

Reptile and Amphibian Responses to Large-Scale Wildfires in Southern California

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ABSTRACT.—In 2003, southern California experienced several large fires that burned thousands of hectares of wildlife habitats and conserved lands. To investigate the effects of these fires on the reptile and amphibian communities, we compared the results from prefire herpetofauna and vegetation sampling to two years of postfire sampling across 38 burned and 17 unburned plots. The sampling plots were spread over four vegetation types and four open space areas within San Diego County. Our capture results indicated that burned chaparral and coastal sage scrub plots lost herpetofaunal species diversity after the fires and displayed a significant shift in overall community structure. Shrub and tree cover at the burned plots, averaged across the second and third postfire years, had decreased by 53% in chaparral and 75% in coastal sage scrub. Additionally, postfire herpetofauna community structure at burned plots was more similar to that found in unburned grasslands. In grassland and woodland/riparian vegetation plots, where shrub and tree cover was not significantly affected by fires, we found no differences in the herpetofaunal species diversity or community composition. At the individual species level, *Sceloporus occidentalis* was the most abundant reptile in these areas both before and after the fires. We saw increases in the net capture rates for several lizard species, including *Aspidoscelis tigris*, *Phrynosoma coronatum*, and *Uta stansburiana* in burned chaparral plots and *Aspidoscelis hyperythra* and *U. stansburiana* in burned coastal sage scrub plots. The toad, *Bufo boreas*, was detected at significantly fewer burned plots in chaparral after the fires. Additionally, we documented decreases in the number of plots occupied by lizards (*Elgaria multicarinata*), salamanders (*Batrachoseps major*), and snakes (*Coluber constrictor*, *Lampropeltis getula*, *Pituophis catenifer*, and *Masticophis lateralis*) in coastal sage scrub and chaparral after the fires. We discuss the individual species results as they relate to such life-history traits as the susceptibility to initial mortality, the response to the altered postfire habitat, and shifts in the availability of potential prey. We foresee that a continued unnatural fire regime will result in a simplification of the southern California reptile and amphibian communities.

Wildfires have long been a part of the natural and human altered environments of southern California, a fact that is unlikely to change anytime in the near future. Native vegetation communities have evolved with some variation of this fire regime and have adapted with various survival strategies (Hanes, 1971; Vogl and Schorr, 1972; Keeley and Keeley, 1984; Keeley and Fotheringham, 2001). Keeley et al. (1999, 2004) have stated that large landscape-level fires occurred in the past and will likely continue to occur into the future as long as southern California experiences episodes of severe fire weather (e.g., fast, dry winds). Despite fire suppression efforts and management plans, large and small wildfires continue to occur from both natural ignition sources and those associated with the increasing human population (Keeley et al., 1999, 2004). This has been reinforced by the findings of Wells et al.

(2004) that have shown that there has been an increase in the burning of coastal sage scrub over the past century. The intervals between fires have been substantially reduced when compared to historic levels, resulting in an overall increased fire frequency. Increased fire frequency can cause the conversion of shrub lands (e.g., chaparral and coastal sage scrub) to grasslands (Zedler et al., 1983; Keeley, 2005).

Direct and indirect effects of fire can have both negative and positive consequences on local species and communities (Kahn, 1960; Lillywhite et al., 1977; Simovich, 1979; Fredericksen and Fredericksen, 2002). Negative effects of fires may include direct mortality, loss of suitable habitat, and the loss of plant and animal food resources (Babbitt and Babbitt, 1951; Erwin and Stasiak, 1979; Shaffer and Laudenslayer, 2006). An additional undesirable effect would be the increased potential for the conversion of herpetologically diverse scrub and chaparral into less diverse grasslands. As the vegetation becomes less diverse, we may expect a concomitant shift to less diverse reptile

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and amphibian communities in southern California. For some species fire may have positive impacts. Species that are able to escape and survive the immediate dangers associated with fires may prefer the open, disturbed habitats of the postfire environment and benefit from the new opportunities.

In October and November of 2003, large-scale fires swept across southern California, burning over 300,000 ha of wild lands. This included nearly 130,000 ha burned in the Cedar and Otay Fires in San Diego County. In addition to the loss of nearly 5,000 structures and 15 human fatalities (CDF, 2003), these large fires impacted local wildlife communities in a region already recognized as being one of the most at-risk areas for loss of biodiversity (Mittermeier et al., 1997). The first large habitat reserve created in San Diego County, the Multiple Species Conservation Plan (MSCP; City of San Diego, 1997) was directly in the footprints of these two fires. Half of the protected lands within the MSCP were affected by the fires, and some protected habitats were entirely within the fire perimeters. Concern over the recovery of these habitats and the species within them motivated our efforts to conduct this research. With the detailed data on vegetation and animal communities that we had collected previously within the fire footprints, we were in a unique position to address this concern.

The primary objective of this study was to increase our understanding of the short-term response of reptiles and amphibians to wildfire in southern California. Through intensive monitoring in burned and unburned areas coupled with comparisons to prefire sampling results, we expected to learn whether (1) species diversity or community structure of the local reptile and amphibians were affected by the fires, (2) any changes in herpetofauna were associated with changes in the vegetative communities, and (3) species-specific responses to the fire were associated with life-history characteristics of the species.

MATERIALS AND METHODS

Study Sites.—We conducted surveys for reptiles and amphibians at four separate locations associated with the 2003 southern California wildfires, Elliott Chaparral Reserve (ELL), Little Cedar Ridge (CED), Rancho Jamul Ecological Reserve–Hollenbeck Canyon Wildlife Area (RAJ), and Santa Ysabel Open Space Preserve (SYR) (Table 1). All sites were in San Diego County, California (Fig. 1) and had been sampled before the fires using identical survey methods (Case and Fisher, 2001; Fisher et al.,

2002; Franklin et al., 2009). The number of study plots included within each site, vegetation type, and burn condition varied depending on the availability of prefire sample data and the extent of the wildfires (Table 2). With a few exceptions, the vegetation at all of the sites had not burned recently and was considered to be senescent. Detailed descriptions of each site are given below.

Elliott Chaparral Reserve: Adjacent to the Marine Corps Air Station Miramar, the Elliott Chaparral Reserve (ELL) was approximately 25 km from the coast. Although ELL itself was only 43 ha, much of the adjacent military lands were also undeveloped wild lands. Our study plots were centered at 32.89217°N and 117.09460°W, with an average elevation of 195 m (Fig. 1). The vegetation at ELL consisted mainly of chaparral and coastal sage scrub, dominated by chamise (*Adenostoma fasciculatum*), California buckwheat (*Eriogonum fasciculatum*), and annual, nonnative grasses (*Avena* and *Bromus*) (Hickman, 1996). ELL was located at the west end of the Cedar Fire footprint, which completely burned the site in October 2003. Before the Cedar Fire, most of ELL had burned in 1944 or 1945 (CDF, 2006). This site was managed by the Nature Reserve System of the University of California at San Diego (UCSD).

Little Cedar Ridge: Located near the international border in southern San Diego County, the Little Cedar Ridge (CED) study site was located on the northern slopes of Otay Mountain and was managed by the Bureau of Land Management (BLM) as part of the Otay Mountain Wilderness. The Otay Mountain Wilderness was approximately 6,800 ha and ranged in elevation from 250–1,000 m. Our study plots covered a small portion of Otay Mountain and were centered around 32.62078°N and 116.86202°W, with an average elevation of 400 m (Fig. 1). The majority of vegetation in the study area was characterized as chaparral and coastal sage scrub based on the dominant plants *A. fasciculatum*, Tecate cypress (*Cupressus forbesii*), wild oats (*Avena*), and *E. fasciculatum* (Hickman, 1996). The entire area surrounding the study plots burned during the Otay Fire in October 2003. No record of previous fire was found for this portion of Otay Mountain (CDF, 2006).

Rancho Jamul Ecological Reserve and Hollenbeck Canyon Wildlife Area: Rancho Jamul Ecological Reserve and Hollenbeck Canyon Wildlife Area, jointly referred to here as RAJ, were located just 6 km north of CED. RAJ was managed by the California Department of Fish and Game. Only the southern portion of the Rancho Jamul Ecological Reserve burned during the 2003 Otay Fire. Three plots on the Hollenbeck Canyon Wildlife Area were burned

TABLE 1. Variables used in the analysis of the responses of the reptile and amphibian species to the 2003 wildfires in southern California.

Variable name	Variable type	Definition	Attributes
Site	Categorical	General location of sample plot	CED (Little Cedar Ridge) ELL (Elliott Chaparral Reserve) RAJ (Rancho Jamul Ecological Reserve) SYR (Santa Ysabel Open Space Preserve)
Vegetation type	Categorical	Dominant plant community at the sample plot, as determined by the results of the vegetation transect survey with a minimum of 25% cover by plant species associated with the identified vegetation community	CHAP (chaparral) CSS (coastal sage scrub) GRASS (grassland) WR (woodland/riparian)
Time	Categorical	Time period during which samples were collected, used in combination with burn condition for BARI univariate analysis	Before (time period up to the 2003 fires, prefire) After (time period following the 2003 fires, postfire)
Burn condition	Categorical	Environmental description of plot condition after the 2003 fires, used in combination with time for BARI univariate analysis	Reference (plots that did not burn in the 2003 fires) Impact (plots that did burn in the 2003 fires)
Condensed fire classification	Categorical	Environmental description of plot conditions during which samples were collected, used in multivariate analysis	Nonrazed (a combination of the before-reference, before-impact, and after-reference samples) Razed (the after-impact samples)

in the 1996 Honey Fire, seven years prior to the initial, prefire surveys conducted in 2003. Based on the level of vegetative cover at these plots after seven years of regeneration, we classified each as unburned for our analyses. One other plot burned in 1968. No other fire records were found for the remaining study plots at this site (CDF, 2006). RAJ was located at 32.67873°N and

116.85431°W, with an average elevation of 250 m (Fig. 1). Rancho Jamul Ecological Reserve covered approximately 1,500 ha and the Hollenbeck Canyon Wildlife Area was approximately 1,450 ha. RAJ encompassed a variety of vegetation communities including native and nonnative grasslands, coastal sage scrub, oak and sycamore woodlands, and riparian environ-

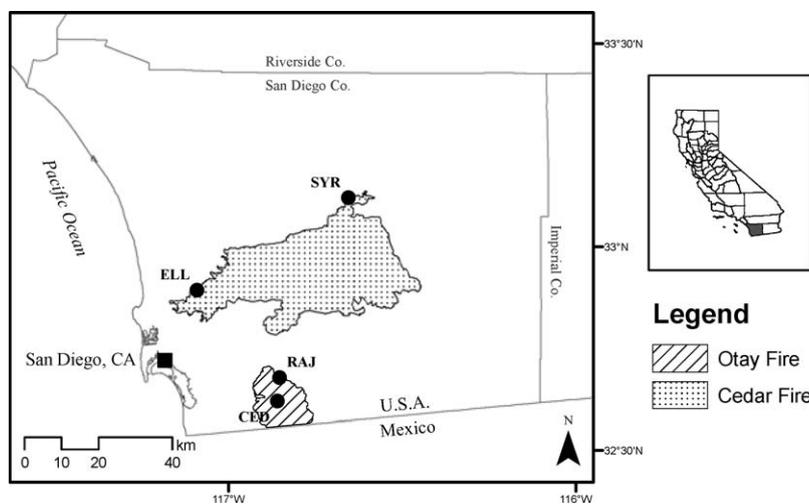


FIG. 1. The four study sites in San Diego, California, were Little Cedar Ridge (CED), Elliott Chaparral Reserve (ELL), Rancho Jamul Ecological Reserve (RAJ), and Santa Ysabel Open Space Preserve (SYR).

TABLE 2. The number of study plots included in this study varied by site, vegetation, and burn condition. This design was based on the availability of prefire sample data and the extent of the wildfires. The vegetation types are chaparral (CHAP), coastal sage scrub (CSS), grassland (GRASS), and woodland/riparian (WR). The availability of reference (R) and impact plots (I) was largely determined by the extent of the fire at each site.

Vegetation:	CHAP		CSS		GRASS		WR		Site total
	R	I	R	I	R	I	R	I	
Site									
Little Cedar Ridge (CED)		5		4					9
Elliott Chaparral Reserve (ELL)		5		5					10
Rancho Jamul Ecological Reserve (RAJ)			4	4	4	4	2	1	19
Santa Ysabel Open Space Preserve (SYR)	2	4	1	1	2	1	2	4	17
Total	2	14	5	14	6	5	4	5	55

ments. In addition to the natural vegetation, there were extensive, fallow agricultural fields. Dominant plant species at the site included brome grass (*Bromus*), *Avena*, *E. fasciculatum*, California sagebrush (*Artemisia californica*), coast live oak (*Quercus agrifolia*), western sycamore (*Platanus racemosa*), laurel sumac (*Malosma laurina*), and San Diego sunflower (*Viguiera laciniata*).

Santa Ysabel Open Space Preserve: At an average elevation of 1,078 m, the Santa Ysabel Open Space Preserve (SYR) was the highest of our four study sites and was located near the small town of Santa Ysabel in the northern portion of San Diego County. The study plots were centered on 33.11984°N and 116.65840°W (Fig. 1). SYR supported oak woodlands and pine forests, native and nonnative grasslands, chaparral, coastal sage scrub, and riparian environments. Dominating the various habitats were *Q. agrifolia*, *Bromus*, *A. fasciculatum*, Engelmann oak (*Quercus engelmannii*), *Avena*, and white sage (*Salvia apiana*). This 1,500-ha site was managed by the Parks and Recreation Department of the County of San Diego. SYR represented the northeastern extent of the Cedar Fire, which burned a portion of the study site in 2003. Of the 17 plots at SYR, one burned in 1938, two others burned in 1929, and no recorded fires were found for the remaining plots at this site (CDF, 2006).

Environmental conditions were relatively uniform across all four study sites. The three lower elevation sites, ELL, CED, and RAJ, all experienced similar weather patterns and temperatures. Average July maximum temperatures ranged between 28°C and 29°C. Average January low temperatures fell between 5°C and 6°C. Annual precipitation averaged between 28 and 31 cm. At SYR, a higher elevation site, the average July high was 33°C, the average January daily low temperature was 1°C, and the annual rainfall was 53 cm. Temperature and precipitation data are 30-yr averages for 1966 through 1995 (see Franklin et al., 2001) and were

extracted for each of our plots using geospatial information system (GIS) tools. We used the same interpolated weather data generated by Franklin et al. (2001) to estimate the general environmental conditions that likely occurred across our sites for the 11-yr time frame over which the sampling occurred. Franklin et al. (2001) generated these weather variables based on data from 104–136 climate stations across southern California.

The fire severity levels within the Otay Fire and Cedar Fire, as measured by the Burned Area Reflectance Classification, were extremely variable across the four study sites. The Burned Area Reflectance Classification (BARC) measured the effect of the fire on the vegetation using a categorical scale of 1–4 with 4 referring to the highest severity. Within the Otay Fire, six of the plots at CED were rated as severity level 4, three plots at CED and one at RAJ were scored as level 3, and the remainder of the impacted plots at RAJ was reported as a level 2 fire severity (USDA, 2003a). None of our study plots in the Otay Fire received the lowest fire severity rating of 1. The full range of fire severity scores were reported within the Cedar Fire; two plots at ELL and three at SYR were rated as level 1, a fire severity level 2 occurred at two of our ELL plots and seven of the SYR pitfall arrays; severity level 3 characterized six ELL and three SYR plots, and only one plot at SYR experienced the highest fire severity rating of 4 (USDA, 2003b).

The proximity of our study plots to the nearest fire perimeter ranged from as little as 50 m to as high as 4,798 m. At CED, all of our plots were 3 km or more inside the perimeter of the Otay Fire. The median distance of the burned plots to the perimeter of the Otay Fire at RAJ was 866 m (range: 73–1,541 m), and 826 m (range: 177–2,279 m) for the unburned plots. With a median distance of 1,025 m (range: 660–1,214 m) to the perimeter of the Cedar Fire, our ELL plots were potentially even more isolated from natural habitat: the closest fire perimeter

included urban development exclusively. At SYR, where the Cedar Fire only burned a portion of the site, our burned samples were a median distance of 614 m (range: 50–1,193 m) inside the perimeter, whereas the unburned samples were a median distance of 886 m (range: 50–4,798) outside of the fire.

Sampling Herpetofaunal Communities.—We sampled herpetofauna using pitfall trap arrays. Pitfall trap arrays have been used widely to sample a variety of animals throughout southern California (Simovich, 1979; Block and Morrison, 1998; Fisher and Case, 2000) and the rest of the United States (Gloyd, 1947; Woodbury, 1953; Semlitsch et al., 1981; Moseley et al., 2003). In this study, we used the same pitfall trap array design to monitor reptiles and amphibians across four vegetation types. Array design and sampling methods were described in Case and Fisher (2001). Briefly, each pitfall array consisted of three 15-m long drift fences, seven 19-L buckets, and three hardware-cloth funnel traps. The three drift fences met at a central point where a bucket was buried flush in the ground. Two additional buckets were buried along each of the radial arms of drift fence, one at the midpoint of the fence, roughly 7.5 m from the central bucket, and the other at the far end of the fence. The final layout of the pitfall array resembled a “Y.” A hardware cloth funnel trap was placed along each arm of the array. Each of the arrays studied here were built and sampled prior to the 2003 wildfires as part of previous studies (Suarez et al., 2000; Case and Fisher, 2001; Fisher et al., 2002). In all four study areas, arrays damaged in the fires were rebuilt. Our postfire sampling efforts began 16–18 months after the 2003 fires. We sampled the pitfall trap arrays after the fires at approximately four- or five-week intervals, resulting in eight to 10 samples per year. Each sampling period lasted five days with the first day used for opening traps. All traps were checked daily on the following four days. When we were not sampling, all traps were secured to prevent incidental captures and mortality.

The length of our prefire sample efforts varied by study site based on the purpose for which the site was originally established (some were long-term monitoring sites, whereas others were established for short-term projects). Postfire efforts were more uniform because of the common purpose for which the sites were rebuilt and maintained (i.e., determining fire effects). Weather permitting, we sampled all four sites across most of the year and all four seasons, beginning typically in February or March and going through October or November (Table 3). One of the most notable differences in the sample effort was the number of prefire

sample periods conducted at the CED and ELL study sites. These two sites were sampled for approximately five years before the fires compared to the one to two years that RAJ and SYR were sampled (Table 3).

Animals captured in the pitfall traps were processed daily and released at the point of capture. We recorded the species, sex, age class, mass, and length (snout-vent) of each animal. To identify animals recaptured within a sample session, each animal was permanently marked with a unique pattern as appropriate for the species; lizards, frogs, and salamanders were toe-clipped, and snakes were scale-clipped.

Vegetation Classification.—We conducted linear vegetation transect surveys three times at each of the study plots. Each vegetation transect consisted of a 50-m point-intercept technique (Sawyer and Keeler-Wolf, 1995) with species composition, vegetation height, substrate, and leaf litter depth recorded every 0.5 m. Bauer's work with linear vegetation transects in southern California (Bauer, 1943) has shown this technique to be comparable to the results of the more time-consuming quadrat technique, especially in chaparral. The original, prefire vegetation surveys were conducted near the time when each plot was originally established (Table 3) and were used to classify each plot into one of four general vegetation types. Postfire vegetation surveys were conducted in 2005 and 2006 and pooled for these analyses.

We grouped the 55 study plots, based on the vegetation transect results, into four general categories: (1) chaparral, (2) coastal sage scrub, (3) grassland, and (4) woodland/riparian (Table 2). We used a 25% coverage level to determine the vegetation classification of each plot. Based on the prefire vegetation survey, if 25% or more of the plants detected along the transect are typically associated with chaparral, coastal sage scrub, or one of the categories making up woodland/riparian (Sawyer and Keeler-Wolf, 1995; Hickman, 1996), the plot was classified as such (Table 1). Where more than one vegetation type represented 25% or more of the transect, the more abundant classification was used. This classification was made regardless of the percent of the plot covered by grassland species. Because much of southern California has experienced some level of disturbance or invasion by exotic grasses, plots were only considered to be grassland if no other vegetation type represented 25% or more of the linear vegetation transect.

Chaparral (CHAP) arrays were dominated by evergreen plant species such as *A. fasciculatum* (Sawyer and Keeler-Wolf, 1995). We classified study plots as coastal sage scrub (CSS) based on the presence of such plant species as *A.*

TABLE 3. Sample efforts at the four study sites showing the number of sample periods per time period. The time frames during which sampling occurred are shown in parentheses.

Study site	Sample periods	
	Prefire	Postfire
Little Cedar Ridge (CED)	58 (JUN 1995–MAR 2001)	20 (MAR 2005–NOV 2006)
Elliott Chaparral Reserve (ELL)	66 (APR 1995–APR 2001)	20 (FEB 2005–NOV 2006)
Rancho Jamul Ecological Reserve (RAJ)	12 (MAR 2001–APR 2002)	20 (FEB 2005–NOV 2006)
Santa Ysabel Open Space Preserve (SYR)	12 (APR 2002–JUL 2003)	16 (MAY 2005–OCT 2006)

californica, *S. apiana* and *E. fasciculatum*. A large percentage of grasslands (GRASS) in southern California are populated with several nonnative genera of grass, including *Avena* and *Bromus*, although some native grasses are interspersed. For our analyses, we made no distinction between native and nonnative grasslands. The woodland/riparian (WR) category included oak woodlands, pine forests, sycamore, and willow riparian areas, as well as seeps. Although these wooded vegetation types were diverse, we did not have sufficient numbers of replicates to test these individually. Most study plots could not be described as 100% one vegetation type or another but were classified based on the results of the vegetation transect surveys. For all vegetation types, data for shrubs and trees were used for analyses of cover as well as plant community composition. Because we did not always conduct vegetation surveys during the same season, we did not include the data for annual forbs and herbs when determining the vegetation community of a study plot. We found that many of the herbs and annual forbs commonly disarticulated in the summer and fall periods, leaving open ground through winter.

Data Classification and Reduction.—We classified and reduced the reptile and amphibian data using two different techniques. For the univariate tests, we used a before–after reference–impact procedure (BARI) to classify our data (Underwood, 1994; Smith, 2002). In this process, we classified each sample plot as either a reference plot or an impact plot (Table 1). Reference plots were pitfall arrays located outside of the burn perimeter, not impacted by the 2003 wildfires. Impact plots were arrays that fell within the burn perimeter and were impacted by the fires. Reference and impact classification applied to both the prefire time period when all arrays existed in an unburned condition and the postfire time period when impact plots burned either wholly or partially. We used this BARI classification for assessing and describing the effects of the fires on

vegetation, reptile and amphibian species diversity, and individual species occupancy and abundance.

For the purposes of conducting multivariate analyses, we reclassified sampled plots as razed or nonrazed (Table 1). In terms of the BARI classifications described above, all data collected during prefire surveys at both reference and impact plots plus data collected during postfire surveys at unburned plots made up the non-razed samples. Razed samples included data from all surveys completed postfire on the burned or impacted plots. Classifying the data in this way allowed us to test whether the postfire herpetofaunal community present at burned plots differed from the community present in all other unburned states. Before combining data from pre- and postfire reference plots, we carefully reviewed the datasets to ensure that there were no systematic effects of time or burn condition that may cause erroneous test results.

Analyses.—Because capture rates of individual reptile and amphibian species varied within and between years, we calculated an average capture rate for each species across sample periods and by time period (i.e., pre- and postfire) for each individual array. Then, we used these averaged capture rates as the basis for all further analyses, with sample arrays serving as replicates.

Prior to measuring the response in amphibian and reptile diversity to fire, we first described the variability in herpetofaunal diversity between the four vegetation types using the prefire data. We calculated the average Shannon Diversity Index (H') (Shannon, 1948) for each vegetation type across all four sites, including data from both the impact and reference plots. We used two sample *t*-tests to determine whether the Shannon Diversity Index was significantly different between each combination of vegetation types.

To test whether fire had an effect on the overall species diversity of the herpetofaunal

community, we additionally calculated the Shannon Diversity Index at each sampling array after the fires. We then subtracted the prefire index from the postfire index to calculate a "net change in diversity" ($\Delta H'$) index for each plot to normalize for the unburned condition. We tested for the effect of burn condition on species diversity by evaluating pairwise differences in $\Delta H'$ for each vegetation type separately using *t*-tests with the variance pooled across all vegetation types. All tests were run using SAS Statistical Software (vers. 9.1, SAS Institute, Cary, NC).

In addition to testing for differences in the herpetofaunal community response to fire using a single diversity measure, we also used a combination of multivariate and univariate techniques to test for changes in the overall community structure, individual species abundance, and plot occupancy following the fires. We performed the multivariate analyses using the statistical software PRIMER-E (vers. 6, Plymouth, U.K.; Clarke, 1993). Before analyzing the data with PRIMER-E, we square-root transformed the data to remove some weight from the most abundant species for a more balanced community analysis and created a Bray-Curtis similarity matrix among all samples (Clarke and Green, 1988). To generate the Bray-Curtis similarity matrix, PRIMER-E calculated the percentage of similarity between each sample in the dataset by comparing the species that occurred in each with the frequency we detected each species (Clarke and Warwick, 2001). PRIMER-E measured the similarity as a percentage, 0–100%, with a similarity of 0% indicating that two samples had no species in common. If all of the same species occur in two samples in exactly the same numbers, the similarity between the two samples would be 100% (Bray and Curtis, 1957). Using the Bray-Curtis similarity matrices, we used PRIMER-E to test our hypotheses in a stepwise fashion using two-way crossed analysis of similarity (ANOSIM) tests, a multivariate permutation-based test similar to the analysis of variance (ANOVA) test in univariate statistics (Clarke and Green, 1988). Using the prefire data only, when all plots were unburned, we first tested whether the factors of vegetation type, site, or both were significantly predictive of the differences in community structure. If vegetation type was significant, the effect of the fire was tested separately for each vegetation type. If site was significant, it was used as a blocking factor within the second series of ANOSIM tests performed for each vegetation type that tested for differences between the razed and nonrazed plots. The test statistic *R* from an ANOSIM test reflects the observed differences between

groups in comparison to within groups and can range from -1 to 1 . An $R = 1$ indicates complete discrimination among groups, whereas $R \leq 0$ indicates no discrimination. PRIMER-E calculates significance by permutation (Clarke and Green, 1988).

To visualize the results of the similarity matrix, PRIMER-E generates nonmetric multidimensional scaling (MDS) plots to ordinate the similarities between the samples (Kruskal, 1964). These plots are a two-dimensional representation of the multidimensional similarity between samples, which can be viewed from multiple angles, from front or back, or rotated and flipped. The only scale in an MDS plot is the relative distance between samples, with similar samples appearing close together and dissimilar samples farther apart (Clarke and Warwick, 2001). Because PRIMER-E limited the MDS to two dimensions, there was some level of distortion or stress incorporated into the ordination to best represent the data. Stress is a measure of the combined deviation from the ideal distance between all samples. Two-dimensional MDS plots with stress values ≤ 0.1 are considered to be a good representation of the similarity matrix, whereas MDS plots with stress > 0.3 are considered to be poor representations of the data (Clarke and Warwick, 2001). Because we used a condensed fire classification to compare our nonrazed samples to the razed samples, we carefully reviewed the MDS plots for each subset of samples to ensure that there were no systematic effects of time or burn condition that may cause erroneous test results.

We used the ANOSIM results as an omnibus test for limiting Type 1 error and determining whether further analyses were warranted. If the condensed fire classification (razed and nonrazed) was not a significant predictor of herpetofauna community structure within each vegetation type, we conducted no further tests. If the fire classification was significant, we conducted two additional tests: the first was to look for patterns between the amount of shrub and tree cover and the herpetofauna community, and the second was to investigate the responses of individual species. We used the biotic-environmental matching (BioEnv) procedure within PRIMER-E to determine whether the total shrub and tree cover was significantly associated with the differences between the herpetofauna communities in the razed and nonrazed samples (Clarke, 1993; Clarke and Ainsworth, 1993). The BioEnv procedure generates similarity matrices of the reptile and amphibian community samples by ranking them from high to low similarity. Similarly, it ranks the percent of shrub and tree cover from high to low values. These are then compared using a weighted Spearman statistic (ρ). The test statistic, ρ , can

range between -1 and 1 , where 1 indicates complete correlation between the herpetofauna community structure and the percentage of shrub and tree cover, $\rho = 0$ indicates no correlation, and -1 represents complete opposition. BioEnv calculates significance by permutation (Clarke and Ainsworth, 1993).

To investigate the potential for community conversion, we averaged the reptile and amphibian capture results across vegetation type and condensed fire classification across all sites. We used PRIMER-E to generate a Bray-Curtis similarity matrix on these averaged data, which in turn was used to produce an MDS plot. The percentage of similarity of the reptile and amphibian communities between each combination of vegetation type (CHAP, CSS, GRASS, and WR) and condensed fire classification (nonrazed and razed) were used to measure whether any of the communities at razed study plots became more like that at one of the alternate vegetation types.

To analyze the relative abundance of individual species within in the community, we first subtracted prefire capture rates from postfire capture rates at each sampling array to calculate the "net change in abundance" at each array. Because there were a large number of species captured across all vegetation types, many of which had low capture rates, we chose to focus our analyses and interpretation on the species that made up the majority of the prefire and postfire communities. Therefore, we report on the species that accounted for $\geq 5\%$ of the captures within each of the four taxonomic units, frogs and toads, salamanders, lizards, and snakes, which resulted in 18 focal species. We used two-sample t -tests to determine whether the changes in abundance at the impact arrays were significantly different from the changes in abundance at the reference arrays. After removing rare species to satisfy assumptions of normality, we pooled variances across the species within each vegetation type. We considered a species to be rare if we detected individuals of the species at $\leq 25\%$ of the samples within the vegetation type at each site. We used the Fisher's Exact test to determine whether there were any significant differences between the impact and reference plots when comparing the occupancy of each species before and after the fires. For the occupancy analysis, we tested all 18 focal species, regardless of the rarity of the species within the vegetation type. Means are given ± 1 SE.

RESULTS

Capture Results.—In total, we sampled 55 study plots with individual plots sampled for

a total time period ranging from three to eight years. Collectively, our pitfall trapping efforts resulted in 6,475 animal captures, of which 6,080 were original (Table 4). Across vegetation types and both prefire and postfire efforts, we detected a total of six frog or toad species, 11 lizard species, two species of salamanders, and 17 species of snakes.

Overall Herpetofaunal Diversity.—Based on the prefire (before) captures, the Shannon Diversity Index for the reptile and amphibian species, averaged across the reference and impact plots and across all sites, differed among the four vegetation types. We found the highest species diversity in CSS ($H' = 1.76 \pm 0.09$), followed closely by CHAP ($H' = 1.64 \pm 0.05$) (Fig. 2). The GRASS plots ranked third with an average diversity of $H' = 1.26 \pm 0.11$, just slightly ahead of our WR plots ($H' = 1.18 \pm 0.11$). There was no difference between the level of species diversity in the CHAP and CSS plots ($t_{26} = -1.17, P = 0.25$) or between the GRASS and WR plots ($t_{27} = 0.55, P = 0.58$). Species diversity in CHAP and CSS differed from that in both GRASS and WR (Fig. 2).

Our analysis of reptile and amphibian captures pre- and postfire indicates that herpetofaunal diversity changed at impact sites following the fires. Impacted or burned plots showed a decrease in diversity ($\Delta H' = -0.196 \pm 0.107$) and reference or unburned plots showing relatively no change in the index ($\Delta H' = 0.098 \pm 0.134$). Across vegetation types, both CHAP and CSS exhibited significant losses in herpetofauna diversity within the impact plots ($\Delta H' = -0.527 \pm 0.263, t_{55} = -2.00, P = 0.05$ and $\Delta H' = -0.491 \pm 0.182, t_{55} = -2.70, P = 0.01$, respectively), whereas we found no change in diversity for either GRASS or WR ($\Delta H' = -0.154 \pm 0.211, t_{55} = -0.73, P = 0.47$ and $\Delta H' = -0.284 \pm 0.234, t_{55} = -1.21, P = 0.23$, respectively; Fig. 2).

Herpetofaunal Community Structure.—Multivariate analysis of the prefire study plots showed that both site (ANOSIM: $R = 0.537, P < 0.001$) and vegetation type (ANOSIM: $R = 0.292, P < 0.001$) were significant factors influencing the similarity of the herpetofaunal communities among study plots. Therefore, all subsequent multivariate analyses controlled for site to examine study plot differences by vegetation type. Reptile and amphibian communities within CHAP and CSS were significantly different in the razed (or burned) plots versus the nonrazed study plots (ANOSIM: CHAP: $R = 0.580, P < 0.001$; CSS: $R = 0.316, P < 0.002$). In both CHAP and CSS plots, the percent of shrub and tree cover tended to be predictive of the clustering of study plots by herpetofaunal community (BioEnv: CHAP $\rho =$

0.095, $P = 0.08$; CSS $\rho = 0.064$, $P = 0.09$). Reptile and amphibian communities within GRASS and WR plots showed no significant differences between the razed versus nonrazed plots, (GRASS: $R = -0.175$, $P = 0.927$; WR: $R = 0.083$, $P = 0.270$).

Changes in Vegetation Structure.—Overall, the percent of shrub and tree cover tended to decline in CHAP and CSS but remained relatively constant in GRASS and WR following the fire. In impacted CHAP plots, the shrub and tree cover dropped from an average of $67\% \pm 5.4$ cover prefire to $31\% \pm 3.9$ postfire, whereas reference plots showed little change, with an average of $68\% \pm 5.5$ prefire cover compared to $66\% \pm 10.75$ postfire cover. Similarly, impact plots in CSS showed large declines in shrub cover, dropping from $50\% \pm 6.3$ prefire cover to $12.6\% \pm 3.7$ postfire, whereas reference plots showed modest differences between prefire ($58\% \pm 8.2$) and postfire ($55\% \pm 8.6$) cover. Both the reference and impact plots in GRASS had very low shrub and tree cover prefire, at $8\% \pm 5.6$ and $1\% \pm 0.8$, respectively. Postfire, we only measured $2\% \pm 1.3$ in the impact plots and $3\% \pm 1.7$ shrub and tree cover in reference plots. Our impact plots in WR did decline in shrub and tree cover when the trees on these plots were burned; prefire averages on the WR impact plots were $35\% \pm 10.8$ and postfire measured $24\% \pm 6.4$. Shrub and tree cover on the reference WR plots remained relatively unchanged prefire to postfire, with $30\% \pm 4.4$ and $37\% \pm 31.3$ cover values, respectively. The WR plots had highly variable shrub and tree coverage because this grouping included not only oak woodlands and pine forest but also seeps, which may have had very little shrub and tree cover.

Species-Specific Responses.—One toad (*B. boreas*) and two lizard species (*Sceloporus occidentalis* and *Aspidoscelis hyperythra*) accounted for nearly 55% of the total captures, across all vegetation types, prefire and postfire. *Sceloporus occidentalis* was the most abundant species in CHAP (Fig. 3) and the second most abundant in CSS (Fig. 4). *Aspidoscelis hyperythra* was the most abundant species in CSS plots (Fig. 4). We detected no change in the capture rate of *S. occidentalis* in CHAP or CSS. However, we did see an increased capture rate for *A. hyperythra* in CSS. We detected *S. occidentalis* in all of the CHAP and CSS plots prefire, which did not change postfire. The only change that we found for *B. boreas* was a decrease in site occupancy in the impacted CHAP plots postfire (Fig. 5).

Within the CHAP study plots, we detected an overall difference in the capture rates or proportion of plots occupied for 10 different species. Capture rates of *Uta stansburiana*,

Aspidoscelis tigris, and *Phrynosoma coronatum* were higher in the postfire impact study plots relative to the reference plots ($\Delta C = 0.736 \pm 0.174$, $t_{247} = 4.24$, $P < 0.001$, $\Delta C = 0.493 \pm 0.174$, $t_{247} = 2.84$, $P < 0.01$ and $\Delta C = 0.369 \pm 0.174$, $t_{247} = 2.13$, $P < 0.05$, respectively; Fig. 3). There was a net decrease in the percent of plots occupied for eight other species, *Batrachoseps major*, *B. boreas*, *Coluber constrictor*, *Elgaria multicarinata*, *Eumeces skiltonianus*, *Lampropeltis getula*, *P. coronatum*, and *Pituophis catenifer* (Fig. 5). The racer (*C. constrictor*) and both salamanders (*B. major* and *Ensatina eschscholtzii*) were not detected in any postfire impact plots in CHAP. However, we were not able to test the lower net capture rate of *E. eschscholtzii* because of the low detection rates for this species in the prefire capture results (Table 4).

In CSS, the capture rates of two species, *U. stansburiana* and *A. hyperythra*, were higher in the postfire impact plots ($\Delta C = 0.574 \pm 0.125$, $t_{418} = 4.59$, $P < 0.001$ and $\Delta C = 0.714 \pm 0.125$, $t_{418} = 5.70$, $P < 0.001$, respectively) when compared to the reference plots (Fig. 4). We detected a net change in plot occupancy for four species, *U. stansburiana*, *E. eschscholtzii*, *Masticophis lateralis*, and *C. constrictor*. *Uta stansburiana* increased in the impact plots when compared to the reference plots. The other three species, *E. eschscholtzii*, *M. lateralis*, and *C. constrictor* were detected on fewer impact sample plots after the fire when adjusted for the changes observed in the reference plots (Fig. 5). Although *M. lateralis* was detected at a substantially higher proportion of the reference CSS plots after the fire ($0\% \pm 0$ prefire to $80\% \pm 0.18$ postfire, $P < 0.01$), this species was detected in a lower proportion of the impact plots (dropping from $85\% \pm 0.10$ prefire to $36\% \pm 0.13$ postfire, $P < 0.05$) (Fig. 5).

Community Conversion.—The MDS plot of the capture results, averaged across vegetation type and condensed fire classification, showed that the reptile and amphibian communities at razed plots were different from those documented in the nonrazed plots. Razed CHAP and CSS communities were more like nonrazed GRASS, with a shared similarity of 75% or higher, than their respective nonrazed states (Fig. 6). All combinations of vegetation type and condensed fire classification had a 50% similarity level based on the species documented and the level of detection.

DISCUSSION

Herpetofaunal Community Response to Fire.—The results of our study indicate the coastal southern California herpetofaunal community exhibits a strong response to wildfire within the

TABLE 4. The results of the pitfall trapping effort have been divided based on the four vegetation types and the southern California wildfires of 2003. The value presented is the percentage that each species contributed to the total captures within each vegetation type for each time period. The vegetation types are chaparral (CHAP), coastal sage scrub (CSS), grassland (GRASS), and woodland/riparian (WR).

Common name	Species	CHAP (N = 1,295)		CSS (N = 1,535)		GRASS (N = 221)		WR (N = 305)	
		Prefire	Postfire	Prefire	Postfire	Prefire	Postfire	Prefire	Postfire
Frog/Toads									
Western Toad	<i>Bufo boreas</i>	16.1	4.1	18.2	2.9	2.7	2.3	0.3	8.1
Arroyo Toad	<i>Bufo californicus</i>						0.4		
Pacific Treefrog	<i>Pseudacris regilla</i>	8.7	0.8	5.2	0.9	0.5	0.4	0.3	2.4
American Bullfrog ^a	<i>Rana catesbeiana</i>						1.7		0.2
Western Spadefoot	<i>Spea hammondi</i>	0.3		0.5	0.1	0.9	1.1		
African Clawed Frog ^a	<i>Xenopus laevis</i>		0.1						
Lizards									
Orange-Throated Whiptail	<i>Aspidoscelis hyperythra</i>	4.1	12.2	21.6	24.0	10.0	3.6	2.0	
Coastal Whiptail	<i>Aspidoscelis tigris</i>	4.1	15.1	2.1	5.6	5.0	6.2	8.2	6.7
Western Banded Gecko	<i>Coleonyx variegatus</i>			0.5	0.4				
Southern Alligator Lizard	<i>Elgaria multicarinata</i>	3.9	1.7	4.9	2.3	1.8	2.3	9.2	9.5
Gilbert's Skink	<i>Eumeces gilberti</i>			0.5	1.0			1.0	0.6
Western Skink	<i>Eumeces skiltonianus</i>	7.0	2.8	9.5	5.1	6.8	6.9	11.5	6.7
Coast Horned Lizard	<i>Phrynosoma coronatum</i>	12.0	3.3	1.8	1.4	0.9	0.4		
Western Fence Lizard	<i>Sceloporus occidentalis</i>	22.9	38.6	17.2	33.8	44.8	49.3	55.7	55.0
Granite Spiny Lizard	<i>Sceloporus orcutti</i>	1.6	2.9	0.3	0.9	0.5	0.2	1.6	0.4
Common Side-Blotched Lizard	<i>Uta stansburiana</i>	2.8	13.5	3.6	9.1	19.0	11.3	4.3	4.9
Granite Night Lizard	<i>Xantusia henshawi</i>	0.1	0.4	0.1					
Salamanders									
Garden Slender Salamander	<i>Batrachoseps major</i>	6.5		4.2	3.2	0.5			
Ensatina	<i>Ensatina eschscholtzii</i>	1.4		1.0					
Snakes									
Racer	<i>Coluber constrictor</i>	1.2		0.6		0.5	0.4	2.0	1.2
Speckled Rattlesnake	<i>Crotalus mitchellii</i>		0.3	0.1					
Red Diamond Rattlesnake	<i>Crotalus ruber</i>	0.1		0.3	0.4			0.3	
Western Rattlesnake	<i>Crotalus oreganus</i>	0.8	0.5	0.7	0.9		2.6		0.8
Ring-Necked Snake	<i>Diadophis punctatus</i>	0.5	0.1	0.3	0.3	0.5	0.2	1.0	0.2
Nightsnake	<i>Hypsiglena torquata</i>	0.5	0.5	0.3	0.1		0.3	0.3	0.2
Common Kingsnake	<i>Lampropeltis getula</i>	1.4	0.4	1.5	1.3	2.3	2.6	0.7	0.8
Western Threadsnake	<i>Leptotyphlops humilis</i>			0.5	1.4	0.5	0.6	1.0	0.4
Rosy Boa	<i>Lichanura trivirgata</i>				0.1				
Coachwhip	<i>Masticophis flagellum</i>	0.2	0.1	0.2	0.3		1.1		
Striped Racer	<i>Masticophis lateralis</i>	1.5	1.8	1.4	2.1	0.5	0.2	0.3	0.6

TABLE 4. Continued.

Common name	Species	CHAP		CSS		GRASS		WR	
		Prefire (N = 1,295)	Postfire (N = 757)	Prefire (N = 1,535)	Postfire (N = 941)	Prefire (N = 221)	Postfire (N = 533)	Prefire (N = 305)	Postfire (N = 493)
Gophersnake	<i>Pituophis catenifer</i>	1.5	0.7	1.6	0.5	1.4	2.1	0.3	1.2
Long-nosed Snake	<i>Rhinocheilus lecontei</i>	0.3	0.1	0.1	0.1		0.2		
Western Patched-Nosed Snake	<i>Salvadora hexalepis</i>		0.1	0.4	0.6				
Western Black-Headed Snake	<i>Tantilla planticeps</i>	0.1	0.1	0.7	0.1	1.4	2.8		
Two-Striped Gartersnake	<i>Thamnophis hammondi</i>	0.5	0.3	0.4	0.5		0.2		
Western Lyresnake	<i>Trimorphodon biscutatus</i>	0.1							

^aSpecies introduced into California.

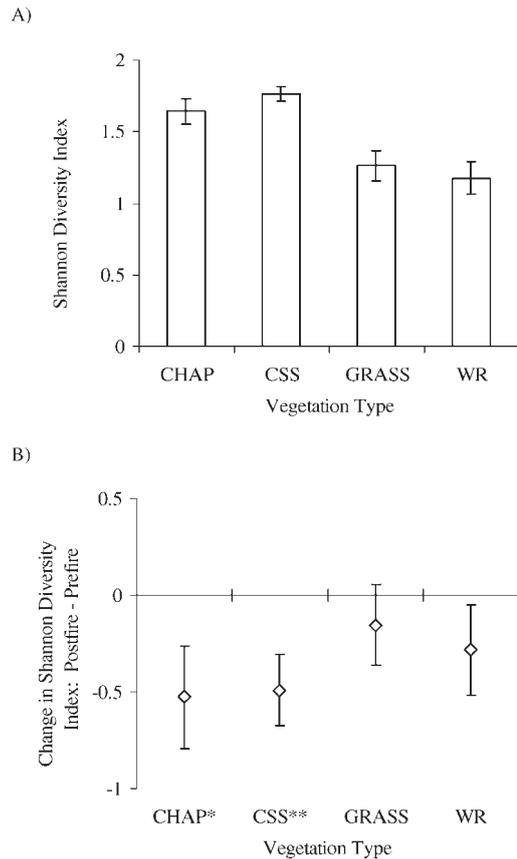


FIG. 2. (A) The average Shannon Diversity Index, with standard error bars, shows that the prefire reptile and amphibian communities in chaparral (CHAP) and coastal sage scrub (CSS) were higher than those in either grassland (GRASS) or woodland/riparian (WR) plots. (B) The net change, prefire to postfire, in the Shannon Diversity Index with standard error bars shows that there were significant losses in diversity within chaparral and coastal sage scrub but not in grasslands or woodland/riparian plots. Levels of significance are indicated as * ($P \leq 0.05$) and ** ($P \leq 0.01$).

first three years postfire. This response is not consistent between vegetation types, because the changes to the herpetofaunal community were great in chaparral and coastal sage scrub habitats, whereas only minimal in grassland and woodland habitats. Within chaparral and coastal sage scrub vegetation structure, measured as shrub and tree cover, decreased by 53% and 75%, respectively, at the impact plots in the two to three years after the fires. This decline in cover was accompanied by significant decreases in herpetofauna species diversity and changes in herpetofauna community composition. Interestingly, razed CHAP and CSS herpetofauna communities were more similar to those

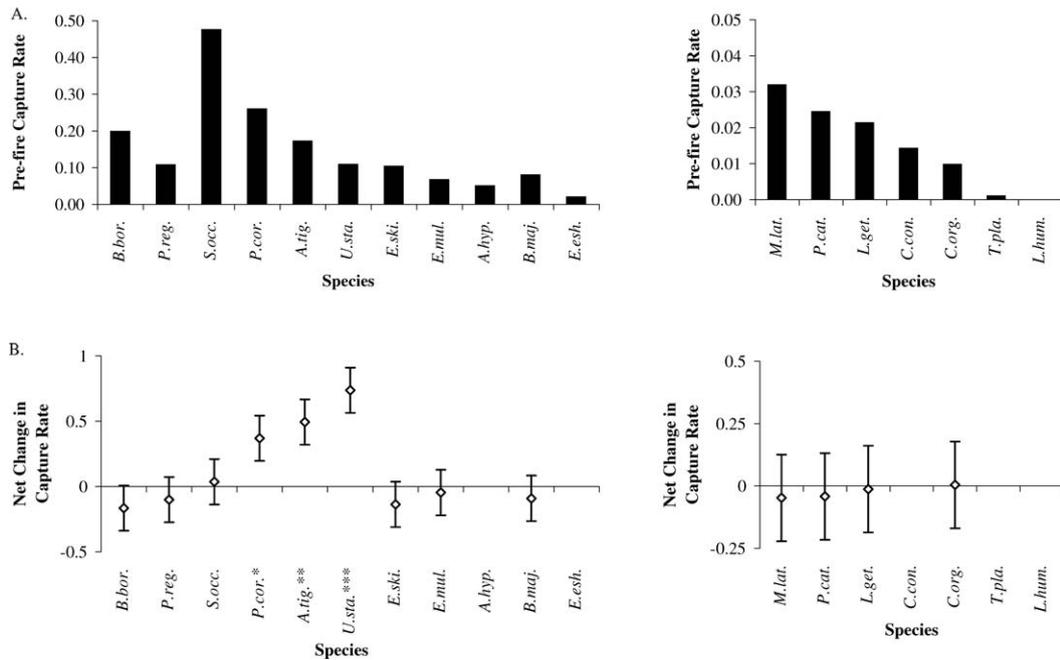


FIG. 3. (A) Prefire capture rates are shown for the 18 focal species in chaparral. (B) The net change in capture rate between the impact and reference study plots prefire to postfire. Error bars represent one standard error. In both A and B, note the difference in the scale of the y-axis. *Aspidoscelis hyperythra*, *Ensatina eschscholtzii*, *Coluber constricto*, *Tantilla planiceps*, and *Leptotyphlops humilis* were not tested for changes in net capture rate due to the limited number of plots at which they were detected. Significance values are presented as * ($P \leq 0.05$), ** ($P \leq 0.01$), and *** ($P \leq 0.001$).

of the less diverse nonrazed GRASS (Fig. 6). For both the CHAP and CSS vegetation communities, postfire recovery can take several years and is likely dependent upon fire return intervals and precipitation patterns (Keeley and Keeley, 1981). Herpetofaunal communities in these vegetation types may also be expected to follow a similar pattern of recovery or community transition. Monitoring efforts of the postfire condition of the impact and reference plots is ongoing, and future analyses will have the ability to track the longer-term response of the herpetofaunal community in these two shrub lands to wildfire.

In contrast to CHAP and CSS, the herpetofaunal communities in our GRASS plots showed little response to fire. The annual grasses that were present before the fires returned the following year, providing nearly the same level of vegetative structure and cover for the same reptile and amphibian communities. Herpetofaunal species diversity and community composition in WR changed little, as in GRASS, but for potentially different reasons. The WR category represents several environments that may be more resistant to the impacts of fires or, as Wells et al. (2004) suggest, may have received higher levels of fire suppression efforts during

the fire events. Riparian environments, containing higher levels of moisture, may burn incompletely, maintaining some of the prefire structure and may act as refugia for the animals sheltering within. In many cases, the large trees in the woodlands and forests survived the fires, as evidenced by little change in the shrub and tree cover after the fires in these environments, but even dead trees can serve as cover for many species. Greenberg et al. (1994) also saw little to no impact to reptiles and amphibians in burned sand-pine scrub forests in their study in the southeastern United States.

Individual Species Responses.—Fire can have both direct and indirect impacts on individual species. Besides direct mortality from the fires, herpetofauna species may be impacted by subsequent postfire changes in habitat suitability and predator-prey dynamics (Lillywhite and North, 1974; Means and Campbell, 1981). We do not believe that direct mortality played a large role in the observed species declines because most reptiles are known to seek refuge in underground rodent burrows, disperse, or find shelter in nearby unburned refugia (see review by Russell et al., 1999). Similarly, many amphibians, such as *Batrachoseps*, shelter underground to avoid the normal heat and dryness

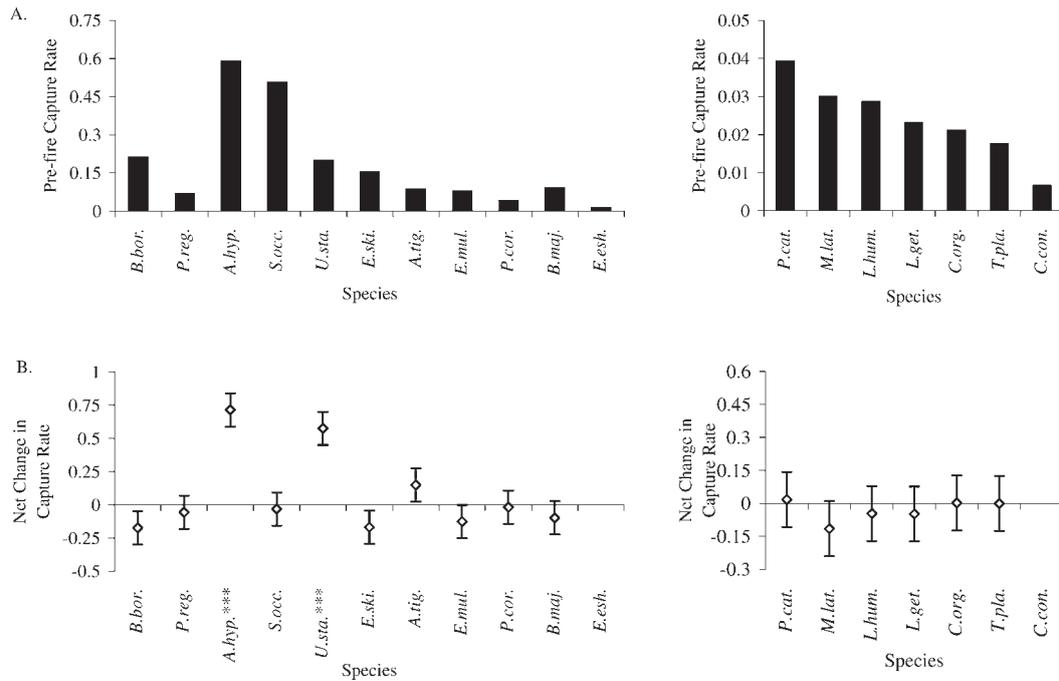


FIG. 4. (A) Prefire capture rates are shown for the 18 focal species in coastal sage scrub. (B) The net change in capture rate between the impact and reference study plots prefire to postfire. Error bars represent one standard error. In both A and B, note the difference in the scale of the y-axis. *Ensatina eschscholtzii* and *Coluber constrictor* were not tested for changes in net capture rate because of the limited number of plots at which they were detected. Significance values are presented as *** ($P \leq 0.001$).

associated with southern California summers (Cunningham, 1960). The 2003 fires occurred when severe weather conditions associated with the wildfires (fast dry winds; Keeley et al., 2004) would not have been conducive to amphibian surface activity. We suspect the indirect effects of the fire, such as changes in habitat suitability and predator-prey dynamics were largely responsible for the changes we observed in the abundance and distribution of herpetofauna species.

The CSS and CHAP plots both lost substantial amounts of shrub and tree cover. The fires also removed much of the downed wood and leaf litter cover in these plots leaving sparse shrubs and vast amounts of open ground. These conditions may be suitable for habitat generalist and open habitat specialist species. Our results support this hypothesis, because the most abundant reptile, *S. occidentalis*, remained so in both CSS and CHAP after the fires. *Sceloporus occidentalis* is a generalist that thrives in many types of habitats across the western United States (Rose, 1976; Stebbins, 1985). We also documented increased numbers for species that specialize in the use of open habitats, such as *U. stansburiana* and *Aspidoscelis* in CSS and CHAP and increased numbers of *P. coronatum* in CSS.

These species all typically prefer to forage on open ground for insects and other arthropods (Stebbins, 1985). *Aspidoscelis* species are known to actively forage in open habitats (Milstead, 1957; Pianka, 1970). The higher detection rates for these species may also be related to changes in behavior associated with the loss of shrub and tree cover, making each more detectable by our sampling technique.

These results largely support those from previous studies. For instance, *S. occidentalis* has been shown to survive fires in chaparral and even selectively favor postburn vegetation (Kahn, 1960; Lillywhite and North, 1974). Increases in *Aspidoscelis* species after disturbance have also been documented elsewhere. In the southeastern United States, *Aspidoscelis sexlineata* increased in burned sandhill plots (Mushinsky, 1986) and preferred disturbed areas in sand-pine scrub (Greenberg et al., 1994).

In CHAP, *P. coronatum* numbers decreased in both impact and reference areas. However, the decrease in the impact arrays was less than that of the reference arrays, indicating a favorable response to the fires. This is consistent with Wilgers and Horne (2006) who found that a closely related species, *P. cornutum*, preferred

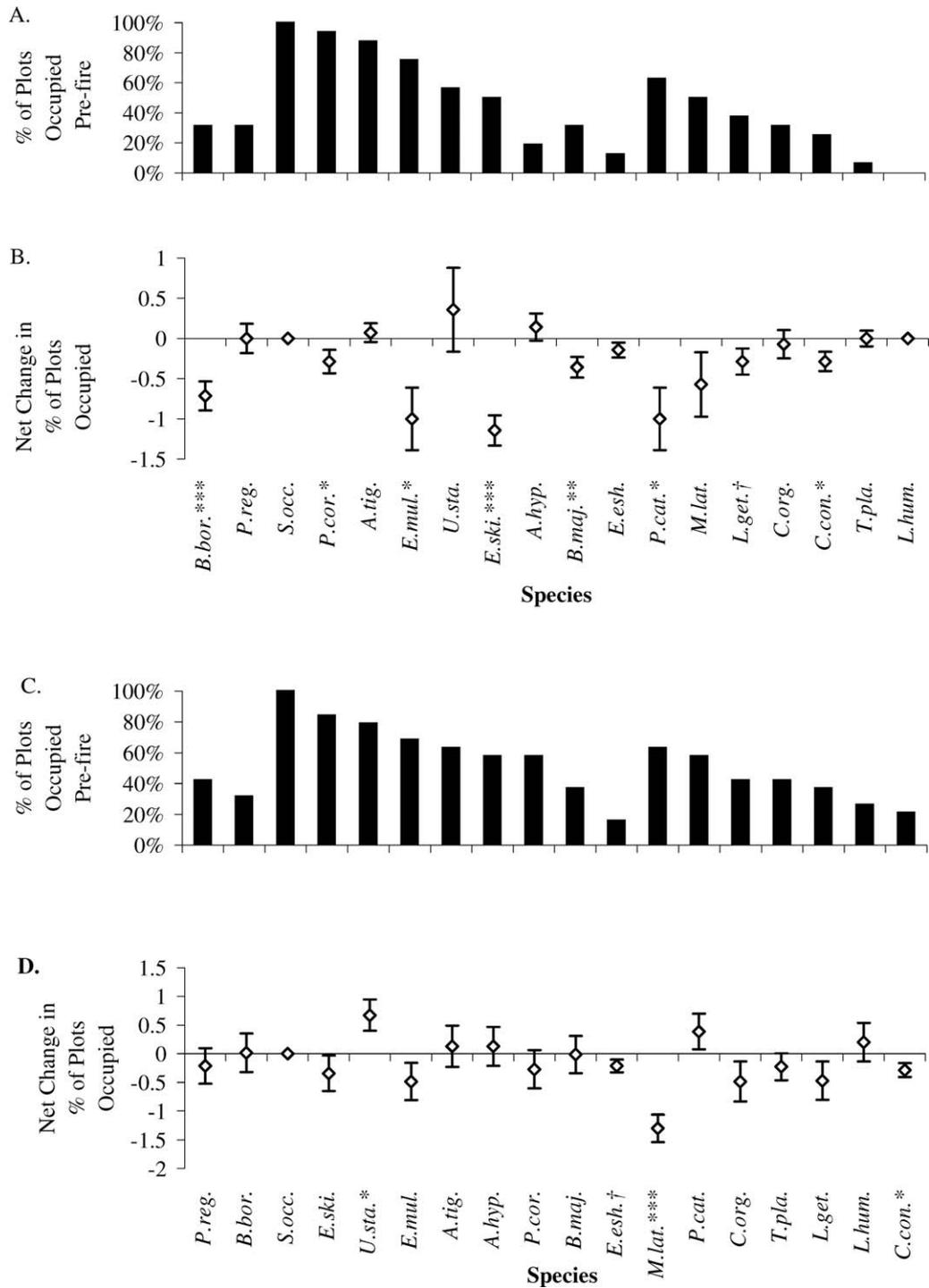


Fig. 5. Occupancy results are shown for chaparral (A and B) and coastal sage scrub (C and D). (A and C) The percent of plots occupied by each species prefire within each vegetation type. (B and D) The net change in the percentage of plots occupied prefire to postfire. Significance values are presented as † ($P \leq 0.10$), * ($P \leq 0.05$), ** ($P \leq 0.01$), and *** ($P \leq 0.001$).

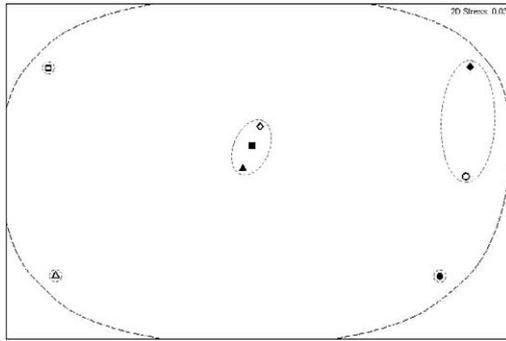


FIG. 6. Nonmetric multidimensional scaling plots (MDS) based on Bray-Curtis similarity matrix using square-root transformed capture data averaged across all plots within each vegetation type show how the reptile and amphibian communities in razed plots have shifted away from the communities detected in the nonrazed plots. Open symbols represent nonrazed plots, and closed symbols represent razed plots. Vegetation types are presented as follows: chaparral = triangles, coastal sage scrub = squares, grassland = diamonds, and woodland/riparian = circles. The outer, dashed, black line represents a 50% similarity level. The inner, dashed, grey line represents a 75% similarity level. The razed chaparral and coastal sage scrub plots are more similar to the nonrazed grass plots than they are to the original prefire and unburned conditions.

tallgrass prairie that underwent annual burn treatments. *Phrynosoma coronatum* is both a habitat and dietary specialist because it is a predator of native harvester ant species that forage in open habitats. Although *P. coronatum* may be highly sensitive to changes in the native invertebrate community (Suarez et al., 2000), we have not detected an overall loss of native harvester ants in our post-fire sample plots (Matsuda et al., unpubl. data). Because its prey base appears intact, this species likely benefited from the increase in open habitat for foraging in the impact areas. This species decreased in both impact and reference plots, and its detection at a lower proportion of plots after the fire may be a result of fire mortalities or other unknown environmental or species demographic factors. We speculate that the movement of *P. coronatum* from unburned refugia into the newly open habitat may help explain their relative increase in the impact areas. Further research may be needed to fully understand the status and response of this species to fires in southern California.

We expected to find an increase in the area occupied by the toad *B. boreas* after the fire in CHAP and CSS, because toads use these habitats for foraging and overwintering. The newly opened habitat should have allowed the toads to move greater distances into the

uplands. Guscio (2007) found *B. boreas* significantly preferred the severely burned habitats in Glacier National Park. Additionally, similar increases have been reported for other Bufonids (*Bufo americanus*, *Bufo quercicus*) in the burned Appalachian deciduous forests and burned long and shortleaf pine stands (Means and Campbell, 1981; Kirkland et al., 1996). In our study, we found increases in the area occupied by *B. boreas* in both impact and reference CHAP and CSS, with relatively greater increases in the reference plots. This resulted in a significant decrease in impacted CHAP and no net change in impacted CSS. In our upland shrub study systems, the impacted habitats did not appear to favor increased toad activity. We suspect that the high rainfall in 2005 may have been responsible for the observed postfire increases in the number of plots occupied.

In contrast to the generalists and open habitat specialists, species that are associated with moist microhabitats, such as the areas under decaying wood and leaf litter, were found in a lower proportion of the impacted CSS and CHAP plots after the fire. These included the salamanders (*B. major* and *E. eschscholtzii*) and the alligator lizard (*Elgaria multicarinata*) (Fig. 5).

In CHAP, *B. major* and *E. eschscholtzii* were detected in 14–36% of study plots before the fire, but neither species was detected after two years of comprehensive postfire sampling. These species, like all salamanders, are associated with moist habitats and understory cover. For instance, Wisely and Golightly (2003) reported *Batrachoseps attenuatus* and *E. eschscholtzii* were found more frequently beneath leaf litter than on bare ground during dry conditions, and Dupuis et al. (1995) found that older stands of habitat, with more cover items and understory, supported larger numbers of salamanders in Canadian forests. Similarly, *E. multicarinata* is known to occupy areas with moist dense vegetation and forage for arthropods in leaf litter (Stebbins, 1985). The San Diego fires, particularly in chaparral, burned nearly all of the leaf litter and understory vegetation. Because of the increased evaporation and reduced ability of water to penetrate exposed burned soils, burned sites have significantly lower soil moisture levels than unburned sites (Christensen and Muller, 1975). As Heisler et al. (2004) found, the loss of aboveground vegetation may result in increased soil surface temperatures at burned plots. The loss of soil moisture, leaf litter, and near-soil surface structure, combined with increased surface temperatures, has likely made the habitat unsuitable for these species.

The snake species that we detected did not appear to follow any pattern that we would have predicted based upon their common life-history characteristics. We detected several species in a lower number of sample plots after the fires in both CHAP and CSS habitats. This included species that are habitat generalists or prefer open grassy habitats. We found decreased occupancy for *L. getula* and *C. constrictor* in both habitats, *P. catenifer* in chaparral, and *M. lateralis* in CSS. Also, these species had lower postfire capture rates, although not significant.

Although there have been several studies documenting the immediate responses of snakes to fire (Mushinsky and Witz, 1993; Rudolph et al., 1998; Smith et al., 2001), few have assessed snake populations in burned habitats several years following a fire (see review by Russell et al., 1999). Also, some studies report conflicting results. For example, in our study, *C. constrictor* ranged in occupancy from 27–29% in CSS and CHAP before the fire (Fig. 5) in contrast to no detections in either vegetation type after the fire (Table 4). These data are consistent with Cavitt's (2000) results in tallgrass prairies, who found that *C. constrictor* respond negatively to burned areas. In the same habitat, Wilgers and Horne (2006) report that *C. constrictor* is found marginally more in burned areas and hypothesize the difference in results was caused by sampling methods. They indicated that their use of coverboards may have increased capture probabilities in the burned area in comparison to Cavitt's (2000) study. We are confident that the technique we used here, pitfall and funnel traps, adequately sampled *C. constrictor* based on our prefire results in CHAP and CSS habitats and the eight animals documented postfire in the other two vegetation types. These differences in findings for *C. constrictor* may relate to preferences at the subspecies level, fire intensity, or other unknown factors.

The loss of cover in the understory of these habitats may have resulted in less favorable conditions, making it more difficult for snakes to hunt and forage for the small mammals and lizards upon which they prey. It is also possible that the declines in snakes are associated with reduced prey availability. Rabbits and rodents are a common food item for many of the larger snake species. Although generalist rodents appear to be plentiful in the postfire CSS and CHAP habitats, the larger prey species, such as rabbits, woodrats, and voles may suffer high levels of mortality during fires and be sparse in postburn areas (Lechleitner, 1958; Wirtz et al., 1988; Clark et al., unpubl. data). Finally, total captures ranged from 39–81 individuals for each of our reported snake species. This is substantial but still low when compared to the 224–1,973 individuals captured for each of our reported

lizard species. The low number of snake captures and the potential biases discussed below likely reduced our ability to detect any changes that may have occurred in this taxonomic group.

Caveats.—Although we were able to show variations in unburned and burned plots within vegetation communities, changes in individual species capture and occupancy rates, and shifts in the overall community structure, there are several potential confounding factors that may have influenced our results and warrant discussion. Natural fluctuations in seasonal weather patterns and the responses of animals to these patterns, may lead to biases in the capture results (Whelan, 1995). For instance, prefire data were collected at different times among our sites. The prefire data for CED and ELL span the years from 1995 through 2001 (Table 3), which, because of an El Niño weather pattern, included an extremely wet year, 1998, possibly bolstering amphibian numbers during this time period. We began collecting prefire data for RAJ and SYR in 2001 and 2002, respectively, both relatively dry years. The postfire data for all sites began in 2005, another wet year. Therefore, the capture data for two of our sites from before the fires may underrepresent those species heavily associated with moisture, whereas prefire data from the other two sites may overrepresent these species. The differences in our sampling efforts may have led to a lower number of detected species within the prefire data for RAJ and SYR. Additional complications may stem from the differences in the fire patterns experienced by the vegetation types in which we conducted our studies; more shrub lands of San Diego have burned more frequently than the other vegetation types that we considered (Wells et al., 2004). Given these limitations, we were careful to test for postburn effects on only the most numerous species and to examine the data thoroughly for any possible biases so as not to present spurious results.

Community Conversion and Future Directions.—In the first two years of research following the wildfires, the reptile and amphibian communities in razed CHAP and CSS have become more similar to that of nonrazed GRASS (Fig. 6). Continuing to study the recovery processes of both the vegetation and animals on these burned plots will serve to tell us whether the herpetofauna follow the same trends as Zedler et al. (1983) and Keeley (2005) have reported for the vegetation on chaparral and coastal sage scrub shrub lands. Under repeated short-return interval fire events, the potential exists that both the vegetation and reptile and amphibian communities will transition to grassland communities and not rebound to those of intact,

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unburned chaparral and coastal sage scrub. As our efforts continue over the three years subsequent to the data presented here, it will be interesting to see whether the communities in the burned shrub lands return to that of the unburned and prefire state.

Although the grasslands we studied did not have the lowest species diversity that we detected, herpetofaunal diversity was substantially lower in grasslands than what we found in either shrub land. Of the 34 native species we detected overall, 10 were never detected in any of the grassland plots (Table 4). Under the scenario of repeated burning, we would expect the shrub lands to become even more like the grasslands, with respect to both the vegetation composition and the herpetofauna community. As wildfires recur in the shrub lands, we expect there to be a decline in the amount of accumulated leaf litter covering the ground and cascading environmental changes that follow this loss. Many of the grasslands in which we work are often dense, monocultures of *Avena* spp. with little structural variability and few open areas, presenting reptiles and amphibians with limited options with regards to foraging behavior and thermoregulation. With the research that we have conducted beyond that presented here, we hope to observe whether the reptile and amphibian community within the impacted shrub land plots recover following a pattern similar to that of the vegetation.

During the preparation of this manuscript, San Diego experienced another severe fire event in October 2007, wherein many of our study plots burned again. We will continue to study these plots to document the processes of recovery and community dynamics. Although this study was not originally designed to investigate the effects of repeated fires on the landscape, it will become one out of necessity. Our postfire survey efforts are scheduled to continue for three additional years, for a total of five years of postfire results. At the conclusion of our efforts, we will reanalyze the dataset to investigate the results and postfire recovery of these study plots and the impacts of repeated, short-return interval fires.

Conclusion.—The southern California wildfires of 2003 impacted the herpetofaunal species diversity and community structure in chaparral and coastal sage scrub study plots. We detected significant shifts in species diversity and community composition in these vegetation types where the fire substantially reduced the cover of shrub and tree species. No changes in diversity or community composition were measured in grasslands or woodland/riparian plots where vegetative structure was not substantially affected by the fires.

We measured changes in the capture rates of individual species in the postfire burned study plots. Many were largely predictable based upon shared life-history characteristics and habitat preferences. In coastal sage scrub and chaparral, we detected increases in the capture and occupancy rates of generalist and open habitat specialists such as *A. tigris*, *A. hyperythra*, *P. coronatum*, *U. stansburiana*, and a decreased occupancy rate of closed habitat specialists, such as the salamanders (*B. major* and *E. eschscholtzii*) and *E. multicolorata*. Several snake species showed a negative response to the burned habitats. Most important, the herpetofauna communities in burned coastal sage scrub and chaparral were more similar to those of unburned grasslands. We will continue to monitor these communities to document the longer-term effects in light of the more frequent fire regime in southern California.

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