The effects of development, vegetation-type conversion, and fire on low-elevation Southern California spider assemblages

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Abstract. California sage scrub (CSS), a native ecosystem type of low-elevation areas of Southern California, is increasingly threatened by urban development, altered fire regimes, and vegetation-type conversion to non-native grasslands. Using pitfall traps, we examined how suburbanization, type conversion, and fire influence ground-dwelling spider assemblages in eastern Los Angeles County, CA, by surveying spiders in three habitats (CSS, non-native grasslands, and suburban areas) before and after a fire that occurred in a small portion of our study site. Spider assemblages in the suburban habitat differed from those in CSS and non-native grassland habitats, but CSS and grassland assemblages did not significantly differ. This suggests that the urban development, but not vegetation-type conversion to non-native grasslands, has significant effects on ground-dwelling spider assemblages. Fire had no observable effect on assemblages. Because ground-dwelling spiders were not impacted by fire and type conversion, increased fire frequencies, which often result in the establishment of non-native grasses, may not deleteriously influence this animal group, a differing pattern from other taxonomic groups. However, the rapid urban development occurring in low-elevation areas of Southern California means that species requiring non-suburban sites for their survival (15 species, 24.1%) may be threatened and require conservation assessment.

Additional key words: Bromus, non-native grasses, sage scrub, suburban, urban

Native to low-elevation areas of Southern California, California sage scrub (CSS), an ecosystem dominated by drought-deciduous shrubs, is one of the most threatened ecosystem types in North America (Burger et al. 2003; Rundel 2007; Riordan & Rundel 2014). It is unique to the semi-arid Mediterranean climate of Southern California, part of the California Floristic province, a world biodiversity "hotspot" (Westman 1981; Myers et al. 2000; Longcore 2003; Kimball et al. 2014). The rich and endemic flora and fauna of CSS make it a habitat of special conservation concern (Davis et al. 1994; Keeley & Swift 1995; Myers et al. 2000). Much of what was once occupied by the sage scrub has been cleared for agriculture and human settlement (Westman 1981; Davis et al. 1994; Riordan & Rundel 2014). It is estimated that only 10–15% of the original CSS distribution remains (Westman 1981; Davis et al. 1994; Rundel 2007), and much of the remaining CSS is found in small, isolated fragments that are increasingly threatened by a variety of disturbances, including urban development and habitat modification, altered fire regimes, and establishment of non-native species (Westman 1981; Davis et al. 1994; Cox et al. 2014; Riordan & Rundel 2014; O'Leary and Westman 1988; O'Leary 1989).

Remaining CSS may be critical to the persistence of CSS-dependent species (Soulé et al. 1988; Bolger et al. 2000), but fragments are increasingly subject to negative impacts of anthropogenic disturbance and activities. Habitat fragmentation increases the likelihood of establishment of non-native species and the negative effects are associated with the invasion (O'Leary 1995; Enserink 1999; Didham et al. 2007). Following a disturbance, the CSS is frequently converted to non-native grasslands, since Eurasian grass species such as *Bromus madritensis* LINNAEUS 1755 and *Avena barbata* POTT EX LINK 1799 are often the first to colonize and become

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established, outcompeting native CSS species (Minnich & Dezzani 1998; Cione et al. 2002; Vila et al. 2003; Gaertner et al. 2009; Cox et al. 2014). Talluto & Suding (2008) estimated that as much as 49% of the plots identified as CSS by the 1930s Vegetation Type Mapping survey (Wieslander et al. 1933) had been converted to non-native grasslands by 2005. High levels of nitrogen deposition from anthropogenic sources reinforce vegetation-type conversion and limit CSS recovery (Talluto & Suding 2008). Such a radical habitat conversion can dramatically change animal community composition and even extirpate native species (Keeley & Swift 1995; Didham et al. 2007; Staubus et al. 2015).

High human population densities and grassland conversion have interacting effects with fire, a primary disturbance of CSS habitats (O'Leary 1995; Syphard et al. 2006; Seager et al. 2007; Klausmeyer & Shaw 2009; Kimball et al. 2014). While fire is a natural part of the Southern California environment, altered vegetation structure and composition, changing climatic conditions, and higher fire ignition probabilities correlated with population density have increased the frequency of fires in Southern California (Keeley et al. 1999; Kimball et al. 2014). Increased fire frequencies negatively impact CSS shrub assemblages by facilitating the establishment of non-native species (Zedler et al. 1983; Callaway & Davis 1993; Keeley et al. 1999, 2005; Syphard et al. 2006; Klausmeyer & Shaw 2009; Keeley & Brennan 2012; Kimball et al. 2014). How fire influences Southern California invertebrates, however, has not been well documented (Matsuda et al. 2011; van Mantgem et al. 2015).

The purpose of this study was to investigate how different types of habitat modification (suburban development and vegetation-type conversion) and fire influence ground-dwelling spider communities (hereafter referred to as spiders or spider communities). We focus on ground-dwelling spiders because only a subset of the complete spider assemblage in an area can be collected using a single sampling approach (Prentice et al. 2001). While spiders are important predators in most systems and have been used to indicate changes in trophic structure in human-altered environments (Niwa & Peck 2002; Shochat et al. 2004), little is understood about the response of spiders to disturbance in the CSS habitat (van Mantgem et al. 2015). In other systems, evidence of the effects of disturbance on spider communities has been contradictory, with some studies demonstrating sensitivity to both burning and habitat modification (Buffington 1967; Miyashita et al. 1998; Bolger et al. 2000; Koponen 2005),

and others finding there to be little effect (Pearse 1943; Riechert & Reeder 1972; Niwa & Peck 2002; Hogg & Daane 2011). To better understand how Southern California spider populations are influenced by urban/suburban development and vegetation-type conversion to non-native grasslands, we examined spider assemblages in adjacent patches of three habitat types: intact CSS, non-native grasslands, and the urban/suburban matrix in eastern Los Angeles County, CA. We also examined spider assemblages before and after a fire that occurred within a small portion of our study area in September 2013, and compared the changes to assemblages in intact CSS and non-native grasslands to determine which changes were due to inter-annual and inter-seasonal variation and which were driven by the fire. Our findings provide critical insight into how major disturbances in Southern California influence the biodiversity of spiders, and potentially some of the many other ground-dwelling invertebrates narrowly endemic to low-elevation areas of Southern California (Pilsbry 1939; Keaton 1960; Hogue 1993).

Methods

Study area

We sampled spiders in four habitat types in the Robert J. Bernard Field Station (BFS) and adjacent suburban areas. The BFS is located at the foot of the San Gabriel Mountains in Claremont, Los Angeles County, CA, and comprising ~35 ha. Summers are hot and dry (average summer maximum temperature is 32°C) and winters are cool and moist (average winter minimum temperature is 4°C). the average annual rainfall is 45.5 cm, but the rainfall over 90% occurs in the winter months, and inter-annual variation is considerable. While we do not have data for our study area, during this study, Los Angeles recorded the driest two consecutive years on record since 1878 (July 2012 through June 2014; Los Angeles Almanac 2015).

California sage scrub is the dominant habitat type at the BFS, covering ~25 ha. Vegetation is typical of CSS stands, featuring drought-deciduous shrubs such as sage scrub (*Artemesia californica* LESSING 1831), flat-top buckwheat brush (*Eriogonum fasciculatum* BENTHAM 1837), yerba santa (*Eriodictyon trichocalyx* HELLER 1906), and sages (*Salvia* spp. BENTHAM 1836) (Westman 1981; Mooney 1988; Rundel 2007). The non-native grassland portion of the BFS covers only ~3.5 ha, but has persisted for more than 40 years. It is dominated by *Bromus* spp.,

native to Europe. A third portion of the BFS origi-
nally comprised ~5.5 ha of transitional habitat
where non-native grasses were being recolonized by
native shrubs. However, in September 2013, a
human-caused fire consumed all the above-ground
plant biomass and burned all sampling sites in the
transitional habitat, as well as small parts along the
edges of the CSS and non-native grassland areas
where arthropod sampling was not conducted. A
small (~1 ha) cluster of administrative buildings sur-
rounded by non-native shrubs and tree vegetation
constitutes the remainder of the BFS.

The suburban habitat, by our definition, consisted
of land directly adjacent to and surrounding the
BFS that receives additional water input through
regular irrigation. Other habitat characteristics, such
as plant composition, soil quality, and management
history, were highly variable. Most suburban sites
were in yards or gardens belonging to private resi-
dences or the Claremont Colleges, and bore little or
no resemblance to native ecosystems. Six sites were
situated within the Rancho Santa Ana Botanic Gar-
den (RSABG), an institution dedicated to the study
and conservation of native California plant species.
These sites, though characterized by the native
plants of California, reflected plant communities
from across the state rather than local ecosystems.
Moreover, RSABG sites, like other suburban sites,
received regular irrigation. As a result, conditions at
those sites more closely reflected a suburban garden
environment than any other habitat type. Two addi-
tional sites were established in the non-native land-
scaping surrounding the BFS buildings. While
within the bounds of the BFS, this area receives
intermittent irrigation and is composed of non-
native plants, and hence was also treated as subur-
ban habitat.

Although our study area is relatively small
(~2.6 km^2), the small spatial scale has two main
advantages. First, a study across a small spatial
extent limits confounding factors such as differences
in species pools and environmental factors such as
temperature, precipitation, and soil type that might
be present in studies conducted over a larger area.
However, these environmental variables are likely to
differ among habitat types based on vegetation and
added water. Second, because spiders are highly
mobile and can easily migrate among habitats over
a small spatial scale (Ferrenberg et al. 2006), differ-
ences in spider assemblages between nearby and
adjacent habitats would more clearly indicate the
differences in the habitat preference or suitability
among species. The disadvantages of a study in an
isolated habitat island are that the extrapolation of

our findings to other sites with different environ-
mental characteristics or disturbance histories may
be inappropriate. In addition, isolation has likely
resulted in loss of some sensitive or specialist spe-
cies, suggesting that we may underestimate the size
of disturbance or conversion effects.

Sampling protocol

We carried out pitfall trapping at 48 sites over
five different 2-week periods. In an effort to obtain
a complete species inventory and examine seasonal
and inter-annual variation in the spider community,
sampling periods were conducted at 3-month inter-
vals: spring 2013 (29–30 March to 11–12 April),
summer 2013 (1–3 to 15–17 July), fall 2013 (28
September to 12 October), winter 2014 (14–16 to
28–30 January), and spring 2014 (12–14 to 26–28
March). Sixteen sites were distributed systematically
throughout the CSS habitat, each at least 75 m
from adjacent sites. Eight sites were distributed
throughout the non-native grassland habitats and
eight throughout the transitional/burned habitat,
but these sites were closer together (~40 m apart)
because of the smaller size of these habitat patches.
In the suburban habitat, 16 sites were randomly
dispersed as a result of accessibility, but still repre-
sented a variety of suburban environments. These
sites ranged from ~30 to 1000 m in distance to
non-suburban sites at the BFS. For a map of our
study area and sampling sites, see Staubus et al.
(2015).

Each site contained three pitfall traps. Sites in the
CSS, non-native grasslands, and transitional habi-
tats were configured so that the three pitfall traps
formed a north-pointing equilateral triangle with
sides 10 m in length. Pitfall traps in the suburban
sites were placed 10 m apart but did not form trian-
gles because obstacles prevented the formation. Pit-
fall traps were constructed using the trap design
employed by Higgins (2010), so that they could
remain in the field for 2 weeks between charging of
a trap and collection of specimens. Pitfall traps con-
sisted of a glass test tube 3.2 cm in diameter and
25 cm deep inserted into a PVC sleeve (3.8 cm
diameter, 28 cm long) that was buried flush with the
soil surface. A pitfall trap cover, constructed by
splitting a 7.5-cm-diameter PVC pipe longitudinally
and drilling holes in each side to attach it to the
sleeve, was used to restrict the access to vertebrates.
When charged, test tubes were filled with ~75 mL of
propylene glycol, a non-toxic, short-term preserva-
tive for arthropods. PVC sleeves were capped
between sampling periods.

After the collection of specimens, trap contents were transferred into 80% ethanol, and spiders were sorted from other arthropods using a dissecting microscope. Adult spiders were identified to species or lowest taxonomic level when species identification was not possible. Juveniles were not included in the analyses because they could not be reliably identified. All specimens are stored in the Bernard Field Station Invertebrate Collection.

Analyses

Effects of habitat modification. To examine the differences in spider richness among habitat types, we first created a species accumulation curve for each habitat type except the transitional habitat (CSS, grassland, and suburban), comparing the number of species collected as the number of sites increased, using the S-curve species accumulation function in PRIMER v.6 (Clarke & Gorley 2006). Each species accumulation curve was created using a site-by-species matrix that combined data from all the five seasons for each site. We considered that richness differed between habitats if 95% confidence intervals did not overlap. Because the spatial extent sampled differed among habitat types because of the small scale of the CSS and non-native grassland habitats relative to the suburban habitat, increased species richness in the suburban sites may indicate that these habitats harbor more species or just that the area surveyed was larger. To examine the species richness among habitats in more detail, we used the non-parametric estimator Chao1 function, executed in PRIMER v.6 (Clarke & Gorley 2006) to extrapolate predicted species richness in each habitat. The Chao 1 also allowed us to estimate the percent inventory completeness by comparing total collected species to predicted species richness.

To determine whether spider assemblages differed among habitat types and seasons, we conducted multiple analysis of similarity (ANOSIM) tests using PRIMER v.6. For each ANOSIM analysis, we used square-root-transformed abundance data and the Bray–Curtis coefficient to generate the resemblance matrices. Because some pitfall traps were destroyed during each sampling period (2.5–9.2% per season), we calculated each resemblance matrix using the average number of individuals of each species found per pitfall trap at each site.

Because we expected the differences in spider assemblages among seasons, we first ran a two-way crossed ANOSIM test (9999 permutations) using habitat and season as factors. This allowed us to test for differences among habitat types while controlling for differences among seasons. Pairwise differences among habitats were examined following a significant ANOSIM result for habitat. We used the conservative Bonferroni correction procedure (three pairwise habitat comparisons within each season: α=0.016) to adjust α-values and correct for multiple testing. A non-metric multidimensional scaling plot (MDS) was generated following these analyses to visualize the relationships among sites according to habitat.

To further test the differences in spider assemblages among habitats and examine how a season may influence our interpretation of differences among habitats, we ran 5 one-way ANOSIM tests using habitat as a factor. Each ANOSIM tested differences among habitats within each season (spring 2013, summer 2013, fall 2013, winter 2014, spring 2014). We used Bonferroni-adjusted α-values (three pairwise habitat comparisons: α=0.016) for pairwise comparisons. To quantify the contribution of each species to any observed differences between pairs of habitats, one-way Similarity Percentage (SIMPER) analyses were conducted following each significant ANOSIM test.

Effects of fire. To determine whether and how fire influences spider assemblages, we performed multiple one-way ANOSIM tests using PRIMER v.6. We used square-root-transformed abundance data and the Bray–Curtis similarity coefficient to perform each ANOSIM test as described above. First, we ran 3 one-way ANOSIMs to test for differences between summer 2013 and fall 2013 collections (the season preceding and the season following the fire) for the transitional (burned), CSS, and non-native grassland habitat types in an initial effort to examine the immediate influence of fire on spider assemblages. If spider assemblages did not differ between seasons in the transitional habitat, it would suggest that fire has little effect on spider assemblages. However, if spider assemblages differed in the transitional habitat between seasons, but not in either the unburned CSS or grassland habitats, it would suggest that fire strongly affects spider assemblages. Alternatively, if there were significant differences in the transitional and at least one other habitat type, further analyses focused on species-specific changes (see below) would be required to ascertain whether differences were caused by fire or inter-seasonal variation. Second, we ran 3 one-way ANOSIMs comparing spider assemblages collected in each habitat during spring 2013 and spring 2014 (the only season sampled twice, once before and after the fire) to evaluate recovery of spider assemblages within the first year following the fire. Again, we use the

unburned CSS and grassland habitats as comparisons to confirm that any differences observed in the transitional habitat were not the result of inter-annual variation.

To examine species-specific responses to fire, we used Fisher's exact tests to compare the abundances of spider species in spring 2013 (pre-fire) to spring 2014 (1 year post-fire), and to compare summer 2013 (season prior to the fire) to fall 2013 (season immediately following the fire) in the transitional habitat, versus the two other BFS habitat types (CSS and non-native grasslands). Differences in the proportion of pre- to post-fire abundance in the transitional area versus the CSS or non-native grassland habitats were used to determine if such changes may be attributed to the effects of the fire or associated with inter-annual or inter-seasonal differences.

Results

We collected 879 adult individuals and 62 spider species representing 51 distinct genera from 21 families (Supporting information Appendix S1). Six species are known non-natives (*Dysdera crocata* KOCH 1838, *Oecobius navus* BLACKWALL 1859, *Metaltella simoni* KEYSERLING 1878, *Zelotes nilicola* CAMBRIDGE 1874, *Urozelotes rusticus* KOCH 1872, and *Trachyzelotes barbatus* KOCH 1866) (Supporting information Appendix S1).

Effects of habitat modification

Species accumulation curves indicated that the suburban habitat may have higher spider richness than either the CSS or grassland habitats, but interpretations should consider the possibility that richness is higher in the suburban area because we surveyed a much larger area for that habitat type (Fig. 1). The Chao1 estimator supported the idea that the suburban habitat has higher species richness than the CSS habitat and suggests that more sampling effort is required to completely inventory spider richness in each habitat type. We achieved >70% inventory completeness in the CSS habitat, >60% inventory completeness in the suburban habitat, and only 26.7% inventory completeness in the invasive grassland habitats (Table 1). The high predicted richness (82 species) in the grasslands and substantial variance associated with this estimate indicated that additional sampling in this habitat is of particular importance.

The two-way ANOSIM test showed that spider assemblages differ among habitats (*R*=0.189, p=0.0001) and seasons (*R*=0.116, p=0.0001). Pairwise
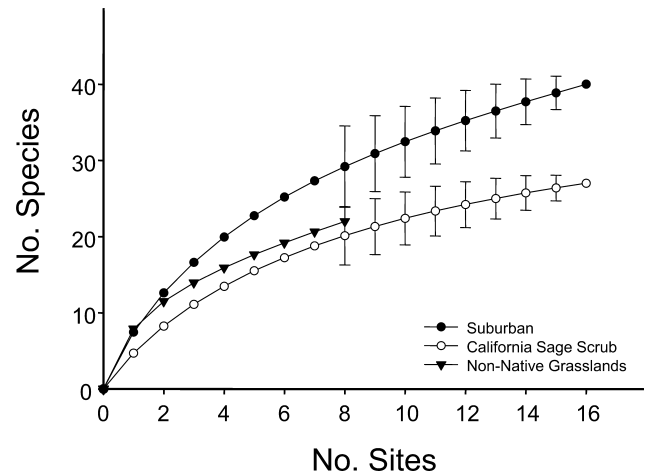

Fig. 1. Species accumulation curves depicting the number of ground-dwelling spider species collected as the number of sites increases in California sage scrub (CSS), non-native grassland, and suburban habitat types. Error bars represent 95% confidence intervals.

Table 1. The total number of ground-dwelling spider species collected in each habitat type, the species richness of each habitat type predicted by the Chao1 estimator and the standard deviation (SD) estimate, and the estimated percent inventory completeness.

Habitat	# Species collected	Predicted species richness (SD)	% Inventory completeness
CSS	27	37.1 (9.0)	72.8
Grassland	22	82.5 (71.1)	26.7
Suburban	40	64.5 (18.6)	62.0

comparisons demonstrated that the spider assemblage in the suburban habitat differed from those in the CSS and non-native grasslands (Table 2, Fig. 2). While assemblages between CSS and grasslands were not distinct (*R*=0.014, p=0.293), a high level of habitat specificity was still observed across all three habitat types. Thirty-three (53%) of the 62 total spider species were found only in one habitat type (Fig. 3; Supporting information Appendix S1): CSS (9 species), grasslands (6), and suburban (18).

One-way ANOSIMs examining differences among habitats within each season revealed a consistent pattern across seasons. The suburban spider assemblage consistently differed from those of the CSS and non-native grasslands, which, in contrast, never differed significantly from each other in any season (Table 3).

The SIMPER analyses revealed the three species most responsible for driving differences among habitats across all seasons: the non-native *Oecobius*

Table 2. Pairwise comparisons examining differences in ground-dwelling spider assemblages between habitat types while controlling for seasons.

Factor	Pairwise comparisons	R	p
Habitat	CSS versus Grassland	0.014	0.293
	CSS versus Suburban	0.184	<0.001*
	Grassland versus Suburban	0.361	<0.001*

*Denotes statistical significance according to α-values adjusted using the Bonferroni correction (three pairwise habitat comparisons: α=0.016).
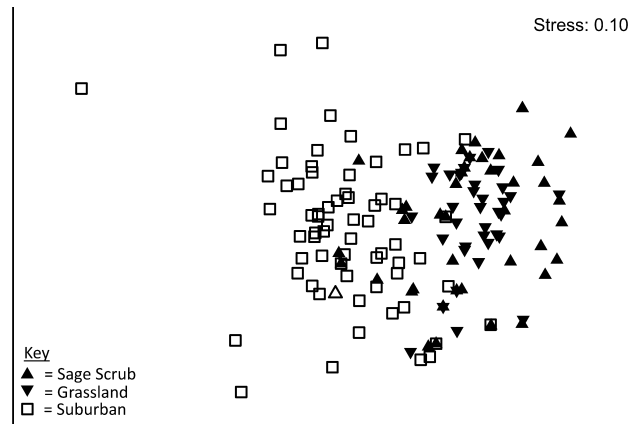

Fig. 2. Multidimensional scaling (MDS) ordination of sites according to composition and abundance (square-root transformed) of ground-dwelling spider species. Sites without any spiders and sites with only species not found at other sites were excluded.
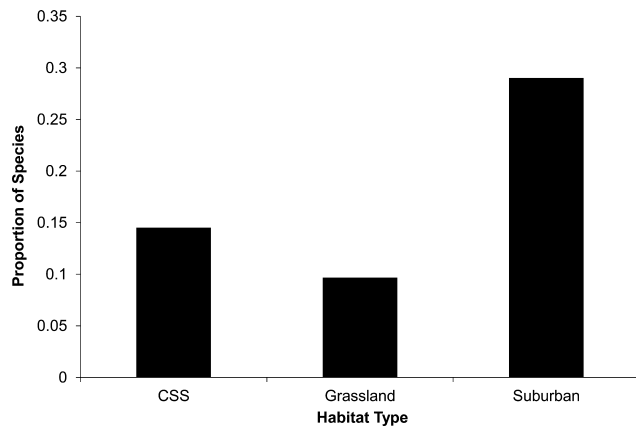

Fig. 3. Proportion of ground-dwelling spider species (presented as a proportion of the total spider richness) found only in one habitat type.

navus and *Dysdera crocata,* and the native *Psilochorus utahensis* CHAMBERLIN 1919 (Supporting information Appendices S2–6). Higher abundance of

Table 3. Pairwise comparisons examining differences in ground-dwelling spider assemblages among habitat types within each season using composition and abundance data.

Season	Pairwise comparison	R	p
Spring13	CSS versus Grassland	0.095	0.081
	CSS versus Suburban	0.154	<0.001*
	Grassland versus Suburban	0.523	<0.001*
Summer13	CSS versus Grassland	0.019	0.356
	CSS versus Suburban	0.311	<0.001*
	Grassland versus Suburban	0.466	<0.001*
Fall13	CSS versus Grassland	−0.069	0.808
	CSS versus Suburban	0.140	0.002*
	Grassland versus Suburban	0.216	0.006*
Winter14	CSS versus Grassland	−0.016	0.577
	CSS versus Suburban	0.103	0.006*
	Grassland versus Suburban	0.091	0.089
Spring14	CSS versus Grassland	0.042	0.216
	CSS versus Suburban	0.213	<0.001*
	Grassland versus Suburban	0.510	<0.001*

*Denotes statistical significance according to α-values adjusted using the Bonferroni correction (three pairwise habitat comparisons: α=0.016).

O. navus and *D. crocata* in suburban sites drove differences between the CSS and suburban habitats across all seasons except winter 2014, when one native species, *Alopecosa kochi* KEYSERLING 1877, and one non-native species, *Metaltella simoni,* drove differences between the habitats (Supporting information Appendices S2–6). Higher abundance of native *P. utahensis* in grassland sites drove differences between grassland and suburban habitats during spring 2013, summer 2013, and fall 2013, while higher abundance of the native *Xysticus montanensis* KEYSERLING 1880 contributed most to differences in spring 2014 (Supporting information Appendices S2–4, S6).

Effects of fire

Spider assemblages differed significantly between the season immediately before the fire (summer 2013) and the season immediately after the fire (fall 2013) in the transitional habitat (R=0.34, p=0.002) and the CSS habitat (R=0.11, p=0.009), but not in the non-native grasslands (R=0.08, p=0.147). Spider assemblages differed in the non-native grassland habitats between the spring 2013 and spring 2014 collections (R=0.449, p<0.001), but not in the CSS (R=−0.02, p=0.837) or the transitional habitats (R=0.133, p=0.077).

Comparison of pre- and post-fire spider abundances in the seasons immediately preceding and

following the fire (summer 2013 and fall 2013), and the spring seasons preceding and following the fire (spring 2013 and spring 2014), showed that several species decreased in abundance after the fire (Supporting information Appendix S7). However, this decrease in abundance was only significantly different for one species, *Drassyllus insularis* Banks 1900, which increased in abundance in the grasslands but decreased in abundance in the transitional habitat type in the spring following the fire (Supporting information Appendix S7).

Discussion

We collected 62 spider species in an area that comprised ~2.6 km². The Chao1 estimator indicates that increased sampling effort would likely yield an even greater number of species. Making comparisons of species richness is difficult among and within regions, particularly with ground-dwelling spiders, because an enormous, resource-intensive effort is required to obtain a relatively complete inventory (Meyer et al. 2015). Because of the number of species we collected and the scale of our study, our results suggest that Southern California, particularly Claremont, CA, harbors a fairly diverse spider assemblage. By comparison, Prentice et al. (2001) collected 78 spider species in an area of ~44 km² in Riverside, CA, from 4032 trap days, while our study area was ~2.6 km² and had fewer (1400) trap days. However, Prentice et al. (2001) focused on CSS that included burned areas with non-native grasses, but excluded suburban habitats. As such, it is difficult to determine if our species richness estimates are high because of increased habitat complexity caused by inclusion of the suburban habitat. Comparisons of spider richness are also limited in the CSS ecosystem because previous studies report only the average number of species per pitfall trap (8.03) and not richness or composition per fragment (Bolger et al. 2000). However, when comparing Southern California species richness to other areas in the southwestern US, Southern California spider assemblage is fairly diverse. For example, Meyer et al. (2015) found 102 spider species in six plant biomes along an elevation gradient in the Santa Catalina Mountains in Arizona using a much higher number of pitfall traps (660 over two seasons; 9240 trap days) and sampling an area with six distinct plant biomes.

Effects of habitat modification

Our results highlight that urban development, but not vegetation-type conversion to non-native grasslands, has significant effects on spider assemblages. Spider assemblages in the suburban habitat differed from those in both the CSS and non-native grasslands each season (except in winter 2014, when no significant differences were observed), indicating that the differences between suburban and non-suburban habitat types are robust. In contrast, differences in spider assemblages between the CSS and non-native grasslands were not observed during any of the seasons.

The lack of difference between the CSS and non-native grassland habitats among seasons suggests that spider assemblages are not impacted by vegetation-type conversion of CSS to non-native grasslands. In our study, these two habitat types shared several highly abundant native species that are likely tolerant to vegetation-type conversion, including *Psilochorus utahensis*, *Zelotes gynethus* Chamberlin 1919, and *Emblyna olympiana* Chamberlin 1919. Many of these species are thought to be generalist predators (Ubick et al. 2009), which may provide an initial explanation as to why this type of habitat modification may not influence spider assemblages. However, this result contrasts with Staubus et al. (2015), who showed that communities of ants varied between the CSS and non-native grassland habitats, and highlights that patterns applicable to one arthropod taxon might not pertain to another.

While spiders seem resilient to vegetation-type conversion, suburbanization (e.g., habitat conversion during suburban development) significantly alters spider assemblages. Differences between suburban and non-suburban (CSS and non-native grasslands) habitats were driven by the large abundance of non-native species, particularly *Oecobius navus* and *Dysdera crocata*, in suburban sites. In contrast, non-suburban habitats were composed primarily of native species, and these habitats seem effective at restricting or limiting the abundance of the non-native spider species. Staubus et al. (2015) reported a similar trend in ant communities at the same sites, particularly with respect to non-native Argentine ants; they attributed increases in non-native ant richness and abundance in suburban areas to increased water availability because of irrigation. While we are uncertain as to how desiccation stress may influence the distribution of spider species, we do know that the suburban areas studied have increased artificial water input and harbor much higher densities of other non-native arthropod species (e.g., isopods and earwigs) (W.M. Meyer unpubl. data). For species such as *D. crocata*, individuals of which consume isopods (Hogue 1993), this change in prey resource availability may significantly influence their

distribution and abundance in the different habitat types. Increased prey availability and changes to microclimate are causes of increased spider abundance and reproduction in other urban systems (Shochat et al. 2004; Lowe et al. 2014). Further research should address whether the spiders in the suburban areas (native and non-native) are less tolerant of desiccation, consume different food resources, and/or evolved in micro-habitats that may make them better suited to persist in suburban habitat.

While the suburban sites may be typified by high abundances of non-native spider species, the suburban habitat also had the highest species richness. Because urban development often increases the numbers of non-native species (Bolger et al. 2000, 2008; Burger et al. 2001; Didham et al. 2007), our initial expectations were that the higher species richness in suburban sites occurred because of higher numbers of introduced species. However, most species, including 16 of the 18 species unique to the suburban sites, were native to Southern California. Of the six non-native species collected (*D. crocata*, *O. navus*, *Metaltella simoni*, *Zelotes nilicola*, *Urozelotes rusticus*, and *Trachyzelotes barbatus*), only *M. simoni* and *T. barbatus* were unique to the suburban sites. Alternatively, the high suburban spider richness may be attributed to the greater sampling area and habitat diversity of the suburban habitat type. However, most of the remaining CSS habitat in Southern California remains in small isolated fragments (Westman 1981; Riordan & Rundel 2014), therefore researchers must consider if their focus is addressing species richness among the CSS and suburban habitats of similar size, or if efforts should be spent trying to characterize the assemblages in the different habitats. In most instances, site choices in the suburban habitats will be strongly influenced by access. Further research should examine which suburban habitat types harbor native spider species and how habitat complexity influences the persistence of spider species in areas where non-native spider species are abundant. Also, further research is needed to determine the contemporary and native ranges of ground-dwelling arthropod species. Although most of the spiders are likely native to Southern California, it is difficult to determine if they are native to our specific study area. Despite having a poor understanding of the mechanisms influencing richness, our research demonstrates that the suburban areas can harbor a rich and distinct native spider assemblage, but suburbanization represents a threat to native spiders that require non-suburban habitats (~25% of the spider species were collected only in the CSS and non-native grasslands). Maintaining a mosaic of suburban and non-suburban habitat types may help maximize native spider richness. In practical terms, however, there is no threat of losing a critical amount of suburban habitat, but a very real threat of losing significant proportions of the remaining non-suburban habitats (Riordan & Rundel 2014).

Effects of fire

The ground-dwelling spider assemblage in the transitional habitat was not impacted by the fire. While assemblages differed significantly between the seasons immediately before and after the fire (summer and fall 2013), significant differences were also observed in the CSS habitat. By examining differences in the abundance of transitional habitat species between seasons, we found that for every change in species abundance in the transitional habitat, there was a corresponding change in that species' abundance in another habitat type. Because of significant inter-seasonal changes in the CSS spider assemblage and no evidence exists that fire influenced the abundance of any single spider species in the transitional habitat, we cannot attribute change in the spider assemblages at the transitional habitat to fire. This is remarkable especially considering that after the fire, there was no above-ground biomass in the transitional habitat until the following April. While our findings are consistent with those of others working in CSS ecosystems who have observed that animal communities quickly recover following fire (Diffendorfer et al. 2012; Schuette et al. 2014), the absence of marked differences in species abundance or community composition in burned and unburned sites just months after the event is striking.

From spring 2013 to spring 2014, only the unburned non-native grasslands had a spider species assemblage that was significantly different from other habitats. The absence of significant differences in species assemblage in the other two habitats, particularly the transitional habitat, indicates that inter-annual variation can differently influence spider assemblages in various habitats, and provides further evidence that fire had little influence on the ground-dwelling spider assemblage. Matsuda et al. (2011) found that diversity in CSS ant communities was impacted for up to 2 years post-fire in CSS habitats. However, these differences between pre-fire and post-fire ant assemblages were largely driven by significant changes in the abundance of one ant species and not loss of species richness. Our results and

those of Matsuda et al. (2011) together suggest that ground-dwelling arthropod assemblages either can survive a fire disturbance, presumably by sheltering underground, or can quickly reestablish populations following the fire (van Mantgem et al. 2015). Both mechanisms may be responsible for the lack of change in spider assemblages observed here. Spider species are highly mobile, so dispersal from adjacent unburned habitats is possible (Ferrenberg et al. 2006), and arthropod species that can shelter in burrows or under rocks can survive a fast-moving fire (van Mantgem et al. 2015).

While species native to Southern California are likely well-adapted to fire (Moretti et al. 2002; Koponen 2005; Keeley et al. 2009; Keeley & Brennan 2012), studies on mammals and Mediterranean climate freshwater streams suggest that succession following fire must involve native plant assemblages, as opposed to the non-native grasses that often become established after a fire, if native animal communities are to fully recover (Diffendorfer et al. 2012; Verkaik et al. 2013; Schuette et al. 2014). This dependence on native plant assemblages arises because some animal species require native habitat for their survival, and because non-native grasses, once established, will promote more frequent fire disturbances (D'Antonio & Vitousek 1992). For ants and mammals, vegetation-type conversion from CSS to a non-native grassland favors some species over others (Matsuda et al. 2011; Diffendorfer et al. 2012; Schuette et al. 2014; Staubus et al. 2015). In contrast, ground-dwelling spiders, given their apparent tolerance of both fire and vegetation-type conversion, may be less impacted. However, we again caution that these patterns are associated with ground-dwelling spiders, and may not apply to web-spiders, which spend most of their time on plants and may not be able to shelter themselves from fast-moving fires or use the habitat left by Southern California fires, which often consume all above-ground plant biomass (Podgaiski et al. 2013; Foster et al. 2015).

Influence of drought

During this study, Los Angeles recorded the driest two consecutive years since 1877–1888 when precipitation records began (July 2012 through June 2014; Los Angeles Almanac 2015). It is possible that spiders were deleteriously impacted by drought, particularly in the non-suburban habitats that do not receive additional water. If the spider faunas were negatively impacted by the drought, it is possible that this impact may reduce our ability to identify the true effects of vegetation-type conversion and fire currently and in future years if stochastic events like extreme drought lead to the extirpation of sensitive species in these isolated habitat fragments. Long-term studies are required to tease out differences associated with drought and isolate the many factors that influence these communities. This study is the first that we know of to have collected data both immediately before and after a natural fire. Continued surveys are planned for subsequent springs to develop a long-term data set that will help us better isolate factors influencing spiders and other ground-dwelling arthropod fauna.

Conclusion

Our results demonstrate that urban development significantly affects spider assemblages. The CSS and non-native grassland habitats harbored native species not found in suburban sites. Therefore, such habitat patches can be important refuges for native species in urban/suburban regions. Similar to findings associated with ant assemblages (Staubus et al. 2015), the conservation value of non-native grasslands should not be discounted, as native spider species may be well-adapted to non-native grassland habitats. The suburban habitat also harbored a unique assemblage of native spider species, demonstrating that individual species are differentially affected by suburbanization, and that some native species may persist and potentially favor this habitat despite widespread vegetation conversion and abiotic and biotic changes. Because spider assemblages do not seem to be negatively impacted by fire or vegetation-type conversion, increased fire regimes may pose less of a threat to spiders compared with other animal assemblages that require reestablishment of native plant species through natural succession (Diffendorfer et al. 2012; Verkaik et al. 2013; Schuette et al. 2014). Combined, our data suggest that spider assemblages may not be negatively impacted by many of the major disturbances influencing Southern California systems (fire and vegetation-type conversion), but that transformation to suburban habitat favors both non-native species and a unique subset of native spider species. As such, both suburban and non-suburban areas are required to preserve the highest native spider richness. While there is little threat of losing suburban areas, there is a very real threat of losing significant proportions of the remaining non-suburban habitats and species that require these habitats for their survival.

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Supporting information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Average number of individuals per pitfall trap for each spider species collected in CSS, grassland, and suburban habitat types during five seasons.
Appendix S2. One-way SIMPER: Spring 2013 with habitat as a factor.
Appendix S3. One-way SIMPER: Summer 2013 with habitat as a factor.
Appendix S4. One-way SIMPER: Fall 2013 with habitat as a factor.
Appendix S5. One-way SIMPER: Winter 2014 with habitat as a factor.
Appendix S6. One-way SIMPER: Spring 2014 with habitat as a factor.
Appendix S7. Pre-fire and post-fire abundance of spider species collected in the transitional habitat the season immediately preceding and immediately following the fire (summer 2013 and fall 2013) and the spring before and after the fire (spring 2013 and spring 2014). Abundance of the same spider species in the CSS and grassland habitats were used for comparison to examine if changes occurred because of fire or inter-seasonal or inter-annual variation.