Effects of fire management practices on butterfly diversity in the forested western United States

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INTRODUCTION

Fire-suppression policies have led to extensive changes in the community composition and ecosystem functioning of forests of the western United States. Without periodic fire, fuel loads and tree densities have increased and plant community structure has shifted to fire-intolerant trees (Agee 1993, McKelvey et al. 1996). These conditions have dramatically increased the risk of catastrophic fire, threatening both to destroy human lives and property and to change forest structure and species diversity. Forest managers in the west have initiated programs of prescribed burning to reduce combustible fuel loads and foster the reestablishment of the historical plant community (e.g., Rose 1983, van Wagendonk 1974, Agee 1993). However, because the landscape has been altered by decades of fire suppression, as well as logging, grazing, and development, the characteristics or effects of prescribed burns may not accurately mimic those of historical fires (van Wagendonk 1974, 1984). Also, because the restoration of fire regimes is an emerging science, it is occurring with incomplete knowledge of its community-level effects.

In general, thorough knowledge of the effects of fire is limited to fire return intervals and forest macrostructure (e.g., Skinner and Chang 1996, Agee 1993). This research has informed managers that fire should return approximately every 8-11 years in ponderosa pine/mixed conifer forests, every 12-17 years in Douglas-fir/mixed conifer forests, and every 11-20 years in red fir forests (Skinner and Chang 1996). When fire is suppressed, certain tree species, such as white fir (Abies concolor), increase in relative abundance (Skinner and Chang 1996, Atzet and Wheeler 1982). However, under historical fire regimes, the predominating species are fire-adapted trees and shrubs, such
as ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), as well as ceanothus (*Ceanothus* spp.) and manzanita (*Arctostaphylos* spp.) (Skinner and Chang 1996, Atzet and Wheeler 1982).

Because trees contribute disproportionately to community macrostructure and because their historical occurrences can be determined through palynology and dendrochronology, it is appropriate that they serve as the cornerstone of fire studies. In addition, Agee (1998) notes that management actions are often implemented with a coarse-filter, or ecosystem-level, approach on the assumption that a functioning ecosystem and appropriate forest macrostructure will maintain all native taxonomic diversity. A good test of this assumption in fire-managed coniferous forests would be to monitor the taxa that are likely to have different requirements for persistence than trees have or to occur at significantly different scales than trees do. Because insects often account for large amounts of diversity, biomass, and nutrient cycling and have markedly different life histories than trees, they are excellent targets for examination. Research has been done on the effects of fire on numerous insect taxa in natural environments (e.g., boreal dendrophagous and soil arthropods, Ehnstrom et al. 1995, Paquin and Coderre 1997; oak savanna arthropods, Siemann et al. 1997; prairie butterflies, Swengel 1996, 1998). However, little research has yet been conducted on the impact of prescribed burning on herbivorous, non-dendrophagous insect taxa of temperate coniferous forests. This is an important class of insects because they consume members of the plant community not assessed by traditional fire research techniques.

In this study, I measured the response of butterflies to multiple burning methods in formerly fire-suppressed forests. No forest butterflies in the study areas are listed as
threatened or endangered at this time; nonetheless, butterflies provide a good opportunity to study the conservation consequences of community-level effects of fire. First, butterflies can serve as a valuable barometer of overall community complexity. Because each species of butterfly tends to be hostplant specific, a diverse butterfly community may potentially indicate a diverse community of herbaceous and shrubby hostplants (Harding 1995). There is a continuing debate on the relative merits of different insect taxa as indicators, however, Harding (1995) emphasizes that butterflies display many of the useful characteristics of indicator taxa and that they are certainly the most well known taxonomically of the potential insect indicator taxa. Also, because butterflies contribute to the diets of numerous and varied arthropods and vertebrates (Douglas 1986), they can potentially suggest much more about the complexity of the community than can vegetative structure or herbaceous plants alone. Second, many butterfly species are associated with early successional communities (Douglas 1986, Scott 1986), and these communities vary greatly in their level of ecological integrity, defined by Kirkpatrick and Gilfedder (1995) as the degree of alteration from their state prior to European settlement. It is quite possible that early successional communities with high ecological integrity are in danger of being overlooked for conservation because of the preponderance of low-integrity (anthropogenically degraded) early successional communities. Because many butterflies only occur in high-quality areas (Scott 1986), they can help shed light on the relative importance of these areas for community-level conservation efforts.

Multiple factors affect the responses of different butterfly species to fire. In general, butterflies usually do not survive fire on site. Planned prescribed burns tend to be conducted in the spring or fall (e.g., Agee 1993, USDA 1996). In either of these
seasons, different butterfly species are likely to have most of their individuals concentrated in one of the different life stages of holometabolous insects—egg, larva, pupa, or adult (Scott 1986). Prescribed natural fires, or fires that start naturally but are allowed to continue burning under certain conditions (van Wagendonk 1995), often burn throughout the summer, at which time a greater proportion of the species will tend to have individuals in the adult (butterfly) stage (Scott 1986). Different life stages are likely to respond differently to fire. For instance, the non-vagile life stages usually suffer direct mortality. The only vagile life stage, the adult, may also suffer high mortality during fire in species that have high site fidelity or slow flight.

In a review of the response of prairie arthropods to fire, Reed (1997) found that prairie arthropods are attracted to the herbaceous growth that follows fire for feeding, nectaring, and ovipositing, a generalization that likely applies to forest butterflies as well. However, Shapiro (1996) cautions that most butterflies specialize on particular host plants, so choice of oviposition plants is nonrandom. In addition, Swengel (1996) observed butterflies on prairie sites burned in different years following fire and found that certain species were significantly associated with sites burned one, two, three, or four years before, indicating that butterflies may undergo a pattern of succession akin to that of vegetation.

Also, colonization of burn sites by butterflies depends on their ability both to reach and to become established on the site (Reed 1997). Because butterfly behavior is highly sensitive to sun and shade (e.g., Grundel et al. 1998a), availability of sunlit corridors into appropriate habitat areas may be a factor in colonization of new sites. Because most butterflies are ectothermic, they may be attracted to openings in the canopy
due to tree mortality following fire (Shapiro 1996). The canopy may open in any of three ways beneficial to butterflies: by increasing the number of canopy gaps, by increasing the average area of each canopy gap, or by providing canopy gap corridors that facilitate butterfly movement.

Another potential benefit of fire to butterflies, increased host plant availability, is less direct. Low-intensity fire stimulates plant growth by releasing N, P, and S into the ash layer (Poff 1996). In addition, the charcoal produced by fire in boreal forests has been shown to absorb allelopathic chemicals from the soil and encourage the growth of tree seedlings (Wardle et al. 1998, Zackrisson et al. 1996) showed that Both of these chemical processes in the soil may lead to increased herbaceous growth following fire. Historical data are difficult to obtain; however, herbaceous vegetation in both ponderosa pine and mixed conifer temperate forests is believed to have been more abundant in the past (Chang 1996). Thus, annual and perennial herbaceous butterfly host plants may consequently increase post-fire.

Because prescribed burning is expensive, risk-laden, and controversial and because different land management agencies have different goals and funding resources, multiple approaches to reintroducing fire are being implemented in the west. In many instances, prescribed fires must remain small and consequently do not burn broadly over heterogeneous areas (e.g., Rose 1983). In addition, when consumption of excess fuels is the primary driving force, upland areas, with their high risk of catastrophic burns, are primary candidates for management. Riparian areas, with their mesic, fire-retarding vegetation, generally are not included in those management plans (e.g., Rose 1983, Agee pers. com.). In national parks, which are under a directive to restore landscapes to the
condition they would be in without technological human intervention where possible (van Wagtendonk 1974), managers may more often have the luxury, not afforded to other management agencies, of letting fires burn indefinitely under prescribed conditions. In these cases, the severity, extent, and heterogeneity of fire are not so bounded as they are in small-scale prescribed burns (van Wagtendonk 1995). Another effective method of combating catastrophic fires is shaded fuel breaks, which are wide corridors of intensively thinned vegetation often created along ridgetops, to reduce fuel loads, slow the spread of wildfires, and provide penetration routes for fire fighters (Agee et al. 2000).

MATERIALS AND METHODS

The study sites

Field studies were conducted in the Ashland Watershed Reserve, Rogue River National Forest, on the eastern side of the Siskiyou Mountains, Oregon, in the summer of 1998, and on the north rim of Yosemite Valley in Yosemite National Park, on the western side of the Sierra Nevada, California, in the summer of 1999. The Ashland Watershed, a late seral-stage reserve, is dominated by a *Pseudotsuga*/hardwood plant community, and the eastern Siskiyou mountains are characterized by warm, dry summers and cool, moist winters with a mean annual precipitation in the Ashland Watershed of approximately 51 cm (Rose 1983). The north rim of Yosemite Valley is dominated by mid- to late-seral stage pines and firs. The western Sierra Nevada is characterized by warm, dry summers and relatively higher annual precipitation (190 cm at 1,675 m), the vast majority of which falls in the winter months (Storer and Usinger 1971).

In the Ashland Watershed, transects were established on 5 prescribed forest burn sites and 5 forest controls (Fig. 1; Table 1). Through the use of GIS maps and ground
truthing, controls were chosen to reflect, as well as possible, the variation found among the forest burn sites with respect to altitude and aspect, dominant plant type, and types and proximity of potential nearby butterfly source habitats. The efficiency with which each of these potential source habitats may provide butterfly propagules is unknown. One forest burn site each has been treated with a prescribed burn in 1991, 1993, 1995, 1996, and 1997. The forest controls are not known to have burned since at least 1978 (Rose 1983). However, because numerous fires have occurred in the Ashland Watershed (Rose 1983) and because occasional burned debris or snags were detectable in each forest control stand, the effects of fire may not have been completely absent from any site.

In Yosemite, transects were established on 5 forest burn sites and 7 forest controls (Fig. 2; Table 2). As in the Ashland Watershed study, GIS maps and ground truthing were used to select controls that reflected, as well as possible, the variation found among the forest burn sites with respect to altitude and aspect, dominant plant type, and types and proximity of potential nearby butterfly source habitats. The efficiency with which each of these potential source habitats may provide butterfly propagules is unknown. In these study sites, potential source habitats were less relevant than in the Ashland Watershed because the fires were on a much larger scale and most transects were established far from roads. In addition, whether the area was strewn with granite boulders was noted because some butterfly species thrive on “rocky outcrops.” One forest burn site each was treated with a burn in 1980, 1986, 1988, 1989, and 1998. Although the broad spread of burn years was not ideal, it was unavoidable in the region of the study. As in the Ashland Watershed study, control sites were chosen to reflect the variation in forest burn sites, and minimal evidence of prior burning was occasionally visible in
control sites. Forest control sites had probably not burned since 1930, when managers first began to keep systematic records.

There was one transect on each site. Because the goal of the study was to quantify maximum diversity, each transect was chosen to maximize opportunities to see adult butterflies. Consequently, a walking visual assessment of the entire site was conducted at the beginning of the field season to determine the transect path that would intersect the most areas with known butterfly attractors, such as sunlight, warm temperatures, and nectar sources. Each transect consisted of 8 connected 30-m sections that followed the contour of the mountainside.

From 28 June 1998 to 28 August 1998 and from 24 June 1999 to 25 August 1999, I walked transects in a regular rotation during conditions of peak butterfly activity to count species and individuals by standard butterfly monitoring methods (Pollard and Yates 1993). I counted each visible adult butterfly within 10 m of the transect in either direction, so that each section was 30-m long x 20-m wide and each whole transect was 240-m long x 20-m wide. I sampled for 5 minutes per section, or until the fauna appeared to be saturated, whichever occurred last. I considered the fauna to be saturated if, during the last 2 minutes in the section, I: a) was not distracted by identification or counting of a species seen in the first 3 minutes, and b) did not see any species new to that section that day. Each site was sampled 6 times in 1998 and 5 times in 1999. Care was taken to sample treatment and control sites under similar weather conditions and at similar times of day whenever possible. Time of day, approximate temperature, percent cloud cover, and general weather conditions were recorded each time but not used in analyses.
Mechanisms Affecting Butterfly Diversity

In 1998, I tested potential mechanisms affecting butterfly richness within sites (alpha richness). Because butterflies are generally ectothermic, I measured the density and area of sunlit patches caused by canopy gaps in each of the forest burn and control sites. Sunlit patches were defined to include only areas where full sunlight penetrated to the bare forest floor or the herbaceous/shrubby understory. I defined density as the number of sunlit patches per 30-m section of transect and area as the 2-dimensional area of sunlit patches per 30-m section of transect. Measurements for both density and entire area were taken parallel to the transect for any sunlit patch occurring partially or completely within 10 m of the transect in either direction. Only patches of at least 5 m in width were included. I used a tape measure and rounded each measurement to the nearest 0.5 m. Measurements were taken between 11 a.m. and 2 p.m. when the sun was highest in the sky. Because certain butterfly species generally prefer sunlit patches and "corridors," I created an index of connectivity of sunlit patches ranging from 1 to 3 to quantify percentage of sunlit corridors connecting sunlit patches (1 = no sunlit corridors linking sunlit patch to other sunlit patch; 2 = dappled sunlight linking patches; 3 = unambiguous sunlit corridor(s) linking patches). Finally, I created an index of habitat quality ranging from 1 to 5 which was based on percentage of herbaceous or shrubby hostplants or nectar sources covering the sunlit portion of the substrate (1 = 0% live understory vegetation; 2 = 1-10%; 3 = 11-20%; 4 = 21-30%; 5 = >31%).

Habitat Heterogeneity

To test whether habitat heterogeneity is a between-site mechanism maintaining butterfly richness at a regional scale (beta richness), I monitored additional sites in
differing habitats. In 1998 in the Ashland Watershed, transects were established on 5 ridgetop fuel breaks and 4 fuel-break controls (Fig. 1; Table 3). Approximate altitude, potential butterfly source habitats, dominant plant types, and understory morphology were noted. Because fuel breaks are long and tend to be vegetationally diverse, the segments that were monitored were assumed to have fuel breaks as potential nearby butterfly sources, even if they were part of the same fuel break. Fuel break understories were dominated by herbs and forbs ("herbaceous"), annual or perennial grasses ("grassy"), or woody shrubs ("shrubby"). Understory plant morphology varied both within and among fuel breaks. Controls were established on untreated ridgetops, again to reflect the variation in the fuel breaks with respect to altitude and proximity to potential butterfly source populations. I was unable to pair treatments and controls by dominant plant type because: a) few untreated ridgetops were available, and b) after treatment, the plant community and morphology of the fuel breaks were significantly altered. Untreated ridgetops were designated as such if they were not treated as heavily as fuel breaks, although some amount of treatment history was evident in one location. In general, however, fuel break controls were much more densely overgrown than the forest controls, with tightly overlapping tree canopies and very little live understory plant cover.

Finally, because it was obvious that certain wet roadside areas in the Ashland Watershed harbored a tremendous diversity of butterflies, 7 30-m sections were established in 1998 along the Ashland Watershed access road at predetermined areas of greatest butterfly diversity and abundance. Each roadside section was situated along a roadside mud puddle (2 sections), seep (3 sections), or creek crossing (2 sections). These sections were used to help ascertain whether the entire regional fauna of the Ashland
Watershed could be found on the treatment sites. In Yosemite in 1999, unlike in the Ashland Watershed study, no roadside (or campground or meadow) areas were found to have butterfly diversity to rival that on the treatment sites, so no additional sites to monitor regional diversity were established.

Because of the butterfly diversity observed at the riparian roadside sections in the Ashland Watershed in 1998, transects were established on 4 riparian burn sites and 5 riparian controls in Yosemite in 1999 (Fig. 2; Table 4). Approximate altitude and aspect, potential butterfly source habitats, presence of granite boulders, and dominant plant types were noted. One riparian burn site each was treated in 1988 and 1998, and two transects were established in different watersheds that were both burned in the same 1986 fire. Because very few riparian burn sites were available, this design was unavoidable; however, both transects were in different watersheds that were located roughly 2 km apart. Before analyzing the data generated from each of those watersheds, I compared numbers of overlapping species in each riparian area and found that the faunas of the two watersheds burned in the same fire were no more closely related than the faunas of other riparian sites (data not presented).

Analyses

I calculated butterfly species richness at each site. Because there was a high degree of variation among the sites, I first verified that the data were approximately normally distributed for each treatment type. I used an ANOVA on square-root transformed ($\sqrt{X} + 0.5$) data to compare species richness on each type of treatment and control as well as between treatments (Zar 1984). I also calculated both Shannon and
Simpson’s diversity indices for each site (Magurran 1988) and did ANOVA tests on the square-root transformed data.

I tested whether either forest burn sites or forest control sites were providing disproportionately more habitat to those butterflies that were common to both habitats. Using an unpaired t-test, I compared the proportion of forest burn and forest control sites in which each of the shared species was observed.

Because certain butterfly species are more readily observable than others and certain sites are more amenable to butterfly observation, it is generally not advisable to compare raw abundance data (Pollard and Yates 1993). However, the sites appeared sufficiently similar to reduce or eliminate that aspect of the problem. Thus, I compared the abundances of species that were shared by both the forest burn and the forest control sites using a chi-square test with a null hypothesis that each treatment type would harbor 50% of each of the shared species.

I performed a backward step-wise regression on the variables hypothesized to contribute to butterfly species richness. I obtained the same results with a forward step-wise regression, so those data are not presented.

Because many butterflies have very narrow habitat requirements, I quantified how many species were unique to each of the different treatment types. In addition, I quantified the average number of species added per unit of sampling effort (8 30-m sections of transect) to help make the number of unique species observed in each treatment type more comparable between treatments.

All butterfly species names follow Scott (1986); all plant references follow Hickman (1993); and all calculations were done using StatView 5.0.1.
RESULTS

A total of 1342 individuals (325 in forest burn sites, 56 in forest burn controls, 635 in fuel breaks, 20 in fuel break controls, and 306 in roadside riparian areas) were recorded in the Ashland Watershed in 1998 (Table 5). A total of 1382 individuals (300 in forest burn sites, 190 in forest burn controls, 703 in riparian burn sites, and 189 in riparian burn controls) were recorded in Yosemite in 1999 (Table 6). By coincidence, a total of 47 species was seen each year; however, the individual species were not the same.

Rarefaction curves were created to determine how thoroughly the fauna was saturated by the sampling method. Individual rarefaction curves for each day sampled for each site were summed for each treatment. Consequently, the cumulative number of species exceeds the total number of species seen in that treatment type. The summed curves were graphed, and logarithmic curves were fitted to the data (Figs. 3a-d, 4a-d). The resulting equation was used to determine what percentage increase in species would have been recorded if sampling effort were doubled to 16 30-m segments per site. Assuming the logarithmic growth would have continued for 16 segments, the doubling of effort would have produced only 21-29% more species. In 1998 in the Ashland Watershed, the increase would have been 25% more species in forest burns; 21% in forest controls; 21% in fuel breaks; 29% in fuel break controls. In 1999 in Yosemite, the increase would have been 27% more species in forest burn sites; 27% in forest controls; 29% in riparian burns; and 26% in riparian controls.

Effects of Prescribed Burning of Upland Forest

In both study sites, significantly greater butterfly species richness occurred in upland prescribed burn areas (hereafter “forest burn sites”) than in forest controls. In the
Ashland Watershed, forest burn sites had 11.2 ± 1.36 (mean ± 1 SE) butterfly species over the course of the summer while forest controls had 4.0 ± 0.71 species (fig. 5). In the 5 forest burn sites, there was a combined total of 24 species; in the 5 forest controls, there were 13 species total. An ANOVA showed that forest burn sites and their controls differed significantly from each other (p = 0.0011). In Yosemite, forest burn sites had on average 13.8 ± 1.46 butterfly species while forest controls had only 6.86 ± 0.94 species (fig. 6). In the 5 forest burn sites, there were 34 species total, and in the 7 forest controls, there was a total of 20 species. In an ANOVA, forest burn sites and forest control sites were significantly different from each other (p = 0.0017).

The Shannon diversity index is sensitive to rarity, while the Simpson’s diversity index is a better measure of dominance (Magurran 1988). Thus, each index measures different aspects of butterfly community structure. In the Ashland Watershed, diversity measured by the Shannon index produced results similar to those for richness (fig. 7). Simpson’s diversity index, however, did not differ significantly between forest burn sites and forest controls (p = 0.4016; fig. 8), which appears to have been due to the superabundance of the pine white (Neophasia menapia), the only conifer feeder in the study area, in 1998. The Simpson’s diversity index did differ significantly for forest burn sites and forest controls when that species was excluded (p = 0.0280; fig. 8). In Yosemite, both the Shannon and Simpson’s diversity indices showed higher diversity in forest burn than forest control sites (p = 0.0011 for Shannon; p = 0.0031 for Simpson’s; fig. 9).

The species that were recorded in both forest burn and forest control sites were analyzed to determine whether forest burn sites more frequently harbored these species.
There was a significant difference in both the Ashland Watershed \((n = 11, p = 0.02)\) and in Yosemite \((n = 15, p = 0.009; \text{fig. 10})\). In addition, chi-square tests on the total abundances of each shared species in forest burn and control sites were performed. Because there were more control sites than burn sites \((7 \text{ vs. } 5)\) in Yosemite, the control site abundances were adjusted before testing. The abundances were significantly different each year, with greater abundances occurring in forest burn sites \(\text{(Table 7)}\).

**Mechanisms**

In a backward stepwise multiple regression, area of sunlight per m\(^2\) was found to be the most important mechanism explaining species richness \(\text{(F-value } = 31.34, \text{ adjusted } R^2 = 0.77\)\). The density of patches also explained some of the variability \(\text{(F-value } = 5.64, \text{ adjusted } R^2 = 0.86\)\). The indices of habitat suitability and connectivity of sunlight did not add significantly to the explanatory power of the model.

**Habitat Diversity**

Fuel breaks in the Ashland Watershed had a significantly greater average number of butterfly species than the fuel-break controls: \(16.4 \pm 1.89 \text{ species compared to } 1.25 \pm 0.95 \text{ species (fig. 5)}\). In the 5 fuel breaks, there were 34 species total, and in the 4 fuel break controls, there were 4 species total. In an ANOVA, fuel breaks and their controls differed significantly from each other \(p < 0.0001\). Also of interest is the fact that fuel breaks harbored greater species richness than forest burn sites \(p = 0.0493\). In the ANOVAs for Shannon and Simpson’s diversity, fuel break and fuel-break controls differed significantly \(p < 0.0001; \text{figs. 7, 8}\). In the roadside riparian areas, 31 species were recorded. In the Ashland Watershed in 1998, forest burn sites harbored 3 unique species, and the fuel breaks harbored 6 unique species \(\text{(fig. 11)}\). Roadside riparian areas
harbored 7 unique species in sections that were sampled at approximately one-fifth the intensity of other sites (fig. 11). On average, each forest burn site contributed 0.6 unique species, each forest control site 0 unique species, each fuel break 1.2 unique species, each fuel break control site 0 unique species, and each equivalent roadside riparian area 7 unique species to regional diversity. In an ANOVA for mean number of species contributed by each site of each treatment type to regional diversity, roadside riparian areas harbored significantly more unique species than any of the treatment types ($p < 0.0001$ in each case).

In Yosemite in 1999, a significantly greater average number of butterfly species occurred in riparian burns than in riparian controls: $25.3 \pm 2.25$ species compared to $10.0 \pm 1.70$ (fig. 6). In the 4 riparian burn sites, there were 37 species total, and in the 5 riparian controls, there were 26 species total. An ANOVA showed that riparian burn and riparian control sites differed significantly ($p < 0.0001$). In a comparison of the two types of burn treatments, it was found that riparian burn sites had a greater number of species than did forest burn sites ($p = 0.0011$). However, forest burn sites did not have a significantly greater number of species than did unburned riparian controls ($p = 0.0893$). Riparian burns had significantly more diversity, as measured by the Shannon and Simpson’s diversity indices, than did riparian controls ($p = 0.0019$ for Shannon; $p = 0.0025$ for Simpson’s; fig. 9). As with the average number of species (fig. 6), riparian burns harbored significantly more diversity than did forest burns ($p = 0.0406$ for Shannon; $p = 0.0297$ for Simpson’s; fig. 9). In Yosemite, forest burn sites had 6 unique species, riparian burn sites had 6 unique species, and riparian controls had 1 unique species (fig. 12). On average, each forest burn site contributed 1.6 unique species, each
forest control site 0 unique species, each riparian site 3 unique species, and each riparian control site 0.2 unique species to the regional fauna. In an ANOVA for mean number of species contributed by each site of each treatment type to regional diversity, riparian burn sites consistently contributed significantly greater average numbers of unique species than other treatments \((p = 0.0176 \text{ for forest burns}; \ p < 0.0001 \text{ for forest controls}; \ p = 0.0003 \text{ for riparian controls}).

**DISCUSSION**

**Species Richness and Diversity**

The hypotheses that butterfly richness and diversity will differ between burn sites and their controls were supported. Shapiro (1996) speculates that fire suppression has not benefited forest-associated butterflies. The results of this study suggest that the converse is also true: restoration of fire seems to increase habitat attractive to butterflies. Burn sites on average each had more butterfly species than unburned controls, and burn sites had higher regional diversity than unburned controls. Also, both measures of diversity were greater in burned forests, and sheer numbers of butterflies were higher in the burned forest sites. Both of these measures suggest that the richness results may be meaningful at the population level as well, at least for certain species. Concern has periodically been raised regarding the insect mortality that accompanies burning. This study, like that of Siemann et al. (1997), shows that burned areas eventually become colonized or recolonized by arthropods, in this case butterflies, so short-term mortality is evidently not a significant concern, at least with these relatively widespread species. This conclusion is obviously sensitive to the size of the burn. Maintenance of species diversity is at least a secondary goal of many management plans (e.g., Husari and McKelvey 1996), and it
appears that reintroducing fire partially attains this goal with respect to certain butterfly species in the process of fulfilling the goals of combustible fuel reduction and restoration of vegetative structure.

Shapiro (1996) indicates that no direct evidence existed (prior to this study) regarding the response of butterflies to the reintroduction of fire in the Sierran forest. However, the response of butterflies to fire in certain other regions has already been addressed. The best known use of fire to manage for a butterfly species is the case of the endangered Karner blue (*Lycaenides melissa samuelis*). The barrens habitats of the Great Lakes region and New York on which these butterflies occur have historically burned on average every 10 to 15 years, which maintains them as early successional habitats (Zaremba and Gebauer 1994, Shuey 1997). The Karner blue’s hostplant, blue lupine (*Lupinus perennis*), persists because of this frequent disturbance. Fire is currently the favored form of management for this butterfly and its hostplant; however, because the barrens communities are often in close proximity to human settlements, fire is sometimes resisted (Shuey 1997). Because forested land in the western United States is in general more extensive and remote than in the eastern barrens and because no butterflies in the study area are currently listed as threatened or endangered, these caveats probably rarely apply to fire management in western forests.

Swengel (1998) examined multiple management strategies on prairies and barrens in central North America and ranked strategies based on their level of “intrusiveness.” Grazing, cutting, and mowing, among others, were considered to be less intrusive than wildfire, which in the study areas had occurred between 4 and 18 years prior to the surveys. “Rotational burning,” or prescribed burning, was considered the most intrusive
because it occurred as frequently as once a year in the study sites. Swengel determined that most specialist butterflies attained higher abundances in areas with less intrusive management. Although at first glance these findings might appear to be a universal indictment against prescribed fire, fire return intervals in the western coniferous forests studied vary from 8 to 20 years (see Introduction), much more rarely than the yearly return of prescribed fire in Swengel’s study. In addition, Swengel found that occasional wildfires, which occurred at intervals similar to those for prescribed fires in western forests, were more favorable to specialists than was rotational burning. Consequently, although management alternatives would be worth examining if resources allow, fire nonetheless appears to be a viable management tool for butterflies in western forests.

Butterflies occurred on a higher proportion of forest burn sites than forest controls. Also, burned areas had significantly higher abundances of shared species than unburned controls did, which may be valuable from a population perspective. Butterflies, like most insects, are subject to large yearly fluctuations in population size due to environmental variations and other factors (Douglas 1986). Consequently, being widespread across the landscape may help butterflies avoid the population “crashes” that can accompany environmental stochasticity (Thomas and Hanski 1997). That is, presence of a butterfly species in large numbers and in multiple microhabitats across a heterogeneous landscape may reduce the risk that environmental stochasticity will cause the simultaneous extinction of each population or subpopulation of that species in all locations at once.

However, richness and abundance data do not address questions of larval residence, viable populations, or source-and-sink dynamics. For example, presence of an
adult butterfly does not indicate residence (see Mechanisms for Butterfly Richness and Diversity, below). Residence can only be ascertained by observation of larvae, which is exceedingly difficult and labor intensive. During this study, oviposition was observed only rarely, as would be expected for this type of monitoring (Pollard and Yates 1993). Also, whether prescribed burns must occur at certain minimum sizes or densities to assure viable populations cannot be ascertained from the data available. Relatedly, presence and even oviposition by butterflies may occur in what is ultimately “sink” habitat for certain species. The effect of the location of prescribed burns on dispersal or metapopulation and source-and-sink dynamics was also not determined by the present study. Furthermore, unlike the Ashland Watershed and Yosemite, much forested land of the western United States is intensively managed for logging, grazing, or other disturbances, which may increase open canopy, herbaceous habitat, and nearby butterfly source populations. However, certain specialist butterflies require early successional but high-integrity habitat (Scott 1986). These other intensive management practices may promote low-integrity early successional habitat and, consequently, only certain common or generalist species of butterflies.

**Mechanisms for Butterfly Richness and Diversity**

Several factors are known to be general requirements of butterflies, including sunlight and availability of hostplants and nectar sources (Scott 1986). In the Ashland Watershed in 1998, only the average area and density of sunlight patches on the forest floor were significant in the backward stepwise multiple regression, and those two measures of the gaps in the tree canopy predicted 86 percent of the variability in butterfly richness. These results are in line with research by Grundel et al. (1998a, b), which has
shown that Karner blue butterflies use canopy gaps significantly more frequently than expected relative to their availability. In addition, Grundel et al. (1998a) found that, even for that single species, burn heterogeneity was required to maintain sufficiently complex canopy structure to ensure mating, oviposition, foraging, and nectaring.

Because high sunlight requirements are common for most butterfly species and because many butterfly species require multiple habitats to complete their life cycles (Dennis 1992), recommendations of burn heterogeneity may be relevant in many other treed landscapes. During the study in the Ashland Watershed, it appeared that many butterflies were moving rapidly through the study sites and were not necessarily resident. Butterflies require host plants and usually nectar sources to complete their life cycle; however, the index of habitat suitability did not significantly explain the slope in the multiple regression. These results tend to confirm that the butterflies were not always resident in the treatment sites of the Ashland Watershed. That is, if butterflies were flying into suitable butterfly habitat more frequently than into unsuitable habitat, they would have been more likely to have been able to establish colonies. In the Yosemite treatment sites, however, butterflies appeared to be much more sedentary (pers. obs.) and are apparently mostly resident (Michael Singer, pers. comm.), so a quantitative herbaceous plant biomass and plant diversity survey in Yosemite would be useful but was beyond the scope of the current study.

Singer and colleagues have studied an interesting system in Yosemite wherein a butterfly species responds to a major disturbance (e.g., Singer 1983, Singer and Thomas 1996). The Edith’s checkerspot butterfly (*Euphydryas editha*) eats a perennial herb, *Pedicularis semibarbata* (Scrophulariaceae), in undisturbed habitats. However, in logged
and slash-burned forests, the butterfly switches to an annual herb, *Collinsia torreyi* (Scrophulariaceae), as a host. This is apparently only possible because of the increased biomass of individual *C. torreyi* plants following the disturbances. Other plants are known to have quantitatively or qualitatively different responses to fire. For example, soap plant, *Chlorogalum pomeridianum* (Liliaceae), a host of the brown elfin (*Callophrys augustus iroides*), flowers following fire (Skinner and Chang 1996), and the larvae of the brown elfin eat buds, flowers, and fruits (Arthur Shapiro, pers. comm.), which are those tissues stimulated by fire. In Yosemite, Hetch Hetchy or slender-stemmed monkeyflower, *Mimulus filicaulis* (Scrophulariaceae), was listed as a rare species until the Ackerson fire of 1996, after which an enormous population covering 5,000 acres appeared (Tait 1999). As discussed above, checkerspot butterflies (*Euphydryas* spp.) feed on perennial scrophs, but may switch to annual hosts in later instars (Singer et al. 1995), and adult females will oviposit on high-biomass *C. torreyi*. Consequently, this newly available patch of *M. filicaulis* provides potential hostplants in enough abundance to support a butterfly colony. The Ackerson fire site was not included in the study area, so whether it does in fact support a checkerspot butterfly colony has not been determined. Butterflies tend to be tightly associated with their hostplants, and many other plants of the forested western United States may potentially be adapted to fire in different ways (Chang 1996). Thus, further research into herbaceous plant responses to fire will undoubtedly provide valuable insight into mechanisms for butterfly colonization of burned forest.
Application of Multiple Management Strategies

Most managers would agree that promoting heterogeneity across the landscape is a desirable goal to increase the likelihood of maintaining all regional species. In fact, some studies have carefully quantified the amount and type of management required each year to maintain an entire landscape in a patchwork of significant portions of each seral stage (e.g., Richards et al. 1999). For butterflies in fire-adapted forests, maintenance of landscape heterogeneity seems to be crucial. Only 51 percent of the species observed in the Ashland Watershed were seen in the forest burn sites, and only 72 percent of the species recorded in the Yosemite study sites were seen in the forest burn sites. Thus, if maintenance of the complete array of regional butterfly species across the landscape is a goal, prescribed burning of upland forested areas alone does not currently appear to be sufficient. One could argue that this result is an artifact of the recent reintroduction of fire following decades of fire suppression. That is, a single burn after long-term fire suppression, which has been accompanied by other anthropogenic disturbances, including extensive logging and grazing, is unlikely to return the forest to its historical condition instantly (van Wagtendonk 1984, Agee 1993). Thus, long-term management with fire may eventually produce landscapes that are much more likely to conserve all butterfly diversity with just upland forest burning; however, it does not appear to be the case at present and whether it will ever become the case remains to be determined.

For the time being, it is important to assess whether additional landscape management more efficiently conserves butterflies (cf. Swengel 1998). If another type of coarse-filter approach conserves butterfly species more effectively, that may suggest either that the resulting landscape provided primary habitat in the past or that it is capable
of doing so in the future. In the Ashland Watershed, fuel breaks had significantly higher numbers of butterfly species on each site than did burn sites. Furthermore, fuel breaks provided habitat for 15 species that were not seen in any of the burn sites. The mechanisms causing ridgetop fuel breaks to be more inviting habitat for many butterfly species were not tested. They may provide larger patches of sunlight, more abundant or denser hostplants, better nectar sources, or more appropriate mating sites (many butterflies “hilltop” when seeking mates). Whatever the mechanism, fuel breaks seem to provide beneficial butterfly habitat. Because fuel breaks are used to slow the spread of catastrophic fire, they are likely to continue to be used as a management tool (Agee et al. 2000), even if biodiversity is not a goal.

However, in the Ashland Watershed in 1998, 31 species of butterfly were seen in roadside riparian areas, and 7 of these species were unique to this treatment type, despite the fact that roadside riparian areas were sampled at approximately one-fifth the intensity of each of the other treatment types. These preliminary data suggest that open canopies in riparian areas may foster high butterfly richness, a hypothesis which was supported by the results comparing burned and unburned riparian areas the following year in Yosemite. Butterflies were significantly richer and more diverse in burned than unburned riparian areas. Moreover, burned riparian areas had higher species richness and diversity than did burned forest areas, so burning riparian areas would seem to be a high priority management practice to maintain and enhance butterfly diversity.

This is an important result because burning riparian areas is currently given very low priority since it is unnecessary for reducing the risk of catastrophic fire (James Agee, pers. comm.). If the goal of management is solely to reduce combustible fuels, riparian
areas can generally be overlooked; however, if the goal is to maintain or enhance biotic diversity, burning riparian areas could be implemented as an adaptive management tool. Riparian burning has received only scant attention thus far. Skinner and Chang (1996), in a review of the relevant literature, were not able to find any dendrochronological studies of riparian fire regimes. Skinner (1997) then examined fire return intervals (FRIs) for riparian areas in the Klamath Mountains in mixed conifer forests. In general, FRIs in the riparian areas were at least twice as long as those for adjacent upland forest sites (16 and 33 years vs. 7 and 8 years median FRIs) although the ranges were essentially the same (5-65 years vs. 3-64 years). Studies of fire regimes in other forested riparian areas throughout the west would be extremely useful. In addition, it is necessary to determine biotic and abiotic effects of riparian burning. The presence of riparian areas disproportionately affects the landscape relative to the amount of land area they occupy (Rundel and Sturmer 1998, Skinner 1997). Thus, although they cover relatively little area, the potential negative side-effects of burning, such as erosion (USDA 1996) and exotic plant encroachment (Agee 1996), may occur more severely in burned riparian than in burned upland areas. These serious issues would require further research if riparian burning were implemented systematically. However, because the ultimate goal of fire management is to restore historical fire regimes, which should eventually serve the dual purposes of fuel reduction and restoration of historical species diversity (van Wagendonk, pers. comm.), the role of riparian fire in historical regimes merits further study.
CONCLUSION

Although fire treatments are being implemented throughout the west to reduce fuel loading and restore vegetative structure, their effects on the entire forest community are just beginning to be studied. Restoration ecology is heavily influenced by the philosophy of “If you build it, they will come,” which means that if the dominant members of the plant community are restored, the other members of the community will reassemble. Consequently, building or maintaining a functioning structure is often the sole focus of management. This research suggests that the philosophy generally holds true with regard to fire and butterflies in the forested west, but that burns must be conducted cautiously to ensure that a full range of habitat heterogeneity is created or maintained. This study indicates that the reintroduction of fire increases attractiveness of the burn site for local butterflies. In upland forest areas, mechanisms for increased butterfly diversity following fire may include density and area of canopy gaps. A greater proportion of the regional diversity appears to be achieved by including other treatments such as fuel breaks and especially prescribed riparian burning. In general, greatest butterfly richness, abundance, and diversity appear to occur in burned riparian areas. In short, varied fire management techniques appear to be useful tool for butterfly conservation in the forested west. However, managing for butterfly conservation may run counter to management for other necessary goals, such as erosion control in riparian areas, so prescribed burning under such circumstances would best be implemented as heavily monitored adaptive management.
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Fig. 1. Site locations in the Ashland Watershed. Heavy line marks perimeter of the Ashland Watershed. Forest burns: 1. 1991; 2. 1993; 3. 1995; 4. 1996; 5. 1997. Forest controls: 6. #1; 7. #2; 8. #3; 9. #4; 10. #5. Fuel breaks: 11. #1; 12. #2; 13. #3; 14. #4; 15. #5. Fuel break controls: 16. #1; 17. #2; 18. #3; 19. #4.
Fig. 2. Site locations in Yosemite. Fires of more than 100 acres are marked. Forest burns: 1. 1980; 2. 1986; 3. 1988; 4. 1989; 5. 1998. Forest controls: 6. #1; 7. #2; 8. #3; 9. #4; 10. #5; 11. #6; 12. #7. Riparian burns: 13. 1986; 14. 1986; 15. 1988; 16. 1997. Riparian controls: 17. #1; 18. #2; 19. #3; 20. #4; 21. #5. Map courtesy of Yosemite National Park.
Fig. 3. Saturation of fauna in each treatment type in the Ashland Watershed.  

a. Forest burn sites.  
b. Forest controls.  
c. Fuel breaks.  
d. Fuel break controls.
Fig. 4. Saturation of fauna in each treatment type in Yosemite. 

a. Forest burn sites.  
b. Forest controls.  
c. Riparian burn sites.  
d. Riparian controls.
Fig. 5. Species richness in the Ashland Watershed. Mean species richness +/- 1 SE. Different letters above bar for each treatment indicate a significant difference at $p < 0.05$ according to Fisher's PLSD test.
Fig. 6. Species richness in Yosemite. Mean species richness +/- 1 SE. Different letters above bar for each treatment indicate a significant difference at $p < 0.05$ according to Fisher's PLSD test.
Fig. 7. Shannon diversity index for butterflies in the Ashland Watershed. Mean diversity +/- 1 SE.
Fig. 8. Simpson's diversity index for butterflies in the Ashland Watershed. Mean diversity +/- 1 SE. Different letters above bar for each treatment indicate a significant difference at $p < 0.05$ according to Fisher's PSLD test.
Fig. 9. Shannon and Simpson's diversity indices for butterflies in Yosemite. Mean diversity +/- 1 SE. Different letters above bar for each treatment indicate a significant difference at $p < 0.05$ according to Fisher's PSLD test.
Fig. 10. Proportions of sampled sites used by species that were seen in both treatment types.
Fig. 12. Species unique to each treatment in Yosemite National Park. Total species in each treatment and number of unique species are shown.
| Year       | Altitude | Aspect | Source Populations | Plant Types               |
|------------|----------|--------|--------------------|----------------------------|
| 1991 burn  | 4500'    | southeast, east | 1                 | Douglas-fir                |
| 1993 burn  | 3000'    | east   | 1, 3               | hardwood/shrub, Douglas-fir|
| 1995 burn  | 3400'    | south, southeast | 1, 3, 4           | Douglas-fir, hardwood/shrub|
| 1996 burn  | 4700'    | southeast | 2, 3, 4           | Douglas-fir, sub-alpine conifer, Jeffrey/ponderosa pine|
| 1997 burn  | 4000'    | southeast | 1                 | Douglas-fir, sub-alpine conifer|
| control 1  | 4600'    | east | 1, 4               | Douglas-fir, sub-alpine conifer|
| control 2  | 3000'    | east   | 1, 3               | Douglas-fir, knobcone pine, hardwood/shrub|
| control 3  | 3200'    | south, southeast | 4                 | Douglas-fir                |
| control 4  | 4600'    | southeast | 1, 2, 4           | Douglas-fir, sub-alpine conifer|
| control 5  | 4100'    | southeast, east | 1                 | Douglas-fir, sub-alpine conifer|

Table 1. Forest burn and control study sites in the Ashland Watershed, including approximate altitude and aspect, types of potential nearby butterfly source populations, and dominant plant types. The source population category numbers indicate whether the site is adjacent to a: 1. substantial length of sunny road, 2. shaded road, 3. wildfire/stand-replacing fire site, or 4. fuel break. (Dominant plant type information from “Draft-Species-Draft, Late Successional Reserve 248” GIS map, courtesy of USFS Rogue River National Forest.)
| approx. alt. | approx. aspect | potential source pop.'s | granite boulders | dominant plant types                  |
|-------------|---------------|-------------------------|------------------|--------------------------------------|
| 1980 forest burn | 6600' southeast | 1, 3                    | no               | Jeffrey pine                         |
| 1986 forest burn | 6400' south   | 2, 3                    | yes              | Jeffrey pine, white fir              |
| 1988 forest burn | 7000' hilltop | 2, 4                    | yes              | Jeffrey and lodgepole pine           |
| 1989 forest burn | 6800' southeast | 2, 4                   | yes              | lodgepole and Jeffrey pine, red fir  |
| 1998 forest burn | 6100' hilltop | 1                      | no               | lodgepole pine                       |
| forest control 1 | 6200' southeast | 1, 2, 3                 | no               | Jeffrey pine, incense-cedar          |
| forest control 2 | 5800' southeast | 2                      | no               | Jeffrey and lodgepole pine, incense-cedar, red fir |
| forest control 3 | 8000' hilltop | 2, 4                    | no               | lodgepole pine                       |
| forest control 4 | 6100' south   | 1, 2, 4                 | yes              | lodgepole pine                       |
| forest control 5 | 7000' hilltop | 2, 4                    | yes              | Jeffrey and lodgepole pine, white fir |
| forest control 6 | 7200' southeast | 2, 4                   | yes              | lodgepole pine                       |
| forest control 7 | 6200' southeast | 2, 4                   | no               | lodgepole pine                       |

Table 2. Forest burn and control study sites in Yosemite, including approximate altitude and aspect, types of potential nearby butterfly source populations, and dominant plant types. The source population category numbers indicate whether the site is adjacent to a: 1. substantial length of sunny road, 2. shaded road, 3. fire site, or 4. meadow.
| Fuel Break    | Approx. Alt. | Potential Source Pop.'s | Dominant Plant Types                                      | Understory Morphology |
|--------------|--------------|-------------------------|-----------------------------------------------------------|-----------------------|
| Break 1      | 3500'        | 1, 4                    | hardwood/shrub, Jeffrey/ponderosa pine                    | herbaceous            |
| Break 2      | 4200'        | 1, 4                    | Douglas-fir, hardwood/shrub                               | grassy                |
| Break 3      | 4700'        | 2, 4                    | hardwood/shrub, Jeffrey/ponderosa pine                    | shrubby               |
| Break 4      | 4400'        | 1, 2, 4                 | hardwood/shrub                                            | grassy                |
| Break 5      | 4400'        | 1, 4                    | hardwood shrub, Jeffrey/ponderosa pine                    | shrubby               |
| Control 1    | 3400'        | 1, 4                    | Douglas-fir                                              | --                   |
| Control 2    | 4300'        | 1                       | hardwood/shrub                                            | --                   |
| Control 3    | 4400'        | 2, 4                    | hardwood/shrub                                            | --                   |
| Control 4    | 4500'        | 2, 4                    | Douglas-fir, sub-alpine conifer                           | --                   |

Table 3. Fuel break and control study sites in the Ashland Watershed, including approximate altitude, types of potential nearby butterfly source populations, plant community type, and (for fuel breaks) dominant understory morphology. The source population category numbers indicate whether the site is adjacent to a: 1. substantial length of sunny road, 2. shaded road, 3. wildfire/stand-replacing fire site, or 4. fuel break. Fuel break controls had very little understory plant cover. (Community type information from “Draft-Species-Draft, Late Successional Reserve 248” GIS map, courtesy of USFS Rogue River National Forest.)
| approx. alt. | approx. aspect | potential source pop.'s | granite boulders | dominant plant types       |
|------------|---------------|-------------------------|------------------|---------------------------|
| 1986 riparian burn | 6400' southwest | 1, 4                    | yes              | Jeffrey pine              |
| 1986 riparian burn | 6300' south | 2                       | partially        | Jeffrey and lodgepole pine |
| 1988 riparian burn | 6400' south | --                      | partially        | lodgepole pine, white fir |
| 1997 riparian burn | 6200' south | 1                       | no               | Jeffrey pine              |
| riparian control 1 | 6200' southeast, south | 1, 2, 3, 4 | no               | Jeffrey pine              |
| riparian control 2 | 4600' east | 1, 2                    | no               | incense cedar, lodgepole pine |
| riparian control 3 | 8000' west | --                      | yes              | red fir                   |
| riparian control 4 | 6200' south | 2                       | no               | Jeffrey and lodgepole pine, incense-cedar |
| riparian control 5 | 7200' south, southwest | 1, 2 | yes              | Jeffrey and lodgepole pine |

Table 4. Riparian burn and control study sites in Yosemite, including approximate altitude and aspect, types of potential nearby butterfly source populations, whether site was heavily strewn with granite boulders, and dominant plant types. The source population category numbers indicate whether the site is adjacent to a: 1. substantial length of sunny road, 2. shaded road, 3. fire site, or 4. meadow.
| SPECIES                        | PRESENCE/ABSENCE | Forest burns | Forest controls | Fuel breaks | Fuel break controls | Roadside riparian |
|-------------------------------|-----------------|--------------|-----------------|-------------|---------------------|-------------------|
| **Family Papilionidae**       |                 |              |                 |             |                     |                   |
| *Papilio rutulus*             | +               | +            | +               | +           | +                   | +                 |
| *P. eurymedon*                | +               | +            | +               | 0           | +                   | +                 |
| *Parnassius clodium*          | 0               | 0            | 0               | 0           | +                   | +                 |
| **Family Pieridae**           |                 |              |                 |             |                     |                   |
| *Colias eurytheme*            | +               | 0            | +               | 0           | +                   | +                 |
| *C. philodice*                | +               | 0            | 0               | 0           | 0                   | 0                 |
| *Pontia occidentalis*         | 0               | 0            | +               | 0           | 0                   | 0                 |
| *Pieris rapae*                | +               | 0            | +               | 0           | 0                   | 0                 |
| *Neophasia menapia*           | +               | +            | +               | +           | +                   | +                 |
| **Family Nymphalidae**        |                 |              |                 |             |                     |                   |
| *Danaus plexippus*            | +               | 0            | +               | 0           | 0                   | 0                 |
| *Coenonympha tullia*          | +               | +            | +               | 0           | +                   | +                 |
| *Cercyonis pegala*            | +               | +            | +               | 0           | 0                   | 0                 |
| *C. sthenile silvestris*      | 0               | 0            | +               | 0           | +                   | +                 |
| *Oeneis nevadensis*           | +               | +            | +               | +           | +                   | +                 |
| *Limenitis lorquini*          | +               | +            | +               | 0           | +                   | +                 |
| *Adelpha bredowii*            | 0               | +            | +               | 0           | +                   | +                 |
| *Vanessa cardui*              | +               | +            | +               | 0           | +                   | +                 |
| *V. atalanta*                 | 0               | 0            | 0               | 0           | 0                   | +                 |
| *V. virginiensis*             | 0               | 0            | 0               | 0           | 0                   | +                 |
| *Polygonia satyrus*           | +               | 0            | 0               | 0           | 0                   | 0                 |
| *P. progne oreas*             | 0               | 0            | 0               | 0           | 0                   | +                 |
| *P. gracilis zephyrus*        | 0               | 0            | 0               | 0           | 0                   | +                 |
| *Nymphalis antiopa*           | 0               | 0            | +               | 0           | 0                   | 0                 |
| *N. californica*              | 0               | 0            | +               | 0           | 0                   | 0                 |
| *Chlosyne leanira*            | +               | +            | +               | 0           | 0                   | 0                 |
| *C. palla*                    | 0               | +            | 0               | 0           | 0                   | +                 |
| *Phyciodes campestris*        | 0               | 0            | +               | 0           | 0                   | +                 |
| *P. mylitta*                  | +               | 0            | +               | 0           | 0                   | +                 |
| *Boloria epithore*            | 0               | 0            | +               | 0           | 0                   | +                 |
Table 5. Presence(+) / absence(0) of 47 butterfly species (by family) found in four different treatment types in Ashland Watershed. (Scientific names from Scott 1986.)

*Difficult to distinguish without genitalic dissection.
| SPECIES                        | PRESENCE/ABSENCE | Forest burns | Forest controls | Riparian burns | Riparian controls |
|-------------------------------|-----------------|--------------|-----------------|----------------|------------------|
| **Family Papilionidae**       |                 |              |                 |                |                  |
| *Papilio eurymedon*           | +               | +            | +               | +              |                  |
| *Papilio rutulus*             | 0               | 0            | +               | +              |                  |
| *Parnassius clodius*          | +               | +            | +               | +              |                  |
| **Total**                     | 2               | 2            | 3               | 3              |                  |
| unique to treatment           | 0               | 0            | 0               | 0              |                  |
| **Family Pieridae**           |                 |              |                 |                |                  |
| *Anthocharis lanceolata*      | +               | 0            | 0               | 0              |                  |
| *Anthocharis stella*          | +               | 0            | 0               | +              |                  |
| *Colias eurytheme*            | +               | +            | +               | +              |                  |
| *Euchloe hyantis*             | +               | 0            | +               | 0              |                  |
| *Neophasia menapia*           | +               | +            | +               | +              |                  |
| *Pieris rapae*                | 0               | +            | +               | +              |                  |
| **Total**                     | 5               | 3            | 4               | 3              |                  |
| unique to treatment           | 1               | 0            | 0               | 0              |                  |
| **Family Nymphalidae**        |                 |              |                 |                |                  |
| *Adelpha bredowii*            | +               | +            | +               | +              |                  |
| *Boloria erithoe*             | +               | +            | +               | +              |                  |
| *Chlosyne palla*              | 0               | 0            | +               | 0              |                  |
| *Limenitis loryi*             | +               | +            | +               | +              |                  |
| *Nymphalis antiopa*           | 0               | 0            | +               | +              |                  |
| *Nymphalis californica*       | +               | +            | +               | +              |                  |
| *Phyciodes campestris*        | +               | +            | +               | 0              |                  |
| *Phyciodes mylitta*           | +               | +            | +               | +              |                  |
| *Polygonia zephyrus*          | +               | 0            | +               | +              |                  |
| *Speyeria atlantis*           | +               | 0            | +               | 0              |                  |
| *Speyeria hydaspe*            | +               | +            | +               | +              |                  |
| *Speyeria mormonia*           | +               | +            | +               | +              |                  |
| *Speyeria zerei*              | +               | 0            | +               | +              |                  |
| *Vanessa cardui*              | 0               | +            | +               | +              |                  |
| *Vanessa virginiensis*        | +               | 0            | 0               | 0              |                  |
| **Total**                     | 12              | 9            | 14              | 11             |                  |
| unique to treatment           | 1               | 0            | 1               | 0              |                  |
| **Family Lycaenidae**         |                 |              |                 |                |                  |
| *Callophrys augustus iroides* | +               | 0            | +               | 0              |                  |
| *Callophrys nelsoni*          | +               | 0            | +               | 0              |                  |
| *Satyrium sylvinus*           | 0               | 0            | +               | 0              |                  |
| *Celastrina echo*             | +               | +            | +               | +              |                  |
| Species                          | + | 0 | + | 0 |
|---------------------------------|---|---|---|---|
| *Euphilotes enoptes*            |   |   |   |   |
| *Everes amyntula*               | + | 0 | + | + |
| *Habrodais grunus*              | + | 0 | 0 | 0 |
| *Lycaena cupreus*               | 0 | 0 | + | 0 |
| *Lycaena editha*                | + | 0 | + | + |
| *Lycaena heteronea*             | + | + | + | + |
| *Lycaena nivalis*               | 0 | 0 | + | 0 |
| *Plebejus acmon*                | 0 | 0 | + | 0 |
| *Plebejus icarioides*           | + | + | + | 0 |
| *Plebejus idas*                 | + | 0 | + | + |
| *Plebejus saepiolus*            | + | + | + | + |
| *Plebejus shasta*               | 0 | 0 | + | + |
| **total**                       | 10| 4 | 15| 7 |
| **unique to treatment**         | 1 | 0 | 5 | 0 |

**Family Hesperiidae**

| Species                          | + | 0 | + | 0 |
|---------------------------------|---|---|---|---|
| *Epargyreus clarus*             |   |   |   |   |
| *Erynnis pacuvius*              | 0 | 0 | 0 | + |
| *Erynnis propertius*            | + | 0 | 0 | 0 |
| *Hesperia juba*                 | 0 | + | 0 | + |
| *Ochlodes sylvanoides*          | + | + | + | 0 |
| *Polites sonora*                | + | 0 | 0 | 0 |
| *Pyrgus ruralis*                | + | 0 | 0 | 0 |
| **total**                       | 5 | 2 | 2 | 2 |
| **unique to treatment**         | 3 | 0 | 0 | 1 |

**TOTAL** 34 20 38 26
**UNIQUE TO** 6 0 6 1

Table 6. Presence(+/absence(0)) of 47 butterfly species (by family) found in four different treatment types in Yosemite. (Scientific names from Scott 1986.)
### Table 7. Chi-square test on the abundances of each species occurring in both burned forest and forest control.

| Species                      | Burn | Control | Control * S / 7 |
|------------------------------|------|---------|-----------------|
| Adelpha bredowii             | 3    | 7       | 5               |
| Boloria epithore             | 42   | 50      | 35.7            |
| Celastrina echo              | 31   | 9       | 6.42            |
| Colias eurytheme             | 7    | 4       | 2.86            |
| Limenitis lorquini           | 1    | 4       | 2.86            |
| Lycaena heteronea            | 4    | 1       | 0.714           |
| Neophasia menapia            | 1    | 10      | 7.14            |
| Nymphalis californica        | 1    | 1       | 0.714           |
| Ochlodes sylvanoides         | 8    | 3       | 2.14            |
| Papilio eurymedon            | 9    | 5       | 3.57            |
| Parnassius clodius           | 19   | 5       | 3.57            |
| Phyciodes campestris         | 4    | 1       | 0.714           |
| Phyciodes mylitta            | 10   | 3       | 2.14            |
| Plebejus icarioides          | 2    | 2       | 1.43            |
| Plebejus saepiolus           | 8    | 5       | 3.57            |

\[ \chi^2 = 77.97 \]
\[ p << 0.001 \]

\[ \chi^2 = 26.09 \]
\[ 0.025 < p < 0.05 \]
