



Transition of Vegetation States Positively Affects Harvester Ants in the Great Basin, United States[☆]



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ABSTRACT

Invasions by non-native plants can alter ecosystems such that new ecological states are reached, but less is known about how these transitions influence animal populations. Sagebrush (*Artemisia tridentata*) ecosystems are experiencing state changes because of fire and invasion by exotic annual grasses. Our goal was to study the effects of these state changes on the Owyhee and western harvester ants (*Pogonomyrmex salinus* Olsen and *P. occidentalis* Cresson, respectively). We sampled 358 1-ha plots across the northern Great Basin, which captured unburned and burned conditions across 1–≥31 years postfire. Our results indicated an immediate and consistent change in vegetation states from shrubland to grassland between 1 and 31 years postfire. Harvester ant occupancy was unrelated to time since fire, whereas we observed a positive effect of fire on nest density. Similarly, we discovered that fire and invasion by exotic annuals were weak predictors of harvester ant occupancy but strong predictors of nest density. Occupancy of harvester ants was more likely in areas with finer-textured soils, low precipitation, abundant native forbs, and low shrub cover. Nest density was higher in arid locations that recently burned and exhibited abundant exotic annual and perennial (exotic and native) grasses. Finally, we discovered that burned areas that received postfire restoration had minimal influence on harvester ant occupancy or nest density compared with burned and untreated areas. These results suggest that fire-induced state changes from native shrublands to grasslands dominated by non-native grasses have a positive effect on density of harvester ants (but not occupancy), and that postfire restoration does not appear to positively or negatively affect harvester ants. Although wildfire and invasion by exotic annual grasses may negatively affect other species, harvester ants may indeed be one of the few winners among a myriad of losers linked to vegetation state changes within sagebrush ecosystems.

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Introduction

Biological invasions of nonnative plants alter ecosystem processes and thus affect native fauna in many direct and indirect ways (D'Antonio and Vitousek, 1992; White et al., 2006; Litt and Pearson, 2013). In some cases, non-native plants have altered ecosystems to such an extent that new, relatively stable ecological states are reached, resulting in novel plant communities (Bestelmeyer et al., 2011). Ecological state transitions caused by non-native plants can directly change demographic rates of animals, such as survival or production, resulting in changes in occupancy and density (e.g., Ostoja et al., 2009; Ostoja and Schupp, 2009; Litt and

Steidl, 2011). By altering population parameters of animals, particularly those with a disproportionate influence on the surrounding ecosystem, biological invasions of non-native plants can cause cascading or indirect effects that further alter animal-animal or plant-animal interactions (e.g., White et al., 2006). These indirect effects could ultimately influence the resilience of an ecosystem to recover from or resist future invasion by non-native species (e.g., Toro et al., 2015).

Sagebrush (*Artemisia tridentata*) ecosystems in lower elevations (i.e., *A. t. wyomingensis*) throughout western North America are experiencing changes in vegetation states because of a synergy between changing fire regimes and biological invasions by exotic annual grasses such as cheatgrass (*Bromus tectorum*; Baker, 2011; Davies et al., 2011; Miller et al., 2011; Chambers et al., 2014). Historically, sagebrush vegetation states were generally composed of shrublands with native perennial grasses as the dominant functional group within the sparsely vegetated understory (Miller et al., 2011). However, invasion by exotic annual grasses (due to human activity, land conversion, and grazing; Knick et al., 2011) has substantially changed fire regimes and resulted in lower fire return intervals, larger area burned per fire, and increased

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probability of fire (Baker, 2011; Miller et al., 2011; Balch et al., 2013). These changes in fire regimes have subsequently enhanced the invasion of exotic annual grasses (Chambers et al., 2007). Remotely sensed data indicate that the extent of cheatgrass dominance exceeded 40 000 km² of the Great Basin Desert (nearly 10%) in 2008 (Bradley and Mustard, 2008), and it has likely increased since then. Indeed, changes in wildfire and biological invasions by exotic annual grasses are synergistically contributing to current vegetation state changes in sagebrush ecosystems: that is, shifts from sagebrush shrublands with native perennial grasses to grasslands dominated by exotic annual grasses (Davies et al., 2011; Miller et al., 2011; Chambers et al., 2014). To understand the consequences of such changes, it is essential to evaluate how fire and exotic annual grasses influence functionally important animals within sagebrush landscapes.

Considering the extent and magnitude of state changes in sagebrush ecosystems, there are surprisingly few studies assessing the effects of these changes on animals. Previous work has demonstrated negative effects of cheatgrass invasion on communities of passerines (Knick and Rotenberry, 1995, 2000), small mammals (Ostoja and Schupp, 2009; Rieder et al., 2010; Freeman et al., 2014), lizards (Newbold, 2005; Rieder et al., 2010), and snakes (Hall et al., 2009). Contrastingly, Ostoja et al. (2009) documented an increase in density of ant assemblages in areas dominated by cheatgrass. Although this information enhances our understanding of how state changes influence animals, most of the previous studies 1) were limited in spatial extent (e.g., $\leq 25 - 400$ km²), 2) were unable to assess how plant and animal parameters change as a function of recovery time (e.g., time since fire or invasion), and 3) could not adequately assess the relative importance of state changes in the context of other environmental gradients. Therefore, our aim was to assess state changes in a sagebrush ecosystem and evaluate the effects on occupancy and density of harvester ants across an extensive spatial gradient capturing a range of time since fire.

We selected Owyhee and western harvester ants (*Pogonomyrmex salinus* Olsen and *P. occidentalis* Cresson, hereafter harvester ant) as target species because they are granivorous and also serve as ecosystem engineers (e.g., Jones et al., 1994, 1997, 2010) in many desert environments (MacMahon et al., 2000). In arid ecosystems seed predation and movement are arguably the most critical plant-animal interactions shaping plant communities (e.g., Brown et al., 1979; Crist and MacMahon, 1992; Heske et al., 1993). Pearson et al. (2014) indicated that harvester ants in Argentina suppressed plant recruitment by 22–89%. Further, harvester ant activities directly and indirectly influence plant communities by removing vegetation (Carlson and Whitford, 1991; Gosselin et al., 2016) and increasing soil nutrients and water absorption (Mandel and Sorenson, 1982; Blom, 1990; Wagner et al., 1997; Wilby et al., 2001; Brown et al., 2012). The trophic and ecosystem engineering interactions associated with harvester ants emphasize the importance of evaluating how state changes influence their occupancy and density.

Our research objectives were to 1) assess state changes in vegetation, occupancy of harvest ants, and nest density of harvester ants (hereafter density) across a gradient of time since fire; 2) determine the relative importance of fire and biological invasions on harvester ants; and 3) assess the effect of postfire restoration on harvester ants. We expected state changes from shrublands to exotic annual grasslands would happen immediately after fire (i.e., 1 year postfire) and remain for all years across our postfire gradient (e.g., Baker, 2011), and that these changes would have positive effects on occupancy and density of harvester ants (Ostoja et al., 2009). We also predicted that the relative importance of fire and exotic annual grasses would be greater for harvester ant density compared with occupancy and that the effects of both factors would be positive. We expected this pattern because evidence indicates that biotic gradients largely influence variation in density, while abiotic gradients tend to drive variation in occupancy (e.g., Boulangeat et al., 2012; Holbrook et al., 2016). Lastly, we expected areas with evidence of postfire restoration (e.g., rows of native or exotic

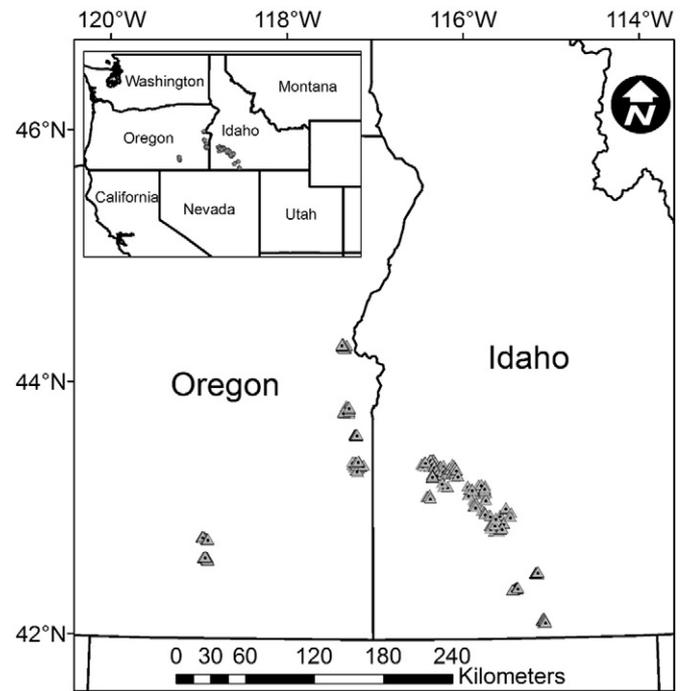


Figure 1. Triangles indicate the distribution of 1-ha plots ($n = 358$) that were sampled for harvester ants (*Pogonomyrmex* spp.) within southern Oregon and Idaho, United States, during 2008–2009 and 2013–2014. Inset shows the distribution of samples in a larger spatial context.

perennial grasses) that suppressed cheatgrass to have little effect or a slight negative effect on harvester ants relative to burned and untreated areas because of the positive effect of exotic annual grasses on harvester ants (Ostoja et al., 2009). Collectively, this work contributes to the understanding of vegetation state changes within sagebrush ecosystems, as well as advances in our understanding of the consequences of such changes on the animal community.

Methods

Study Area and Sampling

We conducted this study across an $\sim 78\,400$ km² extent within publicly managed sagebrush areas throughout southern Idaho and Oregon, United States (Fig. 1). To capture a gradient of vegetation states we combined existing data sets from three separate studies of post-wildfire and seeding treatments (one study took place in 2008–2009, and the second was conducted in 2013–2014). In each study, plant community data and colony density of harvester ants were recorded using identical methods at locations that were selected randomly within each study area (i.e., southeastern Oregon and southwestern Idaho). We used a Geographic Information System (GIS) to randomly place 1-ha plots within 1) areas that were previously burned and seeded (via aerial or rangeland drill methods by the US Bureau of Land Management) with native and exotic perennial plants, 2) areas that were burned and not seeded, and 3) areas that have not burned for at least the past ~ 33 years. Postfire seeding treatment characteristics were derived from the Land Treatment Digital Library (Pilliod and Welty, 2013). The sample size from the 2008–2009 and 2013–2014 study were 225 and 133, respectively, with an allocation of 20–42% burned, 28–39% burned and treated, and 27–39% unburned. Sites ranged in mean annual precipitation from 20 to 64 cm, and fire years ranged from 1980 to 2012. The dominant plant communities we sampled include big sagebrush, winterfat (*Krascheninnikovia lanata*), shadscale saltbrush (*Atriplex confertifolia*), Sandberg bluegrass (*Poa secunda*), and cheatgrass.

Table 1Covariate descriptions, correlations, and collection methods for the variables used in analyses of vegetation states and harvester ant (*Pogonomyrmex* spp.) occupancy and density in Idaho and Oregon, United States

Variable	Units	Mean (Range)	Description	Method
Soil	%	85 (62.5–98.25)	Mean % surface soil passing through a #4 sieve within each map unit key (mukey) code	STATSGO (1:250,000)
Precipitation	cm	32.5 (19.9–63.9)	Mean annual precipitation from 1979–2008	PRISM (800 m)
Time since fire (TSF)	yr	19 (1–33)	Number of years since a fire burned an area using data beginning at 1980, or using 1980 as a reference time for unburned plots	GIS (90 m)
Native perennial grasses (NPGs)	%	20 (0–68)	Mean % cover of native perennial grass at the plot level	PhotoPoint
Exotic perennial grasses (EPGs)	%	3 (0–51)	Mean % cover of exotic perennial grasses at the plot level	PhotoPoint
Exotic forbs (EFs)	%	2 (0–24)	Mean % cover of exotic forbs at the plot level	PhotoPoint
Native forbs (NFs)	%	1 (0–32)	Mean % cover of native forbs at the plot level	PhotoPoint
Exotic annual grasses (EAGs)	%	28 (0–96)	Mean % cover of exotic annual grasses at the plot level (mostly cheatgrass; <i>Bromus tectorum</i>)	PhotoPoint
Shrub	%	6 (0–54)	Mean % cover of shrubs at the plot level	PhotoPoint

Harvester Ant Data

At each 1-ha plot, we surveyed for harvester ant nests during April – August in 2008 – 2009 or 2013 – 2014. Our sampling season was coincident with harvester ant activity, allowing us to identify active nests or colonies. To characterize harvester ant occupancy and colony density during 2008 – 2009, we enumerated colonies within three 100 m × 2 m (600 m²) belt-transects spaced 25 m apart. During 2013 – 2014, we increased our survey effort to three 100 × 4 m (1200 m²) belt-transects because of relatively low ant densities at sites sampled during this time. A three-transect design was an appropriate balance of statistical precision and sampling effort (Holbrook et al., 2015). We classified a nest as active if we observed individual ants in or on the nest. If no individuals were detected, observers disturbed the nest and waited for up to 30 seconds to solicit a response. Previous analyses indicated a high correlation (i.e., $r = 0.99$, slope = 1.01) of counts of harvester ant colonies among independent observers, which was indicative of high survey consistency and detection probabilities (see Holbrook et al., 2015). Finally, we resampled 30 plots in 2014 that we surveyed in 2013 to assess interannual variation in the density of harvester ant colonies. Total counts of ant colonies were similar between years, as indicated by the Pearson's correlation coefficient ($r = 0.95$), suggesting little annual turnover in ant colonies.

Time Since Fire and Vegetation Data

We used GIS and field data to characterize time since fire (Table 1). First, we overlapped a fire perimeter geodatabase (USGS, unpublished data), over our 1-ha plots to determine the most recent fire (≥ 1980) intersecting each plot. We limited our analyses to ≥ 1980 because fire information before 1980 is unreliable (Miller et al., 2011). We then used field data to validate if the plot exhibited characteristics of a burn (i.e., few or no shrubs present; Chambers et al., 2014) but was not seeded (i.e., lack of regularly spaced rows of exotic or perennial grasses); these plots were classified as “burned” and were assigned a time since fire value. We then used all plots with no evidence of fire (i.e., containing a spatially consistent shrub component) as our controls characterizing unburned conditions. This grouping of plots (total $n = 210$) was used to satisfy our first objective of assessing responses of vegetation and harvester ants across a gradient of time since fire (without the influence of management such as postfire seeding). Next, to satisfy our second objective we assigned the appropriate time since fire value to “burned and treated” plots, as well as assigned a value to “unburned” plots (total $n = 337$). We classified plots as “burned and treated” if they fell within known postfire seeding areas and/or exhibited evidence of successful seeding, such as rows of native or exotic perennial grasses.

For our unburned plots, we conservatively assigned the maximum value (e.g., 33 years) of time since fire by subtracting the survey year from 1980. If we did not assign our unburned plots with a time since fire value, we would have not been able to assess the relative importance of shrub cover and all other covariates on harvester ant occupancy or colony density, which was a major component of our second objective.

We characterized the vegetation community at each plot using a sample of 6 – 9 random or systematically placed (depending on the study site) locations within our plots. At each location, we captured a nadir (i.e., 90°) photograph from 2 m above the ground (Pilliod and Arke, 2013). This height corresponded to a 1.5 × 2 m area of ground surface and provided sufficient height above shrubs. We used SamplePoint 1.43 software (Booth et al., 2006) to measure the cover of species and abiotic habitat components (e.g., rock, soil, litter) at 100 computer-selected pixels per image. We classified each pixel to a plant group (see Table 1), which generated a percent cover measurement at each photographed location. We then averaged percentages across the 6 – 9 locations to attain plot-level estimates of percent cover.

Other Environmental Data

We developed an abiotic soil index describing soil texture using STATSGO data (see Table 1; Soil Survey Staff, Natural Resources Conservation Service). We identified the STATSGO map unit key (mukey) at each plot and averaged (across up to 10 soil names) the proportion of soil passing through a number 4 sieve at the first soil depth. This resulted in an index with larger numbers indicating finer-grained soils and low numbers indicating coarse-grained soils. We expected harvester ants to be strongly associated with finer-grained soils (e.g., Johnson, 1992) because they retain soil moisture better than coarse-grained soils (Johnson, 2001). Soil moisture positively influences 1) survival of harvester ant (*Pogonomyrmex rugosus*, *Pogonomyrmex barbatus*) foundresses, 2) wet body mass, and 3) brood production during colony establishment and growth (Johnson, 1998), which are the most vulnerable life stages for colonies.

We used GIS databases to generate climate metrics at each plot (see Table 1). First, we calculated mean annual precipitation and mean annual temperature from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group, Oregon State University, 2004) during the time period 1979–2008. We expected harvester ants to be negatively associated with mean annual precipitation (over our sampled gradient) because harvester ants are evolutionarily adapted for semiarid or arid environments (Johnson, 2001) and tend to be more abundant in these locations (Hanser et al., 2011).

Data Analysis

State Changes

To assess the direction and temporal trend in plant characteristics and occupancy and colony density of harvester ants, we categorized plots according to quantiles of the time since fire distribution. Our categories allowed us to maintain reasonable sample sizes within each bin of time since fire, which resulted in 1–6 years ($n = 32$), 7–21 years ($n = 26$), 21–31 years ($n = 29$), and unburned ($n = 123$). We used our unburned group as our control under the assumption that it closely matched the preburn vegetation state. We elected to group data across our time since fire gradient because we anticipated nonlinear plant responses. At each group, we computed the mean ($\pm 90\%$ CI) for exotic annual grasses (EAGs), native perennial grasses (NPG), and shrubs, as well as the proportion of sites occupied and density of harvester ant colonies. We focused on these plant groups because they are the major groups discussed in terms of vegetation state changes in sagebrush ecosystems (e.g., Chambers et al., 2014) and they are the most dominant groups in our data (see Table 1).

Relative Importance of Fire and Biological Invasions

To evaluate the relative importance of fire and biological invasions on harvester ant occupancy and colony density, we combined vegetation data, time since fire, and other environmental factors potentially important for harvester ants (see Table 1) into generalized linear models. We used a nested approach similar to Boulangeat et al. (2012) and Holbrook et al. (2016), within which we built one model assessing the variation in occupancy ($n = 337$), and then built a second model to evaluate variation in colony density ($n = 162$) for those plots that were occupied. We used generalized linear models with a binomial error distribution for occupancy data and a negative binomial error distribution for density data. In each model, we included an offset describing the difference in area surveyed among study sites to account for differences in survey effort (i.e., 600 vs. 1200 m²). Because our research objectives were focused on general patterns, we evaluated only main effects.

Before model development, we standardized covariates and evaluated multicollinearity. We standardized continuous covariates by $(x_i - \bar{x}) / (2 \times \sigma)$ where x_i equals an observation at plot i , σ is the standard deviation of covariate x , and \bar{x} is the mean of the covariate. This standardization allowed for an equal comparison among effect sizes (Gelman, 2008), which was important for our objective of assessing relative importance of fire and biological invasions. We assessed collinearity among covariates and removed temperature because it was correlated with precipitation ($r = -0.67$).

For each response variable, we developed an initial model with all covariates except exotic annual grasses and time since fire (see Table 1). For these analyses, we kept the continuous scale of time since fire because we expected linear responses by harvester ants. We then added both exotic annual grasses and time since fire to the initial model and tested the drop-in deviance using a likelihood ratio test to evaluate if exotic annual grasses and time since fire increased the fit of our model. For example,

Initial model:

$$\text{logit or log}(Y_i) = \beta_0 + \beta_1(x_{i1}) + \beta_2(x_{i2}) + \beta_3(x_{i3}) + \varepsilon \quad (1)$$

Fire and biological invasion model:

$$\text{logit or log}(Y_i) = \beta_0 + \beta_1(x_{i1}) + \beta_2(x_{i2}) + \beta_3(x_{i3}) + \beta_4(\text{TSF}_i) + \beta_4(\text{EAG}_i) + \varepsilon \quad (2)$$

where Y = response variable at plot i , β = regression coefficient associated with a particular covariate, and x = observation of a particular covariate at plot i . As aforementioned, to provide a conservative estimate of time since fire in unburned plots, we set time since fire to the maximum values on the basis of fire data from ≥ 1980 .

We assessed model fit for our most supported (i.e., either model [1] or [2], depending on results) occupancy and density models. For our occupancy model, we tested goodness of fit (Hosmer and Lemeshow, 2000) and assessed predictive performance by calculating the area under the curve (AUC) of a receiver operating characteristic (ROC; Robin et al., 2011). An ROC plot characterizes true positives against false positives, and the AUC ranges from 0 to 1 providing a measure of the model's ability to correctly discriminate between plots that are occupied versus unoccupied (Hosmer and Lemeshow, 2000; Robin et al., 2011). An AUC of 0.5 indicates random discrimination, whereas values > 0.5 indicate progressively better discrimination (Hosmer and Lemeshow, 2000). For our density model, we computed the Spearman's rank correlation coefficient between the observed and predicted counts as a measure of fit. Finally, we plotted the effect sizes ($\pm 90\%$ confidence interval [CI]) of the estimated parameters describing covariate relationships, which allowed us to assess statistical significance (i.e., different from 0) and determine the effects that were the strongest. To complete these analyses, we used program R (R Core Team, 2015) and packages "MASS" (Venables and Ripley, 2002), "ResourceSelection" (Lele et al., 2014), and "pROC" (Robin et al., 2011).

Effects of Postfire Restoration

We assessed if postfire seeding had an effect on occupancy and colony density of harvester ants that was statistically different than burned plots that were not treated. To characterize the vegetation conditions among burned ($n = 98$) and burned and treated ($n = 124$), we computed the mean ($\pm 90\%$ CI) for the plant groups aforementioned (i.e., exotic annual grasses, native perennial grasses, and shrubs). We also included the unburned category ($n = 123$) for comparative purposes. We then calculated the proportion of sites occupied and density of harvester ant colonies among groups to evaluate statistical differences.

Results

State Changes

Across our sample, we observed 0–2.8 harvester ant colonies per 100 m², and 48% of the 358 plots we surveyed were occupied by ants. The effect of time since fire on shrub cover was immediate and consistent in that the estimated shrub cover for years 1–31 postfire was similar (<4%) and significantly less than shrub cover in unburned areas (14%; Fig. 2). Of our total sample, 64% of plots experienced this state change from shrublands to grasslands (i.e., sites that were burned). Additionally, native perennial grasses increased between 1 and 21 years (12–17%) and 22 and 31 years (32%) postfire, and the estimate for 22–31 years was similar to unburned areas (see Fig. 2). Cover of exotic annual grasses was highest during 1–21 years postfire (47–51%) but was significantly lower 22–31 years postfire (23%) and in unburned areas (12%; see Fig. 2). Collectively, these results indicate that shrub cover was removed after fire and did not recover up to 31 years postfire; however, exotic annual grasses decreased and native perennial grasses increased over time, but this pattern was entirely contingent on the group of 22–31 years postfire.

Occupancy and colony density of harvester ants displayed disparate patterns across our time since fire gradient. The proportion of plots occupied by harvester ants was unrelated to time since fire (see Fig. 2). However, colony density was statistically higher in areas that burned compared with unburned conditions (see Fig. 2). In addition, we observed a decrease in colony density as time since fire increased, which highlighted a positive effect of recent fire (see Fig. 2).

Relative Importance of Fire and Biological Invasions

Our modeling results indicated that biological invasions by exotic annual grasses and the effect of time since fire did not improve model fit for occupancy ($X^2 = 4.33$, $df = 2$, $p = 0.12$) of harvester ants, but

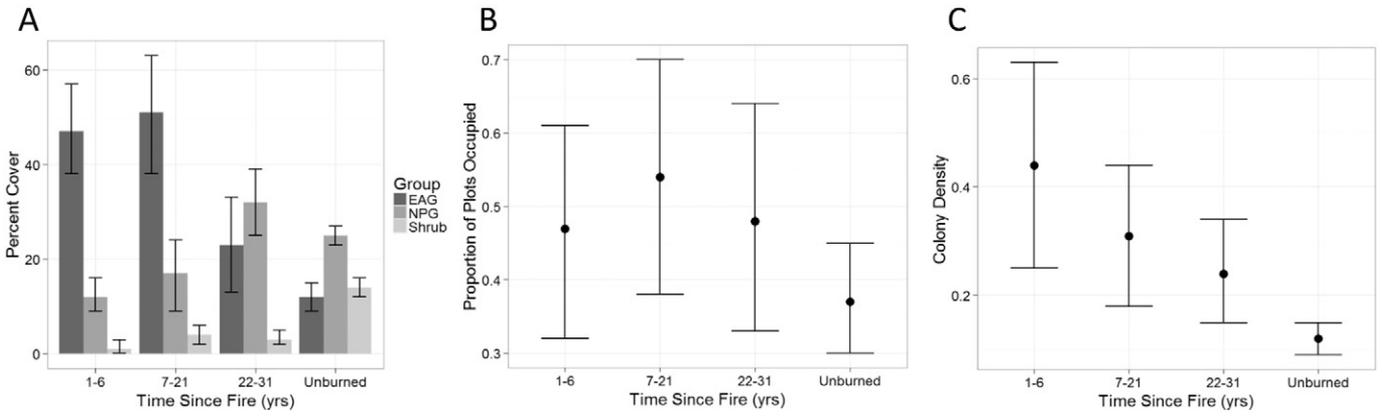


Figure 2. **A**, Percent cover of exotic annual grass (EAG), native perennial grass (NPG), and shrubs as a function of time since fire (x-axis). **B**, Proportion of plots occupied, and **C**, density (colony/100 m²) of harvester ant (*Pogonomyrmex* spp.) colonies as a function of time since fire. Error bars are 90% confidence intervals. Sample sizes for each category were as follows: *n* = 32 (1–6 years), *n* = 26 (7–21 years), *n* = 29 (22–31 years), *n* = 123 (Unburned). Our Unburned group served as our control for comparisons across the time since fire gradient.

it did improve fit for density ($X^2 = 15.79$, $df = 2$, $p < 0.01$). Thus, we continued analyses with our reduced model for characterizing occupancy of harvester ants but used the biological invasion and fire model for characterizing density. For our occupancy model, the goodness-of-fit test indicated appropriate fit ($X^2 = 21.4$, $df = 15$, $p = 0.13$), and predictive performance was high (AUC = 0.91). Our density model suggested reasonable model fit as measured by Spearman’s rank correlation coefficient ($\rho = 0.60$).

The strongest positive effect we observed in our occupancy model was associated with soil texture, and the strongest negative effect was associated with precipitation (Fig. 3). These results indicated that harvester ant occupancy was positively influenced by finer-grained soils and drier locations across our sampling extent. Next, we observed a relatively strong and positive effect of native forbs on harvester ant occupancy, followed by a comparatively weak and negative effect of shrub cover. All other effects were insignificant.

Similar to our occupancy model, our strongest (and negative) effect from our density model was associated with precipitation, reinforcing the positive effect of relatively drier locales on harvester ants (see Fig. 3). In contrast, however, we observed a positive and significant effect of exotic annual grasses and a negative effect of time since fire, indicating a positive effect of increasing exotic annual grasses and recent fires. This was consistent with the patterns we observed when evaluating differences among vegetation and colony density across the time since fire gradient (see Fig. 2). We also documented a positive effect of native and exotic perennial grasses on colony density, suggesting an increase in harvester ants in areas with more perennial grasses. We observed no effect of soil texture, native forbs, or shrub cover on density of ant colonies, which contrasted with our occupancy results. Similarly, we discovered no effect of exotic forbs.

Effects of Postfire Restoration

Lastly, we found no evidence that the vegetation conditions created by postfire seeding (i.e., burned and treated) generated a response in harvester ants that was different than burned areas that had not been seeded (Fig. 4). We did, however, document patterns similar to our previous results highlighting that a reduction in shrubs was associated with occupancy and higher densities of harvester ants.

Discussion

Our results suggest that fire is indeed changing vegetation states from what were historically shrublands to native perennial or exotic annual grasslands and that this process is spatially extensive (e.g., 64% of our sample experienced this state change). Density of harvester ant colonies was positively associated with state changes, whereas occupancy

of harvester ants appears to be driven primarily by abiotic gradients such as climate and soil texture rather than effects of fire or state changes. Overall, our work contributes to the understanding of fire-induced state changes within sagebrush ecosystems and emphasizes the importance of assessing how those changes influence both occupancy and density of animals to gain a better understanding of the relative effects of environmental change on organisms.

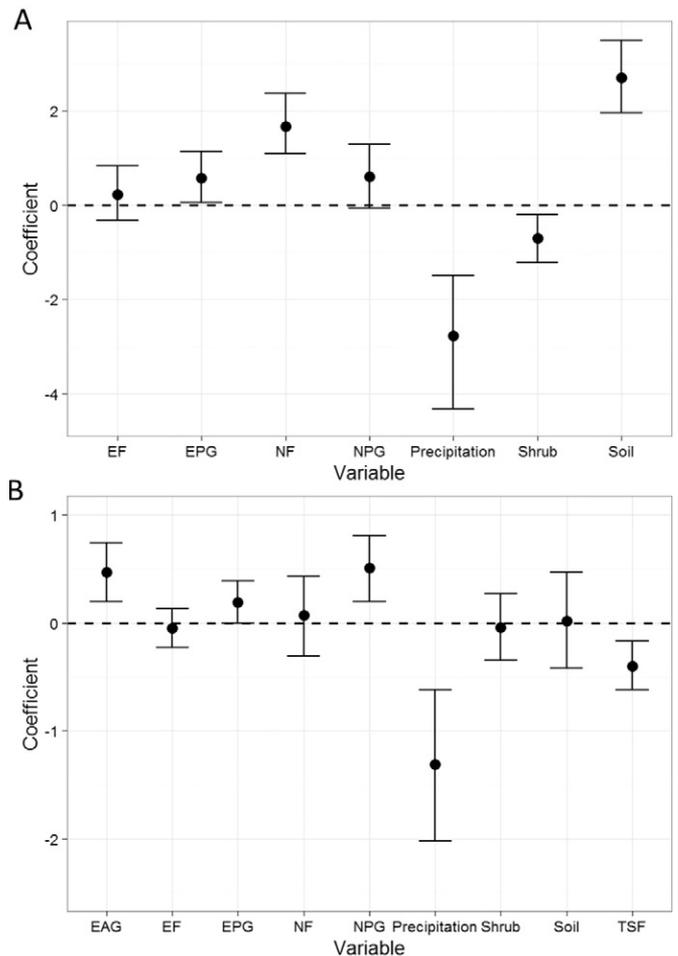


Figure 3. Standardized regression coefficients ($\pm 90\%$ confidence intervals) from our **A**, occupancy model and **B**, density model that described the effect of covariates (x-axis) on harvester ants (*Pogonomyrmex* spp.). See Table 1 for variable descriptions.

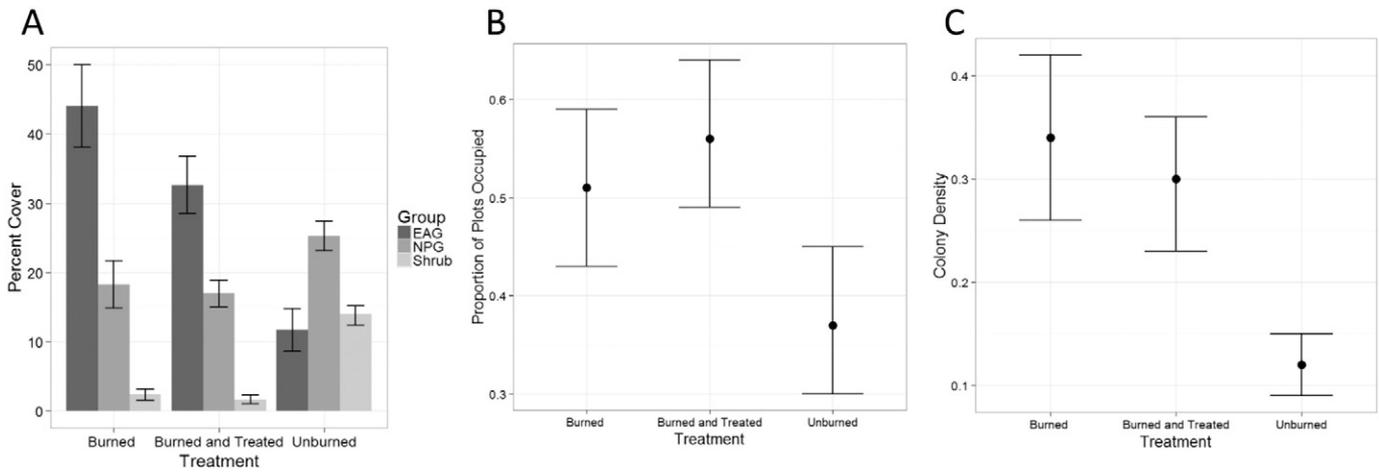


Figure 4. **A**, Percent cover of exotic annual grass (EAG), native perennial grass (NPG), and shrubs as a function of restoration groupings (x-axis). **B**, Proportion of plots occupied and **C**, density (colony/100 m²) of harvester ant (*Pogonomyrmex* spp.) colonies as a function of restoration groupings. Error bars are 90% CIs. Burned ($n = 98$) and Burned and Treated ($n = 124$) groups allow assessment of postfire seeding (restoration) effects. The Unburned ($n = 123$) group was not burned and thus served as a reference state and basis for comparison.

State Changes

Similar to previous work in sagebrush ecosystems (e.g., Baker, 2011), we quantitatively documented an immediate (i.e., 1-year post-fire) and relatively consistent change from shrublands to grasslands that persisted for at least 31 years after fire. Consistent with predictions (Miller et al., 2011), we found that exotic annual grasses were the dominant vegetation state 1–21 years postfire. In addition, the abundance of exotic annual grasses was higher than unburned conditions up to 31 years postfire, which highlights the long-term consequences of fire in Wyoming big sagebrush habitats (Chambers et al., 2014). Finally, native perennial grasses increased over time since fire such that they were similar to exotic annual grasses 22–31 years postfire (see Fig. 2). However, as aforementioned (see Results), the increase in native perennial grasses, as well as the decrease in exotic annual grasses, was entirely dependent on the group of 22–31 years postfire. Therefore, we post-hoc examined the composition of the sample within 22–31 years postfire (as well as the other groups of time since fire). Although the composition of the sample was nearly equal across our larger study areas, a subset of plots receiving more average precipitation (e.g., ~45 cm vs. ~25 cm) was disproportionately driving the patterns for exotic annual and native perennial grasses in the group of 22–31 years postfire. When only including sites with lower precipitation, cover of exotic annual grasses was higher than native perennial grasses 22–31 years postfire. Thus, similar to previous studies (e.g., Chambers et al., 2014), our data suggest that areas within big sagebrush communities that receive lower amounts of precipitation exhibit less recovery potential (in terms of native perennials increasing after fire and exotic annuals decreasing) than areas receiving higher amounts of precipitation.

We expected both occupancy and density of harvester ants to be positively associated with state changes (e.g., Ostoja et al., 2009), but we only observed a pattern consistent with our predictions in density of harvester ant colonies (see Fig. 2). This pattern suggested that high densities of harvester ants were associated with fire and exotic annual grasses, but the relative influence of each of these factors was unclear. Previous work has indicated much higher densities of harvester ants in areas that are dominated by exotic annual grasses (Ostoja et al., 2009; Gosselin et al., 2016). Although harvester ants generally do not prefer cheatgrass seeds (Crist and MacMahon, 1992; Ostoja et al., 2013), our data are consistent with the hypothesis that cheatgrass and other exotic annuals could provide an abundant food resource for harvester ants that may support high-colony densities. However, other indirect mechanisms, such as competitive or predatory release (e.g., Rodriguez, 2006; White et al., 2006; Ostoja et al., 2009) or increased solar radiation and access to deep soil moisture (Wight and

Nichols, 1966; Bucy and Breed, 2006), could be contributing to the positive response we observed between harvester ants and fire and/or exotic annual grasses. Additional data are necessary to disentangle the underlying direct and indirect mechanisms of the positive relationship between harvester ants and state changes in sagebrush habitats.

Relative Influence of Fire, Biological Invasions, and Other Ecological Factors

Although we documented a pattern consistent with a positive effect of exotic annual grasses and fire on density of harvester ants, analyses assessing the relative importance of fire and exotic annual grasses provided a more resolved conclusion in that we were able to assess effects of multiple environmental gradients simultaneously. Exotic annual grasses and time since fire were unrelated to occupancy of harvester ants, while these factors were important for density of harvester ants (i.e., ranked approximately second in terms of their importance when compared with other factors). Other factors characterizing variation in density of harvester ant colonies included precipitation and native perennial grasses. The effect of precipitation was negative, substantiating previous analyses indicating a biogeographical affinity and evolutionary adaptations of harvester ants for arid locations (e.g., Hanser et al., 2011; Johnson, 2001). We predicted a positive effect of perennial (exotic and native) grasses and (as aforementioned) exotic annual grasses because of production of preferred and abundant seed resources, respectively (Crist and MacMahon, 1992; Ostoja et al., 2013). Finally, a negative effect of time since fire on density of harvester ant colonies (indicating an increase in colony density for years immediately postfire) was expected because fires reduce shrub and other surface cover and consequently increase availability of potential nest and foraging sites (e.g., Zimmer and Parmenter, 1998; Ratchford et al., 2005; Arnan et al., 2006; Matsuda et al., 2011). The occurrence of fire might indeed trigger a colonization response from harvester ants because of a spike in resource (e.g., food and nest sites) availability.

In contrast, variation in harvester ant occupancy was best explained by precipitation, soil texture, and native forbs, although effects of shrub cover and exotic perennial grasses were significant. The negative effect of precipitation, which was stronger for occupancy compared with density, further substantiated the affinity of harvester ants for arid locations (Johnson, 2001). Additionally, the positive effect of finer-grained soils on occupancy was expected because they retain soil moisture better than coarse-grained soils, and soil moisture is related to foundress survival and brood production (Johnson, 1998, 2001). The negative effect of shrub cover was consistent with our general predictions in that shrubs may limit nest site locations or inhibit food availability through competition with grasses. Lastly, we observed a positive effect of native forbs

and exotic perennial grasses. Native forb species in our study area, such as slickspot peppergrass (*Lepidium papilliferum*), provide fruits and seeds that harvester ants gather in large quantities when present, consistent with a positive effect of native forbs on occupancy of harvester ants (White and Robertson, 2009). Similarly, exotic perennials are often abundant in areas seeded after fire (Knutson et al., 2014) and may provide an abundant seed source for harvester ants (Gosselin et al., 2016).

Combining our occupancy and density results from our generalized linear models, we observed that effect sizes for a particular variable changed depending on the response and the changes were generally consistent with predictions derived from ecological theory. For example, many authors have provided evidence that broader-scale environmental gradients better predict variation in occupancy patterns, whereas local level dynamics better explain variation in density (e.g., Soberón, 2007; Wiens, 2011; Boulangeat et al., 2012; Holbrook et al., 2016). Indeed, our data contribute to the weight of evidence suggesting that different environmental factors have disproportionate effects on variation in occupancy and density and emphasize the importance of testing alternative hypotheses concerning each factor. These multilevel approaches provide a more complete understanding of how animals are affected by landscape change, which can be directly applied for more precise management actions (Ehrlén and Morris, 2015).

Implications

To our knowledge, our work is among the first to evaluate the *relative* influence of state changes along a time since fire gradient on both occupancy and density of animals in sagebrush ecosystems. We demonstrated that fire-induced changes from shrublands to grasslands are strong predictors of density (but not occupancy) of an important desert granivore, harvester ants. Land managers throughout the sagebrush ecosystem are highly concerned with the conversion from native shrublands and grasslands to exotic annual grasslands and consequently are implementing large-scale restoration efforts that cost millions of dollars per year (Epanchin-Niell et al., 2009). We found no evidence that occupancy or density of harvester ants are responding to these restoration efforts (see Fig. 4), although previous work indicates that other animals (e.g., Piute ground squirrels; *Urocitellus mollis*) are indeed benefiting from postfire rehabilitation and restoration (Holbrook et al., 2016). Extending the assessment of how restoration influences the animal community within sagebrush ecosystems will provide a more refined understanding of the expected benefits and costs associated with the vast and expensive restoration efforts currently being conducted.

As with many environmental changes, such as state changes or restoration activities, there will be winners and losers (e.g., Knick et al., 2014). In our context, it appears density of harvester ant colonies will likely continue to increase following more drought, expansion of exotic annual grasses, and increased wildfire in the Great Basin (Abatzoglou and Kolden, 2011; Cook et al., 2015), while occupancy may be relatively independent of these changes. This suggests that harvester ants are likely winners considering the large-scale state changes within sagebrush ecosystems, which might be somewhat advantageous for restoration efforts. For example, because harvester ants harvest cheatgrass seeds (Ostoja et al., 2013) and can reduce cheatgrass cover and increase native bunchgrasses near their nests (Gosselin et al., 2016), they may help delay the transition from native grasslands to exotic annual grasslands in some locations by removing or reducing seed sources. This hypothesis is consistent with previous work highlighting that granivores can be an important component of biological resistance to exotic plant invasions (e.g., Nuñez et al., 2008; Pearson et al., 2011, 2014). The potential of harvester ants to inhibit plant invasions may be increasingly facilitated given that occupancy of harvester ants was independent of state changes, and thus ants could occupy many locations across a landscape and take advantage of those areas that begin to experience state

changes. Alternatively, however, previous work has also indicated apparent competition between native and exotic grasses mediated by granivores (Orrock et al., 2008), whereby seed consumption of the native species increased with increasing presence of the exotic species. Additional work assessing the role of granivores in reducing or facilitating biological invasions would provide unique opportunities for restoration ecologists to incorporate the ecological roles of animals into their restoration plans to help achieve objectives (sensu Byers et al., 2006). Collectively, our work represents a unique assessment of how state changes within the sagebrush ecosystem are positively influencing an aridland granivore, the harvester ant, which may result in indirect effects that influence future conservation or restoration efforts.

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