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Short-Term Butterfly Response to Sagebrush Steppe Restoration Treatments

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ABSTRACT

As part of the Sagebrush Steppe Treatment Evaluation Project (SageSTEP), butterflies were surveyed pre-treatment and up to four years post-treatment at 16 widely distributed sagebrush steppe sites in the Interior West. Butterfly populations and communities were analyzed in response to treatments (prescribed fire, mechanical, herbicide) designed to restore sagebrush steppe lands encroached by pinyon-juniper woodlands (*Pinus, Juniperus* spp.) and invaded by cheatgrass (*Bromus tectorum*). Butterflies exhibited distinct regional patterns of species composition, with communities showing marked variability among sites. Some variation was explained by the plant community, with the Mantel's test indicating that ordinations of butterflies and plants were closely similar for both woodland sites and for lower elevation treeless (sage-cheat) sites. At woodland sites, responses to stand replacement prescribed fire, clearcutting, and tree mastication treatments applied to 10-20 ha plots were subtle: 1) no changes were observed in community structure; 2) Melissa blues (*Plebejus melissa*) and sulfurs (*Colias* spp.) increased in abundance after either burning or mechanical treatments, possibly due to increase in larval and nectar food resource respectively; and 3) the juniper hairstreak (*Callophrys gryneus*) declined at sites at which it was initially present, probably due to removal of its larval food source. At sage-cheat sites, after prescribed fire was applied to 25-75 ha plots, we observed: 1) an increase in species richness and abundance at most sites, possibly due to increased nectar resource for adults; and 2) an increase in the abundance of skippers (Hesperiidae) and small white butterflies. Linkages between woody species removal, the release of herbaceous vegetation, and butterfly response to treatments demonstrate the importance of monitoring an array of ecosystem components, in order to document the extent to which management practices cause unintended consequences.

KEY WORDS

insect-plant relations, mastication, cut and leave, mowing, prescribed fire, pinyon-juniper, cheatgrass

INTRODUCTION

Sagebrush ecosystems have long been considered among the most endangered in North America (Noss et al. 1995; Knick et al. 2003), with perhaps a third of pre-settlement area of sagebrush already converted to other land uses or highly degraded. Over the past 100 years, fire suppression, livestock grazing, urban expansion, oil and gas extraction, expansion of native conifers like juniper and pinyon pine (*Juniperus occidentalis, J. osteosperma*; *Pinus monophylla, P. edulis*), and invasion of exotic weeds such as cheatgrass (*Bromus tectorum*) have contributed most to the decline of sagebrush communities in the Intermountain Region (Pellant 1994; Miller and Tausch 2001; Ingelfinger and Anderson 2004). At higher elevations, conifer expansion and depletion of fine fuels due to heavy livestock grazing has shifted fire regimes from relatively frequent, low (< 50 years mean fire return interval) to more infrequent and high severity (>50 years mean fire interval) (Miller and Rose 1999; Miller and Tausch 2001; Miller and Heyerdahl 2008). At lower elevation treeless sagebrush ecosystems, cheatgrass has invaded at the expense of native perennial species, and mean fire return intervals have shifted from >50 years to <10 years in some places (Whisenant 1990; D'Antonio and Vitousek 1992). Under current climatic conditions, both pinyon and juniper woodlands and exotic annual grasses have the potential to dominate an even greater area (Wisdom et. al 2002), and global warming is likely to exacerbate this trend (Pyke and Knick 2003; Tausch and Nowak 2000; Neilson et al. 2005; Balch et al. 2013; Bradley 2010).

For several years now, land managers have attempted to arrest the conversion of sagebrush steppe lands into woodland and cheatgrass systems, restore a desirable herbaceous understory, and reduce fuel loads by applying treatments such as prescribed fire, mowing, chaining, cutting, masticating, and/or herbicides. Although site-specific information exists on the effectiveness and ecological effects of some treatments, there is scant multivariate scientific information available on treatment outcomes over the range of environmental and ecological conditions that occur across sagebrush ecosystems. The Sagebrush Steppe Treatment Evaluation Project (SageSTEP) evaluates the ecological effects of prescribed fire and its surrogates (mechanical and herbicide treatments) at 21 sagebrush steppe sites in the Great Basin and surrounding areas (McIver et al. 2010). The multi-site design of SageSTEP is intended to provide information on how different site conditions influence treatment response, while the multivariate design is intended to understand how treatments influence relationships within systems, and to identify potential tradeoffs among variables.

Butterflies have long been considered as indicators of ecosystem condition, thus allowing insights about the likely responses of a larger set of fauna of conservation concern (Thomas 1983; Swengel 1998; Fleishman 2000). Furthermore, the decline of several species of threatened and endangered butterflies has been linked to habitat loss due to invasive plant invasion (Russell and Schultz 2010). This is primarily because native butterflies are closely linked to native plants (Ehrlich and Raven 1965). Since sagebrush steppe restoration is keenly concerned with the control of invasive species, it makes sense to monitor faunal components that would likely be sensitive to changes in the balance between native and exotic plant species. More generally, butterflies are good indicators of ecosystem condition due to their sensitivity to changes in the distribution and abundance of native host plants (Ehrlich and Raven 1965) and to native and exotic nectar sources (Holl 1995).

Butterflies are also easy to count and identify on the wing (Pollard 1977), and so can be sampled with relatively little impact to their populations. Further, butterfly larvae are intimately linked to native host plants, particularly perennial forbs and grasses, and so assessing the effects on them will tell us something about effects of treatment on the plant community, and linkages between flora and fauna (Ehrlich and Raven 1965). Finally, testing the effects of land management treatments on the fauna can give us more insight on the extent to which management practices, especially those with which flora and fauna have no evolutionary history (mechanical and herbicide treatments), result in unintended or undesirable consequences. Although some butterfly species can adapt to sudden loss of host plants or nectar sources (Singer et al. 1994; Boughton 1999), mechanical or herbicide treatments may have other structural or functional effects that are unique enough to cause problems for native species.

In this paper, we describe butterfly species composition across a network of 16 of the 21 SageSTEP sites, and relate this to plant species composition, habitat structure, and site characteristics. We then report on the response of butterfly species, species groups, and communities to prescribed fire and fire surrogate treatments. We expected that butterfly community composition would vary in accordance with known species distributions in the Great Basin, and that it would correspond roughly to native plant community composition. We also expected that prescribed fire would have somewhat different effects on butterflies when compared to its 'fire surrogates', such as herbicides and mechanical treatments, and that effects would decrease with time after treatment.

METHODS

Study Sites and Treatment Plots

Butterflies were sampled between 2006 and 2012 at 16 sites within the SageSTEP Network, on sagebrush steppe lands in the Great Basin and surrounding areas. Nine sites comprise the SageSTEP 'woodland' experiment, representing sagebrush systems that are relatively mesic (259-462 mm annual precipitation) (Table 1) and characterized by expansion of Piñyon and Juniper into areas that were historically sagebrush steppe. The nine sites are divided into three regions, each dominated by a different woodland overstory: 1) Western Juniper Region: four sites in Oregon and N. California, dominated by Western Juniper (*Juniperus occidentalis* Hook.); 2) Pinyon-Juniper Region: three sites in Nevada, with overstory shared by singleleaf piñon (*Pinus monophylla* Torr.& Frém.) and Utah juniper (*Juniperus osteosperma* [Torr.] Little); and 3) Juniper-Pinyon Region: two sites in Utah, with overstory dominated by Utah juniper, with minor representation of Colorado piñon (*Pinus edulis* Engelm.) (McIver et al. 2010). Seven sites comprise the 'sage-cheat' experiment, representing sagebrush systems that are treeless, lower elevation, more xeric (214-364 mm annual precipitation), and characterized by cheatgrass invasion of sagebrush steppe. The Sage-Cheat experiment is composed of three sites in Utah, Nevada, and western Idaho, two sites in Oregon and two in Washington (Table 1). Although all 16 sites are classified as cool desert, and have similar vegetation and land use patterns (Bestelmeyer et al. 2009), weather patterns differ markedly across this geographic range. Sites in California, Oregon, Washington, and southwest Idaho have a Pacific Maritime climate, with nearly all precipitation originating in the Pacific Ocean, and falling between November and June. Sites in Nevada, Utah, and eastern Idaho have a more Continental climate, with less precipitation falling from November to June, and relatively more summer rains originating from the Gulf of Mexico, usually in July and August.

For the woodland experiment, each site comprised three or four 10-20 ha plots, with each plot receiving one distinct treatment, randomly assigned (Table 1). We selected one plot as un-manipulated control, applied prescribed fire to a second plot, and clearcut all trees on a third plot. At both Utah Juniper-Pinyon woodland sites, we masticated all trees within a fourth plot, with a Bullhog® rotary mower (McIver and Brunson 2013). Prescribed fire was applied first, between August and November of 2006, 2007, or 2008. The goal was to accomplish 100 percent tree mortality by fire within each prescribed fire plot, in an effort to release the residual understory; due to variation in weather conditions, prescribed fires burned between 38 and 95 percent of each plot area (Table 1). Clearcut and mastication treatments were implemented within six months of fire treatments. For the clearcut treatment, all trees >2 m tall were cut down and left on the ground across the contour. For the mastication treatment, all trees >2 m tall were shredded with the rotary mower and residue left where initially deposited.

For the sage-cheat experiment, each site comprised four 25-75 ha plots, with each plot receiving one distinct treatment, randomly assigned (Table 1). We selected one plot as un-manipulated control, and applied prescribed fire, a mowing treatment, and a broadleaf herbicide treatment to the remaining three plots. Prescribed fire was applied first, from May to October 2006, 2007, or 2008, and was intended to blacken 100% of each plot area. For six of the seven sites, prescribed fires burned between 40 and 79% of each plot area (Table 1); at Roberts, only 8% of the plot area burned, and so the prescribed fire treatment was not evaluated for this site. Once fire was implemented for each site, both herbicide and mowing treatments were applied to two other plots within the following eight months. Both treatments were designed to remove about 50% of sagebrush cover to reduce woody fuels and release the understory herbaceous species. The herbicide tebuthiuron (N -[5-1,1-dimethylethyl-1,3,4-thiadiazol-2-yl]- N,N' –dimethylurea) was applied over the entire plot at a rate dictated by prior testing to remove 50 percent of the overstory. Rotary mowers were set at a pre-determined height to remove and distribute roughly 50% of sagebrush biomass, over each entire plot. It should be noted that the Roberts sage-cheat site experienced a severe wildfire (Jefferson Fire) on July 13, 2010, which killed nearly all vegetation in two of the four plots. Since treatments were applied in 2007 at Roberts, we present only three years post-treatment data for this site (2008-2010), with the 2010 butterfly sample collected just three weeks prior to the wildfire.

Data Collection and Analysis

Butterflies were surveyed within each plot at each site prior to treatment (2006), and up to six years after treatment (2007-2012). A belt-transect survey method was used (Pollard 1977), with a single 1000 m transect permanently established within each plot. Since several sites had adjacent plots, we attempted to minimize inter-plot influence by positioning plot transects as far as possible from one another. At 15 of the 16 sites, we were able to position transects at least 200 m from one another; at one site with adjacent plots however (Bridge Creek), plot shapes were highly irregular, necessitating the placement of transects 100 m apart (Table 1). All plots at each site were surveyed on the same day for a given sampling session, by walking transects at a pace of 20 m/min for a total of 1000 m in a 50-minute period. Only those butterflies observed to the front and sides of the transect and within 5 m of the observer were counted. Sampling took place on warm, sunny, and calm days (>60^{o}F, >70% clear sky, and <10mph wind), between 0800 and 1700 from 1 May to 15 July of each year. Prior to each sampling day at a given site, problem species (e.g. fritillaries, checkerspots) were netted, identified in hand, and in some cases retained for confirmation by Dana Ross (affiliated with Oregon State University, Corvallis, Oregon). Once a sample began, butterflies were identified on the wing if possible; in some cases butterflies were captured, identified, and released, or kept for later confirmation. Sites were sampled as much as possible during a sampling season, however due to the large geographic scope of the study, unpredictable weather, and a relatively short sampling window, we typically could only sample each site between one and three times each season. Total counts for each observed species were recorded during each survey. Butterfly nectar sources were noted if observed within or near a plot, or along a transect. Plant species data were collected by SageSTEP vegetation field crews, uploaded to the SageSTEP Data Store (see McIver et al. 2010 for description of sampling protocols), and then downloaded for comparison with butterfly species data in the present study. In every case, we averaged sub-plot level vegetation data to the entire plot, in order to make vegetation and butterfly data comparable in scale. Plant data were used to identify potential mechanisms behind butterfly response (e.g. whether the treatment response of larval host plants or adult nectaring sources were correlated with butterfly response), and to relate butterfly and plant community structure.

Butterfly count data were analyzed using both univariate and multivariate methods. Treatment effects were evaluated with a two-factor general linear model, with treatment and time since treatment as main effects {$Y_{ijk} = \mu + A_i + B_j + AB_{ij} + S(AB)_{ijk}$; where A = treatment, B = time since treatment, S = Interaction}. First, species were defined as either ‘transient’ or ‘local’, and these two groups were always analyzed separately (Appendix 1). Transients included those species that are strong-fliers as adults, with individuals observed to cover distances sufficient to carry them through treatment plots and beyond; for these species, we did not assume that larvae developed in the treatment plot within which the adult was observed. Local species included those species in which individual adults tended to fly only short distances, rarely carrying them outside the treatment plots; for these species, we assumed that the adult developed as a larva in the same treatment plot within which it was observed and counted. The distinction in adult flying behavior is important for interpretation of results, because only for local species could we infer that an observed treatment effect might have been due to a change in the status of a larval host plant. A total of 20 variables were analyzed with the general linear model. First, to gain an understanding of the generality of treatment effect across all sites, mean survey abundance and richness of both transients and local butterflies were evaluated for the network as a whole (4 variables; N=16 sites). Next, total abundance (either local and transient species), and total species richness (either local and transient species) were analyzed for each experiment (8 variables; Woodland, Sage-Cheat). Finally, 8 species that were sufficiently common and widespread were analyzed for either the Woodland or Sage-Cheat experiment (Appendix 1: indicated with asterisk). For each *local* butterfly species for which a treatment effect was demonstrated, we correlated the observed butterfly Effect Size {Hedge's D = (mean count in control plot – mean count in treatment plot)/ pooled standard deviation; Cooper and Hedges 1994} with the Effect Size for its presumed larval host plants, in order to identify a potential 'host plant' mechanism behind observed response. Finally, we analyzed eight 'functional' groups of related species for which larvae are known to feed on similar species of host plants (Appendix 1): 1) SK-Poa: grass-feeding skippers (*Hesperia* spp., local); 2) BL-Fab: legume-feeding blues (*Everes, Glaucopsyche, Plebejus,* local); 3) CH-Scr: scroph-feeding checkerspots (*Euphydryas,* local); 4) FR-Vio: violet-feeding fritillaries (*Speyeria,* local); 5) NY-Poa: grass-feeding nymphs (*Coenonympha, Neominois, Cercyonis,* local); 6) SU-Fab: legume-feeding sulphurs (*Colias*); 7) WT-Bra: mustard-feeding 'transient' whites (*Pieris, Pontia*); and 8) WL-Bra: mustard-feeding 'local' whites (*Euchloe, Anthocharis*).

Community data were ordinated with non-metric, multidimensional scaling (NMS) (Clarke 1993) a method that finds optimal solutions for community data iteratively, without reliance on an underlying parametric model. NMS has become the preferred ordination technique for most community data, which are typically non-normal (McCune and Grace 2002). We used NMS to illustrate community patterns of butterfly distribution, inter-annual variation, and treatment response. Because we were most interested in treatment effects, and less interested in species distribution patterns, we collapsed species data to the generic level for the ordinations. We tested for group differences among regions and sites, among years, and among treatments with the Multi-Response Permutation Procedure (MRPP), which uses the distance matrix produced by NMS, and then compares the sums of distances within and among groups to generate a group 'effect size', a measure of the separation among groups (Mielke and Berry 2001). We also ordinated plant floral data for each site, using a main matrix of sub-plot-level data for plant species identified and recorded by vegetation crews. A secondary matrix to accompany the plant floral data was also constructed with sub-plot and plot-level data collected by vegetation crews. We then correlated butterfly and plant species richness at the site level (using species lists for both taxonomic groups generated from the same number of sampling years), and tested for similarities between butterfly and flora ordinations with the Mantel Test (McCune and Grace 2002), comparing butterfly and plant matrices that were identical in size and attributes (year, treatment, plot, etc.).

RESULTS

A total of 5933 butterflies were observed at the 16 sites during the 7-year study period, comprising 5 families and 52 species (Appendix 1). Over 72% of the total count was represented by the ten most commonly observed species; ten species were observed fewer than four times. The average number of butterflies counted per 1000 m survey across all years at all sites was 13.52 (+/- 1.57 S.E.) and was reasonably consistent over the 7 years, except in 2007 (35% of average), and 2009 (153% of average). Woodland sites had about three times the average count per 1000 m survey (Woodland = 17.16 +/- 2.23 S.E. individuals; Sage-Cheat = 5.46+/- 0.53 S.E. individuals) and nearly twice the average survey richness (Woodland = 3.09 +/- 0.13 S.E. species; Sage-Cheat = 1.79 +/- 0.08 S.E. species) compared to sage-cheat sites. Butterfly species richness was correlated with overall plant species richness at the plot scale ($r^2 = 0.45$; $p<0.01$; $y=0.3x – 0.9$), with average plot-level plant species richness per year nearly twice as high at woodland sites (43.5 +/- 1.66 S.E. spp.) compared to the relatively lower elevation sage-cheat sites (25.6 +/- 1.56 S.E. spp.).

At woodland sites, NMS ordination distinguished the three woodland regions along axis 1, and sites within each region along axis 2 (Fig. 1a). In the western juniper region, the principal indicator taxa for the Blue Mt site include common blues (*PLIC*), juniper hairstreaks (*CAGR*), and Edith's checkerspot (*EUED*), with ochre ringlets (*COTU*) indicating the other three western juniper sites. The pinyon-juniper sites ordinated toward the center, and include several indicator taxa, principally the pine elfin (*INER*) and large whites (*POIA*) for Seven Mile, skippers (*HEIA*), Melissa blues (*PLME*), and fritillaries (*SPIA*) for South Ruby, and sulfurs (*COAS*), Riding's satyr (*NERI*), and Anicia Checkerspots (*EUAN*) for Marking Corral. In the juniper-pinyon region, the principal indicator taxa for Greenville Bench include checkered skippers (*PYCO*), and for Onaqui desert marbles (*EULO*). Principal environmental correlates ($r^2 > 0.50$) include higher cover of duff, embedded litter and Idaho fescue (*Festuca idahoensis*) toward the western juniper region, versus higher mean gap sizes and bluebunch wheatgrass cover

(*Pseudoregneria spicata*) toward the juniper-pinyon region. Overall butterfly abundance was higher toward the sites ordinating toward the bottom of the graph (BM, SV). Analysis with multi-response permutation procedure (MRPP) demonstrated highly significant separation of each region in ordination space, with all pairwise p-values < 0.001. Moreover, when MRPPs were run for *site* comparisons, the majority of pairwise p-values (84%) were < 0.03; the remainder were all < 0.05. Likewise, MRPP analyses for pairwise inter-annual comparisons were all significant (p < 0.02) with the exception of the comparison between 2009 and 2010; thus, community structure of butterflies not only varied markedly among woodland sites, but also varied markedly among survey years. On the other hand, MRPP yielded no significant community structure differences among woodland *treatments* for any pairwise treatment comparison (p > 0.10).

At sage-cheat sites, NMS ordination yielded similar results as observed for the woodlands, with four more or less distinct groups of sites recognizable (Fig. 1b). The most compositionally diverse of the sage-cheat sites was Moses Coulee, which ordinated by itself as a distinct group of plots, with four key indicator taxa [gray hairstreak (*STME*), common blue (*PLIC*), ochre ringlet (*COTU*), and wood nymphs (*CEPE*)]. The two geographically close Hart Mountain Refuge sites (Gray Butte and Rock Creek) clustered together, with both sites featuring a dominance of desert marbles (*EULO*). Interestingly, despite their greater geographic separation, Saddle Mountain and Owyhee had very similar compositions of butterfly genera, with both sites featuring an abundance of skippers (*HEIA*) and large whites (*POIA*). Finally, the Onaqui and Roberts sites (the two most eastern sage-cheat sites) were also quite similar in generic composition, with each site featuring an abundance of Melissa blues (*PLME*), ladies (*VACA*), sulfurs (*COAS*), and checkered skippers (*PYCO*). The principal environmental correlates ($r^2 > 0.40$) of axis 1 were shallow-rooted native bunchgrasses (PSG), particularly Sandberg's bluegrass (POSE) in the northwest and squirreltail (ELEL5) in the east}, and weather factors at the time of survey [higher wind in the northwest (Wind), higher temperature in the east (TEMP)]. Higher axis 2 scores are correlated with plant species richness (Prich) and cover of perennial forbs (PFb), both of which were attributes of the sites ordinating toward the top of the graph. Analysis with MRPP indicated that most site-level pairwise comparisons were significantly different (all < 0.03), with the exception of the two Hart Mountain Refuge sites Gray Butte v. Rock Creek ($p = 0.12$), and the two most easterly sites Onaqui v. Roberts ($p = 0.07$). Like the woodland sites, inter-annual variation was also marked, with each year different from every other year, with the exception of 2009 and 2010 ($p < 0.03$ for all pairwise comparisons except 2009 and 2010). However, MRPP analysis of treated sites yielded no significant differences in community structure among sage-cheat *treatments* for any pairwise treatment comparison ($p > 0.10$ for all pairwise comparisons). Finally, when the woodland and sage-cheat butterfly main matrices were each compared statistically to their floral matrix counterparts (Mantel Test), the null hypothesis of no relationship between each pair of main matrices was rejected ($p < 0.000001$), indicating distinct among-site similarity in the ordination of butterfly and floral communities.

High spatial variation in butterfly community structure, together with marked inter-annual variation in counts at most sites, made determination of treatment effects challenging. Within the context of substantial spatial and temporal variation however, certain patterns of treatment response were observed. When all sites were analyzed as a whole (N=16 sites), treated plots had higher transient abundance and richness compared to untreated controls (Table 2), starting in the second year after treatment, and lasting through year 4 (Fig. 2). No treatment effects were observed for local butterflies at the network level, although both abundance and richness increased with time after treatment in most plots, regardless of treatment.

In the woodland experiment, two of the eight functional groups and two of the eight common and widespread species exhibiting significant treatment response. Among transients, the number of legume-feeding sulfurs (SU-Fab) and the number of transient whites (WT-Bra) were higher in plots treated with either fire or by mechanical means (Table 3). Sulfurs were consistently more abundant in treated plots throughout the 4-year post-treatment time period (Fig. 3a), while transient whites were more abundant in treated plots only in post-treatment years 2 and 3 (Fig. 3b). Higher numbers of transients (both sulfurs and whites) in treated plots were mirrored by vegetation data, which showed that both annual and perennial percent forb cover increased with treatment of any kind relative to untreated controls (Table

4). In particular, annual forb cover increased markedly in burn plots, with mean post-treatment cover averaging nearly fourfold that of untreated controls (13.76% in burn plots v. 3.53% in control plots). Among local butterflies, numbers of Melissa Blues increased in burned and clearcut plots, and the effect size of its plot-level response was correlated with the effect size of the cover of its *Astragalus* host plants (Fig. 4; $r^2 = 0.30$; $y = 0.64x – 0.03$; $p<0.05$). Although the mean multi-site effect size correlation for fire and mechanical treatment plots were very similar (two symbols labeled with 'TOT' in Fig. 4), individual sites typically varied markedly in effect size correlations for fire versus mechanical treatments (Fig. 4). For example, effect sizes for both *Astragalus* and Melissa blue were high for the Blue Mountain (BM) prescribed fire plot but low for the mechanical plot there, while Walker Butte (WB) site showed the opposite pattern. We observed no other effect size correlation between local butterflies and their principal larval host plants. The only observed *decreases* in butterfly numbers observed in the woodland experiment were for legume-feeding blues in bullhog plots, and for the Juniper Hairstreak (Table 3). The difference in blues was due entirely to a region effect, in which numbers were lower for all plots in the juniper-pinyon region. Since the bullhog treatment was applied only to the two juniper-pinyon sites, this led to the apparent bullhog plot effect. The juniper hairstreak on the other hand, declined in abundance after treatment at all sites where it was initially common, primarily the western juniper and the pinyon-juniper sites Marking Corral and South Ruby (Table 3). Having a larva that feeds on juniper, removal of its host plant had clear effects on abundance of this species, and this effect persisted through four years of post-treatment time. Finally, significant inter-annual variation was observed for nearly every analyzed taxon in the woodland experiment, with numbers generally increasing with time after treatment, due to relatively low counts in 2007, and generally high counts in 2009 and 2011. The only taxon that did not exhibit inter-annual variation was the Juniper Hairstreak, which had consistent survey counts relative to treatment, throughout the study period (Table 3).

In the sage-cheat experiment, we observed persistently higher local species abundance and richness in mowed plots and in burn plots at five of the six sites at which our prescribed burn blackened at least 40% of the plot area (Gray Butte, Moses, Rock Creek, Owyhee, Saddle Mt);

local butterfly abundance and richness in plots treated with the broadleaf herbicide-tebuthirion were no different than controls (Table 5). The treatment effect on the abundance of local butterflies persisted through four years post-treatment, with control and treated plot abundance similar only in year 2 (Fig. 5). We also observed persistently higher numbers of grass-feeding skippers (SK-Poa) and local mustard-feeding whites (WL-Bra) after burning, but mowing or herbicide application had no apparent effect on these taxa (Table 5). Local butterfly abundance declined with time since treatment in most plots, with relatively higher counts in 2008 and 2009, and lower counts in 2010 and 2011. Much of this effect was due to decreases over time in the numbers of western branded skippers and in local whites (primarily marbles; see Appendix 1). Local species richness also varied through time, but variability was not clearly or consistently linked to year effects. Among transients, numbers of Becker's White (*Pontia beckerii*) were lower in mowed plots relative to control or burn plots, with this effect persisting through four years post-treatment (Table 5). Neither transient abundance nor richness varied markedly at sage-cheat sites over time.

DISCUSSION

Observed butterfly community structure generally conformed to known patterns of species distribution in the Great Basin, and showed a close relationship to native plant communities across the SageSTEP network of sites. Both spatial (among-site) and temporal (among-year) variation in butterfly community structure was very high however, and tended to overwhelm patterns of treatment response. When species and species groups did respond to treatment, response was generally positive regardless of treatment type, with response to prescribed fire versus its mechanical surrogates (clearcutting, mastication) more similar than expected. Similarity in response among treatments was likely due to the fact that woody vegetation removal, whether by fire or machine, tended to increase soil water availability (Roundy 2014), which enhanced grass and forb production (Table 4), and in turn provided more resources for butterfly larvae (host plants) and adults (nectar). Finally, observed treatment responses were persistent, with most variables showing divergent trajectories between control and treated plots through four years of post-treatment time.

A total of 52 species of butterflies were observed at the 16 SageSTEP study sites over a seven-year period of time, a relatively low number compared to other butterfly studies of comparable scope conducted in the Great Basin. For example, in a 3-year montane canyon study examining the principal factors that explain patterns of butterfly species richness, Fleishman et al. (2000), observed 33 and 40 butterfly species from only two mountain ranges in central Nevada (Toiyabe and Toquima respectively), nearly double the maximum richness we found at our most diverse woodland sites, after seven years of observations (Blue Mountain – 18 species; Marking Corral – 17 species). Lack of available water (Murphy and Wilcox 1986), proximity to water (Fleishman et al. 1997), and restriction of sampling to an early phenological window (May through mid-July), all probably contributed to the relatively low species richness observed in the current study, especially at the sage-cheat sites. In addition, the higher species richness we observed at the higher elevation woodland sites was likely due in part to the positive correlation with plant species richness, which has been reported in other studies (Hogsden and Hutchinson 2004).

The pronounced differences in butterfly community structure among sites, at the species, generic, and group level, is one of the most striking results of the current study. The broad geographic extent of the SageSTEP study might explain some among-site differences in species composition, due to geographic range limits of individual species. But nearly 64% of Great Basin butterfly species are widespread in distribution, occurring in their preferred habitats not only in the Great Basin, but in the Sierra Nevada to the west, as well as in the Rocky Mountains to the east (Austin and Murphy 1987). More likely, among-site differences are due to several factors including availability of host plants, landscape context, and topographic features, as well as site history. Certainly, when ordinations of butterflies and plants are compared within each experiment (woodland and sage-cheat), patterns of among-site distances in ordination space are remarkably similar (Mantel Test), reflecting the strong relationship between butterflies and the native flora. In any case, the magnitude of among-site variability observed in the current study is not unprecedented. For example, working at a number of sites within the Toquima Range, Fleishman (2000) observed substantial spatial and temporal variability in butterfly species composition and richness. Her data also indicated that butterfly community similarity decreased with the distance between inventoried units, with the most distant units tending to be markedly dissimilar. Furthermore, Fleishman et al. (2000) also reported considerable among-site differences in the *relationship* between butterfly communities and environmental gradients, with surveys in the Toquima and Toiyabe ranges indicating opposite correlations between species richness and elevation. Although we do not yet have the sample sizes necessary to quantify patterns of inter-annual variation in butterfly communities, it is also clear from other work that temporal variation tends to be considerable as well, with year to year surveys producing distinctively different results at the same sites (Ross and Miller 2000; Pollard et al. 1998; Fleishman 2000; Fleishman et al. 2000; Kleintjes et al. 2004).

At the level of the butterfly community, treatments designed to restore degraded sagebrush steppe habitat produced measurable impact only on transient richness and abundance, which both increased after treatment (Table 2; Fig. 2). However, when community response was measured by the combination of relative abundance and species composition (community structure), no measurable effects were observed. Part of the reason for this is that marked spatial (among-site) and temporal (among-year) variability in butterfly numbers and species composition created so much ‘noise’ in the data, that treatment-induced ‘signals’ were difficult to pick out of community-level data. Indeed, variation in butterfly communities among sites and through the years often produced a much stronger signal in community data than did treatments, as demonstrated by the significant inter-annual variation observed for eight of the 20 variables analyzed. Neither Fleishman (2000) nor Ross and Miller (2000) reported marked effects of prescribed fire on butterflies, when effects were evaluated at the community level (total richness or abundance). Rather, both studies identified among-site, among-plot, or among-year variability as a major contributing factor in their determination of no-effect. In a study on prairie restoration however, Vogel et al. (2007) were able to detect a compositional effect of treatment, with burning and grazing treatments generating similar richness but somewhat different community structures. They suggest that no one practice will benefit all species, or even all species within habitat-specialist or habitat-generalist guilds.

At the species and species-group level however, a few notable treatment effects were observed. The most obvious was the decline in the number of juniper hairstreaks in woodlands after the removal of trees by either prescribed fire or mechanical treatments. The reason for hairstreak decline is obvious: larvae feed on juniper vegetation, and treatments thus decreased the availability of larval host plants. But nearly every other species or species group that was measurably affected *increased* in numbers after treatment in both sage-cheat and woodland experiments, indicating that butterfly habitat generally improved as a result of treatment. Moreover, these effects generally persisted through four years post-treatment, indicating that the mechanisms behind treatment response are long-lasting.

At sage-cheat sites, prescribed fire had the most obvious effect, with local butterfly abundance and richness consistently higher in fire-treated plots (Table 5). These effects were largely due to higher abundance of grass-feeding skippers (SK-Poa), and mustard-feeding local whites (WL-Bra) in fire plots relative to controls. Skippers are relatively sedentary as adults and so it is possible that these modest differences were due to improved larval feeding habitat, which included a variety of native bunchgrasses. It is also possible that larval host plant resource for desert marbles (the most common representative of the local white group) improved with burning, although at no site at which it was common did any of its known mustard host plants (*Arabis, Descuriana, Lepidium, Sisymbrium, Streptanthus*) increase in cover in burned plots. The fire effect was also persistent through four years of post-treatment time, and there was no evidence that numbers of these groups were converging over time in fire versus controls or other treated plots. The only species for which negative treatment effects was observed was the transient Becker's White (*Pontia beckerii*), which declined in mowed plots relative to controls or fire-treated plots. The mechanism for this decline is unclear, as annual forb nectar resources were generally higher in mowed plots (Table 4), and there was no evidence that potential larval host plants (mustards) declined after mowing.

At woodland sites, mechanical treatments, including both clearcutting and mastication, caused increases in the abundance of legume-feeding sulfurs (SU-Fab) and mustard feeding transient whites (WT-Bra)(Table 3; Fig. 3). Similarly, numbers of Melissa Blues were higher after both prescribed fire and clearcutting (Table 3; Fig. 4). Positive responses to treatment are most likely due to the fact that removal of trees by any means begins a cascade of effects that has the ultimate result of improving both larval and adult feeding habitat for most sagebrush steppe butterfly species. In particular, water is the most important limiting resource in sagebrush steppe systems (Chambers et al. 2007; 2014), and pinyon and juniper trees are the most effective competitors for it. When trees are removed, soil water availability markedly increases (Roundy 2014), and these increases are accompanied by shifts in resource utilization toward shrubs (mechanical treatments only) and herbaceous vegetation (both mechanical and burning treatments). Since many sagebrush steppe butterfly species, as well as prairie species, are linked to native herbaceous vegetation (grasses and forbs) for larval feeding (Ehrlich and Raven 1965; Boggs and Freeman 2005; Moranz et al. 2012), and since many adults depend on forb flowers for adult feeding (Murphy 1983; Boggs and Freeman 2005), increases in the production of particular larval host plant species (e.g. *Astragalus*; Fig. 4), and forb cover in general (e.g. Table 4), will tend to improve butterfly foraging habitat. In any case, the fact that increases in soil water availability have, like observed butterfly effects, persisted through four years treatment (Roundy 2014), suggests that enhanced soil water availability is the root mechanism behind increases in butterfly abundance at most sites.

Enhancement of larval food plant availability by both fire and mechanical treatments is the most likely mechanism behind observed increases in Melissa Blues. This interpretation is supported by the positive correlation between the plot-level effect size of Melissa Blues and that of one of its primary host plants *Astragalus* spp. (Fig. 4). Certainly, larval food resources can have significant impacts on adult life history features of holometabolous insects, including body size, which can in turn influence population growth (Boggs 2003). In our study, while Melissa Blues clearly responded positively to restoration treatments, Juniper Hairstreaks responded negatively, because of the removal of their larval host plants. This underlines the fact that any significant habitat alteration is likely to benefit some species and impact others (Vogel et al. 2007). One would expect however, that as long as restoration practices are implemented on sufficiently small scales, positive and negative effects on species will tend to balance out at the landscape level.

Ross and Miller (2000) also suggested that increases in specific larval host plants (e.g. lupine) were linked to increases in the abundance of butterflies that feed on them (Common Blue: *Plebejus icariodes*), but also identified improved nectar resources as the primary mechanism behind increased butterfly abundance one year after burning in western juniper woodlands in eastern Oregon. Most likely, improvement of adult nectar habitat is the most likely mechanism behind treatment-induced increases in the number of transients like sulfurs and large whites. Since many nectar species are annual forbs, which generally increased in cover after treatment (Table 4)(see also Miller et al. 2014), tree-removal treatments essentially created 'bulls-eyes' of nectar resource at the plot scale, which could have attracted strong-flying adult species of butterflies from outside the plots, such as large whites and sulfurs. Similar results were found by Kleintjes et al. (2004), who reported increases in butterfly abundance and richness after mechanical treatments to remove trees in pinyon-woodlands in northern New Mexico. They also reported increases in herbaceous cover overall, and increases in five of the ten most common nectar and larval host plants after treatment, and suggested that the treated watershed became an 'oasis' that attracted nectaring adults from adjacent areas. In prairie habitat, Vogel et al. (2007) reported similar linkages between butterfly response and vegetation, with butterfly abundance and diversity responding positively to burning or mowing treatments, and best explained by a negative association to bare ground, and by a positive association to percent forb cover. It is also possible however, that increases in the number of sulfurs was due in part to the creation of more 'open' habitat that some of these species are known to prefer (e.g. *Colias eurytheme*; Scott 1986; Meyer and Sisk 2001), or to increased insolation of treated stands (Waltz and Covington 2004). Whatever the mechanism, the negative correlation between woody cover and butterfly abundance and richness has been noted elsewhere (Erhardt 1985), reinforcing the close linkage between butterflies and herbaceous vegetation (Pollard et al 1998; Grill et al. 2005; Vogel et al. 2007). Certainly, for most butterfly studies in which investigators have evaluated treatments designed to remove or reduce woody vegetation in semi-arid systems, the linkages between butterflies and herbaceous vegetation have been emphasized. This suggests that treatment effects on the herbaceous flora and the butterfly fauna will likely move in parallel for the most part, even though it will always be necessary to monitor both components to be certain that no unintended consequences arise from management treatments.

MANAGEMENT IMPLICATIONS

Management activities, especially those that replace stands, are very likely to change species composition of invertebrates, due to habitat changes that favor some species and impact others. With a juniper-feeding larva, juniper hairstreaks exhibited a decline in numbers, short of local extirpation, at all sites at which they were common. This result was expected, and is no cause for alarm, but emphasizes the importance of maintaining a balance across the landscape in the spatial extent of management activities that replace stands. While most other butterfly species and species-group variables did not change with treatment, most of those that did change increased in numbers. This is most likely due to the fact that removal of woody vegetation by any means (fire or fire surrogate treatments) increased water availability for herbaceous vegetation, which increased its cover in the short term, and led to improvement in both larval food and adult nectar resources. Most of the significant effects observed in this study persisted for four years after treatment. That trend would be expected to continue for some time, until enhanced soil water resources are captured by re-growing vegetation.

Strong ties to the native plant community favors butterflies as a monitoring tool to assess environmental change in the Great Basin. Yet high temporal and spatial variability in numbers suggests that monitoring would have to be long-term and of considerable spatial extent, in order to yield meaningful information.

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FIGURE CAPTIONS

Figure 1. See Accompanying Table.

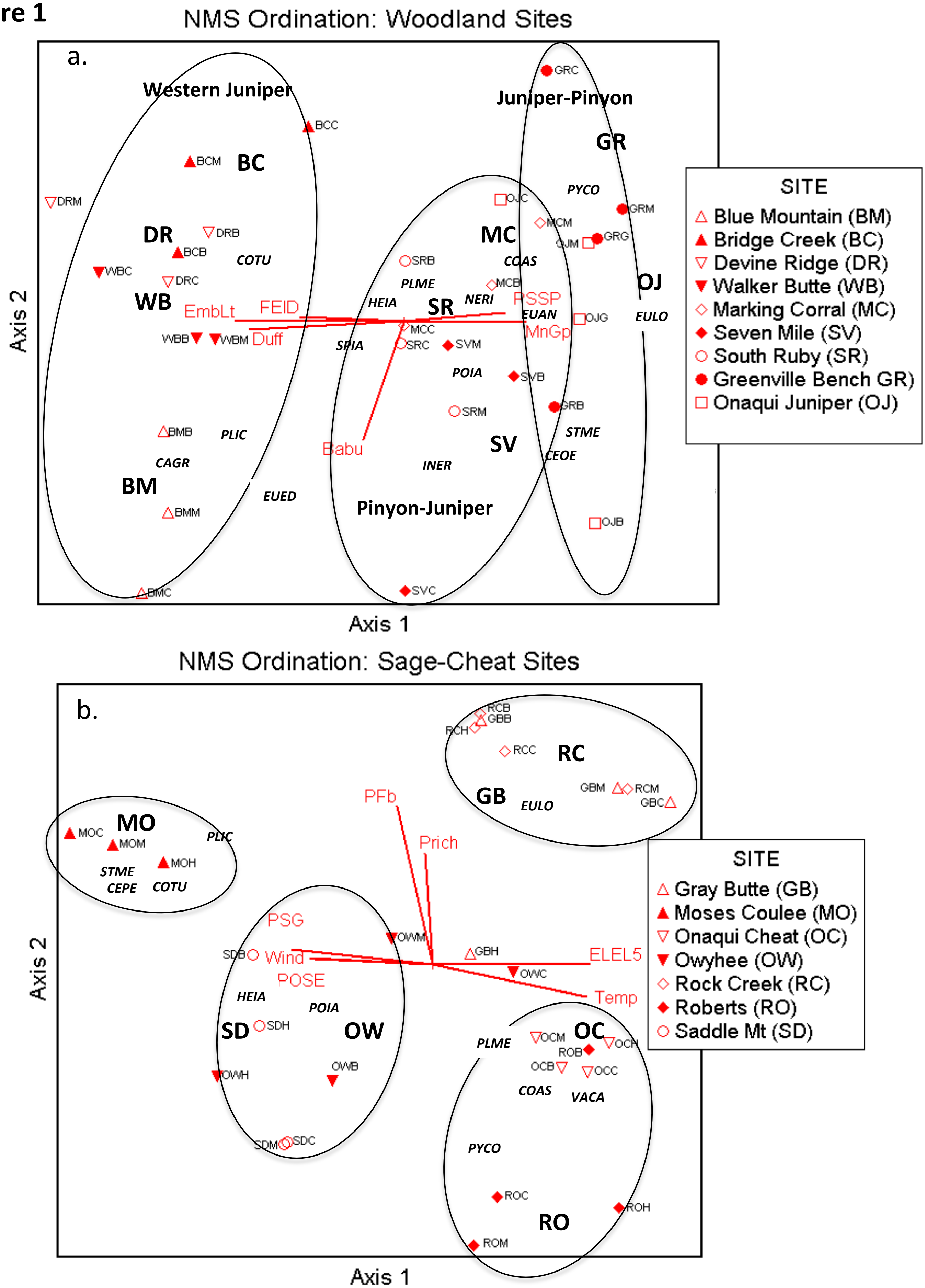
Figure 2. Mean (+/- S.E.) transient richness (a) and abundance (b) at the Network Level (N = 16 Sites), for untreated control plots and combined fire and mechanical plots, one through four years after treatment. *Above fire/mechanical error bar indicates significant difference ($p < 0.05$) between treatment and control for comparison at each year after treatment.

Figure 3. Mean (+/- S.E.) abundance of sulfurs (a) and transient whites (b) for the Woodland Experiment (N = 9 Sites), for untreated control plots and combined fire and mechanical plots, one through four years after treatment. *Above fire/mechanical error bar indicates significant difference ($p < 0.05$) between treatment and control for comparison at each year after treatment.

Figure 4. Effect size of Melissa Blues (*Plebejus melissa*) versus the effect size of one of it's primary larval host plants *Astragalus* spp., for pooled post-treatment samples taken in prescribed burn and mechanically-treated plots at those woodland sites at which Melissa Blues were present. Effect size metric used was: Hedge's D = (mean count in control plot – mean count in treatment plot)/ pooled standard deviation. Woodland site acronyms: BM: Blue Mountain; GR: Greenville Bench; MC: Marking Corral; ON: Onaqui; SR: South Ruby; SV: Seven Mile; WB: Walker Butte; and TOT: All Site Average.

Figure 5. Mean (+/- S.E.) local abundance for the Sage-Cheat Experiment (N = 7 Sites), for untreated control plots and combined fire and mechanical plots, one through four years after treatment. *Above fire/mechanical error bar indicates significant difference ($p < 0.05$) between treatment and control for comparison at each year after treatment.

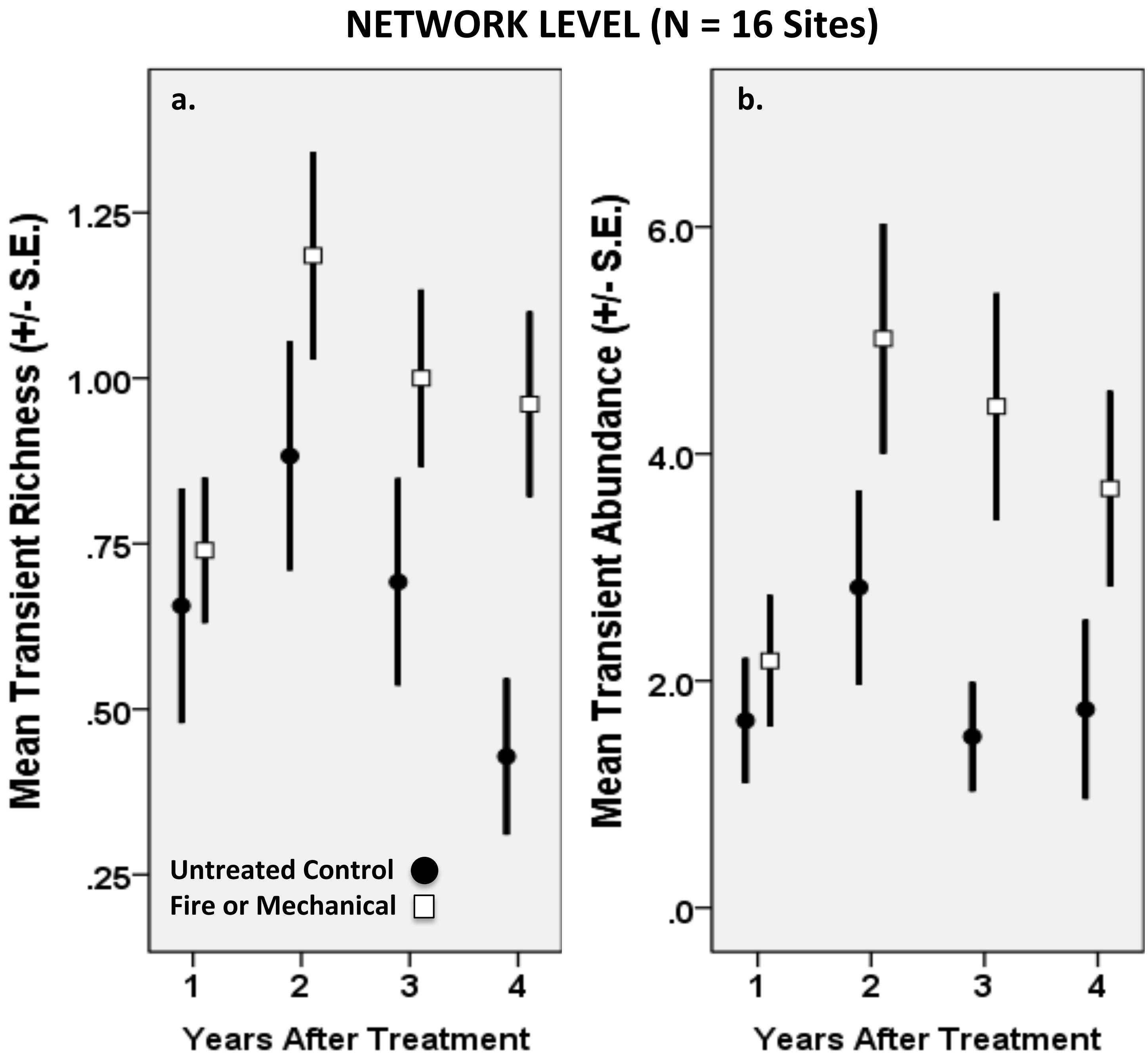
Figure 1


NMS Ordination: Woodland Sites
a.
Western Juniper
Juniper-Pinyon
Pinyon-Juniper
BC
DR
WB
BM
MC
SR
SV
GR
OJ
COTU
PLME
HEIA
NERI
COAS
PYCO
EUAN
EULO
SPIA
POIA
STME
CEOE
PLIC
CAGR
EUED
INER
EmbLt
FEID
Duff
PSSP
MnGp
Babu
Axis 1
Axis 2
SITE
Blue Mountain (BM)
Bridge Creek (BC)
Devine Ridge (DR)
Walker Butte (WB)
Marking Corral (MC)
Seven Mile (SV)
South Ruby (SR)
Greenville Bench GR)
Onaqui Juniper (OJ)
NMS Ordination: Sage-Cheat Sites
b.
MO
RC
GB
SD
OW
OC
RO
PLIC
STME
CEPE
COTU
EULO
HEIA
POIA
PLME
COAS
VACA
PYCO
PFb
Prich
PSG
Wind
POSE
ELEL5
Temp
Axis 1
Axis 2
SITE
Gray Butte (GB)
Moses Coulee (MO)
Onaqui Cheat (OC)
Owyhee (OW)
Rock Creek (RC)
Roberts (RO)
Saddle Mt (SD)

Caption for Figure 1: Non-metric multi-dimensional scaling (NMS) ordinations of butterfly survey data, all sampling years combined, for woodland and sage-cheat experiments, with emphasis on site differences. Vectors indicate significant correlations between main species matrix and variables in the environmental matrix (r > 0.50). Ellipses encircle clusters of plots with similar coordinate values, as discussed in text.

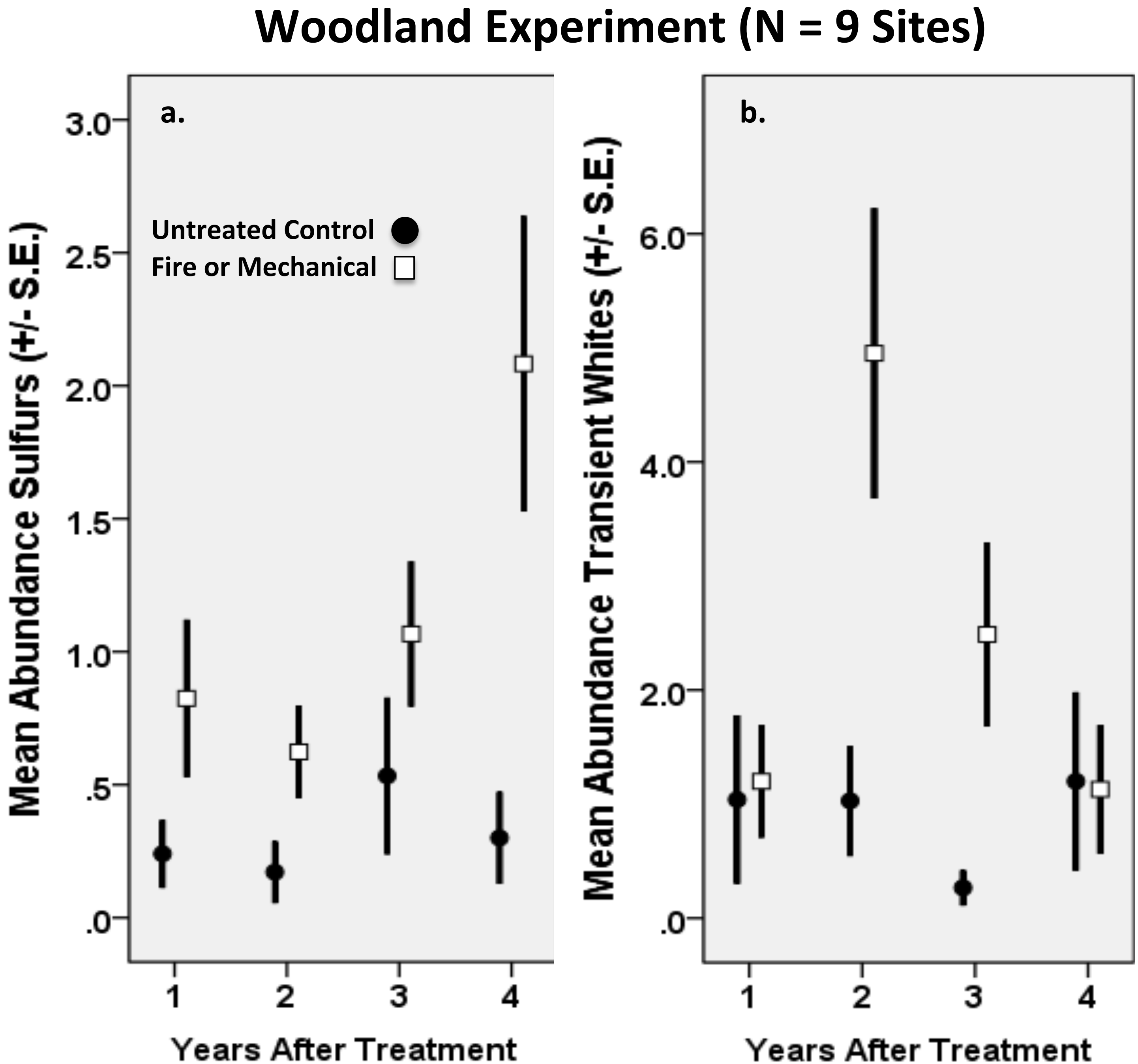
Type of Code	Acronym	Definition
Environmental Codes	MnGap	Mean Gap Diameter
	EmbLit	Embedded Litter Cover
	PFb	Perennial Forb cover
	Prich	Plant Species Richness
	Temp	Mean High Daily Temperature
	PSG	Perennial Short Grass Cover
	Wind	Mean Wind Speed at Survey Time
Plant Species Codes	ELEL5	*Elymus elymoides* (Squirreltail)
	FEID	*Festuca idahoensis* (Idaho Fescue)
	POSE	*Poa secunda* (Sandberg;s Bluegrass)
	PSSP	*Pseudoroegneria spicata* (Bluebunch Wheatgrass)
Treatment Plot Codes	C	Control
	B	Prescribed Fire
	M	Clearcut -- Woodland Experiment
	M	Mow -- Sage-Cheat Experiment
	H	Herbicide -- Sage-Cheat Experiment
	G	Bullhog -- Woodland, Juniper-Pinyon Sites
Butterfly Species Codes	CAGR	*Callophrys gryneus* (Juniper Hairstreak)
	CEOE	*Cercyonis oetus* (Dark Wood Nymph)
	CEPE	*Cercyonis pegala* (Common Wood Nymph)
	COAS	*Colias alexandra* (Queen Alexandra)
	COTU	*Coenonympha tullia* (Ochre Ringlet)
	EUED	*Euphydras editha* (Edith Checkerspot)
	EULO	*Euchloe lotta* (Desert Marble)
	EUAN	*Euphydras anicia* (Anicia Checkerspot)
	HEIA	*Hesperia* spp. (Hesperia Skippers)
	INER	*Incisalia eryphon* (Western Pine Elfin)
	PLME	*Plebejus melissa* (Melissa Blue)
	NERI	*Neominois ridingsii* (Riding's Satyr)
	PLIC	*Plebejus icarioides* (Common Blue)
	POIA	*Pontia* spp. (Large Whites)
	PYCO	*Pyrgus communis* (Checkered Skipper)
	SPIA	*Speyeria* spp. (Fritillaries)
	STME	*Strymon melinus* (Gray Hairstreak)
	VACA	*Vanessa cardui* (Painted Lady)

Figure 2



NETWORK LEVEL (N = 16 Sites)
a.
Mean Transient Richness (+/- S.E.)
1.25
1.00
.75
.50
.25
Untreated Control
Fire or Mechanical
1
2
3
4
Years After Treatment
b.
Mean Transient Abundance (+/- S.E.)
6.0
4.0
2.0
.0
1
2
3
4
Years After Treatment

Figure 3



Woodland Experiment (N = 9 Sites)
a.
b.
Untreated Control
Fire or Mechanical
Mean Abundance Sulfurs (+/- S.E.)
Mean Abundance Transient Whites (+/- S.E.)
3.0
2.5
2.0
1.5
1.0
.5
.0
6.0
4.0
2.0
.0
1
2
3
4
Years After Treatment
Years After Treatment

Figure 4

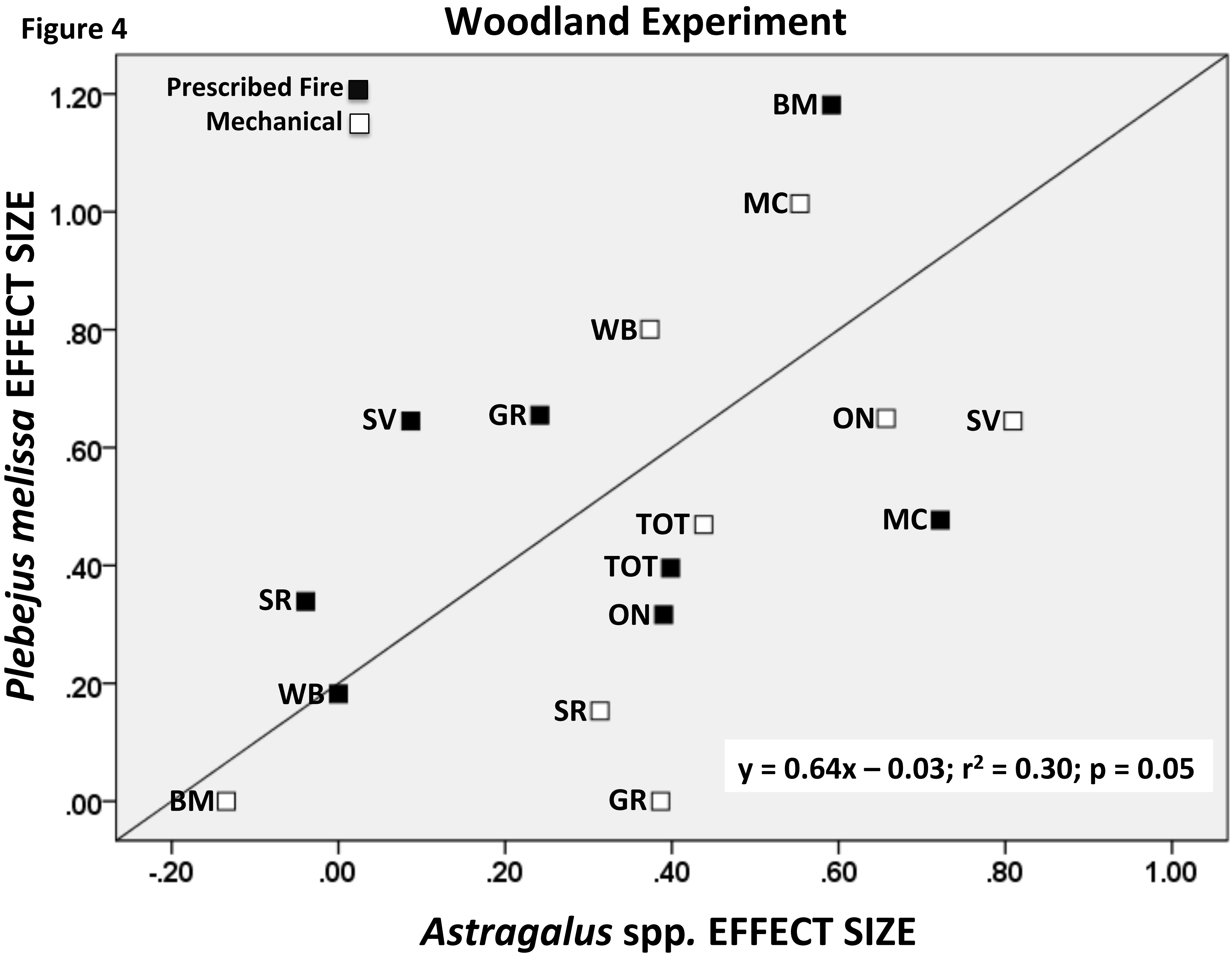
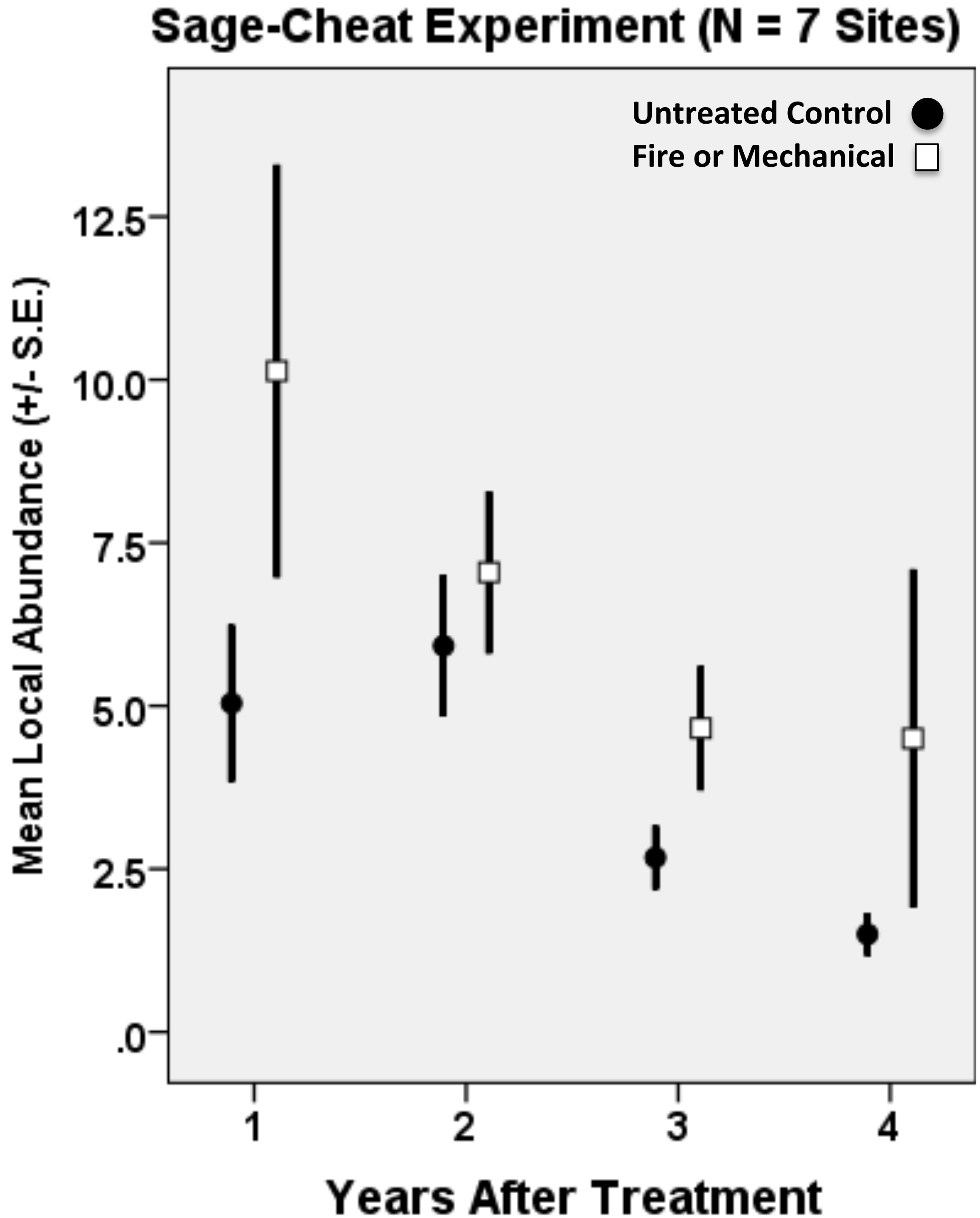

Woodland Experiment
Prescribed Fire
Mechanical
BM
MC
WB
SV
GR
ON
SV
TOT
MC
TOT
SR
ON
WB
SR
BM
GR
y = 0.64x – 0.03; r2 = 0.30; p = 0.05
1.20
1.00
.80
.60
.40
.20
.00
-.20
.00
.20
.40
.60
.80
1.00
Plebejus melissa EFFECT SIZE
Astragalus spp. EFFECT SIZE

Figure 5



Sage-Cheat Experiment (N = 7 Sites)
Untreated Control
Fire or Mechanical
Mean Local Abundance (+/- S.E.)
12.5
10.0
7.5
5.0
2.5
.0
1
2
3
4
Years After Treatment

Table 1. SageSTEP site information, including site acronym and name, state, year treated, percent plot area burned in prescribed fire (parentheses after year), elevation, slope, aspect, current native vegetation, plot position within site (plots separated or adjacent), mean plot area (ha), and minimum distance between plot transects at each site (m). **Moses Coulee burn treatment applied 2008, followed by mowing and herbicide treatments in 2009; [WF1] Site burned by wildfire after treatment: Roberts – 2010 {Jefferson Fire}

SITE, STATE, YEAR TREATED (% BURN) **ELEVATION; SLOPE; ASPECT**	**TREE SPECIES** **CURRENT NATIVE VEGETATION**	**PLOT POSITION W/IN SITE;** **MEAN PLOT AREA;** **MIN. INTER-TRANSECT DISTANCE**
Woodland Experiment	**Western Juniper**	
BM: Blue Mt., CA – 2007 (75%) 1500 – 1700 m; 5%; N	Mountain Big Sage, ID Fescue Sandberg bluegrass, Bluebunch wheatgrass	Separate; 10 ha; 1000 m
BC: Bridge Creek, OR – 2006 (56%) 800 – 900 m; 25%; NW	Basin Big Sage, Bluebunch wheatgrass, Sandberg bluegrass, ID fescue	Adjacent; 15 ha; 100 m
DR: Devine Ridge, OR – 2007 (62%) 1600-1700m; 0-8%; W	Mountain Big Sage, Squirreltail, Sandberg Bluegrass, Thurber needlegrass,	Burn & Control Adjacent, Mech. Separate; 20 ha; 200 m
WB: Walker Butte, OR – 2006 (77%) 1400-1500m; Flat	Mountain Big Sage, Squirreltail, ID fescue, Thurber needlegrass,	Adjacent; 16 ha; 200 m
	Pinyon-Utah Juniper	
MC: Marking Corral, NV -- 2006 (66%) 2300-2400m; 6-20%; NW, NE, SE	Wyoming Big Sage Thurber needlegrass	Separate; 20 ha; 1000 m
SV: Seven Mile, NV -- 2007 (40%) 2300-2500m; 6-15%; NW, E, SE	Mt. Mahogony/Mountain Big Sage Bluebunch wheatgrass, muttongrass	Separate; 16 ha; 1000 m
SR: South Ruby, NV – 2008 (40%) 2100-2200m; 8-30%; All Aspects	Wyoming Big Sage/Bitterbrush, Bluebunch, Sandberg bluegrass, Thurber needlegrass	Separate; 20 ha; 1000 m
	Utah Juniper	
GR: Greenville Bench, UT–2007 (38%) 1750-1850; 2-28%; N	Wyoming Big Sage Needle and Thread, Bluebunch wheatgrass	Adjacent; 12 ha; 1000 m
OJ: Onaqui Mt., UT -- 2006 (85%) 1700-2100m; 2-30%; E	Wyoming Big Sage Bluebunch wheatgrass	Mech & Bull. Adjacent, Burn & Cont. Separate; 15 ha; 1000 m
Sage-Cheat Experiment	**Treeless**	
OC: Onaqui Flat, UT – 2006 (79%) 1750-1850m; 3-4%; E	Wyoming Big Sage/Antelope bitterbrush Bluebunch wheatgrass, Slender wheatgrass	Separate; 25 ha; 500 m
OW: Owyhee, NV – 2008 (45%) 1700-1750m; 0-10%; All Aspects	Wyoming Big Sage, Thurber needlegrass, Bluebunch wheatgrass, Squirreltail, Sandberg bluegrass, Wildrye	Adjacent; 75 ha; 500 m
RO: Roberts [WF1], ID – 2007 (8%) 1550-1600m; 0-10%; All Aspects	Wyoming Big Sage, Bluebunch wheatgrass	Adjacent; 40 ha; 500 m
GB: Grey Butte, OR – 2008 (50%) 1450-1600m; 0-10%; All Aspects	Wyoming Big Sage Squirreltail, Thurber needlegrass	Adjacent; 25 ha; 400 m
RC: Rock Creek, OR – 2008 (40%) 1450-1600m; 0-10%; All Aspects	Wyoming Big Sage Squirreltail, Thurber needlegrass	Adjacent; 75 ha; 800 m
MO: Moses, WA** -- 2008, '09 (55%) 515-530m; 0-10%; S	Wyoming Big Sage, Bluebunch, Squirreltail, Sandberg bluegrass	Adjacent; 25 ha; 250 m
SM: Saddle Mt., WA – 2008 (65%) 262-286m; 1-5%; S	Wyoming Big Sage, Bluebunch, Indian ricegrass, Bottlebrush squirreltail	Adjacent; 25 ha; 250 m

Table 2. Post-treatment means and standard errors for local and transient butterfly richness and abundance, and indication of interannual variation (*), analyzed for the network as a whole (N=16) with 2-factor general linear modeling (treatment x time since treatment). Different superscript letters indicate significant pairwise difference between treatment and control ($p < 0.05$).

	Control		Treatment		Interannual Variation
NETWORK (All Sites)	**Mean**	**S.E.**	**Mean**	**S.E.**	
RICHNESS: Local Butterflies	1.65	0.12	1.91	0.11	*P = 0.006; Increasing with time
RICHNESS: Transients	0.68[a]	0.08	0.97[b]	0.07	P = 0.19
ABUNDANCE: Local Butterflies	8.25	1.39	9.02	1.14	*P = 0.02; Increasing with time
ABUNDANCE: Transients	1.96[a]	0.35	3.88[b]	0.46	P = 0.22

Table 3. Post-treatment means and standard errors for variables in the Woodland Experiment, for which significant treatment effects or internnual variation (*) was observed with 2-factor general linear model (treatment x time since treatment). Different superscript letter indicate significant differences between treatment and control (P < 0.05). WJ=Western Juniper; PJ=Pinyon-Juniper; JP=Juniper-Pinyon.

WOODLAND EXPERIMENT		Treatment: Control		Presc. Fire		Cut & Leave		Bullhog		Interannual
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Variation
RICHNESS	WJ	2.92	0.38	2.79	0.42	2.52	0.38			
(Local Butterflies)	PJ	2.27	0.24	1.91	0.26	2.22	0.29			*P = 0.001;
	JP	0.63	0.30	1.63	0.40	1.69	0.47	1.44	0.40	Increasing
	TOTAL	2.11	0.22	2.18	0.22	2.20	0.22	1.44	0.40	with time
ABUNDANCE	WJ	15.26	5.22	15.40	5.02	18.29	6.78			
(Local Butterflies)	PJ	18.66	4.97	9.00	2.80	8.92	2.18			*P = 0.001;
	JP	2.18	1.15	6.45	2.59	6.18	1.97	7.25	3.41	Increasing
	TOTAL	13.12	2.81	10.82	2.30	11.89	2.85	7.25	3.41	with time
BLUES (BL-Fab)	WJ	6.53	2.49	8.90	2.97	6.34	2.10			
	PJ	2.02	0.77	2.67	0.75	2.87	0.88			*P = 0.008;
	JP	0.30	0.30	0.68	0.39	0.31	0.23	0.38	0.30	Increasing
(Host Plant: Fabaceae)	TOTAL	[ab]3.37	1.07	[a]4.57	1.25	[ab]3.58	0.92	[b]0.38	0.30	with time
FRITILLARIES (FR-Vio)	WJ	1.39	0.72	0.90	0.52	0.38	0.29			*P = 0.03;
	PJ	7.36	4.36	4.58	2.60	3.86	2.06			abundance
	JP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	higher 2011,
(Host Plant: *Viola*)	TOTAL	3.12	1.58	1.97	0.96	1.54	0.77	0.00	0.00	2012
SULFURS (SU-Fab)	WJ	0.05	0.05	0.65	0.25	0.43	0.18			
(Host Plant: Fabaceae)	PJ	0.44	0.17	1.13	0.35	0.68	0.29			*P = 0.04;
	JP	0.60	0.31	0.75	0.27	2.88	0.93	2.38	0.83	Increasing
	TOTAL	[a]0.32	0.10	[ab]0.84	0.17	[b]1.13	0.29	[c]2.38	0.83	with time
TRANSIENT WHITES (WT-Bra)	WJ	0.72	0.50	0.30	0.13	0.91	0.72			*P = 0.04;
(Host Plants: Brassicaceae)	PJ	1.20	0.52	3.07	0.88	2.77	1.00			Abundance
	JP	0.60	0.41	3.68	1.78	2.25	1.01	5.78	2.29	higher 2008,
	TOTAL	[a]0.86	0.29	[a]2.16	0.58	[a]1.91	0.53	[b]5.78	2.29	2009
LOCAL WHITES (WL-Bra)	WJ	0.77	0.54	0.00	0.00	0.10	0.07			*P = 0.04;
(Host Plant: Brassicaceae)	PJ	1.20	0.55	0.38	0.28	0.57	0.42			Numbers
	JP	0.90	0.62	1.05	0.62	1.43	0.81	1.55	0.82	variable year
	TOTAL	0.95	0.32	0.41	0.19	0.60	0.26	1.55	0.82	to year
MELISSA BLUE	WJ	0.05	0.05	0.65	0.29	0.58	0.42			
(*Plebejus melissa*)	PJ	0.38	0.23	1.91	0.70	1.46	0.61			*P = 0.02;
(Host Plant: Fabaceae)	JP	0.00	0.00	0.30	0.20	0.31	0.23	0.30	0.30	Increasing
	TOTAL	[a]0.15	0.08	[b]1.01	0.29	[b]0.83	0.28	[a]0.30	0.30	with time
JUNIPER HAIRSTREAK	WJ	30.91	12.91	3.65	1.41	7.44	2.53			
(*Callophrys gryneus*)	PJ	1.31	0.68	0.44	0.28	0.26	0.15			
(Host Plant: *Juniperus* spp.)	JP	0.08	0.08	0.38	0.24	0.00	0.00	0.00	0.00	
	TOTAL	[a]12.74	5.40	[b]1.67	0.59	[b]3.00	1.08	[c]0.00	0.00	P = 0.54

Table 4. Post-treatment means and standard errors (years 1 - 3) for annual and perennial forb cover in Sage-Cheat and Woodland Experiments. Different superscript letters indicate significant difference in pairwise comparisons with 2-factor general linear model (treatment x time since treatment); *Indicates significant interannual variation.

SAGE-CHEAT SITES (N = 7)

	Control		Burn		Mow		Herbicide		
Forb Type	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	
Annual	[a]4.67	1.22	[b]8.26	1.57	[b]6.31	1.32	[a]4.23	1.00	P = 0.65
Perennial	2.80	0.63	2.17	0.51	2.67	0.64	1.85	0.48	*P = 0.001; Increasing with time -- all plots

WOODLAND SITES (N = 9)

	Control		Burn		Clearcut		Bullhog		
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	
Annual	[a]3.53	0.60	[b]13.76	1.58	[a]5.55	0.69	[a]6.22	1.39	*P = 0.001; Increasing with time; Year 3 cover > in treated plots
Perennial	[a]3.08	0.21	[b]4.71	0.51	[b]3.96	0.27	[a]2.50	0.27	*P = 0.001; Increasing with time in treated plots

Table 5. Post-treatment means and standard errors for variables in the Sage-Cheat experiment, for which significant treatment effects or interannual variation (*) was observed in analysis with 2-factor general linear modeling (treatment x time since treatment). Different superscript letters indicate significant pairwise difference between treatment and control (P < 0.05).

SAGE-CHEAT EXPERIMENT	**Control**		**Prescribed Fire**		**Mow**		**Herbicide**		**Interannual Variation**
	Mean	**S.E.**	**Mean**	**S.E.**	**Mean**	**S.E.**	**Mean**	**S.E.**	
RICHNESS (Local Butterflies)	1.17^{a}	0.17	1.67^{b}	0.15	1.39^{a}	0.18	1.32^{a}	0.15	*P = 0.005; Variable among years
ABUNDANCE (Local Butterflies)	4.87^{ab}	1.04	6.91^{b}	1.07	3.71^{a}	0.58	3.24^{a}	0.71	*P = 0.02; 2008 Peak
SKIPPERS (SK-Poa) (Host Plant: Poaceae)	0.47^{a}	0.19	1.87^{b}	0.67	0.70^{a}	0.31	0.88^{ab}	0.23	P = 0.83
LOCAL WHITES (WL-Bra) (Host Plant: Brassicaceae)	2.70^{ab}	0.69	3.87^{b}	0.93	1.90^{a}	0.44	1.52^{a}	0.61	*P = 0.02; Decreasing with time; 2008 Peak
BECKER'S WHITE (*Pontia beckerii*)	0.73^{a}	0.31	0.71^{a}	0.17	0.13^{b}	0.06	0.29^{ab}	0.11	P = 0.42

Appendix 1. List of butterfly species annotated with site fidelity description (local v. transient), analysis group (based on host plant preferences), observed nectar sources, regional affinities (sage-cheat, woodland sites), total count during study period, and relative abundance for each year of study period (2006 -- 2012).

						SAGE-CHEAT REGION		WOOD-LAND REGION			INTER-ANNUAL VARIATION (Survey Years)						
Species	**Common Name**	**Analysis Group**	**Site Fidelity**	**Observed Nectar Sources**	**Total Count**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**
HESPERIIDAE (Skippers)																	
*Hesperia colorado**	W Branded Skipper	SK-Poa	local	*Crepis, Senecio*	118	3	3	3	1	2	3	1	2	3	3	3	2
Hesperia juba	Juba Skipper	SK-Poa	local	*Arnica, Balsamorhiza, Phlox,* Brassicaceae	150	3	2	1	2	3	0	0	2	2	2	2	3
Hesperia uncas	Uncas Skipper	SK-Poa	local		17	0	0	2	1	0	0	2	1	0	0	0	0
Pyrgus communis	Checkered Skipper		local	*Sphaeralcea,* Brassicaceae	156	1	2	0	1	4	0	1	3	4	3	2	4
LYCAENIDAE (Blues, Elfins, Hairtreaks)																	
Euphilotes ancilla	Rcky Mt Dotted Blue		local		4	0	0	1	0	0	1	0	0	1	0	0	0
Euphilotes battoides	Buckwheat Blue		local	*Erigonum*	36	1	0	2	0	3	1	0	0	0	3	2	1
Everes amyntula	W Tailed Blue	Bl-Fab	local		40	0	1	0	2	0	0	0	0	0	0	2	0
Glaucopsyche piasus	Arrowhead Blue	Bl-Fab	local		4	0	0	1	0	0	0	1	0	0	0	0	0
Plebejus acmon	Acmon Blue	Bl-Fab	local	*Achillea, Eriogonum, Senecio, Sphaeralcea*	45	1	0	3	1	2	1	0	0	3	2	1	1
*Plebejus icarioides**	Common Blue	Bl-Fab	local	*Balsamorhiza, Erigeron, Eriogonum, Lupinus, Phacelia, Phlox, Senecio*	777	4	2	4	4	1	4	2	3	4	4	4	4
*Plejebus melissa**	Melissa's Blue	Bl-Fab	local	*Astragalus, Erigeron*	138	0	1	3	3	2	3	3	1	3	3	3	3
Incisalia eryphon	W Pine Elfin		local		7	0	0	0	1	0	0	0	1	0	1	1	0
*Callophrys gryneus**	Juniper Hairstreak		local	*Achillea, Allium, Amsinckia, Arnica, Astragalus, Balsamorhiza, Crepis, Erigeron, Eriogonum, Senecio, Sphaeralcea*	1316	0	0	4	3	3	4	4	3	4	4	4	4
Callophrys spinetorum	Thicket Hairstreak		local	*Crepis*	19	0	0	1	2	1	0	0	0	3	0	0	0
Strymon melinus	Gray Hairstreak		local	*Arnica*	20	1	0	1	0	0	0	0	1	0	0	2	0
NYMPHALIDAE (Checkerspots, Fritillaries, Admirals, Ladies, Wood Nymphs, Ringlets, Satyrs)																	
Chlosyne acastus	Sage Checkerspot		local		4	0	0	1	0	0	2	0	0	0	0	0	0
Chlosyne whitneyi	Sierra Checkerspot		local		46	0	0	0	0	3	0	0	0	0	2	0	3
*Euphydryas anicia**	Anicia Checkerspot	CH-Scr	local	*Agoseris, Balsamorhiza, Eriogonum, Lomatium,* Compositae, Umbelliferae	382	1	2	4	4	2	0	0	2	2	4	4	3
Euphydryas chalcedona	Chalc. Checkerspot	CH-Scr	local		22	0	0	3	0	0	3	0	1	0	0	0	0
Euphydryas editha	Edith's Checkerspot	CH-Scr	local		81	0	0	2	4	1	0	0	0	4	0	0	0
Speyeria callippe	Callippe Fritillary	FR-Vio	local	*Amsinckia, Antennaria, Balsamorhiza, Crepis, Eriogonum, Lomatium*	359	0	0	3	4	1	2	4	3	1	2	4	4
Speyeria coronis	Coronis Fritillary	FR-Vio	local	*Allium*	52	0	0	2	1	0	3	1	1	0	0	3	0
Limenitis lorquini	Lorquin's Admiral		transient		10	0	0	1	1	0	1	1	0	1	1	1	0
Vanessa annabella	W Coast Lady		transient		35	0	0	0	0	1	0	0	2	0	0	0	0
Vanessa cardui	Painted Lady		transient	*Allium, Balsamorhiza, Crepis, Erigeron*	164	1	3	2	3	4	0	0	4	4	3	1	1
*Coenonympha tullia**	Ochre Ringlet	NY-Poa	local	*Achillea, Crepis, Eriogonum*	388	3	1	4	2	1	1	1	3	4	4	4	3
Neominois ridingsii	Riding's Satyr	NY-Poa	local		180	0	0	1	4	0	0	0	3	1	2	3	4
Cercyonis oetus	Dark Wood Nymph	NY-Poa	local		21	0	0	1	4	1	3	3	0	0	3	1	0
Cercyonis pegala	Co. Wood Nymph	NY-Poa	local		3	1	0	0	0	0	0	0	0	0	1	0	0
Cercyonis sthenele	GB Wood Nymph	NY-Poa	local		43	0	0	1	0	3	4	0	0	0	0	0	0
PAPILIONIDAE (Swallowtails)																	
Papilio rutulus	W Tiger Swallowtail		transient		16	2	0	1	1	0	0	0	0	1	1	1	0
Papilio zelicaon	Anise Swallowtail		local	*Astragalus*	36	1	0	3	0	2	0	0	3	1	1	3	1
PIERIDAE (Whites, Marbles, Sulfurs)																	
Colias alexandra	Queen Alex. Sulfur	SU-Fab	transient		157	1	3	2	3	4	3	3	1	3	3	3	3
Colias eurytheme	Orange Sulfur	SU-Fab	transient	*Achillea*	24	0	1	1	2	1	0	0	3	1	1	1	0
Colias philodice	Clouded Sulfur	SU-Fab	transient		152	0	3	1	3	3	0	3	3	3	3	3	4
Pieris rapae	Cabbage White	WT-Bra	transient		9	1	1	0	1	1	0	0	0	1	0	1	0
*Pontia beckerii**	Becker's White	WT-Bra	transient	*Aster,* Brassicaceae	130	3	3	3	1	3	1	1	1	3	2	3	3
Pontia occidentalis	Western White	WT-Bra	transient		98	2	1	1	3	3	0	0	4	3	1	2	1
Pontia protodice	Checkered White	WT-Bra	transient		182	0	1	0	4	4	1	1	4	3	1	3	0
Pontia sisymbrii	Spring White	WT-Bra	transient		45	0	1	3	1	1	0	0	2	1	1	3	1
Euchloe ausonides	Large Marble	WL-Bra	local		22	0	1	1	3	2	0	1	2	0	3	0	0
*Euchloe lotta**	Desert Marble	WL-Bra	local	*Allium, Crepis, Descuriana, Erigeron,* Brassicaceae	415	4	3	1	3	4	0	3	4	4	3	4	2
Anthocharis sara	Sara's Orange Tip	WL-Bra	local		30	0	0	3	1	1	0	0	2	1	0	2	3

*Species abundant enough to be analyzed as separate response variables; Current Species Names ex. **ButterfliesofAmerica.com**; accessed 31 January 2013

Analysis Groups: SK-Poa:Grass-feeding skippers; BL-Fab:Legume-feeding blues; CH-Scr:Scroph-feeding checkerspots;FR-Vio: Violet-feeding fritillaries; NY-Poa:Grass-feeding nypmhs; SU-Fab:Legume-feeding sulphurs; WT-Bra:Mustard-feeding transient whites; WL-Bra:Mustard-feeding local whites

Abundance Codes: 4:Abundant (>1.0/sample); 3:Common (0.20-0.99/sample); 2:Uncommon (0.10-0.19/sample); 1:Rare (<0.09/sample); 0:Absent

Region Codes: 1: Sage West; 2: Sage East; 3: Western Juniper; 4: Pinyon-Juniper; 5: Juniper-Pinyon

Species observed < 3 TIMES*: Danaus plexippus, Euchloe hyantis, Limenitis weidemeyerii, Lycaena helloides, Nymphalis antiopa, Nymphalis milberti, Pholisora catullus, Polygonia zephyrus, Satyrium californicum, Speyeria hydaspe*