RESPONSE OF AN AVIFAUNAL COMMUNITY TO THE LA TUNA FIRE IN THE VERDUGO MOUNTAINS OF SOUTHERN CALIFORNIA

SHANE E. JORDAN, Department of Biology, California State University, Northridge, California 91330; shane.jordan@csun.edu

RICHARD RACHMAN, Department of Biological Sciences, Boise State University, Boise, Idaho 83725; richardrachman@u.boisestate.edu

ABSTRACT: In California's coastal sage scrub and chaparral, fire reshapes the distribution of vegetation and the composition of bird communities, although the direction of the response in various habitats remains unclear. We investigated changes in the bird community at one site following the 2017 La Tuna Fire in the Verdugo Mountains of southern California. We found that the community's diversity and evenness did not change, but the structure of foraging guilds did. Counts of omnivores and aerial and generalist foragers increased significantly, whereas counts of granivores and shrub foragers decreased. The number of insectivores decreased slightly, and ground foragers appeared unaffected. Principal components analysis suggests positive, neutral, and negative responses of birds associated with these guilds were driving differences in their abundances after the fire. We show how post-fire bird distributions may be related to fire severity, vegetation structure, and interspecific interactions. However, differences between our results and those of other studies suggest that patterns of bird community response to wildfire may be dictated by factors both related and unrelated to the fire over broader time scales.

The effect of wildfire on southern California's flora and fauna is an area of continuing interest in ecology. However, post-fire changes to avifaunal communities in disturbed coastal sage scrub and chaparral have received limited attention and thus remain poorly understood. Some researchers have reported a decrease in avian species diversity in these habitats after fire (Moriarty et al. 1985, Stanton 1986, Newman et al. 2018), but others have reported an increase (Wirtz 1982, Mendelsohn et al. 2008). Studies of the effects on the proportions of feeding guilds have been more consistent but still not uniform (Wirtz 1979, 1982, Newman et al. 2018). For example, Newman et al. (2018) found that in chaparral prescribed fire had no effect on avian foraging guilds, whereas mechanical vegetation removal was associated with increased numbers of granivorous species. Additional study is needed to improve our understanding of the consequences that various fire regimes in California's shrublands have for bird distribution and community structure, especially as these regimes change.

Various environmental factors can affect avian communities after disturbance. Longhurst (1978) hypothesized that heterogeneous seral plant communities provide better habitat for many bird species as well as their prey because fire stimulates an abundance of new plant growth that may be more nutritious than older vegetative foods. Likewise, Knick et al. (2005) emphasized the importance of fire-mediated landscape heterogeneity for maintaining avian diversity in sagebrush-dominated habitats. From these studies one might predict that wildfire should benefit birds. In addition, many birds may favor the edge effects arising from disturbance (Brawn et al. 2001). Research in these seral communities has shown that changes in vegetation cover can

Western Birds 55:116–129, 2024; doi 10.21199/WB55.2.3

be predictors of avian community structure (Stanton 1986, Brawn et al. 2001, Mendelsohn et al. 2008). Successional periods after chaparral wildfires can be positive, neutral, or negative for birds (Hargrove and Unitt 2018). Thus species vary in their responses to wildfire, probably because of differences in habitat preference. Birds that prefer open habitat for foraging may benefit, whereas those that require cover may not. It should therefore be expected that wildfire reshapes the diversity and guild structure of bird communities.

The 2017 La Tuna Fire provided an opportunity to study a bird community's response to environmental change that may be related to an altered disturbance regime. We assessed whether (1) bird diversity and community evenness increased or decreased after the fire and (2) whether the structure of feeding guilds and use of foraging substrates changed. Because the fire regime in coastal sage scrub and chaparral is likely to be affected by future climate change, monitoring birds' response is important to understanding changes in biodiversity within this ecosystem. These communities will be particularly sensitive as urbanization and environmental change encroach upon ecosystem processes (Brawn et al. 2001). Frequent and intense fires can drive type conversion of these habitats (Keeley 2005, Keeley and Pausas 2019), especially as more invasive non-native species become naturalized in disturbed areas of southern California's shrublands, causing subsequent biodiversity losses.

METHODS

In September 2017 the La Tuna Fire burned 29.11 km^2 within the Verdugo Mountains (Figure 1). Previously, the area was covered by climax mixed coastal sage scrub and chaparral, characterized by a high density of shrubs mostly 1–3 meters tall (Figure 2, Jordan pers. obs.). Dominant plant species included the California Sagebrush (*Artemisia californica*), California Buckwheat (*Eriogonum fasciculatum*), Laurel Sumac (*Malosma laurina*), Black Sage (*Salvia mellifera*), Blue Elderberry (*Sambucus cerulea*), and Lemonadeberry (*Rhus integrifolia*). By the spring of 2019, few new shoots in the study area exceeded a height of 1 meter, although taller snags remained (Figure 2, Jordan pers. obs.). At this time the vegetation included a few recovering native shrubs such as *A. californica*, *M. laurina*, and *S. cerulea*, but the most abundant plant species were the native subshrub Deerweed (*Acmispon glaber*), invasive grasses such as *Bromus* spp., and the invasive forb *Brassica nigra*.

In 2016, Jordan selected a site in the Verdugo Mountains for monitoring bird communities in mixed coastal sage scrub and chaparral. All birds within ~25 m of a 2–km transect on a ridge above La Tuna Canyon, at an average elevation of 410 meters were recorded (Figures 1 and 2). From 19 April to 6 June 2016, six late-afternoon surveys each with 2.5 hours duration were completed (14 hours total). Following the same protocol 18 months after the fire, from 26 March to 2 May 2019, another six surveys were completed along the same transect (14.5 hours total).

Remote-sensing data, based on spectral reflectance in satellite imagery (Landsat 8 with 30 × 30-meter resolution; $n = 126$ quadrats), allowed us to quantify the magnitude of vegetation change due to the fire along the survey transect by means of the normalized difference vegetation index (NDVI).

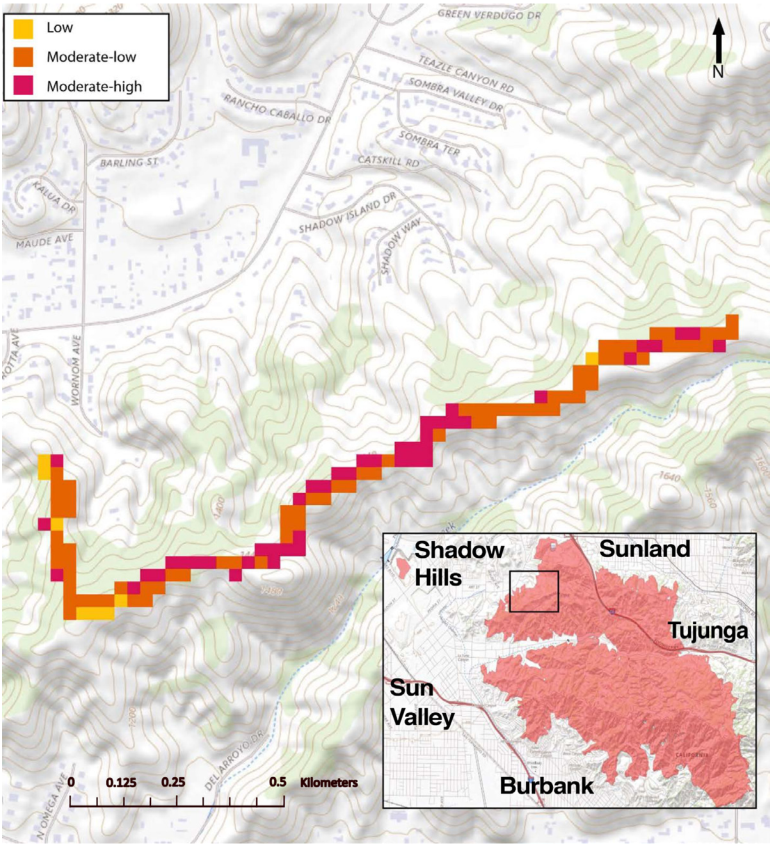

FIGURE 1. Area of sampling location in the Verdugo Mountains with 30 × 30-m burn-severity quadrats along the transect coded by categories of the difference-normalized burn ratio (dNBR). Inset map at lower right shows the 2017 La Tuna Fire's perimeter with black rectangle showing the location of the monitoring transect; fire perimeter from Monitoring Trends in Burn Severity (https://www.mtbs.gov/).

Values greater than 0.3 indicated cover by a canopy, whereas values near zero indicated bare soil. We then used the difference normalized burn ratio (dNBR), based on changes in spectral reflectance along the transect before and after the fire, to estimate the fire's severity. Following Key and Benson (2006), we classified values of this ratio into three categories: low (<0.27), moderate-low (0.27–0.44), and moderate-high (0.44–0.66). We selected these categories because patchy shrublands are less prone to high-intensity crown fires than are areas with more contiguous woody vegetation (Keeley et al. 2008). This ratio was calculated from both pre-fire and post-fire values as (band 5 – band 7)/(band 5 + band 7). The NDVI was calculated as (band 5 – band 4)/(band 5 + band 4). Using this imagery, band 4 has a wavelength of

Figure 2. Vegetation along the transect through the Verdugo Mountains showing the severity of the 2017 La Tuna Fire and the ensuing habitat change. (A) 1½ years before the fire (spring 2016); (B) 1½ years after the fire (spring 2019).

0.64–0.67 μm (red), band 5 has a wavelength of 0.85–0.88 μm (near-infrared), and band 7 has a wavelength of 2.11–2.29 μm (short-wave infrared II). Pre-fire data were based on images taken in August 2017; post-fire images were taken in September 2017. Rachman processed the data in ERDAS Imagine (Hexagon, Stockholm) and generated the maps in ArcMap (ESRI, Redlands, CA).

Because observations were limited to one site, we treated bird counts along each transect as replicate samples. We quantified diversity with Shannon's index (H') and compared pre-fire and post-fire results with a two-sample t-test in Microsoft Excel (version 2206). Evenness was then calculated as $H'/\ln s$, where s = species richness, and likewise compared with a two-sample t-test. The assumptions of a general linear model were met for both variables. Following De Graaf et al. (1985), we categorized each species' feeding guild as (1) granivore, (2) insectivore, (3) nectarivore, (4) carnivore, or (5) omnivore. Likewise, we categorized foraging substrates as (1) aerial, (2) shrub, (3) ground, or (4) generalist. Feeding-guild and substrate classifications were based on main food preferences (according to apparent breeding or nonbreeding status) and most common foraging locations, as described in the life-history accounts for each species available from the California Department of Fish and Wildlife document library (https://nrm.dfg.ca.gov/documents/Default.aspx; Table 1).

To analyze the difference between pre-fire and post-fire surveys in the counts of birds by feeding guild and foraging substrate, we performed two separate likelihood-ratio (G) tests of independence by using the function *GTest* in R (R Core Team 2020). Because counts of flower-specialist shrub foragers also represent counts of nectarivores, we did not include them in the test for substrate differences. Then we used a covariance matrix of the count data in a principal-components analysis (by means of the function *princomp* in R) to investigate which guilds and substrates might explain the difference between pre-fire and post-fire transects. We determined the number of principal components to be analyzed from a scree plot showing the explained variance of each axis, generated with the function *fviz_eig* in R (Figure 3). Finally, using general linear models created with the function *anova* in R, we tested the principal-component scores from the axes explaining the most variance in guilds and substrates as one-way analyses of variance (ANOVA).

RESULTS

The mean NDVI within the study site changed from 0.3527 before the fire to 0.1668 one month after the fire, illustrating a significant loss in vegetation cover (paired t-test: $t = 43.4$, df = 125, $P < 0.0001$; Figure 4a). The post-fire dNBR of the 126 quadrats within our study site ranged from 0.20 to 0.58; 6.4% ranked low, 59.5% moderate-low, and 34.1% moderate-high (Figures 1 and 4b), showing how fire intensity varied. Lower severity is typical of forb and grasslands, whereas higher severity is typical of sage scrub and chaparral (Moreno and Oechel 1991). Generally, severity increases with the abundance of woody vegetation (Bolger 2002, Keeley and Brennan 2012). Before the fire, the transect site comprised a patchy mix of these vegetation types, so it is not surprising that most of our dNBR values indicated the fire was of moderate-low severity.

As measured by Shannon's index, the bird diversity on pre-fire and post-fire

Table 1 Numbers of Birds Counted in Pre-Fire and Post-Fire Transects of the Verdugo Mountains, and the Assignment of Species to Guild

Species	Common name	Pre-fire	Post-fire	Feeding guild	Foraging substrate
Accipiter cooperii	Cooper's Hawk	1	2	Carnivore	Aerial
Aphelocoma californica	California Scrub Jay	21	44	Omnivore	Generalist
Baeolophus inornatus	Oak Titmouse	1		Omnivore	Generalist
Buteo jamaicensis	Red-tailed Hawk	4	7	Carnivore	Aerial
Callipepla californica	California Quail	4	4	Granivore	Ground
Calypte anna	Anna's Hummingbird	5	12	Nectarivore	Flower[a]
Cardellina pusilla	Wilson's Warbler		2	Insectivore	Shrub
Cathartes aura	Turkey Vulture	4	2	Carnivore	Ground
Corvus brachyrhynchos	American Crow	16		Omnivore	Ground
Chamaea fasciata	Wrentit	33	7	Insectivore	Shrub
Chordeiles acutipennis	Lesser Nighthawk	2		Insectivore	Aerial
Corvus corax	Common Raven		38	Omnivore	Ground
Dryobates nuttallii	Nuttall's Woodpecker	1		Insectivore	Shrub
Haemorhous mexicanus	House Finch	31		Granivore	Ground
Icterus cucullatus	Hooded Oriole	1		Insectivore	Shrub
Melospiza melodia	Song Sparrow		1	Omnivore	Ground
Melozone crissalis	California Towhee	21	24	Omnivore	Ground
Mimus polyglottos	Northern Mockingbird	1	2	Insectivore	Generalist
Passerina amoena	Lazuli Bunting		13	Omnivore	Generalist
Phainopepla nitens	Phainopepla	4		Omnivore	Generalist
Pipilo maculatus	Spotted Towhee	18	11	Omnivore	Ground
Piranga ludoviciana	Western Tanager		1	Omnivore	Generalist
Pheucticus melanocephalus	Black-headed Grosbeak	2	4	Insectivore	Generalist
Psaltriparus minimus	Bushtit	36	4	Insectivore	Shrub
Sayornis saya	Say's Phoebe		2	Insectivore	Aerial
Selasphorus sasin	Allen's Hummingbird		4	Nectarivore	Flower[a]
Setophaga coronata	Yellow-rumped Warbler	1	14	Insectivore	Generalist
Setophaga nigrescens	Black-throated Gray Warbler		1	Insectivore	Shrub
Setophaga townsendi	Townsend's Warbler		1	Insectivore	Shrub
Sialia mexicana	Western Bluebird	1	11	Omnivore	Generalist
Spinus psaltria	Lesser Goldfinch	17	28	Granivore	Shrub
Sturnella neglecta	Western Meadowlark		2	Insectivore	Ground
Thryomanes bewickii	Bewick's Wren	9		Insectivore	Shrub
Toxostoma redivivum	California Thrasher	12	12	Insectivore	Ground
Tyrannus verticalis	Western Kingbird		44	Insectivore	Aerial
Zenaida macroura	Mourning Dove	53	17	Granivore	Ground
Zonotrichia leucophrys	White-crowned Sparrow		36	Omnivore	Ground

[a] Shrub forager that feeds on flowers.

surveys did not differ significantly ($t = -0.73$, df = 10, $P = 0.48$; Figure 5a), and neither did evenness ($t = 0.24$, df = 10, $P = 0.82$; Figure 5b). There was, however, a highly significant difference in the counts of species by feeding guild ($G = 69.6$, df = 4, $P < 0.0001$; Figure 6a) and foraging substrate ($G = 90.8$, df = 3, $P < 0.0001$; Figure 6b). Counts of granivores were lower (105 pre-fire vs. 49 post-fire, a 53% decrease), whereas those of omnivores were higher (83 pre-fire vs. 193 post-fire, a 133% increase). Counts of insectivores decreased only

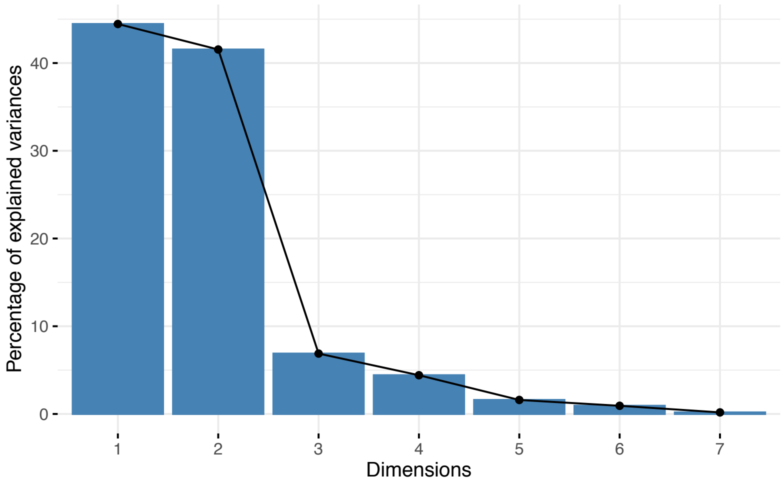

FIGURE 3. Scree plot showing variance explained by each principal component (i.e., dimension). The first two components explained 86% of the variance and were selected for analysis.

slightly (97 pre-fire vs. 81 post-fire). Assessing the response of nectarivores (9 pre-fire vs. 16 post-fire) and carnivores (9 pre-fire vs. 11 post-fire) is impaired by their low sample sizes. The comparison of foraging substrates revealed increases in counts of aerial foragers (7 pre-fire vs. 55 post-fire, a 686% increase) and generalists (31 pre-fire vs. 89 post-fire, a 187% increase), but a decrease in counts of shrub foragers (97 pre-fire vs. 43 post-fire, a 56% decrease). The abundance of ground foragers changed little (159 pre-fire vs. 147 post-fire).

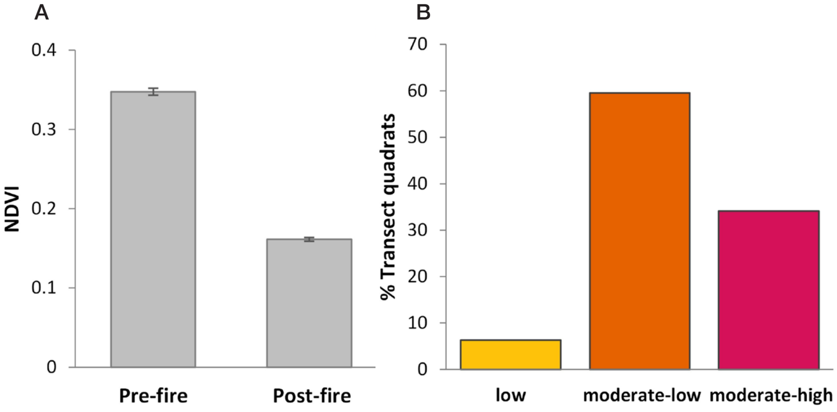

FIGURE 4. (A) Means ± standard errors of the normalized-difference vegetation index (NDVI) before and after the La Tuna fire, showing a significant difference ($n = 126$ for each level). (B) Percentage of 30 × 30-m quadrats along the transect in three categories of the difference-normalized burn ratio (dNBR).

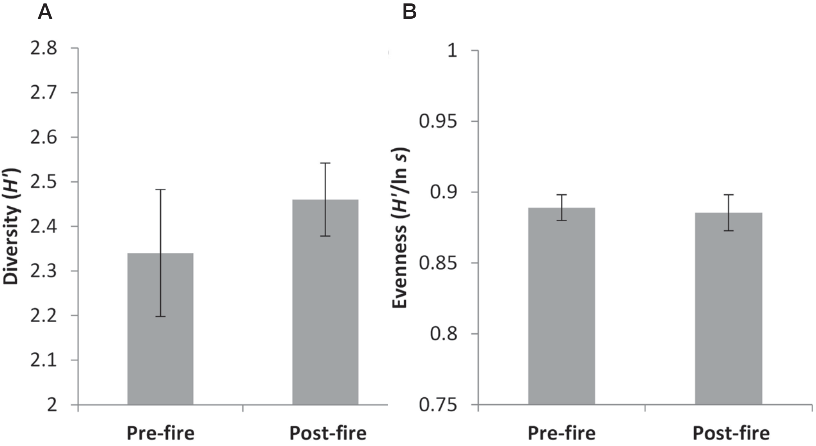

FIGURE 5. Means ± standard errors of (A) diversity and (B) evenness of bird species before ($n = 6$) and after ($n = 6$) the La Tuna fire. Between neither pair of measures is the difference significant.

The first two principal components combined to explain 86% of the variance and reflect the results of the *G* tests (Figure 7, Table 2). Changes in numbers of omnivores and aerial and generalist foragers were each correlated and associated with the first principal component. In contrast, changes in granivores and shrub foragers were correlated and associated with the second principal component, as were insectivores to a much lesser extent. Ground foragers were not strongly associated with either axis. Nectarivores and carnivores were poorly represented with principal components, so we excluded them from the analysis during model selection. The first principal component explained 44.5% of the variance and drove most of the difference between pre-fire and post-fire transects ($F_{1,10} = 11.3$, $P = 0.007$), whereas the second explained 41.5% of the variance but contributed less significance to the differences ($F_{1,10} = 3.7$, $P = 0.083$). Although these results reflect short-term change, they illustrate the variability of positive, neutral, and negative responses of different birds to fire as found previously by Hargrove and Unitt (2018).

DISCUSSION

Previous studies have reported significant changes in bird community diversity following wildfire (Wirtz 1982, Moriarty et al. 1985, Stanton 1986, Mendelsohn et al. 2008, Newman et al. 2018), but our results did not identify such a pattern. Mendelsohn et al. (2008) proposed that differences in habitat preference by species are likely to drive patterns of post-fire bird distribution. In addition, those authors speculated that wide variation in vegetation structure after wildfire is likely to determine such patterns of distribution. Other studies similarly postulated that avian communities may benefit from habitat heterogeneity caused by wildfire (e.g., Longhurst 1978, Brawn et al. 2001, Bock and Block 2005). In our study area, specific patterns of vegeta-

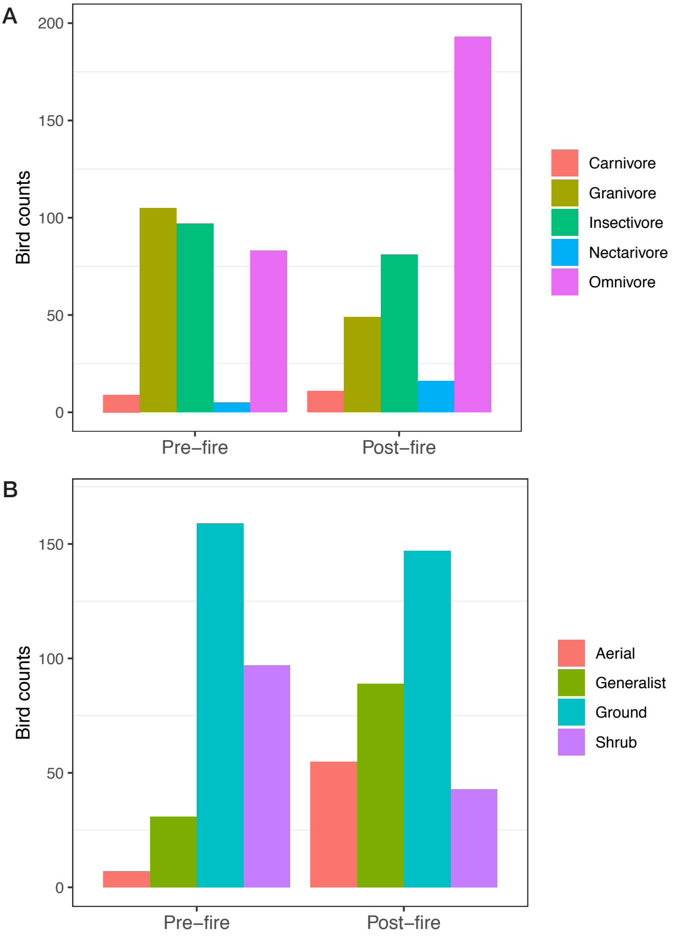

FIGURE 6. Counts of individual birds on transects before (*n* = 6) and after (*n* = 6) the La Tuna fire, by (A) feeding guild and (B) foraging substrate. The difference between each pair of measures is significant.

tion response to the heterogeneity of the fire's severity (Figure 1) may have generated a habitat mosaic with multiple effects on avian diversity. Furthermore, the process of recolonization also depends upon time (Smucker et al. 2005) and species (Winchell and Doherty 2014). Moriarty et al. (1985) demonstrated that within one year of wildfire, avian diversity should increase gradually as habitats are recolonized. Since our post-fire surveys took place 18 months after the study site had burned, the level of diversity observed was presumably due to colonization following subsequent periods of low diversity immediately after the fire. Wirtz (1982) reported a gradual increase in avian diversity over 42 months after wildfire in chaparral. However, our results

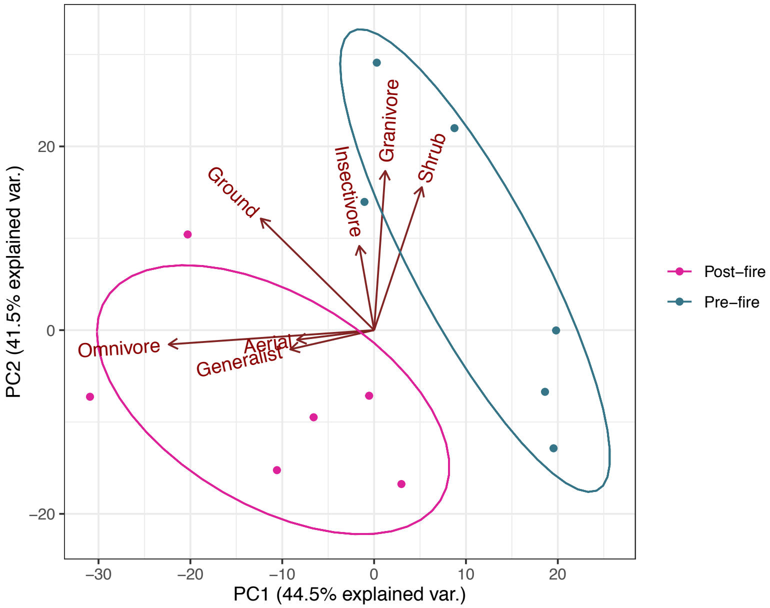

FIGURE 7. Principal-components analysis showing the association of feeding guilds and foraging substrates with pre-fire (blue) and post-fire (magenta) transects. The percentage of variance explained by each axis is given in parentheses.

could also indicate that the fire's severity along this transect was not sufficient to alter the richness and relative abundance of species (e.g., Smucker et al. 2005). Because 66% of dNBR values represent plots burned at moderate to low severity (Figures 1 and 4b), it is possible that the habitat was not altered sufficiently to change avian community diversity.

Although changes in an avian community's evenness after wildfire in California are not discussed in previous research, species' abundances may reflect patterns of adaptation to disturbance. Sufficient niche space may

TABLE 2 Loadings of Variables for Each Principal Component in Analysis of Species by Foraging Guild and Substrate

	Principal component						
Foraging guild	1	2	3	4	5	6	7
Granivore		**0.620**[a]	0.263	0.637		0.227	0.294
Insectivore		**0.328**	0.108	−0.576	−0.555		0.482
Omnivore	**−0.773**		0.124	−0.169	0.496	0.210	0.256
Aerial	**−0.290**		0.242		−0.434	0.565	−0.588
Shrub	0.180	**0.557**	0.275	−0.440	0.408	−0.112	−0.458
Ground	−0.427	0.434	−0.676	0.101	−0.175	−0.283	−0.229
Generalist	**−0.315**		0.560	0.165	−0.245	−0.698	

[a] Boldface signifies a significant difference between the first two axes.

allow the birds of coastal sage scrub and chaparral to occupy the variable habitats created by wildfire. Longhurst (1978) suggested that such species may be adapted to heterogeneous vegetation presumably because it offers better habitat for their prey. Fire may maintain evenness if species are able to use a broader range of niches after it reshapes vegetation. In addition, the timing of wildfires may be related to the community's response. Newman et al. (2018) suggested that chaparral birds are adapted to wildfires in fall, the usual season that this habitat burns. Because the 2017 La Tuna Fire burned in fall, perhaps evenness was maintained by species' behavioral adaptations to the historic fire regime. One hypothesis is that plasticity in bird behavior causes the foraging strategies of some species to shift as resources change after disturbance.

The prediction that this fire prompted a change in guild structure due to a change in vegetation structure was supported by our results (Figures 6a, b). Although Wirtz (1979, 1982) did not detect a significant change in guild structures after a previous shrubland wildfire in southern California, we found that such a change is possible. Newman et al. (2018) did find a significant change in guild structure following fire in chaparral but recorded higher numbers of granivores and ground foragers in response, contrary to our results. The association of omnivores and generalist foragers with principal component axis 1 suggests that increases in these guilds were driving important differences between our pre-fire and post-fire surveys (Figure 7). Although flexible foraging strategies could benefit resident birds after shrubland fire, the abundance of omnivores and substrate generalists in the post-fire surveys also reflects the presence of migrants such as the Yellow-rumped Warbler and White-crowned Sparrow. Moriarty (2013) reported increases in both species after wildfires in coastal sage scrub, and suggested they could benefit from foraging in disturbed habitat. In our study, granivores and shrub foragers were instead associated with principal component axis 2, suggesting that decreases in these guilds after the fire were also important. These results could reflect mortalities in some bird species (e.g., McClure 1981), but it is not surprising that strategies of foraging on plants would be unfavorable when perennial vegetation was just beginning to recover. In contrast to these explanations, the weak association of ground foragers with these axes indicates that they were unaffected by the fire. Birds can demonstrate neutral or resilient responses to wildfire over successional stages (Hargrove and Unitt 2018), which may have occurred in our post-fire surveys with ground foragers such as the California and Spotted Towhees. Our results further illustrate that the avian community's response to wildfire in shrubland habitats may not always follow the same patterns and depends upon the constituent species' life histories, seasonality, and habitat suitability related to vegetation recovery.

Over the first 18 months after the 2017 La Tuna Fire, the vegetation shifted from predominantly mature perennial shrubs to herbaceous annuals. Our results suggest that granivores were more strongly associated with perennials, whereas omnivores had a stronger association with annuals that proliferate rapidly while attracting insect prey for birds. Force (1981) predicted that insect diversity should increase substantially in response to the emergence of pioneer plant species immediately after wildfire in chaparral. Van Mantgem et al. (2015) specifically pointed to increases in ground-dwelling harvester ants immediately after wildfire in coastal sage scrub and chaparral. Other insects also may survive the fire below ground or recolonize from adjacent unburned areas. Force (1982) reported conspicuous post-fire colonization by flower-visiting hymenopterans, phytophagous aphids and acridid grasshoppers, and more predatory syrphid, asilid, and bombyliid flies and coccinellid beetles. Whereas insectivores showed a weak negative response to the fire, omnivores and aerial foragers responded positively (Figure 7). It follows that post-fire omnivores frequently fed on flying insects in mid-air (e.g., hawking by Western Kingbirds, Jordan pers. obs.). In contrast, birds that strictly take insects from shrubs (e.g., foliage gleaners) were probably negatively affected after perennial vegetation had burned.

Patterns of species turnover present additional questions about what may cause shifts in avian community structure in burned habitat over time. Some migrants such as the Western Kingbird and Lazuli Bunting observed following the fire were not observed in the study site previously. However, resident shrub-foraging insectivores such as the Bushtit, Wrentit, and Bewick's Wren that were observed before the fire were less abundant in all post-fire surveys (Table 1). Very similar responses in bird abundance have been observed in burned coastal sage scrub (Stanton 1986), in chaparral cleared mechanically to simulate the effects of fire (Seavy et al. 2008), and after large shrubland wildfires (Mendelsohn et al. 2008, Hargrove and Unitt 2018). By comparison, whereas all granivores observed before the fire (except for the House Finch) were also observed in post-fire surveys, their abundance was reduced, as indicated by their association with the second principal component axis (Figure 7). The apparent negative response of residents likely reflects their presence at the time the fire burned, whereas the positive response of migrants probably reflects their absence and more successful post-fire colonization (McClure 1981). In addition, some residents are resilient and can gradually recolonize post-fire habitat over longer time periods (Hargrove and Unitt 2018). Moriarty (2013) found that an avian community had largely returned to its pre-fire composition within three years after coastal sage scrub had burned. Thus our results provide only a snapshot of avifaunal change shown at one phase of early succession.

Changes to bird communities' diversity and structure in response to fire in coastal sage scrub and chaparral remain uncertain. Various studies' results differ, implying that these communities may not always follow the same patterns (Jones and Tingley 2021). Underlying variables such as differences in vegetation structure, fire intensity, season, and periods of post-fire colonization each have potential to influence community composition. A unique history of adaptation in bird species inhabiting sage scrub and chaparral may allow these avian communities to coexist with a natural fire regime and maintain diversity despite disturbance. Although it seems likely that guild structures will change following wildfire, we suggest that the response varies temporally.

Coastal sage scrub and chaparral are facing novel environmental pressures that may lead to the extirpation of sensitive bird species in areas such as the Verdugo Mountains. As fire regimes in shrublands are altered by climate change and anthropogenic influence, long-term monitoring of their response to disturbance will become increasingly important for conservation. If replacement of these shrub-dominated habitats by invasive forbs and grasses becomes prevalent, this information may guide management and help predict how bird species' ranges may shift as the environment changes.

ACKNOWLEDGMENTS

Thank you to Mark B. Mendelsohn of the National Park Service at the Santa Monica Mountains National Recreation Area for commenting on the research, Sanchayeeta Adhikari for providing remote-sensing consultation, and Fritz Hertel and two anonymous reviewers for providing valuable comments that aided in revision of the manuscript. Philip Unitt suggested additional revisions and provided insight that improved our evaluation of the results.

LITERATURE CITED

Bock, C. E., and Block, W. M. 2005. Fire and birds in the southwestern United States. Studies Avian Biol. 30:14–32.

Bolger, D. T. 2002. Habitat fragmentation effects on birds in southern California: Contrast to the "top-down" paradigm. Studies Avian Biol. 25:141–157.

Brawn, J. D., Robinson, S. K., and Thompson, F. R. III. 2001. The role of disturbance in the ecology and conservation of birds. Annu. Rev. Ecol. Syst. 32:251–276; doi.org/10.1146/annurev.ecolsys.32.081501.114031.

De Graaf, R. M., Tilghman, N. G., and Anderson, S. H. 1985. Foraging guilds of North American birds. Env. Mgmt. 9:493–536; doi.org/10.1007/BF01867324.

Force, D. C. 1981. Postfire insect succession in southern California chaparral. Am. Nat. 117: 575–582; doi.org/10.1086/283742.

Force, D. C. 1982. Post-burn insect fauna in southern California chaparral. U.S. Forest Service Gen. Tech. Rep. PSW-58:234–240, Pacific Southwest Forest and Range Experiment Station, Albany, CA.

Hargrove, L., and Unitt, P. 2018. Responses of birds to large-scale wildfires in southern California, *in* Trends and traditions: Avifaunal change in western North America (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, eds.), pp. 374–399. Studies of Western Birds 3. W. Field Ornithol., Camarillo, CA; doi.org/10.21199/SWB3.20.

Jones, G. H., and Tingley, M. W. 2021. Pyrodiversity and biodiversity: A history, synthesis and outlook. Divers. Distrib. 28: 386–403; doi.org/10.1111/ddi.13280.

Keeley, J. E. 2005. Fire as a threat to biodiversity in fire-type shrublands. U.S. Forest Service Gen. Tech. Rep. 97–106.

Keeley, J. E., and Brennan, T. J. 2012. Fire-driven alien invasion in a fire-adapted ecosystem. Oecologia 169:1043–1052; doi.org/10.1007/s00442-012-2253-8.

Keeley J. E., and Pausas J. G. 2019. Distinguishing disturbance from perturbations in fire-prone ecosystems. Int. J. Wildland Fire 28:282–287; doi.org/10.1071/WF18203.

Keeley, J. E., Brennan, T., and Pfaff, A. H. 2008. Fire severity and ecosystem responses following crown fires in California shrublands. Ecol. Appl. 18:1530–1546; https://doi.org/10.1890/07-0836.1.

Key, C. H., and Benson, N. C. 2006. Landscape assessment: Ground measure of severity, the composite burn index; and remote sensing of severity, the normalized burn ratio, *in* FIREMON: Fire effects monitoring and inventory system (D. C. Lutes, R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi, eds.). U.S. Forest Service Gen. Tech. Rep. RMRS-GTR-164-CD, Rocky Mountain Research Station, Ogden, UT.

Knick, S. T., Holmes, A. L., and Miller, R. F. 2005. The role of fire in structuring sagebrush habitats and bird communities. Studies Avian Biol. 30:63–75.

Longhurst, W. M. 1978. Responses of bird and mammal populations to fire in chaparral. Calif. Agric. 32:9–12.

McClure, H. E. 1981. Some responses of resident animals to the effects of fire in a coastal chaparral environment in southern California. Trans. W. Sect. Wildlife Soc. 17: 86–99.

Mendelsohn, M. B., Brehme, C. S., Rochester, C. J., Stokes, D. C., Hathaway, S. A., and Fisher, R. N. 2008. Response in bird communities to wildland fires in southern California. Fire Ecol. 4:63–81; doi.org/10.4996/fireecology.0402063.

Moreno, J. M., and Oechel, W. C. 1991. Fire intensity effects on germination of shrubs and herbs in southern California chaparral. Ecology 72:1993–2004; doi.org/10.2307/1941554.

Moriarty, D. J. 2013. A twenty-year investigation of the effects of fire on a coastal sage scrub bird community. W. Birds 44: 2–16.

Moriarty, D. J., Farris, R. E., Noda, D. K., and Stanton, P. A. 1985. Effects of fire on a coastal sage scrub bird community. Southwest. Nat. 30:452–453; doi.org/10.2307/3671284.

Newman, E. A., Potts, J. B., Tingley, M. W., Vaughn, C., and Stephens, S. L. 2018. Chaparral bird community responses to prescribed fire and shrub removal in three management seasons. J. Appl. Ecol. 55:1615–1625; doi.org/10.1111/1365-2664.13099. R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; https://www.R-project.org/

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; https://www.R-project.org/.

Seavy, N. E., Alexander, J. D., and Hosten, P. E. 2008. Bird community composition after mechanical mastication fuel treatments in southwest Oregon oak woodland and chaparral. Forest Ecol. and Mgmt. 256:774–778; doi.org/10.1016/j.foreco.2008.05.034.

Smucker, K. M., Hutto, R. L., and Steele, B. M. 2005. Changes in bird abundance after wildfire: Importance of fire severity and time since fire. Ecol. Appl. 15:1535–1549; doi.org/10.1890/04-1353.

Stanton, P. A. 1986. Comparison of avian community dynamics of burned and unburned coastal sage scrub. Condor 88:285–289; doi.org/10.2307/1368874.

Van Mantgem, E. F., Keeley, J. E., and Witter, M. 2015. Faunal responses to fire in chaparral and sage scrub in California, USA. Fire Ecol. 11:128–148; doi.org/10.4996/fireecology.1103128.

Winchell, C. S., and Doherty, P. F. Jr. 2014. Effects of habitat quality and wildfire on occupancy dynamics of coastal California Gnatcatcher (*Polioptila californica californica*). Condor 116:538–545; doi.org/10.1650/CONDOR-13-156.1.

Wirtz, W. O. II. 1979. Effects of fire on birds in chaparral. Cal-Neva Wildlife Trans., pp. 114–124.

Wirtz, W. O. II. 1982. Postfire community structure of birds and rodents in southern California chaparral, *in* Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems (C. E. Conrad and W. C. Oechel, eds.), pp. 241–246. U.S. Forest Service Gen. Tech. Rep. PSW-58, Pacific Southwest Forest and Range Experiment Station, Berkeley.

Accepted 28 September 2022
Assiciate editor: Ryan S. Terrill