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RESEARCH ARTICLE

Environmental Associations with Post-Fire Butterfly Occupancy in the Sierra Nevada, California

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ABSTRACT: Fire affects environmental attributes associated with the distribution, abundance, and reproduction of butterflies, and studies have demonstrated that species richness and abundance of butterflies respond to fire. However, the effects of fire on resources used by adult butterflies, and on butterfly occupancy, are largely unknown. In 2014 and 2015, we surveyed butterflies and elements of their habitat within the boundary of the Rim Fire (Stanislaus National Forest, Tuolumne County, California), one of the largest fires known to occur in California during the past century. We examined the extent to which butterfly occupancy and abundance in the first two years following the Rim Fire were associated with environmental attributes that were affected by fire. We also tested whether vegetation and soil burn severity, two indices used by resource management agencies, explained variation in the environmental attributes that we included in models of butterfly occupancy and abundance. We found that the percentage of live ground cover and canopy cover were strongly associated with occupancy of the majority of the species we modeled. In some cases, environmental attributes associated with occupancy also were associated with the abundances of those species. Values of environmental attributes that explained substantial variation in butterfly occupancy and abundance were associated with vegetation and soil burn severity. Understanding how fire affects environmental attributes that are associated with butterfly occupancy and abundance may inform strategies for managing these species with prescribed fire or following wildfire, or when fire treatments are applied for other reasons.

Index terms: abundance, canopy, nectar, Rim Fire, vegetation

INTRODUCTION

Adults of many species of butterflies feed exclusively on nectar, and availability of nectar affects the distribution, population sizes, or fecundity of certain species (Murphy et al. 1983; Boggs and Ross 1993; Schultz and Dlugosch 1999). Regardless of the ignition source, fire affects nectar availability and quantity. Prescribed fire is among the treatments applied by resource managers who aim to decrease fuel loads and wildfire probability, and also has been used to increase the abundance of nectar sources used by butterflies. For example, the abundance of nectar sources for *Lycaeides melissa samuelis* (Nabokov), a subspecies listed as endangered under the US Endangered Species Act, increased after a prescribed fire in Wisconsin, USA (King 2003). In forests of eastern Texas, USA, the abundances of nectar sources used by butterflies were greatest in areas maintained by prescribed fire (Rudolph and Ely 2000). Abundance and species richness of butterflies also respond to fire. For example, following fires in riparian areas within coniferous forests in Oregon and California, USA, the number of butterflies in burned areas was two to three times greater than the number in comparable areas that were not burned (Huntzinger 2003). Although the responses of butterflies to fire have been studied, these studies did not address variables such as vegetation burn severity and soil burn severity. It is possible that vegetation burn severity and soil burn severity could have different effects on different species of butterflies, or resources used by butterflies, and understanding these relations could support butterfly conservation and habitat management. Additionally, the effects of fire on other resources that may be associated with the abundance of adult butterflies, and on butterfly occupancy (the probability that a given site is occupied by a given species after accounting for imperfect detection; MacKenzie et al. 2002), are largely unknown.

Understanding the effects of fire on environmental attributes that are associated with butterfly occupancy and abundance can inform management of fire that is used to maintain or increase habitat quality for this taxonomic group. Such understanding also can be used to project potential unanticipated consequences of fire management that is intended to meet other objectives, from maintenance of military training areas to reduction of fuels at the wildland–urban interface.

Occupancy is relevant to both population monitoring and assessment of habitat associations. Although estimates of abundance and reproduction are more-informative measures of population status than estimates of occupancy, collection of the data necessary to estimate abundance or

reproductive success generally requires more time and money than collection of occurrence data (MacKenzie et al. 2004). Effective modeling of occupancy depends on whether five assumptions are met or, if violated, overcome: first, occupancy remains constant, or changes in occupancy are modeled effectively; second, probability of detection (observing the species given its presence) remains constant, or changes in probability of detection are modeled effectively; third, detections of individuals at each site are independent; fourth, species are not falsely detected; and fifth, occupancy status does not change among surveys (the closure assumption; MacKenzie et al. 2002). Butterfly occupancy has been estimated with models that relax the assumption of closure by allowing for a single entry and exit of the species from each sampling location (Kendall et al. 2013; Roth et al. 2014; Fleishman et al. in review). Environmental covariates can be added to these models to explore whether they are associated with detection probability and occupancy.

We examined the extent to which butterfly occupancy and abundance in the first two years following the Rim Fire, one of the largest fires in California since accurate fire records for that region have been maintained (1932–present), were associated with environmental attributes that were known or hypothesized to be affected strongly by the fire. We expected occupancy and abundance to increase as canopy cover decreased, and as nectar availability and the percentage of live ground cover increased. We also tested whether variation in the environmental attributes that we included in models of butterfly occupancy and abundance was explained by local differences in fire severity. We studied butterfly occupancy and abundance after fire, not changes in occupancy and abundance before and after fire or on differences in areas that were burned or unburned.

There is a solid theoretical basis for using occupancy as a surrogate measure of a species' abundance (He and Gaston 2003; Nichols et al. 2007; Green et al. 2011). Abundance, in turn, is strongly related to probability of persistence (Gaston et al. 2000; Zuckerberg et al. 2009). However, empirical tests of relations between occupancy and other state variables, and whether environmental variables have similar relations to multiple state variables, are relatively uncommon. To our knowledge, this is the first study to compare the relations between environmental attributes and both butterfly occupancy and abundance.

METHODS

Field Methods

The Rim Fire burned on the west slope of the Sierra Nevada from August through October 2013 and encompassed more than 1040 km^2 (257,000 acres) of public and private land (USFS 2014). We collected data within the Rim Fire boundary on the Groveland Ranger District of the Stanislaus National Forest (Tuolumne County, California). The vegetation in the areas in which we worked is classified as Sierran yellow pine forest and Sierran montane forest (Miksicek et al. 1996). These forests are dominated by ponderosa pine (*Pinus ponderosa* Lawson & Lawson), white fir (*Abies concolor* Gordon & Glend), Douglas fir (*Pseudotsuga menziesii* Franco), sugar pine (*P. lambertiana* Douglas), incense cedar (*Calocedrus decurrens* Florin), and black oak (*Quercus kelloggii* Newberry). Understory species include manzanita (*Arctostaphylos* spp.), buckbrush (*Ceanothus* spp.), mountain misery (*Chamaebatia foliolosa* Bentham), chinquapin (*Castanopsis sempervirens* Dudley), and various berries (Miksicek et al. 1996).

Random selection of sampling locations was not possible due to complex topography, the lack of roads, and limited time available for travel. In 2014, we established eight 300–500-m transects in burned areas in which pre-fire vegetation composition and structure were relatively homogeneous. We established an additional four transects (300–500 m in length) in 2015. The fire was sufficiently patchy to draw reasonable inference to pre-fire vegetation. Some unburned vegetation remained in burned areas, and some vegetation regenerated by spring 2014. Transect length varied because in some cases we could not locate 500 m with apparently homogeneous pre-fire vegetation composition and structure. We placed transects along vegetated or non-vegetated dirt roads or trails. The elevation of each transect fell between approximately 1350 and 1450 m, and transects were placed along relatively flat terrain. In all but one case, the endpoints of different transects were separated by ≥100 m. In that one case, the endpoints were separated by 60 m, and the transects were orthogonal. On the basis of the behavior of the butterflies we observed, we believe that detections of individuals along the two transects were independent. The maximum linear distance between transects was approximately 24 km. We sampled each transect that was established in 2014 five times during June and July 2014 and we sampled all transects five times from May through July 2015, which encompassed the majority of the butterfly flight seasons in those years.

We divided each transect into linear, 20-m segments, which were the sample units for analysis. During each survey, a single observer walked along the center of the segment at a constant pace and identified each butterfly using the area within 10 m on either side of the center line (e.g., taking nectar, mating, perching). Where necessary, we captured individual butterflies for identification. We noted whether each butterfly was taking nectar (proboscis observed probing flowers or florets) and, if so, the species on which it was feeding. In some cases, we observed the same individual taking nectar from more than one plant species. In these cases, we recorded one observation of feeding on each nectar source. We estimated abundance as the total number of individuals of each species that we observed during the season. It is possible that a small number of individuals were recorded on more than one survey day, but we considered this situation unlikely given the time between surveys and the fact that in temperate ecosystems, the average lifespan of an adult butterfly is about one week (Scott 1986).

We collected data on vegetation along each transect within one day of each butterfly survey except in one case, when we measured vegetation nine days after butterfly

surveys on a subset of the transects due to inclement weather. During each survey, we used a random-number generator to select 1 m^2 in each 20-m segment for fine-resolution vegetation sampling. Within that 1 m^2, we used a concave spherical densiometer to measure the percentage of canopy cover, visually estimated the percentage of live ground cover, identified all known or potential nectar sources, and counted the number of florets of each nectar source. As canopy cover decreases, solar insolation in the understory increases. Solar insolation may affect butterflies either physiologically (Clench 1966; Weiss et al. 1988, 1991) or indirectly, via responses of host plants, nectar sources, and other plants that provide shelter or perches in the understory. We measured ground cover because as the cover of understory vegetation increases, the distribution and abundance of host plants also may increase. Additionally, ground cover affects microclimatic factors, such as temperature, that may affect butterflies (Calvert et al. 1986). We did not attempt to measure host plants directly given uncertainty in local use of particular species and in dispersal distances (therefore in the area over which presence or density of host plants might be associated with our observations of adult butterflies).

For each plant species on which we observed adult butterflies feeding, we collected from multiple plants a total of five florets that showed no signs of senescence. We covered each floret overnight with a fine-mesh cloth bag, secured with a rubber band, to prevent feeding by insects and to allow nectar to regenerate following any previous feeding (Bentley and Ellas 1983; Morrant et al. 2009). We collected the florets during the following afternoon. We placed each floret in a 30-ml plastic vial with 2 ml of distilled water and shook the vial for 60 s to wash the nectar from the floret (Grünfeld et al. 1989; Morrant et al. 2009). We maintained the samples on ice (typically for less than a week) and then transferred the samples to a −80 °C freezer.

We used high performance liquid chromatography–mass spectrometry to quantify the masses (mg) of glucose, fructose, and sucrose for all plant species from which we collected florets. In most cases, we analyzed each of the five samples (florets) from each nectar source. In two cases, we analyzed four rather than five samples due to improper handling or storage of one sample. We multiplied the mean mass of sugar (sum of glucose, fructose, and sucrose) for each nectar source by the number of florets in each 20-m segment to estimate the mass of sugar available to butterflies in that segment. Full methods for extraction and estimation of sugar mass are available from the corresponding author.

We initially derived five environmental covariates for each segment. We calculated the number of florets across each season (June–July 2014 and May–July 2015) as the sum of the survey-specific number of florets. For each season, we calculated the average percentage of canopy cover, percentage of live ground cover, sugar mass, and categorical abundance of florets that serve as nectar sources. Because the number of florets summed across each season was highly correlated with sugar mass ($r = 0.99$ and 0.91 in 2014 and 2015, respectively), we did not retain sugar mass as a covariate for analysis.

We previously found that detection probabilities and occupancy of a considerable proportion of butterflies in three ecosystems increased as the categorical abundance of nectar sources increased (Fleishman et al. in review). Those categorical estimates were intended to classify abundance relatively quickly along an approximately logarithmic or semi-logarithmic scale. The estimates were comparable among observers in a given geographic area (Fleishman and Pavlik, unpub. data), but the relation between categorical and absolute estimates of abundance might vary among years and likely would vary among regions. Here, we measured abundance of nectar sources quantitatively, as a continuous variable. Nevertheless, to explore whether inferences about the strength of associations between occupancy and nectar abundance depended on the precision with which the latter was assessed, we created post-hoc categories of abundance of nectar sources (none, low, moderate, and high) on the basis of our previous field experience. In 2014, we classified segment-level abundances of 1–49, 50–399, and >399 florets as low, moderate, and high, respectively. In 2015, the abundance of florets was greater than in 2014, and we classified segment-level abundances of 1–99, 100–499, and >499 florets as low, moderate, and high, respectively. We acknowledge that it would have been preferable to conduct a categorical assessment in the field, but felt that the comparison still provided useful information.

Analytical Methods

We used single-season occupancy models with relaxed closure assumptions in Program MARK (White and Burnham 1999) to estimate detection probabilities and occupancy (Kendall et al. 2013). We standardized all continuous covariates. We limited analyses to species with naïve occupancy (i.e., the proportion of sites in which the species was observed, not accounting for detection probability) ≥0.28 and ≤0.70 in each year (Fleishman et al. 2017). Models for species that are relatively rare or common generally have limited ability to discriminate covariates associated with occurrence or occupancy.

We implemented model selection in two stages: modeling probability of detection and modeling occupancy. In both stages, we used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to compare models (Burnham and Anderson 2002). In the first stage, we evaluated associations between covariates and probabilities of detection (p_{ij}), entry (β_{ij}), and departure (d_{ij}), where i is location and j is visit. We estimated p_{ij} as a time-varying effect of visit (i.e., we estimated p_{ij} for each of the five surveys). We also tested whether the survey-specific number of florets was associated with p_{ij} estimates. We used survey five as the intercept in our models. We estimated β_{ij} and d_{ij} as linear functions of time. If univariate models were ranked lower than the null models, we did not retain the covariates in the univariate models for further modeling. We fit multivariate models that contained every possible combination of covariates from the univariate models that were ranked higher than the null model. We included the highest-ranked model (or, if the AIC_c value of a competing model was

within two units of our highest-ranked model, the most parsimonious model) in the second stage of modeling. Complete model-selection results are available from the corresponding author. In the second stage, we modeled occupancy as a function of the four covariates described above.

Initially, we fit univariate models of occupancy. Because we fit models with two different measures of nectar abundance (number of florets and categorical abundance), we included only the covariate from the highest-ranked univariate model (or, if the AIC_c value of a competing model was within two units of our highest-ranked model, from the most parsimonious model) in our multivariate models. If the null model had a higher rank than the univariate models, we did not retain the covariates from the univariate models. If multiple univariate models had higher ranks than the null model, we fit models with every combination of those covariates. Complete model-selection results are available from the corresponding author.

If the 95% confidence interval of the regression coefficient for a given covariate in the most highly ranked model did not overlap zero, we considered the covariate to be associated strongly with the response variable. We report detection probabilities and occupancy from the highest-ranked model for each species. If the AIC_c value of a competing model was within two units of our highest-ranked model, we report values of detection probabilities and occupancy from the most parsimonious model.

Because the counts of the butterfly species were overdispersed, we used univariate, negative binomial generalized linear models to examine relations between the abundances of the species for which we modeled occupancy and canopy cover, live ground cover, number of florets, and categorical abundance of nectar sources.

We used single-factor, one-way analysis of variance (ANOVA) to examine relations between soil burn severity and vegetation burn severity with canopy cover, live ground cover, and number of florets in 2014 and 2015. Between the 2014 and 2015 field seasons, two of the transects that we surveyed in 2014 were logged. We excluded these transects from our analysis of canopy cover in 2015 because the 2015 canopy cover estimates would reflect logging rather than burn severity. We used Tukey's post-hoc tests to quantify pairwise differences between fire severity classes. During the first survey in 2014, we qualitatively classified the proportion of each segment that burned (none, some, or all). We used ArcGIS v. 10.3 (ESRI, Redlands, California) to compare these classifications with remotely sensed measures of vegetation burn severity from the US Forest Service's Rapid Assessment of Vegetation Condition after Wildfire (RAVG) process (USFS 2016). The RAVG classification and our classification generally matched. The RAVG process derives vegetation burn severity by applying a Relative Differenced Normalized Burn Ratio to pre-fire and post-fire images from the Landsat Thematic Mapper. Vegetation burn severity was classified by RAVG as unchanged, low, moderate, or high. We obtained estimates of soil burn severity from the US Forest Service's Burned Area Emergency Response (BAER) team (USFS 2013), which derives soil burn severity by measuring the difference in spectral reflectivity in pre-fire and post-fire satellite images. Soil burn severity was classified by BAER as unburned or very low, low, moderate, or high. If any of our segments overlapped multiple severity classes, we assigned the segment to the severity class that covered the majority of that segment. If multiple severity classes appeared to be equally represented in a segment, we assigned the segment to the lower severity class.

RESULTS

In 2014, we recorded 29 species of butterflies (1–198 individuals per species; Table 1). One species, *Icaricia lupini* (Boisduval), met our criteria for modeling occupancy. In 2015, we observed 44 species of butterflies (1–974 individuals per season; Table 1). Five species—*Colias eurytheme* (Boisduval), *Icaricia lupini*, *Junonia coenia* (Hübner), *Phyciodes mylitta* (Edwards), and *Erynnis persius* (Scudder)—met our criteria for modeling occupancy. Naïve estimates of occupancy were 0.63 for *C. eurytheme*; 0.38 and 0.66 for *I. lupini* in 2014 and 2015, respectively; 0.52 for *J. coenia*; 0.44 for *P. mylitta*; and 0.28 for *E. persius*. The number of florets of nectar sources per segment was 83.8 ± 322.6 (mean ± SD) in 2014 and 143.0 ± 341.6 in 2015.

Maximum detection probabilities on a given survey ranged from 0.35 for *J. coenia* to 0.81 for *I. lupini* (2015) and *E. persius* (Table 2). The model with a time-varying effect of visit was associated with the probability of detection of *J. coenia*, *P. mylitta*, and *E. persius* (effect sizes varied among surveys). Survey-specific number of florets was associated with the probability of detection of *I. lupini* (0.95) in 2015. None of the covariates we measured was associated with the probability of detecting *I. lupini* in 2014 or *C. eurytheme* in 2015.

Estimates of occupancy ranged from 0.22 (*E. persius*) to 0.85 (*C. eurytheme*) (Table 2). Occupancy of each species was associated with at least one covariate (Table 2). Canopy cover was negatively associated with occupancy of *C. eurytheme*, *I. lupini* (2015), *P. mylitta*, and *E. persius*. Live ground cover was positively associated with occupancy of *C. eurytheme*, *I. lupini*, *J. coenia*, and *P. mylitta*. Number of florets was positively associated with occupancy of *I. lupini* (2014) and *E. persius*. Categorical abundance of nectar was not associated with occupancy of any species. The highest-ranked or most parsimonious models for all species except *J. coenia* included multiple covariates (Table 2).

For all species, univariate occupancy models that included number of florets were supported more strongly than models that included categorical abundance of nectar. However, the difference between AIC_c values for the two models for *I. lupini* in 2014 was <1.

The percentage of canopy cover was significantly and negatively associated with the abundances of *C. eurytheme*, *I. lupini* (2015), *P. mylitta*, and *E. persius* (Table 3). The percentage of live ground cover was significantly associated with the abundances of all five species (Table 3). Categorical nectar abundance was significantly associated with the abundances of

Table 1. Number of butterflies observed during surveys in the Stanislaus National Forest, Sierra Nevada, California, during 2014 and 2015. Taxonomy and nomenclature follow Pelham (2015).

	Number of individuals observed	
Species	2014	2015
Parnassius clodius	3	3
Papilio rutulus	0	5
Papilio eurymedon	3	31
Papilio multicaudatus	0	1
Colias eurytheme	79	482
Anthocharis sara	0	3
Pieris rapae	0	1
Pontia protodice	1	5
Pontia occidentalis	0	1
Lycaena cupreus	4	1
Satyrium californica	0	3
Satyrium saepium	0	3
Callophrys gryneus	1	14
Callophrys augustinus	6	3
Strymon melinus	15	10
Celastrina ladon	2	16
Glaucopsyche piasus	2	23
Leptotes marina	0	1
Cupido amyntula	2	14
Icaricia saepiolus	5	4
Icaricia icarioides	17	71
Icaricia lupini	198	974
Danaus plexippus	5	11
Boloria epithore	6	4
Speyeria hydaspe	11	28
Limenitis lorquini	1	32
Adelpha californica	37	23
Vanessa virginiensis	0	18
Vanessa cardui	90	22
Vanessa atalanta	0	1
Nymphalis californica	0	1
Polygonia gracilis	3	2
Junonia coenia	1	189
Euphydryas chalcedona	1	1
Chlosyne palla	0	1
Phyciodes mylitta	15	181
Coenonympha tullia	2	12
Epargyreus clarus	3	4
Thorybes pylades	0	1
Erynnis propertius	0	1
Erynnis persius	6	207
Pyrgus communis	2	0
Hesperia juba	0	1
Polites sonora	0	5
Poanes melane	1	1
Total	522	2415

Table 2. Detection probability and occupancy of butterflies in the Stanislaus National Forest, Sierra Nevada, California, in 2014 and 2015, and estimates of regression coefficients in the highest-ranked or most parsimonious models of occupancy (95% confidence intervals in parentheses). Canopy cover and live ground cover measured as percentages. Categorical abundance of nectar was not associated with occupancy of any species.

Species and year	Detection	Occupancy	Canopy cover	Live ground cover	Number of florets
Colias eurytheme (2015)	0.71 (0.63–0.78)	0.85 (0.71–0.93)	−1.75 (−2.50 to −1.00)	0.53 (0.10–0.95)	
Icaricia lupini (2014)	0.78 (0.53–0.91)	0.58 (0.41–0.73)		0.47 (0.07–0.86)	4.04 (1.34–6.74)
Icaricia lupini (2015)	0.81 (0.73–0.87)	0.78 (0.69–0.85)	−1.30 (−1.83 to −0.78)	0.72 (0.28–1.16)	
Junonia coenia (2015)	0.35 (0.27–0.45)	0.85 (0.46–0.97)		1.62 (0.21–3.04)	
Phyciodes mylitta (2015)	0.67 (0.33–0.90)	0.83 (0.45–0.96)	−1.20 (−2.12 to −0.28)	1.75 (0.27–3.23)	
Erynnis persius (2015)	0.73 (0.54–0.86)	0.22 (0.15–0.32)	−1.76 (−2.26 to −1.25)		1.18 (0.20–2.16)

Table 3. Relations between environmental covariates and abundances of butterflies in the Stanislaus National Forest, Sierra Nevada, California, during 2014 and 2015. *P* values derived from negative binomial generalized linear models. Canopy cover and live ground cover measured as percentages.

Species and year	Canopy cover	Live ground cover	Categorical abundance of nectar	Number of florets
Colias eurytheme (2015)	< 0.01	< 0.01	< 0.01	< 0.01
Icaricia lupini (2014)	0.20	< 0.01	0.06	0.48
Icaricia lupini (2015)	< 0.01	< 0.01	< 0.01	< 0.01
Junonia coenia (2015)	0.17	< 0.01	0.40	0.22
Phyciodes mylitta (2015)	< 0.01	< 0.01	< 0.01	0.13
Erynnis persius (2015)	< 0.01	0.01	0.01	< 0.01

C. eurytheme, *I. lupini* (2015), *P. mylitta*, and *E. persius* (Table 3). Number of florets was significantly associated with the abundances of *C. eurytheme*, *I. lupini* (2015), and *E. persius* (Table 3).

In 2014, canopy cover was significantly associated with vegetation burn severity (Table 4). Average canopy cover in areas with low, moderate, and high vegetation burn severity was significantly lower than in unchanged areas (Tables 5, 6). In 2015, all environmental covariates were significantly associated with vegetation burn severity (Table 4). Canopy cover decreased significantly as vegetation burn severity increased (Tables 5, 6). Live ground cover was significantly greater in areas with moderate or high vegetation burn severity than in unchanged areas or areas with low vegetation burn severity. Number of florets was significantly greater in areas with high vegetation burn severity than in unchanged areas or areas with low vegetation burn severity.

In 2014, no covariates were significantly associated with soil burn severity (Table 4). In 2015, however, all environmental covariates were significantly associated with soil burn severity. Canopy cover was significantly greater in areas that were unburned or had very low or low soil burn severity than in areas with moderate soil burn severity (Tables 5, 6). Live ground cover was significantly greater in areas with moderate soil burn severity than in areas with any other severity level. Number of florets was significantly greater in areas with moderate soil burn severity than in areas that were unburned or had very low or low soil burn severity.

DISCUSSION

We identified environmental covariates associated with post-fire detection probabilities and occupancy of five species of butterflies at fine spatial resolution. In 2015, survey-specific number of florets was strongly associated with the detection probability of *I. lupini*. The number of *I. lupini* that we observed taking nectar in 2015 was greater than that of any other butterfly species. Butterflies generally are easier to detect when they are feeding on nectar than when they are hidden in vegetation or flying. Observers also may spend more time searching for butterflies near known nectar sources. However, the number of florets of nectar sources did not appear to be associated with detection probabilities of species that rarely, if ever, took nectar within our study area. For example, we observed relatively few *P. mylitta* and *E. persius* taking nectar, and the null models of detection for these species were ranked higher than univariate models that included the survey-specific number of florets.

Detection probabilities of three species varied temporally. Flight periods differ among species and among years. If surveys are conducted outside of the flight period for a species, or when few individuals are present, detection probabilities will be lower than if surveys are conducted during peak flight periods or when many individuals are present. However, if the flight period is sufficiently long (e.g., if the species has multiple broods) and individuals are available for detection throughout the sampling period, the probability of detection may not change over time. *Icaricia lupini* and *C. eurytheme* were present during all surveys, and detection probabilities of these species were not associated with time. We noted temporal changes in the presence and abundance of the three species for which time was associated with detection probability.

The percentage of live ground cover was positively associated with occupancy of four species. We observed each of the five species that we modeled laying eggs on plants in the understory. As noted above, ground cover may be correlated with the distribution and abundance of host plants and microclimate. Additionally, ground cover may be positively correlated with the number of florets of nectar sources, and we found a low correlation between these two covariates ($r = 0.28$, 2015). The percentage of canopy cover was strongly and negatively associated with occupancy of four species.

We previously included categorical abundance of nectar in occupancy models for butterflies (Fleishman et al. in review). Our results suggest that continuous measures of nectar abundance may explain a greater proportion of the variance in detection probability and occupancy than categorical measures. In all models, the number of florets was more strongly associated with occupancy than were categorical estimates of nectar abundance. As noted above, we found that sugar mass and number of flo-

Table 4. Results of analyses of variance assessing the relations between covariates included in occupancy models and abundance analyses and vegetation burn severity and soil burn severity in the Stanislaus National Forest, Sierra Nevada, California, during 2014 and 2015. Canopy cover and live ground cover measured as percentages.

2014	Treatment	*F*	*P*
Canopy cover	Vegetation burn severity	6.40	< 0.01
Live ground cover	Vegetation burn severity	2.23	0.09
Number of florets	Vegetation burn severity	2.51	0.06
Canopy cover	Soil burn severity	0.46	0.71
Live ground cover	Soil burn severity	2.37	0.07
Number of florets	Soil burn severity	2.04	0.11
2015			
Canopy cover	Vegetation burn severity	22.44	< 0.01
Live ground cover	Vegetation burn severity	17.40	< 0.01
Number of florets	Vegetation burn severity	5.65	< 0.01
Canopy cover	Soil burn severity	12.97	< 0.01
Live ground cover	Soil burn severity	15.79	< 0.01
Number of florets	Soil burn severity	7.68	< 0.01

rets were highly correlated. Additionally, the time and cost necessary to estimate sugar mass with high performance liquid chromatography–mass spectrometry is considerably higher than that necessary to estimate the number of florets.

Abundances of butterflies increased substantially between the first and second growing seasons after the Rim Fire despite empirical evidence (E. Fleishman, unpub. data) and credible, albeit anecdotal, reports of decreases in abundance of many species across the southwestern United States between 2014 and 2015 (D. Wagner, pers. comm.; A. Warren, pers. comm.). For example, we detected 198 *I. lupini* in 2014 and 974 in 2015. Canopy cover was associated with both abundance and occupancy of all species except *J. coenia*. Live ground cover was associated with the abundances of all five species and with occupancy of all species except *E. persius*. Categorical nectar abundance was not associated with occupancy of any species, but was significantly associated with the abundances of four species. Number of florets generally was more strongly associated with abundance than with occupancy of butterflies.

Fire severity as measured by resource management agencies affected values of environmental variables associated with butterfly occupancy, such as canopy cover and live ground cover. Many plant species that are used by butterflies are early successional species, and high levels of soil nutrients after the fire may have supported growth of understory plants (Rice 1993). Our results suggest that fires of high and moderate severity, or patches in which severity was relatively high, may stimulate regrowth of understory plants and increase nectar source abundance more than low-severity fires, while decreasing canopy cover. Butterfly occupancy and abundance ultimately may be greater in areas in which fire severity was moderate or high than in areas with low-severity fires.

Although, to the best of our knowledge, this

Table 5. *P* values derived from Tukey's pairwise comparisons between vegetation and soil burn severity classes and environmental covariates in the Stanislaus National Forest, Sierra Nevada, California, during 2014 and 2015. Canopy cover and live ground cover measured as percentages.

	2014	2015		
Vegetation burn severity classes	Canopy cover	Canopy cover	Live ground cover	Number of florets
Unchanged : Low	0.01	0.02	0.52	0.83
Unchanged : Moderate	< 0.01	0.00	0.01	0.27
Unchanged : High	0.01	0.00	0.00	0.01
Low : Moderate	0.32	0.00	0.04	0.45
Low : High	0.99	0.00	0.00	0.00
Moderate : High	0.21	0.14	0.09	0.53
Soil burn severity classes				
Unburned /very low : Low		0.90	0.99	0.99
Unburned /very low : Moderate		0.00	0.00	0.02
Unburned /very low : High		0.65	0.99	0.52
Low : Moderate		0.00	0.00	0.00
Low : High		0.49	0.99	0.31
Moderate : High		0.97	0.01	0.93

Table 6. Average values (± SE) of environmental covariates associated with different vegetation and soil burn severity classes for statistically significant analyses of variance in 2014 and 2015 (see Table 4). Canopy cover and live ground cover measured as percentages.

Covariate	Treatment	Vegetation or soil burn severity class			
		Unchanged (vegetation) or unburned/very low (soil)	Low	Moderate	High
2014					
Canopy cover	Vegetation burn severity	88.51 ± 2.52	69.60 ± 2.96	61.86 ± 3.95	70.97 ± 2.80
2015					
Canopy cover	Vegetation burn severity	87.57 ± 1.90	71.91 ± 2.16	56.82 ± 3.78	46.46 ± 4.17
Live ground cover	Vegetation burn severity	28.24 ± 3.56	33.99 ± 1.57	42.79 ± 2.61	50.73 ± 2.23
Number of florets	Vegetation burn severity	6.22 ± 2.14	71.31 ± 17.28	162.26 ± 61.56	245.72 ± 47.50
Canopy cover	Soil burn severity	68.01 ± 4.42	71.18 ± 1.93	45.20 ± 4.26	51.39 ± 20.74
Live ground cover	Soil burn severity	36.47 ± 2.87	35.37 ± 1.54	52.89 ± 2.35	36.90 ± 4.39
Number of florets	Soil burn severity	82.76 ± 27.89	65.22 ± 18.18	283.92 ± 57.76	225.21 ± 89.85

is the first study that quantified interactions between butterflies and fire severity, several have examined the effects of fire severity on other taxonomic groups. For example, five years after a wildfire in central Idaho, the biomass of benthic insects and frequency of bat echolocation calls was greater in areas in which fire severity was high than in areas in which fire severity was low or that were not burned (Malison and Baxter 2010). One year after a wildfire in the Sierra Nevada, California, bat activity was equal or higher in burned areas than unburned areas, and activity of some phonic groups was greater in areas in which fire severity was high than in areas in which fire severity was moderate or that were not burned (Buchalski et al. 2013). It is conceivable that increases in invertebrate abundance or biomass in areas in which fire severity is high have cascading effects on food webs in the years following a fire.

Life history traits of butterflies also may affect their spatial distribution or colonization rates after a fire. *C. eurytheme* and *J. coenia* typically travel long distances as adults (Scott 1986; Fleishman et al. 1997) and species with high vagility may be able to colonize severely burned areas more quickly than species with low vagility. However, we recorded numerous species with low vagility in areas with high burn severity in the first growing season after the Rim Fire. *Icaricia lupini*, the only species with sufficiently high naïve occupancy in 2014 to facilitate occupancy analysis, typically does not move large distances as an adult (Scott 1986; Fleishman et al. 1997). The distance from the transects to the nearest unburned patches was greater than the reported vagility of this species. Our data and observations suggest that some eggs, larvae, pupae, or adults can survive high-severity fire, are capable of moving longer distances than reported, or move in association with smoke plumes. For example, some species of beetles can detect smoke from fires and use these signals as cues for dispersal (Schütz et al. 1999). However, this behavior has not been observed in butterflies.

Environmental attributes other than the abundance of host plants and nectar sources were associated with occupancy of butter-

flies after a major fire in the Sierra Nevada, California. There are reasonable mechanistic hypotheses of relations between many of these attributes, such as percentage of live ground cover, and the abundance of host plants and nectar sources. Some of these environmental attributes also were directly associated with abundances of butterflies, although the consistency of associations varied among species. Vegetation and soil burn severity, in turn, affected the environmental attributes that were associated with occupancy and abundance. Understanding how vegetation and soil burn severity affect environmental attributes that are associated with butterfly occupancy and abundance may inform strategies for managing these species with prescribed fire, when fire is prescribed for other reasons, or following wildfire. For example, if fire is used to maintain or restore habitat for butterflies, a prescription that allows relatively high vegetation burn severity could decrease canopy cover, increase nectar abundance, and increase live ground cover, all of which may facilitate increases in occupancy and abundance.

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Rick Scherer's research examines the effects of environmental attributes on the demography and spatial distribution of species.

Rob Blair's research focuses on how land use affects bird communities, especially those in urban-dominated landscapes.

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