

THESIS

SPATIAL AND TEMPORAL CONTROLS ON PINYON AND JUNIPER SEEDLING  
ESTABLISHMENT IN THE UNCOMPAHGRE PLATEAU, WESTERN COLORADO

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Phillip Jay Graeve

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Master's Committee:

Advisor: Monique Rocca

Peter Brown  
Jason Sibold

## ABSTRACT

### SPATIAL AND TEMPORAL CONTROLS ON PINYON AND JUNIPER SEEDLING ESTABLISHMENT IN THE UNCOMPAHGRE PLATEAU, WESTERN COLORADO

Moderate and extreme climate events have the potential to cause sudden shifts with long-lasting relictual effects in ecological communities. In this study I investigated the direct and indirect effects of climate on Colorado pinyon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) on the Uncompahgre Plateau in western Colorado. I determined age structure of pinyon seedlings and tested for the effects of current year and antecedent year climate on seedling establishment. Finally, I described microhabitat preferences (substrate microhabitat and overstory canopy) for pinyon and juniper seedlings and assessed whether suitable microhabitats may have changed as a consequence of overstory die-off. No relationships between climate and pinyon establishment were detected, and pinyon establishment appears to have been relatively constant over the past 30 years. I found that both pinyon and juniper exhibited distinct preferences for certain substrate microhabitats, especially different types of litter. Pinyon seedlings avoided bare soil microhabitats. While both pinyon and juniper seedlings avoided open overstory microhabitat, pinyon preferred juniper overstory microhabitat. Microhabitat preferences of pinyon seedlings may buffer seedlings from climate-induced stress. Pinyon overstory declined rapidly due to a severe drought from 2000-2004, but juniper overstory was not affected. My results indicate that episodic overstory mortality events and continuous pinyon establishment characterize pinyon dynamics on the Uncompahgre Plateau, at least within the 30 year time frame investigated here. In contrast, juniper seedlings are less abundant but likely more resilient to climate-induced changes in microhabitat structure. Future pinyon establishment and

overstory survival may be reduced due to direct and indirect effects of climate, especially if predictions for increased drought frequency and severity for this area are realized.

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## INTRODUCTION

Colorado pinyon (*Pinus edulis*) and juniper (*Juniperus osteosperma*) communities dominate low elevation forested areas covering over 16 million ha in the Colorado Plateau. Changes in woodland structure and composition in these communities are commonly attributed to past management practices, including grazing and fire suppression, or favorable climatic conditions (i.e. cool and wet periods), yet the mechanisms by which these changes occur are unknown (Baker, 2004; Eisenhart, 2005; Greenwood and Weisberg, 2009; Romme, Allen, et al., 2009; Romme, Floyd, et al., 2009; Weisberg et al., 2007). Here, the relative role exerted by climatic fluctuations and structural characteristics in determining seedling establishment and recruitment in these systems is examined, with emphasis on the effects of climate and microhabitat preferences on seedling establishment (Tausch et al., 1988; Swetnam et al., 1999; Romme et al., 2008; Romme, Floyd, et al., 2009).

Pinyon-juniper ecosystem resilience to climate-induced disturbances, such as extensive pinyon mortality seen during an historic and extensive regional drought from 2000-2004, is dependent on many factors including changes in seedling establishment patterns in response to structural habitat changes (Elmqvist et al., 2003; Folke et al., 2004). With increasing average temperatures and decreasing annual precipitation predicted for the intermountain west (Hanson and Weltzin, 2000), understanding the impacts of climate on ecological communities is important for predictions of future changes in ecotones and significant alterations in Colorado pinyon communities.

In this study, I investigated climate controls on pinyon and juniper seedling establishment over the past 30 years on the Uncompahgre Plateau, Colorado. I tested whether climate controls on seedling establishment vary across an elevation gradient as might be expected if recruitment is



moisture or temperature limited. Furthermore, I explored the degree to which establishment is affected by the availability of facilitating microhabitats, including substrate microhabitat (the surface material on which a seedling germinates and grows) and overstory microhabitat (the nurse structures such as shrub and tree canopies under which seedlings establish). Microhabitats have the potential to modulate the temperature and moisture environment experienced by young seedlings, and may also facilitate moisture and nutrient acquisition strategies through mycorrhizal associations. Finally, I explored the implications of my findings and the potential for feedback mechanisms in the context of climate projections and predictions of subsequent changes in forest structure.

Abundant evidence from other aridland pine ecosystems suggests strong relationships between seedling establishment and favorable climate conditions (Savage et al., 1996; Breshears et al., 2005; Brown and Wu, 2005; Gray et al., 2006). The importance of climate for pine seedling establishment spans historical to contemporary periods (Breshears et al., 2005; Brown and Wu, 2005; League and Veblen, 2006). It follows that species which colonize the most marginal microsites are the most susceptible to climate-induced changes in establishment (Woodward et al., 1995). The episodic nature of microbial activity in arid ecosystems may further illustrate that significant changes in climate-mediated processes such as seedling establishment are related to the episodic availability of resources and nutrients in the system (Collins et al., 2008). This relationship could be especially evident during extended (2-3 year) episodes of favorable climate conditions (Collins et al., 2008).

Recent research on the eastern Uncompahgre Plateau indicates the important role of climate in pinyon-juniper establishment and growth over decadal time scales. Pinyon and juniper differ in their response to large-scale climate teleconnections including Atlantic Multidecadal

Oscillation (AMO) and the Pacific Decadal Oscillation (PDO), two indicators of ocean temperatures which have been shown to exert significant regional impacts on climate (Betancourt et al., 1993; Shinneman, 2009). Juniper densities appear to increase during droughts, while increases in pinyon establishment coincide with generally above average moisture periods (Shinneman, 2009). Other research on the Uncompahgre Plateau indicates pinyon growth release related to cool season moisture in the early 1900's, with patterns most evident after 1930, and a positive relationship with above average moisture in the antecedent fall and current spring (Eisenhart, 2005). While climate effects were observed at all elevations, they were most pronounced near the lower ecotone, indicating the importance of climate was increased at marginal sites (Eisenhart, 2005). How these dynamics play out at annual times scales in the recent past (~30 years) has not yet been addressed.

Further indication of the relative importance of climate in pinyon establishment is the observed importance of facilitative microhabitats in pinyon and juniper establishment. Single-leaf pinyon pine (*Pinus monophylla*) is known to regenerate most effectively in the presence of facilitating substrate microhabitat structures such as logs, rocks and litter in conjunction with overstory structure (Chambers, 1999). It has been suggested that nitrogen-fixing shrubs like curl-leaf mountain mahogany (*Cercocarpus ledifolius*) may enable pinyon establishment by providing microsites with increased local nitrogen levels (L. Floyd, Prescott College, personal communication). Additionally, several studies have indicated that pinyon regenerate most frequently in pinyon litter under pinyon overstory microhabitat, and least commonly in the interspaces between overstory structures (Johnsen, 1962; Jameson, 1965). These associations are possibly due to mycorrhizal symbionts which provide favorable substrate microhabitat conditions by increasing nutrient and moisture availability and favorably improving substrate

microhabitat temperatures due to shading effects (Chambers, 2001; Haskins and Gehring, 2004). Warm spring temperatures combined with bare soil substrates have been shown to be positively related to pinyon germination, but negatively related to pinyon seedling survival, likely as a result of lethal summer temperatures and depressed soil moistures (Chambers et al., 1999; Schupp et al., 1999; Chambers, 2001). These relationships have been studied almost exclusively in *Pinus monophylla* but it is presumed that Colorado pinyon (*Pinus edulis*) exhibits the same substrate microhabitat preferences (Lanner, 1974). Though *Pinus edulis* seedling substrate microhabitat studies are underrepresented in the literature, studies indicate the two species are closely related and that the phenotypical differentiation of single or two-needled fascicles is dependent on the presence, intensity and duration of summer monsoonal precipitation (Lanner 1974). Though the relative importance of microhabitat is possibly diminished in areas of bimodal precipitation such as the Uncompahgre Plateau (Chambers et al, 1999), Colorado pinyon establishment success is still likely dependent on these microhabitat associations (Schupp et al, 1999; Chambers et al, 1999).

While episodic establishment has been observed at grassland-ponderosa ecotones, and long-term impacts of climate on age structure of Colorado pinyon have been investigated (Eisenhart, 2005; Gray et al., 2006; Shinneman, 2009), there is still uncertainty regarding pinyon establishment dynamics relative to extreme drought and changes in overstory composition and substrate microhabitat structures (League & Veblen, 2006; Shinneman, 2009). The impacts of recent discrete drought events, particularly of the severity of the 5-year drought from 2000-2004, are poorly understood (Baker, 2004; Eisenhart, 2005; Gray et al., 2006; Shinneman, 2009), despite the potential for widespread impacts over a significant proportion of the lower-elevation montane zones of the intermountain west and Colorado Plateau. Developing greater

understanding of short-term (<30 years) seedling establishment dynamics, especially with changes in community composition and increases in severity of drought events, will better inform management plans as stakeholders adapt to what could be abrupt community transformations in the future.

## **METHODS & ANALYSIS**

### **Study Area**

The Uncompahgre Plateau is a 600,000 ha cuesta with a northwest-southeast orientation on the eastern edge of the Colorado Plateau in western Colorado (Figure 1). The northeastern aspect of this landform is a gradual monocline, rising gradually but steadily from 1600 meters to nearly 3200 meters at the crest, which is a distinguished southwest escarpment. Deeply dissected canyons along intermittent waterways distinguish this gradual uplift, though most of the eastern aspect is flat or gradually sloping mesa formations.

The soils found on these mesas, especially in areas of pinyon and juniper dominance, are sandy with shallow and well-drained infiltration properties (Hughes et al., 1995). Pinyon juniper communities occupy, in variable community types, the middle elevations of the Plateau, dominating areas from 1700-2300 meters. These communities range from sparse pinyon communities dominated mostly by juniper and sagebrush at low elevations to pinyon dominated stands with few juniper and developed grass understory at high elevations (Romme, Allen, et al., 2009). Precipitation is bimodal, with winter snowpack and summer monsoon providing the majority of precipitation. Total annual precipitation averages ~20 cm at lower elevations with maximum temperatures of ~31 degrees C in July and minimum temperatures of 2.1 degrees C in Jan. (WRCC, 2012). The eastern Uncompahgre has a consistent disturbance history characterized by moderate grazing intensity, firewood cutting, and localized intensive chaining and hydro-axing of pinyon-juniper communities for grazing forage. Though fire suppression has been the official policy in these woodlands for over a century, historical evidence indicates fire was likely a very infrequent occurrence in the eastern Uncompahgre pinyon-juniper forest communities (Eisenhart, 2005; Romme, 2010).

The Uncompahgre Plateau experienced a severe and widespread mortality event in pinyon-juniper woodlands caused by a multi-year regional drought from 2000-2004. Colorado pinyon pine (*Pinus edulis*) experienced mortality of up to 65 % in reproductive trees and 35 % in pre-reproductive pinyon with much lower mortality in seedlings (Selby, 2004; Floyd et al., 2009). Mortality was likely caused by the interacting effects of drought-induced water stress, pinyon ips beetle (*Ips confusus*), and black stain root disease (*Leptographium wagneri*) (Floyd et al., 2009). Areas of marginal pinyon habitat suitability such as low elevation mesic sites and high elevation xeric sites, typically shrub-dominated areas, are generally thought to have experienced encroachment of pinyon woodlands in the last 60 years (Gray et al., 2006).

### **Sampling Area**

I established 75 plots on the eastern aspect of the Uncompahgre Plateau during June and July 2010. Plots were located in pinyon- and juniper-dominated areas south of the Escalante River canyon and north of Ridgeway Reservoir on US Forest Service and US Bureau of Land Management administered lands (Figure 1). Within this study area I stratified plots in three elevation strata: low elevation (1700 - 2000 m), medium elevation (2000-2200 m) and high elevation (2200 m – 2300; Figure 1). I randomly selected plot locations using GIS mapping software (ESRI, 2010) in areas of pinyon-juniper (PJ) dominance according to National Land Cover Data (USGS, 2010). I excluded from the sampling design random points which, upon field inspection, did not exhibit dominant pinyon or juniper composition. Within each 50 x 20 m (0.05 ha) plot, I measured and harvested all pinyon and juniper seedlings (specimens < 3 cm diameter at root collar (DRC)). In the immediate vicinity of each seedlings (10 cm radius of the seedling), the specific substrate microhabitat associated with each seedling was indicated. This substrate microhabitat was an open-ended category, meaning there were an unlimited number of

categories possible. The most common categories (and those used in analysis) were; bare ground, rock, non-specific shrub litter, nitrogen fixing shrub litter, non-nitrogen fixing shrub litter, tree litter, juniper litter, pinyon litter, mixed pinyon and juniper litter, unidentified litter, biological soil crust and log/root. The dominant primary substrate microhabitat association was always indicated. For example, if a seedling established in sage litter but associated with herbaceous forbs, the likely dominant substrate microhabitat (sage litter) was indicated. Shrub overstory presence (e.g., big sagebrush (*Artemisia tridentata*), black sage (*Artemisia nova*), ephedra (*Ephedra viridis*), greasewood (*Sarcobatus baileyi*), mountain mahogany (*Cercocarpus montanus*), serviceberry (*Amelanchier alnifolia*), Gambel oak (*Quercus gambelii*)) was indicated when present. Additionally overstory tree presence was identified by species (pinyon or juniper) or as co-dominant. At the plot level, overstory composition was assessed by measuring diameter at root collar, species, live/dead status and, if dead, decay condition class of the snag (Table 1). Finally, the point intercept method was used to measure substrate microhabitat cover, shrub cover and overstory cover (as described above) at one-meter increments along a 50-meter transect bisecting the 50 meter by 10 meter plot.

### **Tree Ring Analysis**

Field sampling yielded 3311 pinyon and 531 juniper seedling specimens which were returned to the laboratory for further analysis. An additional 900 pinyons were determined by field reference to have cotyledons and were thus confidently aged in the field. Due to the difficulty inherent in aging juniper seedlings with any degree of accuracy, only pinyon seedlings were aged for this study. When possible, all specimens were assigned a binary pre- or post- drought (2000-2004) age. If the age was determined to be during the drought-mortality event (i.e., 2000-2004), it was not given a pre or post age determination. Ten samples were randomly selected

from each plot for precise dating with standard dendrochronological techniques under a dissecting scope (Stokes & Smiley, 1968). This procedure included serial sectioning and sanding to identify embryonic pith structures at the root-shoot boundary of each sample (Telewski, 1995). In many cases this required razor blade surfacing and sanding up to 1500 grit sandpaper. Samples were aged by crossdating, using analogous or matching ring patterns based on climate synchronization of growth between trees, beginning with the outermost ring (harvest year 2010) inwards to the pith or root-shoot interface to establish germination year. At least 861 pinyon seedlings were aged using the dissecting microscope.

### **Analyses**

To determine whether climate exhibited a relationship with pinyon establishment, I examined the age frequency distribution of pinyon seedlings. An exponential decay pattern, or inverse J distribution, would be expected if seedling establishment and mortality were constant through time. Superimposed on this background of exponential decay, episodic “pulses” of recruitment and intervening gaps would be expected if climate patterns impacted pinyon establishment. After examining the age distribution of pinyons, I factored out the climate-independent exponential decay by regressing the log of seedling density (seedlings \* ha<sup>-1</sup>) against year of establishment. Then, I regressed the residual variability in seedling density against annual and seasonal climatic indicators including Palmer Drought Severity Index (PDSI), mean precipitation and mean temperature (source data in Table 2). Seasonal values were limited to dormant season (Nov-Apr) and growing season (May-Oct) averages for each climate variable. Each year had a growing season average and a dormant season average. Similar analyses using state and local datasets were performed (NOAA, 2012; source data Table 2).



To test the climate-establishment relationship on an intra-annual resolution, I conducted Response Function Analyses using DendroCLIM 2002 (Biondi and Waikul, 2004). These tests corrected for temporal autocorrelation and examined monthly variables of interest including precipitation, minimum temperature, maximum temperature, mean temperature, and PDSI (NOAA, 2012; see list of data and sources in Table 2). Monthly climate datasets for these analyses included local weather data from Montrose, CO as well as a regional dataset covering western Colorado NOAA Climate Division 2 (WRCC, 2012; Table 2). An annual hemispherical North American Monsoon Index which measures the strength of the summer monsoons was also examined, though only for the summer monsoon months of July, August and September (Jianping and Zeng, 2003) (Table 2). For the other Response Function Analyses, a temporal window of 13 months was used including from August in the year preceding establishment through September of the year of establishment. One-year lags in establishment date also were analyzed to explore the relationship between multi-year monthly climate variables and establishment. The significant results of these analyses were further explored with correlation coefficients determined by standard Pearson's Correlation tests. All analyses of climate data and pinyon establishment were conducted on a landscape scale as well as stratified by elevation.

I compared the proportion of seedlings establishing in a substrate microhabitat (or overstory microhabitat) with the proportional representation of that microhabitat in the plot to test whether seedling establishment preferentially established in specific substrate microhabitats or overstory microhabitats. If seedlings found in a particular substrate microhabitat exceeded the proportion of that substrate microhabitat in the plot; that plot was assigned a "yes". Otherwise, a plot was assigned to the "no" category. Under the null expectation (i.e. seedlings distributed at random), roughly half of the plots would be "yes" and the other half "no". I used two-sided binomial tests

to determine whether the proportion of “yes” or “no” exceeded the null expectation of 0.5. To account for the major loss of tree overstory during the 2000-2004 drought, separate tests were run for pinyons established prior to the drought (with the estimated pre-outbreak tree cover) and pinyons established after the drought (with the post-outbreak tree cover). Microhabitat preference tests were not performed with plots at different elevations due to sample size limitations. Instead, qualitative analyses at varying elevations were examined in lieu of statistical testing.

With the exception of Response Function Analysis which was conducted in DendroCLIM 2002 (Biondi and Waikul, 2004), all statistical analyses were conducted using the R 2.13.2 statistical environment (R Development Core Team, 2011).

## RESULTS

Pinyon and juniper seedling and overstory dynamics varied with elevation. Pinyon seedling densities were lower at low elevation plots than at medium elevation (Tukey HSD  $p=0.020$ ) and high elevation plots (Tukey HSD  $p=0.004$ ) (Table 3). Juniper seedling densities were lower at low elevation plots relative to medium elevations (Tukey HSD  $p=0.010$ ) but not high elevation plots (Table 3).

Overstory basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of pinyon and juniper varied significantly at all three elevation levels ( $p < 0.01$ ; Table 4). Live overstory pinyon density (trees  $\text{ha}^{-1}$ ) at low elevations was lower than medium (Tukey HSD  $p=0.0035$ ) and high elevation (Tukey HSD  $p=0.001$ ) plots though the medium and high elevation plot basal area did not differ (Table 4). The percent change of live pinyon overstory basal area ( $\text{m}^2 \text{ha}^{-1}$ ) due to drought-induced mortality at low elevation was lower than medium (Tukey HSD  $p=0.003$ ) and high elevation (Tukey HSD  $p=0.005$ ) plots.

### Climate variability and pinyon establishment

The frequency histograms of pinyon seedling establishment by year indicated no visually discernible patterns of pulse establishment or obvious time periods of episodic establishment (Figure 2). In contrast to my prediction, a reverse J distribution, suggestive of constant establishment and constant mortality and a static age structure, was observed at all elevations and at the landscape scale (Figure 2). Furthermore, the linear regression of log-transformed pinyon seedling density against year of establishment showed that most of the variability in seedling density was a simple function of establishment year ( $p < 0.001$ ,  $R^2=0.82$ ; Figure 3). This relationship was also consistent in all three elevations zones. Regressions of the residual variability in seedling density against annual and seasonal climatic indicators displayed no climate relationship, with annual establishment unrelated to climatic indicators such as PDSI,

precipitation and temperature. The lack of a climate-establishment relationship was consistently absent across all elevations. Additionally, lag-year analyses failed to yield any associations between establishment and climate.

While the regression mentioned above looked at annual or seasonal indicators on an annual basis, the Response Function Analysis results looked at finer scale monthly climate variables to examine climate-establishment relationships with the residual variations in pinyon establishment. Regional climate data indicated no relationships between monthly climate variables and pinyon establishment. Data from a local climate station in Montrose, CO, however, identified three climate variables associated with seedling establishment. For the thirty year period of analysis, mean February temperature was positively correlated with pinyon establishment ( $r=0.395$ ,  $p=0.0252$ ). Additionally, minimum June temperature at low elevation plots was negatively related to pinyon establishment ( $r=-0.427$ ,  $p=0.015$ ). Finally, the antecedent November minimum monthly temperature at high elevation plots was also negatively related to pinyon seedling establishment density ( $r=-0.453$ ,  $p=0.011$ ).

### **Microhabitat associations of pinyon and juniper seedlings**

Overstory microhabitat preference tests indicated that pinyon seedlings preferentially established under juniper overstory ( $p<0.001$ ). Pinyon seedlings which germinated before the 2000-2004 drought avoided open overstory ( $p<0.001$ ) as did pinyon seedlings which established post-drought ( $p<0.001$ ) (Table 5, Figure 4). When all overstory categories were aggregated into one overstory presence category, pinyon seedlings preferred all overstory ( $p<0.001$ ) (Table 5, Figure 4). All pinyon seedling establishment patterns related to microhabitat preferences were consistent across all elevations, though pinyon preference for

juniper overstory may display a skewed relationship with low and medium elevation plots (Figure 4a).

Across the landscape, pinyon seedlings were not found in bare ground ( $p < 0.001$ ) and non-specific litter ( $p < 0.001$ ), indicating avoidance relative to expected establishment (Table 6, Figure 6). Conversely, pinyon seedlings exhibited a preferential relationship with non-nitrogen fixing shrub litter ( $p < 0.001$ ) and log/rock substrate microhabitats ( $p < 0.001$ ) (Table 6, Figure 6). Additionally, pinyon seedlings were preferentially found in shrub litter ( $p < 0.001$ ) and tree litter ( $p < 0.001$ ) (Table 6, Figure 6).

Juniper seedlings displayed a pattern of avoidance of juniper, open and pinyon overstory microhabitats ( $p < 0.001$ ) (Table 5, Figure 4). When all overstory categories were aggregated, juniper seedlings avoided all overstory ( $p < 0.001$ ) (Table 5, Figure 5).

Juniper seedlings preferentially established in: rock, shrub litter, non-nitrogen-fixing shrub litter, tree litter, juniper litter, and biological soil crusts ( $p < 0.001$ ), (Table 6, Figure 7). There were no patterns of avoidance related to juniper seedling establishment. All juniper seedling establishment patterns related to microhabitat preferences were consistent across all elevations.

## **DISCUSSION**

The episodic association between favorable climate and pinyon seedling establishment that I had anticipated was not supported by the data I collected. Annual variability in temperatures, precipitation, and Palmer Severity Drought Indices did not affect pinyon establishment, even at historic extremes of these variables. Pinyon and juniper establishment does, however, associate with specific microhabitats. These microhabitat associations, likely modulate the effects of climate on seedling survival. Although I did not find any evidence of direct effects of climate on establishment, the microhabitat associations I found may indirectly mitigate or buffer the effects of climate on seedling establishment. Overstory pinyon basal area was severely reduced during the historic drought from 2000-2004, most severely at the more droughty lower elevations. Additionally, overstory survivorship is clearly climate-limited, particularly in older and larger trees, with increasing effects seen at lower elevations. These results point to the probable indirect effects of climate as drivers of pinyon-juniper community dynamics and trajectories.

### **Climate variability and pinyon establishment**

Overall, my results indicate continuous seedling establishment through time that was largely independent of annual and monthly climate variables, suggesting a static age distribution and population size for seedlings up to 30 years old. If mortality rates of older trees were also static, one would predict relatively steady pinyon populations through time. Studies have demonstrated that adult overstory canopy recruitment is sensitive to climate, at least on multi-decadal to centuries-long time scales. Other research indicates that young pinyon seedlings on the Colorado Plateau are unaffected by climate variability (J. Betancourt, USGS, personal communication; Martens et al., 2001). Shinneman (2009) found definite climate-dependent relationships with

pinyon establishment (determined by origin dates from dendrochronological analysis) for multiple periods in the past 300 years, including the period from 1980-2000. These results may indicate recent observations of changes in pinyon community composition are the consequence of climate limitations on mature trees (overstory sensitivity) rather than on seedlings (recruitment sensitivity), and that the effects of climate on pinyon seedling establishment may be buffered by microhabitats and their sheltering impacts. While Shinneman's results appear to contradict the results highlighted here, the annular resolution (rather than multi-year averages) of the seedling age structure in this study is likely a stronger indicator of establishment and sensitivity to annual climate indicators. The lack of a climate-establishment relationship even during an historically intense drought indicates that the pinyon seedling establishment niche is definitively resistant to climate and that there is likely a substantial difference between establishment niches and overstory survival niches in pinyon-juniper systems.

The pinyon overstory mortality observed from the early 2000's drought indicates that both climatic events and elevation influence overstory pinyon dynamics. Similar patterns of mortality and vegetation shifts related to drought have been seen in the Colorado Plateau and have strong implications for plant communities, affecting dominance shifts and community migrations (Allen and Breshears, 1998). It is possible that the pinyon regeneration niche may be more tolerant or complacent relative to climate fluctuations on the Uncompahgre, but that the adult niche and life-history niche at later stages are far more sensitive to these events. Indeed, at each stage of tree development, different sensitivities may emerge (Grubb, 1977; Mueller et al., 2005; van Mantgem et al., 2009 in Jackson et al., 2009). My results indicate that severe and extended droughts impact overstory mortality while not influencing establishment patterns, at least on a 30-year annular time scale. This time interval includes the early 2000's drought, a period unique

in terms of its severity, though not duration, based on reconstructed PDSI over the past 1000 years, and is certainly unequalled in the past 100 years (Cooke et al., 2004).

### **Microhabitat associations of pinyon and juniper seedlings**

Overstory microhabitat associations of pinyon seedlings include positive associations with juniper overstory microhabitat and, as predicted, a negative association with open canopy. Pinyon seedlings avoided open overstory microhabitat areas, both before and after pinyon overstory mortality. While I expected pinyon seedlings to preferentially establish under tree canopies in general, the preference for juniper overstory microhabitat specifically was somewhat unexpected. The result may be an artifact of the low pinyon cover and relatively high junipers cover in the lower and middle elevations, and the fact that, at high elevations where pinyon comprises most of the tree overstory, microhabitat preferences are more difficult to statistically detect because pinyon overstory cover is so dense.

The lack of an overstory canopy appears to be a consistent detriment to pinyon seedling establishment. In general, pinyon seedlings prefer overstory microhabitat, while not differentiating between specific (i.e. pinyon or juniper) overstories. The avoidance of bare areas and preference for generic overstory microhabitat displayed by pinyon seedlings could be an indication of the deleterious effects that losses of structural overstory diversity in a landscape could mean for pinyon establishment dynamics.

Juniper seedling establishment exhibited negative associations with juniper overstory microhabitat, open overstory microhabitat and pinyon overstory microhabitat. This lack of a need for overstory microhabitat facilitation, and indeed avoidance of most types of overstory microhabitat, lends credence to previous predictions of juniper expansion in marginal areas of



current pinyon dominance. Especially under predicted climate scenarios of increased intensity and frequency of droughts, the tendency of juniper seedlings to avoid establishing under any type of canopy may become increasingly important if pinyon-juniper woodland structural changes occur or range contractions occur as theorized (Allen and Breshears, 1998; Breshears et al., 2005; Gitlin et al., 2006). Under these scenarios, juniper range expansion into areas of current or recent pinyon pine dominance is likely.

Bare ground is a definitive deterrent to pinyon establishment, while various forms of litter tend to favor establishment, perhaps by inoculating germinants from moisture and temperature stresses or facilitating nutrient absorption abilities through mycorrhizal symbionts. Intense heat during the summer likely decreases seedling survival in bare ground, even if initial germination is more successful there due to favorable warm early spring temperatures (Chambers 2001; Chambers et al. 1999).

Neither species preferred or avoided pinyon or juniper litter, an unexpected result given presumed mycorrhizal benefits to moisture and resource acquisition (Haskins and Gehring, 2004; Hubert and Gehring, 2008). While the results do not indicate obvious avoidance or deterrence of these litter types, litter in general is clearly beneficial for establishment, but the type of litter is less important.

Seedling establishment is generally facilitated by substrate microhabitat and overstory presence. The absence of these microhabitats exerts strong negative influence on establishment success. Significant changes in these spatiotemporal patterns of seedling dynamics may cause long-term relictual impacts on future population dynamics, ultimately impacting spatial structure of plant populations and the long-term viability of these communities in select areas (Gómez-Aparicio et al., 2005; Jackson et al., 2009).

## **Implications**

It is widely accepted that pinyon overstory is highly susceptible to drought-induced overstory mortality events, a pattern established repeatedly in pinyon communities at varying temporal scales (Allen and Breshears, 1998; Martens et al., 2001; Shinneman, 2009). Indeed, decadal and centuries-long age structure studies indicate the strong role climate plays in shaping pinyon communities (Shinneman, 2009). Under this scenario, the influence of climate-resistant seedling establishment is likely to be mediated sharply by sudden and severe overstory mortality, a pattern manifested by rapid vegetation and community shifts impacted more by mortality induced changes than by plant establishment and migration (Allen and Breshears, 1998; Martens et al., 2001). Relative to other pines, pinyon establishment may be favored by novel climate scenarios including warmer and earlier springs as well as increased CO<sup>2</sup> levels due to evolutionary advantages in water-use efficiency strategies (Betancourt et al., 1993; Lajtha and Getz, 1993). It is difficult to envision, however, a future when changes in community composition related to tree establishment circumvent sudden mortality-based, geographically widespread changes created by drought (Allen and Breshears, 1998). Evolutionary advantages such as water-use efficiencies, furthermore, are likely tempered by the presence of extremely plastic competitors such as juniper and sagebrush. These competitors, while providing some substrate and overstory microhabitat benefits, will likely change the trajectory of long-term community dynamics by competing directly for resources but also by increased drought-resilience relative to mature pinyons (Betancourt et al., 1993; Martens et al., 2001).

Given recent pinyon overstory loss and its likely impact on suitable substrate microhabitats for pinyon and juniper seedlings, rapid loss of overstory canopy will likely preclude subsequent pinyon establishment in areas of heavy mortality due to the decreased incidence of microhabitats,

notably pinyon litter and pinyon overstory microhabitat (Haskins & Gehring, 2004). While pinyon litter and pinyon overstory were not specifically associated with pinyon establishment, the patterns of bare ground and bare overstory avoidance, coupled with pinyon preference for generic overstory and generic types of litter, indicate litter and overstory are important components of pinyon establishment dynamics. In the short term, pinyon litter may persist in a landscape with sudden overstory mortality, limiting the incidence of pinyon-avoiding bare substrate microhabitats and contributing to favorable pinyon establishment. In the long run, however, these persistent conditions will diminish as litter decays or is wind-swept off site, thus limiting pinyon establishment. While juniper seedlings also exhibited microhabitat preferences, the nature of these associations, (i.e. avoiding overstory microhabitat) indicate in a scenario with decreased pinyon overstory, juniper seedlings establishment will be less impacted.

The results described here have strong implications for managers and stakeholders interested in the long-term future of areas of pinyon-juniper dominated communities. In many areas, pinyon-juniper communities are actively discouraged from perpetuating themselves through chaining and hydro-axing programs to encourage grasses for forage. Consistent use of these tactics should presumably hinder pinyon seedling regeneration since the loss of suitable microhabitats, and the climate-resistant microclimates they presumably provide seedlings, would hinder continuous pinyon establishment and switch the feedback from one of persistence to one of diminishing survival. Under different management objectives, pinyon-juniper communities are encouraged for wildlife and conservation objectives. In these areas, managing for structural complexity and specific microhabitats may encourage pinyon community persistence in spite of severe drought events.

A sequence of overstory-altering drought events in rapid succession would assuredly cause cascading positive feedbacks, limiting the ability of pinyon seedlings to effectively establish in a landscape. By diminishing the types of substrate microhabitat and overstory microhabitat structures which facilitate pinyon establishment success, the direct compensating effect of climate-resistant pinyon seedling establishment could be negated by the indirect effects climate exerts on microhabitat and forest structural complexity. Under this scenario, the pinyon-juniper communities would transition from pinyon-dominated forests in many areas, to shrub and juniper-dominated communities and localized pinyon extirpation at marginal sites. Areas which have seen significant changes in pinyon extent or density in the last 100 years, essentially areas of marginal but obviously viable resource availability for pinyon establishment and survival, will likely see the greatest reduction in pinyon prevalence. As overstory mortality events occur, and potentially with greater frequency, these trajectories will be reversed.

These trends are predicted due to the positive feedback mechanisms which will likely inhibit pinyon establishment in the event of losses in forest structure and microhabitats, and the relative inoculation of juniper seedlings to such microhabitat limitations as well as higher resistance to drought mortality exhibited by juniper communities.

**Table 1 - Decay condition classes of pinyon pine snags on the Uncompahgre Plateau.**

Condition Classes 1 & 2 confidently categorized as mortality caused by the 2000-2004 drought and Ips beetle infestation. Condition Classes adapted from (Harmon et al., 1986; Kearns et al., 2005; Eisenhart, 2005)

| Snag Characteristics      | Decay Condition Class              |                                     |  |   |
|---------------------------|------------------------------------|-------------------------------------|--|---|
|                           | 1                                  | 2                                   | 3  | 4   |
| <b>Bark</b>               | Intact                             | Slightly Peeling (< 50%)            | Mostly Bare (< 90% Missing)                                    | Bark > 90 % Missing   |
| <b>Twigs</b>              | Dendritic - terminal twigs present | Some terminal twigs missing (< 50%) | Fine twigs and 2° twigs missing (> 50%)                        | None - All twigs missing (> 90%)                                    |
| <b>Branches</b>           | Intact                             | Intact                              | Some branches missing  | Most branches missing   |
| <b>Aerial Arrangement</b> | Standing vertical                  | Standing vertical                   | Downed w/ min. 2 points of contact - trunk mostly above ground | Downed w/ no structural support - entire trunk in contact w/ ground |

**Table 2 - Climatic datasets used in temporal pinyon establishment analysis.**

|                       | <b>Regional</b>              | <b>State</b>  | <b>Local</b>  |
|-----------------------|------------------------------|---|---|
| <b>Spatial Scale</b>  | North America                | Western Colorado<br>Climate Division 2  | Montrose, CO<br>Station ID - 055717   |
| <b>Temporal Scale</b> | Annual                       | Annual  | Monthly   |
| <b>Data Variables</b> | North American Monsoon Index | Palmer Drought Severity Index<br>Precipitation (Mean)<br>Temperature (Mean)         | Palmer Drought Severity Index<br>Precipitation (Mean)<br>Temperature (Maximum)<br>Temperature (Minimum)<br>Temperature (Mean) |
| <b>Data Source</b>    | Li & Zeng, 2002              | <a href="http://www.esrl.noaa.gov/psd/data/">http://www.esrl.noaa.gov/psd/data/</a> | <a href="http://www.wrcc.dri.edu/">http://www.wrcc.dri.edu/</a>   |
| <b>Organization</b>   | Chinese Academy of Sciences  | National Oceanic & Atmospheric Administration                                       | Western Regional Climate Center   |

**Table 3 - Summary statistics for pinyon and juniper seedlings by elevation strata (L=low, M=middle, H=high).**

| <b>Category</b>  | <b>L</b>                  | <b>M</b>                 | <b>H</b>                 | <b>p-value</b> |
|--|---------------------------|--------------------------|--------------------------|----------------|
| <b>Average Diameter at Root Collar (cm)</b>              |                           |                          |                          |                |
| Pinyon   | 1.42 (0.11) <sup>a</sup>  | 0.91 (0.07) <sup>b</sup> | 0.87 (0.08) <sup>b</sup> | <0.001         |
| Juniper  | 1.53 (0.15)               | 1.03 (0.12)              | 0.99 (0.11)              | NS             |
| Pinyon & Juniper   | 0.81 (0.08) <sup>a</sup>  | 0.90 (0.08) <sup>b</sup> | 0.99 (0.08) <sup>b</sup> | <0.001         |
| <b><u>Average Age (yr)</u></b>                           |                           |                          |                          |                |
| Pinyon   | 11.18 (0.93) <sup>a</sup> | 8.50 (0.65) <sup>b</sup> | 7.79 (0.76) <sup>b</sup> | 0.0081         |
| <b><u>Seedling Density (stems * ha<sup>-1</sup>)</u></b> |                           |                          |                          |                |
| Pinyon   | 588 (135) <sup>a</sup>    | 1,362 (139) <sup>b</sup> | 1,540 (288) <sup>b</sup> | 0.0028         |
| Juniper  | 155 (29.7) <sup>a</sup>   | 320 (42.7) <sup>b</sup>  | 269 (43.2) <sup>ab</sup> | 0.012          |
| Pinyon & Juniper   | 879 (183) <sup>a</sup>    | 2,167 (179) <sup>b</sup> | 2,571 (472) <sup>b</sup> | <0.001         |

*Notes:* Standard deviations are in parentheses. Means within rows (i.e., between elevation strata) that do not share superscripts differ by <0.05 according to Tukey's HSD. P-values reported are from one-way ANOVA.

**Table 4 - Summary statistics for pinyon and juniper overstory trees by elevation strata**  
Basal area, diameter, and density were calculated post-drought, with percent change calculated with the difference in basal area between live and recent dead.

| <b>Category</b>   | <b>L</b>                  | <b>M</b>                  | <b>H</b>                 | <b>p-value</b> |
|---|---------------------------|---------------------------|--------------------------|----------------|
| <b>Basal Area (m<sup>2</sup> * ha<sup>-1</sup>)</b>                                       |                           |                           |                          |                |
| Pinyon (live)   | 2.8 (0.7) <sup>a</sup>    | 9.1 (1.5) <sup>b</sup>    | 14.2 (1.5) <sup>c</sup>  | < 0.001        |
| Pinyon (dead)   | 3.2 (0.7)                 | 4.8 (1.1)                 | 4.3 (1.2)                | NS             |
| Juniper (live)  | 25.6 (2.8) <sup>a</sup>   | 17.8 (2.1) <sup>ab</sup>  | 16.1 (2.8) <sup>b</sup>  | 0.035          |
| Juniper (dead)  | 0.9 (0.3)                 | 1.8 (0.6)                 | 1.2 (0.5)                | NS             |
| <b>Percent change in live canopy due to disturbance (m<sup>2</sup> * ha<sup>-1</sup>)</b> |                           |                           |                          |                |
| Pinyon  | -58.5 (6.3) <sup>a</sup>  | -35.50 (7.6) <sup>b</sup> | -21.6 (5.5) <sup>b</sup> | < 0.001        |
| Juniper   | -3.8 (1.4)                | -6.7 (1.9)                | -5.1 (1.7)               | NS             |
|   |                           |                           |                          | NS             |
| <b>Diameter at Root Collar (cm)</b>   |                           |                           |                          |                |
| Pinyon (live)   | 24.2 (0.9) <sup>a</sup>   | 25.01 (0.9) <sup>ab</sup> | 29.1 (0.9) <sup>b</sup>  | 0.011          |
| Pinyon (dead)   | 13.6 (1.3)                | 16.64 (1.2)               | 16.1 (1.7)               | NS             |
| Juniper (live)  | 27.4 (1.4) <sup>a</sup>   | 29.53 (1.6) <sup>ab</sup> | 29.3 (1.6) <sup>b</sup>  | 0.025          |
| Juniper (dead)  | 37.8 (2.8)                | 36.32 (1.4)               | 31.6 (2.2)               | NS             |
| <b>Overstory Density (stems * ha<sup>-1</sup>)</b>  |                           |                           |                          |                |
| Pinyon (live)   | 173.6 (40.9) <sup>a</sup> | 500 (60.2) <sup>b</sup>   | 632 (93.6) <sup>b</sup>  | < 0.001        |
| Pinyon (dead)   | 146.4 (18.6)              | 200 (40.3)                | 132 (34.9)               | NS             |
| Juniper (live)  | 374.4 (35.8)              | 325.6 (32.4)              | 286.4 (30.7)             | NS             |
| Juniper (dead)  | 15.2 (4.9)                | 22.4 (7.2)                | 15.2 (5.3)               | NS             |

*Notes:* Standard deviations are in parentheses. Means that do not share superscripts differ by <0.05 according to Tukey's HSD. P-values reported are from one-way ANOVA.



**Table 5 - Pinyon and juniper seedling overstory microhabitat preferences**

Positive values indicate seedling "Preference" for a specific overstory microhabitat ( $p < 0.025$ ). Negative values indicate seedling "Avoidance" of a specific overstory microhabitat category ( $p < 0.025$ ).

| Overstory Microhabitat Category | Pinyon | Juniper |
|---------------------------------|--------|---------|
| Juniper                         | +      | -       |
| Pre-Drought Open                | -      | -       |
| Post-Drought Open               | -      |         |
| Pinyon                          |        | -       |
| Pinyon & Juniper                |        |         |
| Shrub                           |        |         |
| All Overstory                   | +      | -       |

**Table 6 - Pinyon and juniper seedling substrate microhabitat preferences**

Positive values indicate seedling "Preference" for specific substrate microhabitat ( $p < 0.025$ ). Negative values indicate seedling "Avoidance" of specific substrate microhabitat ( $p < 0.025$ ).

| Substrate Microhabitat Category  | Pinyon | Juniper |
|----------------------------------|--------|---------|
| Bare Ground                      | —      |         |
| Rock                             |        | +       |
| Shrub Litter                     | +      | +       |
| Nitrogen-Fixing Shrub Litter     |        |         |
| Non-Nitrogen-Fixing Shrub Litter | +      | +       |
| Tree Litter                      | +      | +       |
| Juniper Litter                   |        | +       |
| Mixed Pinyon & Juniper Litter    |        |         |
| Pinyon Litter                    |        |         |
| Unidentified Litter              | —      |         |
| Biological Soil Crust            |        | +       |
| Log or Root                      | +      |         |

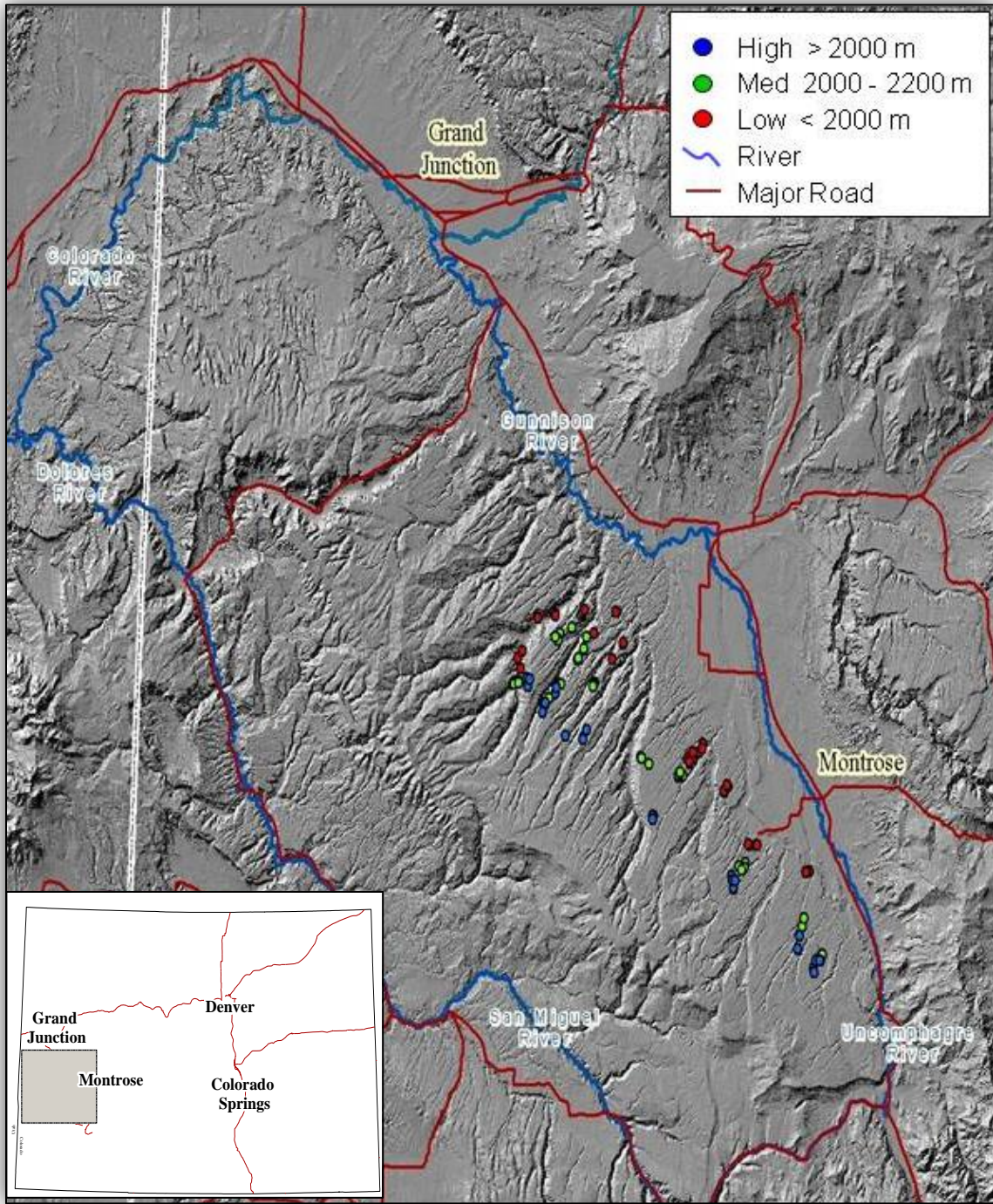
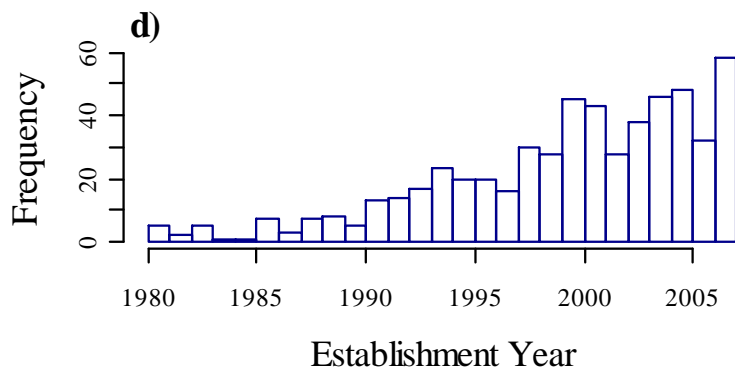
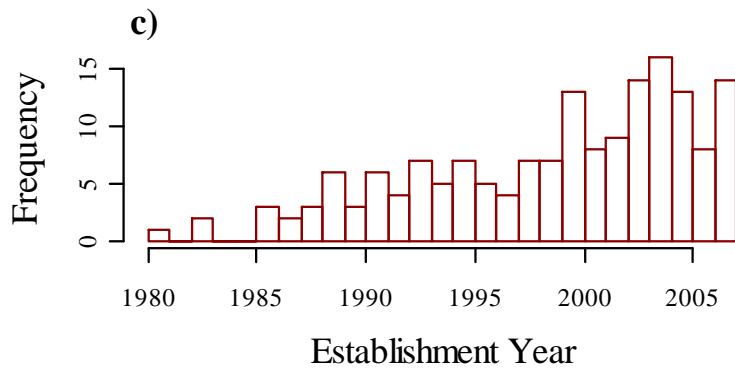
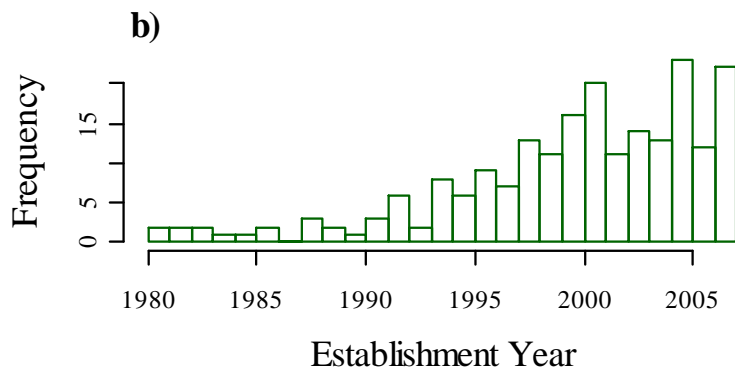
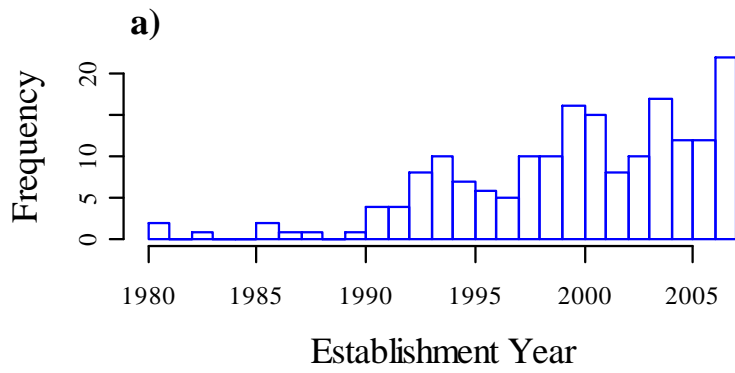
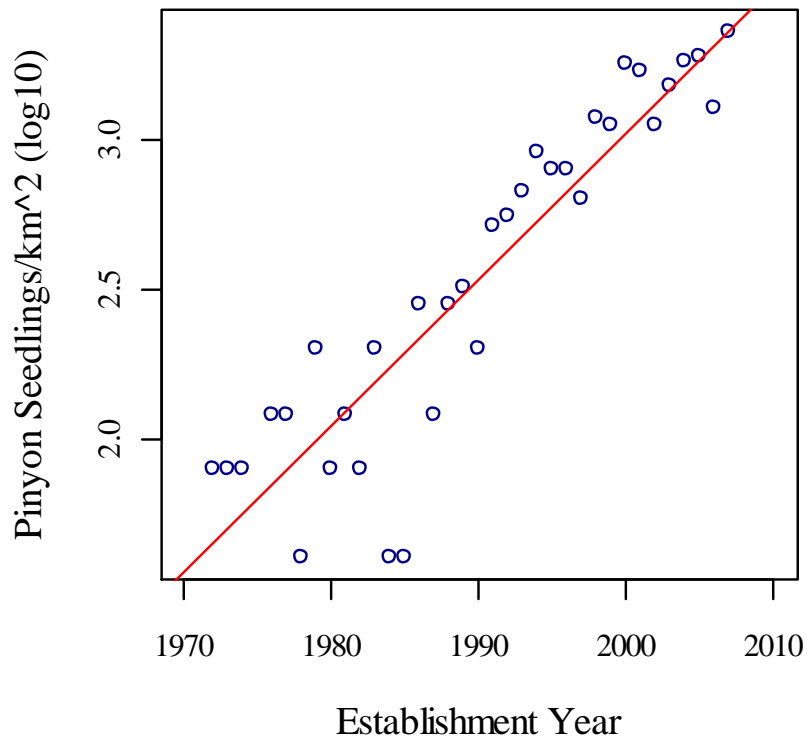


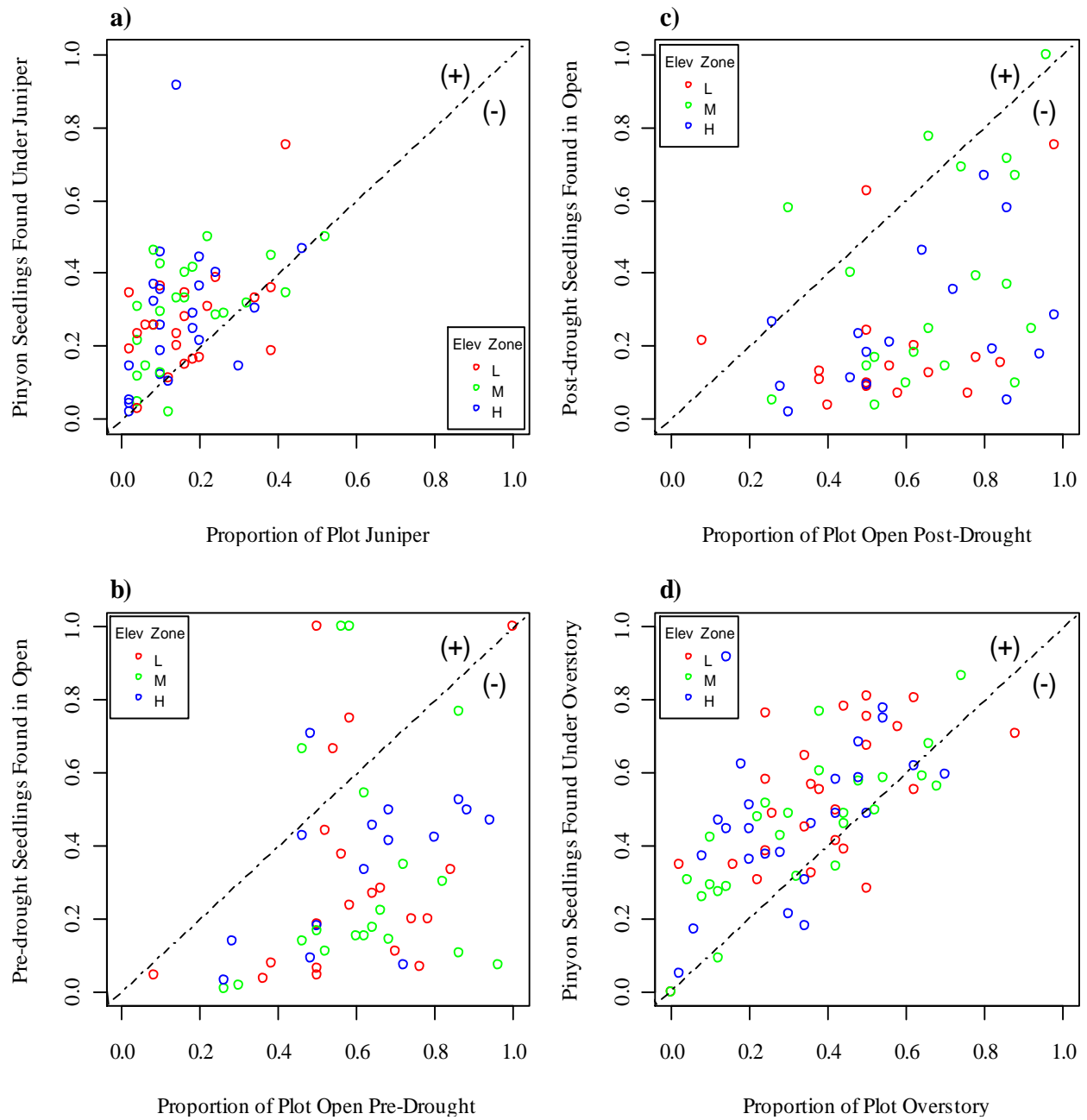
Figure 1 - Study area with plot locations on the Uncompahgre Plateau in western Colorado



**Figure 2 - Age frequency histograms of establishment year for pinyon seedlings.**  
 a) High elevation plots, b) Medium elevation plots, c) Low elevation plots. d) All plots

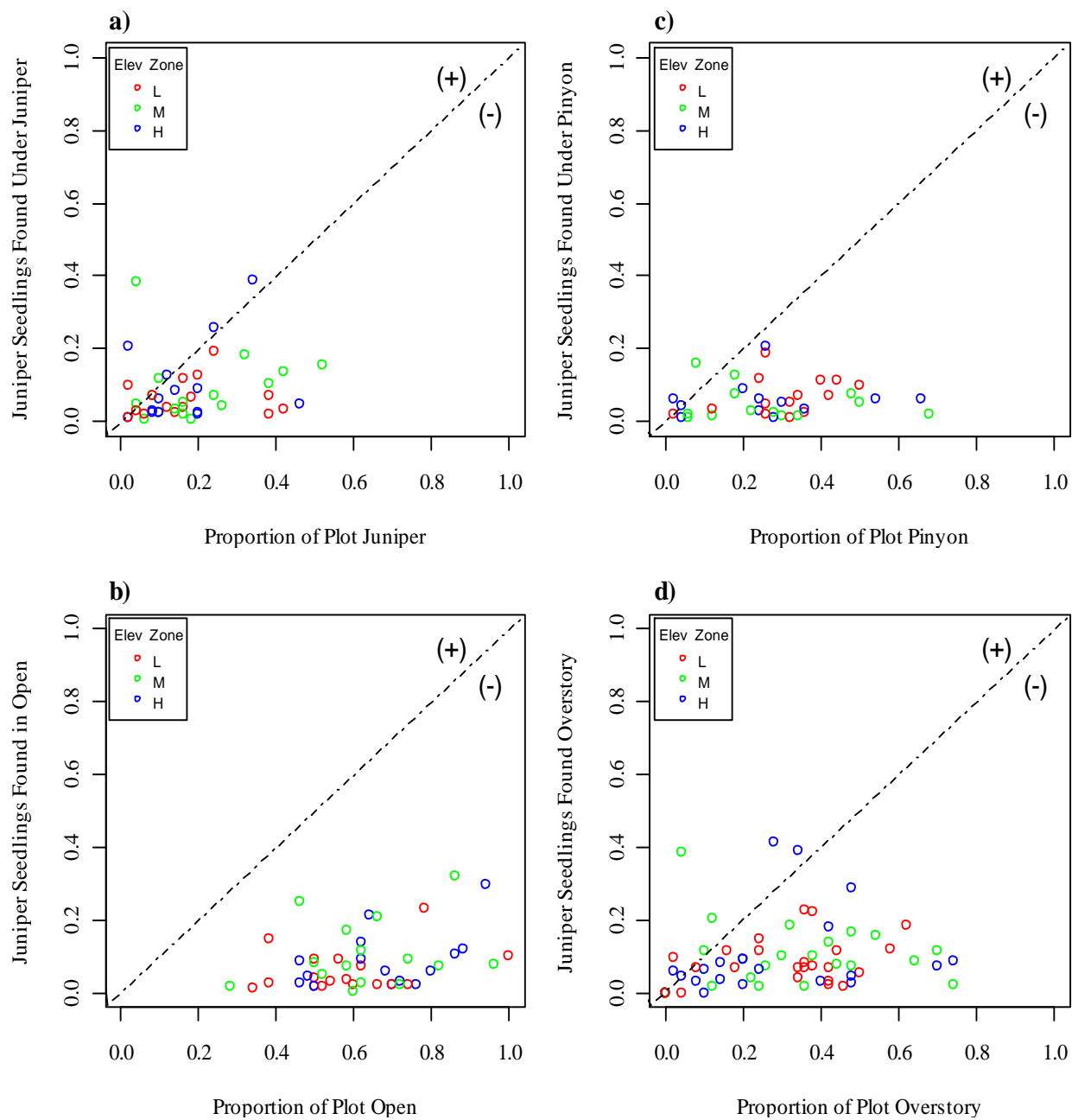


**Figure 3 - Density of pinyon (all plots) establishing by year.**  
( $R^2 = 0.82$ ,  $p < 0.001$ ).



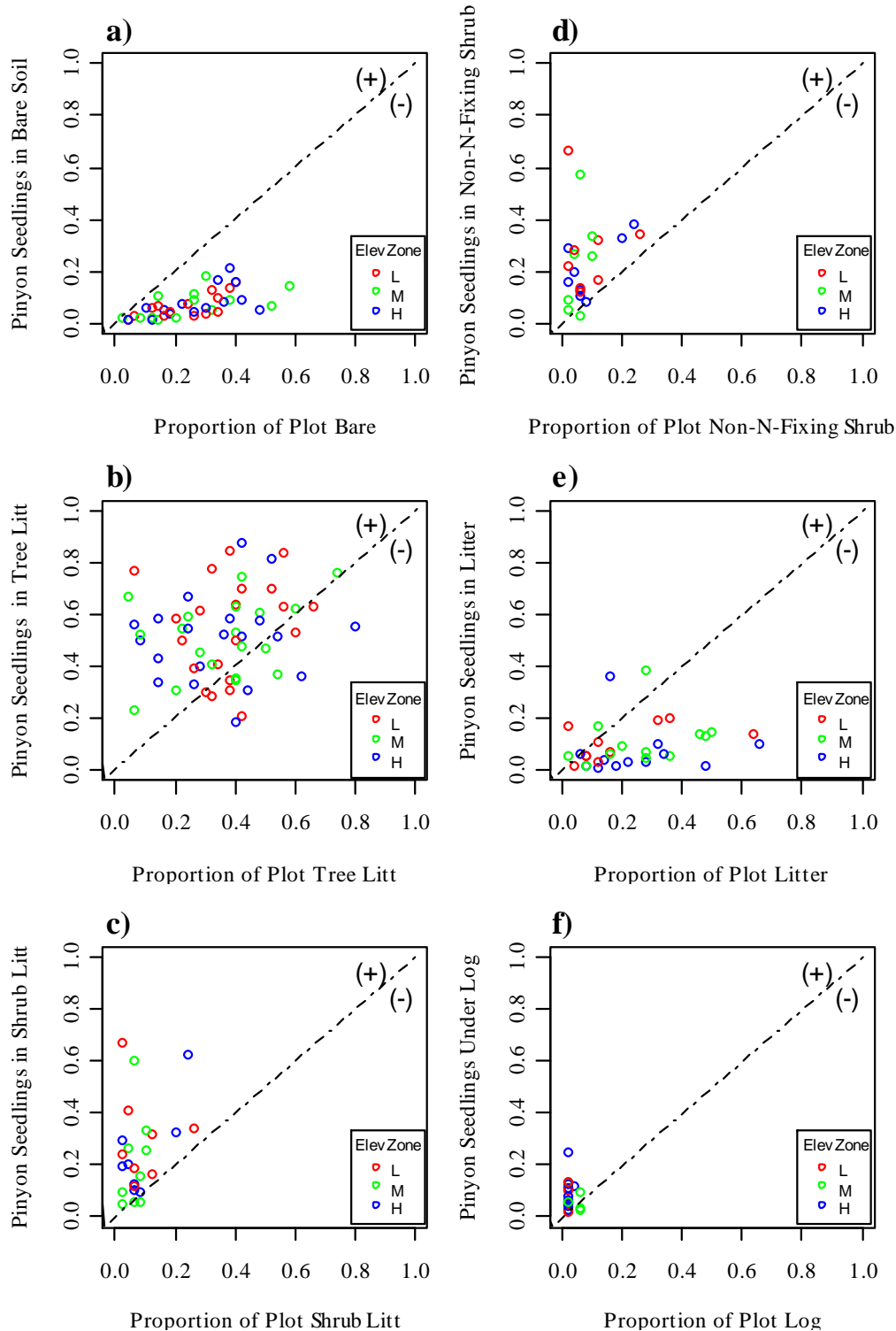
**Figure 4 - Pinyon seedling overstory microhabitat preferences.**

Proportion of each plot covered by specific overstory microhabitat vs. proportion of pinyon seedlings found under the same overstory microhabitat category. a) Pinyon seedlings prefer juniper overstory microhabitat ( $p < 0.001$ ). Pinyon seedlings avoided open overstory microhabitat both a) pre-drought, and b) post-drought ( $p < 0.001$ ), but d) prefer all overstory ( $p < 0.001$ ).



**Figure 5 - Juniper seedling overstory microhabitat preferences.**

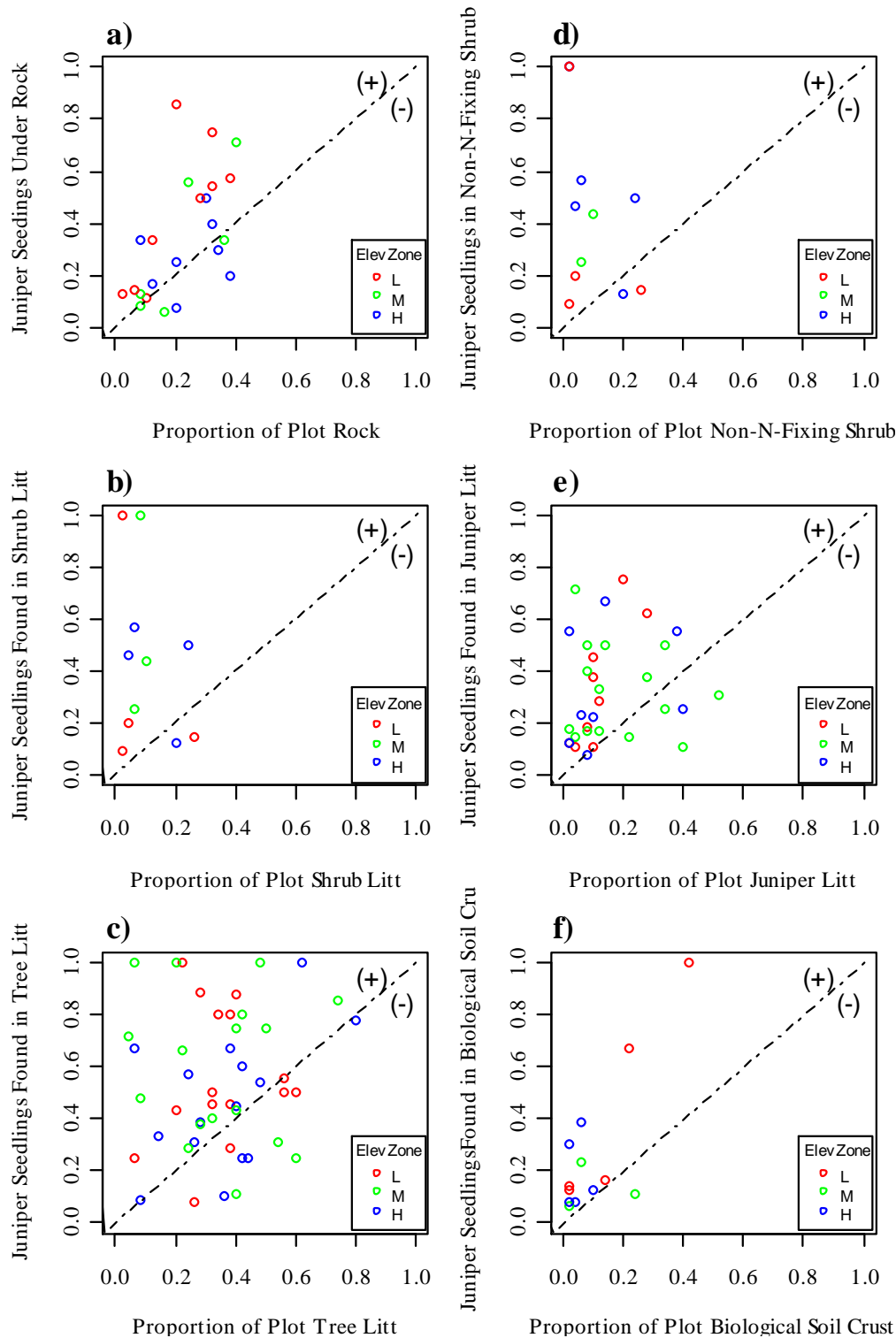
Proportion of a specific overstory microhabitat in each plot vs. proportion of juniper seedlings found in that overstory microhabitat; a) Seedlings avoid juniper overstory microhabitat ( $p < 0.001$ ), b) avoid open overstory microhabitat ( $p < 0.001$ ), c) avoid pinyon overstory microhabitat ( $p < 0.001$ ), and d) avoid all overstory ( $p < 0.001$ ).



**Figure 6 - Pinyon seedling substrate microhabitat preferences.**

Proportion of a specific substrate microhabitat in each plot vs. proportion of seedlings found in that substrate microhabitat; a) Seedlings avoid bare substrate microhabitat ( $p < 0.001$ ) but b) prefer tree litter ( $p < 0.001$ ). c) Seedlings prefer shrub litter ( $p < 0.001$ ) and d) non-nitrogen-fixing litter ( $p < 0.001$ ) but e) avoid non-specific litter ( $p < 0.001$ ). f) Seedlings prefer log or rock ( $p < 0.001$ ).





**Figure 7 - Juniper seedling substrate microhabitat preferences.**

Proportion of a specific substrate microhabitat in each plot vs. proportion of juniper seedlings found in that specific substrate microhabitat; a) Juniper seedlings prefer rock ( $p < 0.001$ ), b) shrub litter ( $p < 0.001$ ), c) non-Nitrogen-fixing ( $p < 0.001$ ), d) tree litter ( $p < 0.001$ ), e) juniper litter ( $p < 0.001$ ), f) and biological soil crust substrate microhabitat ( $p < 0.001$ ).

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