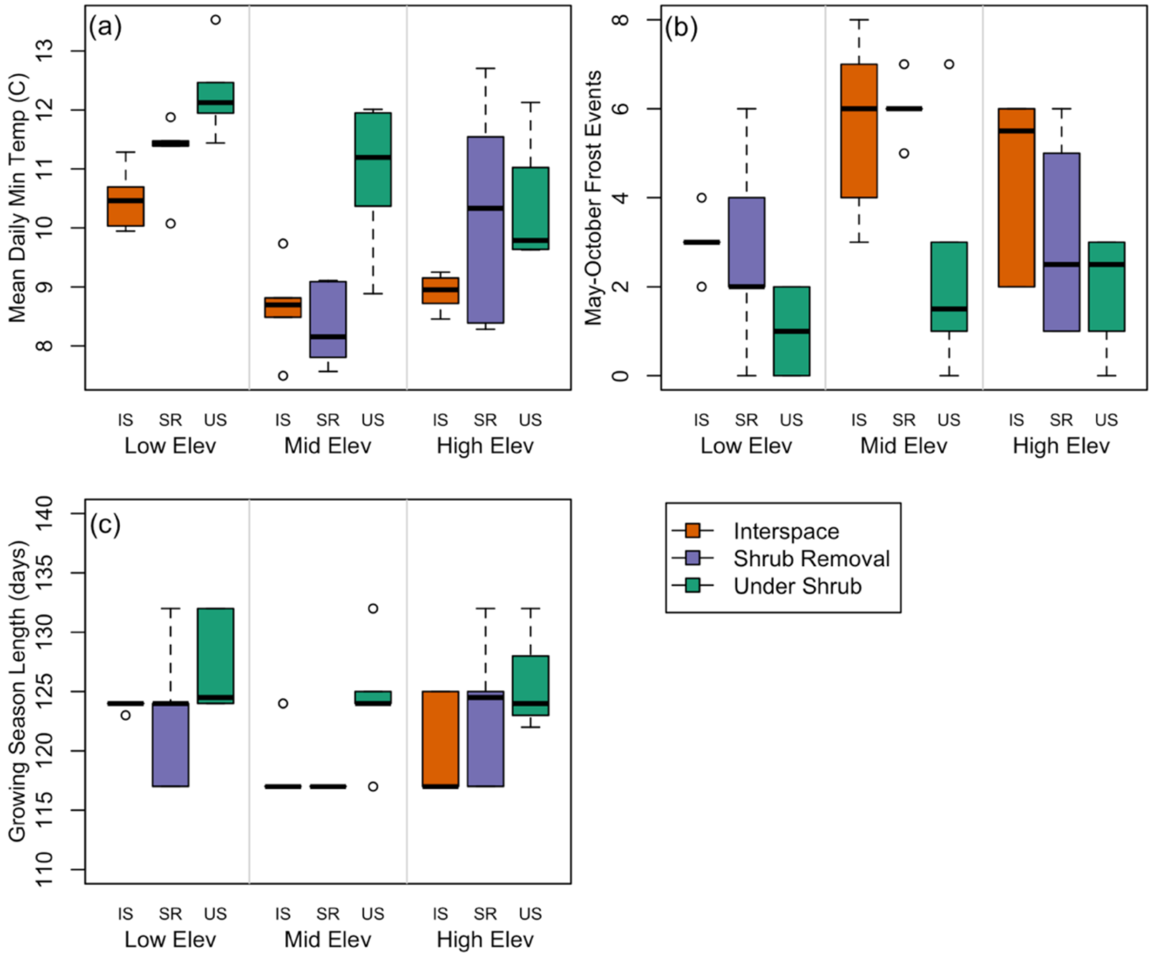


Figure C2. Frequency distribution of the location of pinyon juveniles in relation to the stem of associated sagebrush plants. The radius of each arc represents the proportion of pinyon juveniles that were found in each cardinal direction.