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COYOTE BRUSH AS FACILITATOR OF NATIVE CALIFORNIA PLANT RECOVERY IN THE SANTA MONICA MOUNTAINS

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ABSTRACT

Exotic annual grasses now cover large areas of southern California that were once stands of native California sage scrub (CSS), or a mixture of native grasses, forbs, and CSS. Both CSS and California grasslands are threatened habitats, where restorations of type-converted landscapes are often burdened by the persistent dominance of non-native annual grasses. Research finds that once exotic grasses take hold in these areas, native plant communities are extremely slow to recover, if they recover at all. Coyote brush (*Baccharis pilularis* DC) is a native shrub common to CSS habitat and often appears in a complex mosaic with other vegetation types including grasslands. Coyote brush has been documented invading grasslands, resulting in a change of state from grassland to shrubland in northern California. This study investigates the long-term consequences of coyote brush invasion in a type-converted landscape of southern California. Stands of expanding coyote brush were transected to identify species composition along a spatial and temporal continuum. Results show that, following initial invasion, non-native species are gradually replaced by, not only coyote brush, but also several other noteworthy native species. This study finds that over the 37 yr timeframe, exotic grasses gradually decline while native plant cover increases in landscapes invaded by coyote brush. We conclude that in the Santa Monica Mountain areas studied, coyote brush invasion of type-converted landscapes leads to increased native plant diversity that includes native grasses and a variety of shrubs.

Key Words: *Baccharis pilularis*, California sage scrub (CSS), coastal sage scrub, facilitation, native bunchgrasses, passive restoration.

Exotic annual grasses now cover large areas of southern California that were once stands of native California sage scrub (CSS), or a mixture of CSS and native perennial grasses and forbs (Westman 1981; Freudenberger et al. 1987; Minnich 2008). These landscapes were invaded and replaced by exotic grasses of mostly European origin (Burcham 1957; Stromberg et al. 2007; Minnich 2008). Numerous studies find that once exotic grasses take hold in these areas, native plant communities are extremely slow to recover, if they recover at all (Hobbs 1983; Davis 1994; Stylinski and Allen 1999; Engelberg et al. 2013). In part, this is because invasive grasses are competitive with native species, as experimental studies have shown, and thus grass control is necessary before natives can reestablish (Eliason and Allen 1997; Gillespie and Allen 2004). Fragments of coastal sage scrub or native bunch grasses that do remain are often intermixed with persistent stands of exotic grasses (e.g., Freudenberger et al. 1987), even after removal of disturbances that promote grass colonization, such as grazing, frequent fire, or mechanical disking (Davis 1994; Zink et al. 1995; Engelberg et al. 2013; Laris et al. 2017).

In cases where CSS shrubs have recovered in areas formerly type-converted to exotic grasses, the diver-

sity of shrub species is often lower than neighboring existing stands of CSS. This has been particularly true in instances where areas formerly dominated by CSS, which were forcibly converted to grassland by mechanical means, eventually recovered after release from intensive disturbance (Davis 1994; Stylinski and Allen 1999; Engelberg et al. 2013; Laris et al. 2017). In some cases, a single species, such as coyote brush (*Baccharis pilularis*), becomes a dominant monotypic shrub cover at least temporarily (Laris et al. 2017). Indeed, coyote brush is one of few CSS species that has proven capable of readily (re)colonizing landscapes invaded by exotic annual grasses (Fig. 1, McBride 1974; Williams and Hobbs 1989; Zavaleta and Kettley 2006).

In spite of the fact that coyote brush is a native shrub common in coastal areas and other locales, its propensity to colonize and expand into areas forming monotypic stands has been the subject of some debate in terms of its perceived pros and cons by different land management agents. From the perspective of some managers of California State Park lands, for example, who view the grasslands as historical relics of a lost landscape, the coyote brush invasion is seen as a negative change. Contrastingly, many conservationists view coyote brush expansion



FIG. 1. Coyote brush-annual grassland boundary. Note the dense band of coyote brush and individuals expanding into the grassland (Photograph by Paul Laris).

in a positive light primarily because it is a *native* shrub expanding into largely *exotic* grasslands. In the first case the vegetation form—grassland—is deemed most critical, while in the latter case it is the vegetation origin—nativeness—that matters most (Laris et al. 2017).

In part the debate over the role of coyote brush invasion is due to the fact that the “original” vegetation cover of exotic grasslands remains uncertain. Until relatively recently, it was believed that prior to exotic grass invasion, the valleys and slopes of coastal California mountains and foothills were covered primarily by native California bunch grasses (e.g., *Stipa*) (Clements 1934; Burcham 1957; Barry 1972; Heady 1977). However, recent research casts doubt on this so-called “bunch-grass” hypothesis by arguing that forbs were predominant prior to the Colombian exchange (Hamilton 1997; Schiffman 2005; Minnich 2008). As such, a shift from grassland to a coyote brush shrubland constituted a type conversion in its own right (Russell and McBride 2003), suggesting the landscape may be governed by multiple states and transitions. Still others argue that CSS shrubs were common in areas now covered by exotic grasses and that grazing management practices, which included mechanical disking, primarily caused the type conversion (Laris et al. 2017).

Coyote brush has a number of key traits that give it advantages for rapidly expanding into grasslands. First, wind dispersal, in particular, may give it an advantage over many CSS shrubs, which lack a similar dispersal mechanism (DeSimone and Zedler 2001; Steinberg, 2002). Second, *B. pilularis* grows rapidly and after only two to three yr forms a closed canopy that can shade out exotic grasses. Third, and most importantly perhaps, *B. pilularis* stands are known to provide excellent refuge for small mammals, such as rabbits and rodents, which find safe cover under the shrub canopy and consume exotic grasses and seed. Feeding activity of these small animals is concentrated in grassland areas immedi-

ately adjacent to stands of shrubs and beneath the shrub canopy. The adjacent annual grassland provides poor cover for most of these animals, yet furnishes an excellent food supply for grazers and seed eaters. The activity can be so intense as to create trails of bare soil along the grass/shrub border, which may facilitate additional shrub establishment (Bartholomew 1970; Halligan 1973, 1974). As such, herbaceous-seed dispersal into and seedling survival in *B. pilularis* stands is very low (Hobbs and Mooney 1986), as small rodents and birds consume most developing herbaceous seedlings, perhaps facilitating a shrub domination (Bartholomew 1970; Christensen and Muller 1975; Hobbs and Mooney 1986; DeSimone and Zedler 2001).

It has been well documented that exotic grasses suppress the recovery of native CSS plants by outcompeting juvenile shrubs for resources (Eliaison and Allen 1997; Cox and Allen 2008; Fleming et al. 2009). By harboring small mammals that reduce the competition from exotic grasses, *B. pilularis* appears to facilitate conversion of grasslands to dense coyote brush stands (DaSilva and Bartolome 1984). Indeed, Hobbs and Mooney (1986) found that abundances of all herbaceous species declined greatly after *Baccharis* formed a closed canopy, usually within two to three yr of colonizing grassland. At this point, little seed of herbaceous species was dispersed into shrub stands or stored in the soil.

Importantly, *B. pilularis* is thought to have a relatively short lifespan (Hobbs and Mooney 1986). In addition, the coyote brush canopy, which is dense and closed during the plant's youth, can become progressively open over time as the plant ages. After ten yr or more, the canopy of coyote brush may be sufficiently fragmented such that herbaceous seedlings are able to establish (Fig. 2). It is possible, therefore, that coyote brush could facilitate a recovery of a more diverse mixture of species on the landscape by removing or damping the competition from exotic grasses—a phenomenon appropriately dubbed the “*Baccharis* hypothesis” by DeSimone and Zedler (2001).

In one of the few well-documented long-term studies of coyote brush invasion of a grassland, McBride (1974) found that the coyote brush colonization was a step in the succession of exotic grassland to woodland. McBride found that *Quercus agrifolia* and *Umbellularia californica* became established as seedlings under the canopy of coyote brush. In a related study, Zavaleta and Kettley (2006) found herbaceous biomass and competition from grasses strongly influenced the establishment of woody plants in grassland. They found that progressive increase in *B. pilularis* stand age and decline in herbaceous understory biomass likely increased the probability of successful oak recruitment under older shrubs. It is noteworthy that their study area was on San Francisco Bay Area lands formerly subjected to grazing and mechanical disturbance.

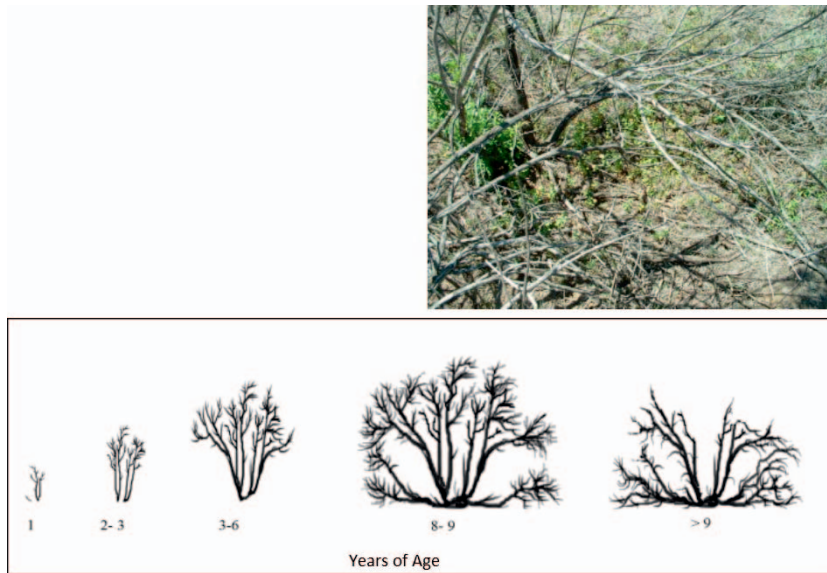


FIG. 2. Photograph of seedlings sprouting beneath a mature coyote brush canopy. Illustration of coyote brush structure over time [reproduced from Hobbs and Mooney (1986)] and Note the opening of the canopy occurs in more mature stands (Photograph by Paul Laris).

To our knowledge, the phenomenon of coyote brush invasion has not been studied systematically in southern California. To explore the possibility that coyote brush plays a facilitating role in native CSS shrubland reestablishment in southern California, and test the *Baccharis pilularis* hypothesis, we sampled plots of coyote brush known to have recently colonized exotic grasslands at numerous sites in the Santa Monica Mountains. We hypothesized that the relative frequency of native plants (shrubs and grasses) would increase, and exotic cover decrease, over time in areas covered by coyote brush stands. We sampled coyote brush stands of known age classes and then compared the results between age classes to determine to effect of coyote brush on native plant establishment over time.

METHODS

Study Area

The Santa Monica Mountains are one of the Transverse Ranges of southern California. They directly border the California Bight from Point Mugu on the west to Pacific Palisades on the coast to the east and continuing eastward inland to the Hollywood Hills. They constitute an anticline thrust southward along the Malibu/Santa Monica fault zone running along the coast. The study areas lie in the western Santa Monica Mountains and adjacent sections of the Simi Hills to the north (Fig. 3).

Miocene Conejo volcanics and lava intrusions are exposed along the western and central core with Miocene mostly marine sedimentary rocks to the

north and south (e.g., Vaqueros, Topanga Canyon, and Modelo formations). Peak elevations in the western Santa Monica Mountains are taller than found in the eastern Santa Monica Mountains, ranging from roughly 400 m to over 900 m. The general east-west trend of the range is interrupted by a few major north-south trending canyons, such as Malibu Canyon, Sepulveda Canyon, and Cahuenga Canyon. Small valleys and canyons are found throughout, making for a complex and high-relief landscape. Soils vary dramatically with elevation, slope, underlying geological substrate, and weathering (Yerkes and Campbell 2005).

The climate is Mediterranean in character, with the warm summer variant along the south-facing slopes along the beach and the hot summer on the north-facing slopes inland. Prevailing air and winter storm circulation is generally from the west, occasionally disrupted by Santa Ana foehn winds from the northeast and diurnal onshore and downslope breezes. Higher elevations experience more precipitation annually and during individual storms, through orographic effects. Lower elevations are drier due to less frequent attainment of saturation vapor pressure on the coast, coupled with and intensified by leeward descending circulation inland. The microclimatic pattern, thus, is extremely diverse and changeable over short distances (National Oceanic and Atmospheric Administration 1985; Barbour et al. 1993; Rundel and Gustafson 2005).

Vegetation reflects the climatic, edaphic, topographical, and geological diversity as well as land use history and fire regime. Chaparral dominates at higher elevations and north-facing slopes, often on the steepest slopes with the most skeletal and



FIG. 3. Study areas in Santa Monica Mountains of southern California.

unstable soils, while California sage scrub is common on lower slopes and drier situations, with a distinctive variant on coastal bluffs. Oak-dominated woodlands are common in canyons and hill slopes with deeper, well-developed and well-drained soils. Grasslands today dominate valleys and lower slopes and terraces, generally with histories of grazing, cultivation and/or mechanical disturbances to reduce shrub cover (Laris et al. 2017). The fire regime for the Santa Monica Mountains varies by location, but there were major fire events in 1973, 1993, and 2013, giving the specific study areas a fire return interval of twenty yr or less. The extent and floristic character of pre-European California grasslands are poorly understood (Minnich 2008) but, whatever their original character, grasslands in the Santa Monica Mountains today are dominated by exotic annual grasses and forbs and exotic perennial bunch grasses.

CSS, the focus of this study, is a sage-scrub community extending from the central California coast through northwestern Baja. CSS is dominated by semiwoody shrub species, and most of the flora is drought-deciduous, with a smaller portion represented by evergreens and succulents. Common shrub species include a number of sage species, such as *Salvia mellifera* Greene (Lamiaceae), *S. leucophylla*

Greene (Lamiaceae), and *S. apiana* Jeps. (Lamiaceae); two species of the composite family (Asteraceae): *Artemisia californica* Less. and *Encelia californica* Nutt.; and two buckwheat species: *Eriogonum fasciculatum* Benth. and *E. cinereum* Benth (Polygonaceae). The evergreen species *Rhus integrifolia* (Nutt.) Benth. & Hook. f. ex Roth (Anacardiaceae), *Malosma laurina* (Nutt.) Nutt. ex Abrams (Anacardiaceae), and *Heteromeles arbutifolia* (Lindl.) M. Roem. (Rosaceae) are present, too. CSS also supports the Cactaceae succulents *Opuntia littoralis* (Engelm.) Cockerell, *O. oricola* Philbrick, and *Cylindropuntia prolifera* (Engelm.) F.M. Knuth. CSS tends to be a floristically diverse combination of annuals, perennials, and geophytes, although some of the species can dominate large areas (Rundel and Gustafson 2005; Rundel 2007).

Baccharis pilularis, is a native shrub common to the coastal sage scrub (CSS) habitat of California and often appears in a complex mosaic with other vegetation types including grasslands. *Baccharis pilularis* is common in coastal areas and is found occasionally in the interior grassland and shrubland areas (Rundel and Gustafson 2005).



FIG. 4. View from above a *Baccharis pilularis* stand advancement over time based on image analysis for the four dates (Photograph by Sean Brennan).

Site Selection

To assess changes in species composition beneath coyote brush canopy, we selected stands of *B. pilularis* that had advanced over a 37 yr period, into several adjacent type-converted landscapes dominated by exotic grasses. We identified stands of *B. pilularis* using a vegetation map provided by the Santa Monica Mountains National Recreation Area (SMMNRA) that was constructed using 2001 aerial imagery and ground surveys. *Baccharis pilularis* shrub stand extents were then compared to historical imagery from aerial photographs for 2013, 2001, 1989, and 1976 acquired from SMMNRA. Google Earth's online historical imagery was also used to facilitate the identification of appropriate study sites (Google Earth, Google, Inc., Mountain View, CA).

The SMMNRA vegetation map provided a highly accurate and reliable source of vegetation data down to the species association level. This dataset was provided in a geographic information system (GIS) shapefile format, allowing for stands of *B. pilularis* polygons to be identified separately from all other vegetation association polygons. Polygons, or stands of *B. pilularis* based on 2001 imagery, were then compared to 2013, 1989, and 1976 imagery. Eleven stands showing the greatest expansion of *B. pilularis* and accessibility were identified, then transected to determine species composition (Fig. 4).

A belt transect sampling method was used to determine species composition at each sampling

location along each transect. Classifying transect portions and associated vegetation by age involved visual comparisons with historical imagery in GIS. Each 50 m transect location was entered into GIS using the field-recorded GPS locations. Then, each transect was separately analyzed across the four imagery dates. When viewing transects over 1976 imagery, most transects appeared as entirely open grassland. Portions of transects where shrubs appear for the first time in 1989 were classified as being at least 23 yr of age, and were assigned to the C-group. When viewing transects over 2001 imagery, portions of transects where newer shrubs appear were classified as being between 12 and 23 yr of age, and were assigned to the B-group. Finally, when viewing transects over 2013 imagery, portions of transects where the newest shrubs appear were classified as less than 12 yr of age, and were assigned to the A-group (Fig. 5).

A belt transect sampling method was used to determine species composition for each sampling location along each transect. Classifying transect portions and associated vegetation by age involved visual comparisons with historical imagery in GIS. Each 50 m transect location was entered into ArcGIS using the field recorded Global Positioning Sensor (GPS) locations (ArcGIS, Release 10.1, Environmental Systems Resource Institute, Redlands, CA). Then each transect was separately analyzed across the four imagery dates.



FIG. 5. Schematic of study design showing progression of coyote brush advancement.

Field Sampling

Transect placement began at the shrub stand edge and proceeded 50 m into the shrub stand, perpendicular to the expanding *B. pilularis* stand's boundary with grassland. Data collection began at the zero mark, followed then at each half meter. As a visual aid, a 1 m wide rod was held at its middle, horizontally to the ground, and perpendicular to the belt transect. Any new plant that touched the 1 m wide vertical plane (0.5 m on each side of the data point) would be counted according to species and transect location. This included all vascular vegetation from surface level into the shrub or tree canopy if applicable. If a plant that had been previously identified continued into the next data sampling point or beyond and no new individual plant was identified, "no change" was attributed to that data point. Areas completely void of vegetation received an attribute of "bare". A data point could contain multiple species as well as having more than one of any single species. All exotic grasses were categorized together as non-native grasses, while all native grasses were also categorized together with the exception of *Elymus condensatus*, a large grass that competes with CSS shrubs. In addition, all non-native mustards were also categorized together. There were 101 data points for each of the 11 transects, for a total of 1,111. Each transect was separately entered into a spreadsheet program listing species and counts for each data point. Transect locations were recorded using a GPS logger.

Transects were separately analyzed by age class using a spreadsheet. While all transects were 50 m in length, each individual age class portion along them

uniquely varied in length along each transect. Each datum, or sampling point, typically had more than one data entry along the crossbar set up at that point, and there would be varying numbers of sampling points within each class depending on the distribution of the age classes along that transect. Therefore, each transect was separately analyzed by age class as a percentage of the age class having any one species. Most transects had three age classes, all with varying lengths. Species within each age class were calculated by percentage of age class containing that species. A final tally of the three age classes across all eleven transects was summarized and also calculated as a percentage of age class containing a species.

Statistical Testing

Since the interest here is evaluating whether *B. pilularis* generally facilitates the re-establishment of native species in exotic dominated annual grasslands, our analyses focused on the counts and relative frequencies of *B. pilularis*, other native species, and exotic species as they change over the three age classes for *B. pilularis*. Frequency counts of native species and non-native species in general and then *B. pilularis* in particular, against all other native species and against all non-native species were cross-tabulated by the three age classes. Given that the sample sizes for our three contingency tables ranged from 710 to 1218 and that the smallest observed cell count was 28, we selected Chi-square tests to judge significance ($\alpha = 0.05$) for these three tests. Additionally, we evaluated the frequency of the no change attribute for shrub canopy extents with a Chi-square

TABLE 1. SPECIES COUNTS BY AGE CLASS (A < 12; 12 < B < 23; C < 23 YR OF AGE). * = NON-NATIVE SPECIES

Species	Count	Age class		
		A	B	C
<i>Adenostoma fasciculatum</i> var. <i>fasciculatum</i>	1	0	0	1
<i>Anagallis arvensis</i> *	27	11	11	5
<i>Artemisia californica</i>	130	12	54	64
<i>Astragalus brauntonii</i>	15	2	2	11
<i>Asclepias fascicularis</i>	6	0	3	3
<i>Baccharis pilularis</i>	215	38	85	92
<i>Brassica nigra</i> * or <i>Hirschfeldia incana</i> *	24	6	16	2
<i>Centaurea melitensis</i>	172	108	59	9
<i>Diplacus aurantiacus</i>	51	14	37	0
<i>Dichelostemma capitatum</i> ssp. <i>capitatum</i>	2	0	2	0
<i>Eriogonum cinereum</i>	4	0	3	1
<i>Hazardia squarrosa</i>	1	1	0	0
<i>Leymus condensatus</i>	26	0	17	9
<i>Malacothamnus fasciculatus</i> var. <i>fasciculatus</i>	20	7	9	4
<i>Malosma laurina</i>	24	1	4	19
<i>Marrubium vulgare</i> *	3	3	0	0
<i>Nassella pulchra</i> or <i>Nassella lepida</i>	108	10	59	32
Non-native grass: <i>Avena</i> sp*, <i>Bromus</i> sp*, <i>Erharta</i> sp*, or <i>Phalaris</i> sp*	284	182	90	12
<i>Pseudognaphalium californicum</i>	3	2	1	0
<i>Phacelia ramosissima</i>	4	0	2	2
<i>Quercus agrifolia</i> var. <i>agrifolia</i>	1	1	0	0
<i>Quercus lobata</i>	1	1	0	0
<i>Rhamnus ilicifolia</i>	1	1	0	0
<i>Salvia leucophylla</i>	33	3	13	17
<i>Sambucus nigra</i>	2	0	1	1
<i>Acmispon glaber</i> [formerly <i>Lotus scoparius</i>]	40	7	31	2
<i>Toxicodendron diversilobum</i>	2	0	0	2
<i>Trichostema lanceolatum</i>	4	0	1	3
Unknown	9	9	0	0
No Change	247	39	105	103

goodness-of-fit test, using the uniform probability distribution for the expected probabilities.

Sample size selection was governed by the availability of suitable sites, so we ran scenarios to learn if we had a sample large enough to minimize the probability of a Type II error (β). Not knowing ahead of time if there would be an effect of *B. pilularis* on the re-establishment of native species or what magnitude such an effect might have, we estimated the statistical power of our sample sizes, using G*Power (Faul et al. 2007), hoping to achieve at least a 0.80 probability of avoiding a false negative finding ($1 - \beta$). Conservatively assuming the effect (w) would be “weak” in Cohen’s usage (effect size, w , of 0.20), even the smallest of the three tables attained power in excess of 0.99 (Cohen 1992). Post-hoc power achieved and effect size are noted for each result in addition to statistical significance (P-value).

RESULTS

The surveys encountered 1218 individual plants over the 1090 data collection points (due to problems of access, 21 of the original 1111 data locations were not considered for analysis). There were 30 designations assigned that included 23 native species, five non-native species, no change, or unknown (Table 1, Fig. 6). As expected, *B. pilularis*, non-native grasses,

and no change were the most commonly encountered designations.

Age classification revealed spatial variations across all transects (Fig. 6). While photo analysis revealed shrub stand expansion occurred in general since 1976, each specific transect location contained varying proportions of age classes.

Separating each summarized age class into native and non-native vegetation types revealed distinct patterns. Vegetation in age class A showed non-native species were found in 95 percent of the sampling data points, as opposed to 38 percent for native species. Of the 436 plants encountered in class A, 29% were native, while 71% were non-native. Vegetation in age class B showed a marked increase in native species while non-natives declined sharply (Fig. 7): 74% of sampling data points contained native species, while only 39% of them contained non-natives. Of the 492 plants encountered in class B, 65% were native and 35% non-native. Vegetation in age class C showed a moderate relative increase in natives with 80% of sampling points containing natives, while non-natives again declined sharply, with only 10% of sampling points containing non-natives (Table 2). Interestingly, the number of plants subsides in these oldest classes to 290. Of these 90% were natives and 10% were non-natives. The observed counts of native and non-native plants

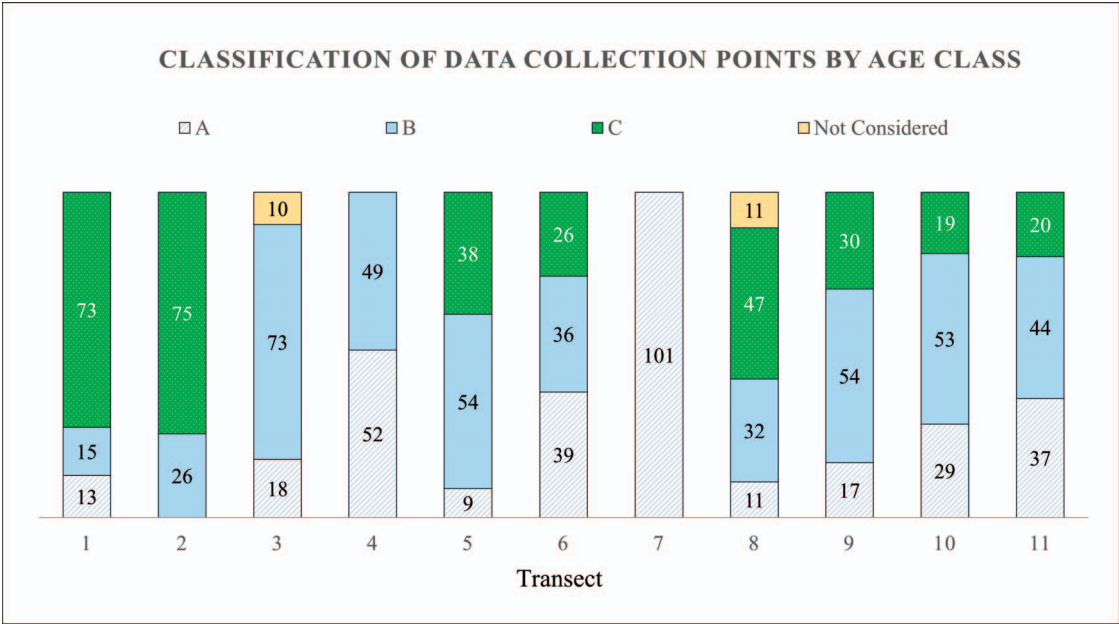


FIG. 6. Classification of data collection points and quantities within each respective age class. A < 12 yr in age; 12 < B < 23 yr in age and C > 23 yr in age.

were significantly different among age classes ($\chi^2 = 290.103$, $df = 2$, $P < 0.001$). The effect size is moderate (0.485), so the sample size ($n = 1218$) was sufficient to achieve a power of 0.999.

When examining *B. pilularis* abundance within each age classification for signs of facilitation of other CSS species, results show a non-monotonic increase in native species (Table 3). Of the 125 native plants encountered in class A, 30% were *B. pilularis*. The number of natives increased in class B to 322, as did the number of *B. pilularis*. Coyote brush, however, comprised only 26% of natives in this age class. In class C, the number of natives decreased to 262, but the 92 *B. pilularis* made up 35% of them.



FIG. 7. Age class A (foreground) transitioning to age class B (background) (Photograph by Sean Brennan).

However, these changes in the percentage of *B. pilularis* are roughly similar across the three age classes. *Stipa pulchra* Hitchc. (Poaceae), and *S. lepida* Hitchc. (Poaceae) were among the native species whose numbers increased non-monotonically with the age of the *B. pilularis* cover. These native bunchgrasses increased from 10 in class A to 59 in class B, thereafter subsiding to 39 under class C. This increase in *Stipa* species accompanies a strong decline in non-native grasses, from 182 in class A, through 90 in class B, down to only 12 in class C.

A Chi-square analysis of *B. pilularis* frequency relative to all other native species frequency revealed no significant differences ($\chi^2 = 5.196$, $df = 2$, $P = 0.074$, $1 - \beta = 0.509$) with almost no shift in the balance between *B. pilularis* and the other native species over the three time classes ($w = 0.086$).

When comparing summations of *B. pilularis* within each age class to the presence of non-native vegetation, however, results show a substantial negative association. As age classes became more populated with *B. pilularis* over time, non-native vegetation noticeably declined. A Chi-square analysis

TABLE 2. FREQUENCY OF NATIVE AND NON-NATIVE SPECIES BY AGE CLASS (A < 12; 12 < B < 23; C < 23 YR OF AGE).

Age Class	Native	Native %	Non-native	Non-native %
A	125	38	311	95
B	322	74	170	39
C	262	80	28	9

TABLE 3. FREQUENCY OF *B. PILULARIS* AND ALL OTHER NATIVE SPECIES BY AGE CLASS (A < 12; 12 < B < 23; C < 23 YR OF AGE).

Age class	Native species	Coyote brush	%	All other natives	%
A	125	38	30	87	70
B	322	85	26	237	74
C	262	92	35	170	65
Total	709	215	30	494	70

reveals a small, but significant, inverse association between the frequencies of *B. pilularis* and non-native species ($\chi^2 = 187.558$, $df = 2$, $P < 0.001$, $1 - \beta = 0.997$, $w = 0.136$).

Finally, shrub canopy extents most often featured the attribute of no change. No change values increased with shrub stand age as the vegetation approached a stable, native-dominated equilibrium (i.e., type-conversion back from exotic-dominated grassland to a native-dominated scrub). Most noticeable is the 83% increase from age class A to age class B, followed by a 41% increase from age class B to age class C ($\chi^2 = 31.941$, $df = 2$, $P < 0.001$, $w = 0.368$, $1 - \beta = 0.961$).

DISCUSSION

Our analyses indicate that expanding stands of *B. pilularis* support increased native plant cover. Following initial shrub invasion (age class A < 12 yr), a modest diversity of native species was found to exist. Then, following expansion or establishment of additional *B. pilularis* (age class 12 < B < 23 yr), non-native species declined precipitously while native shrubs, such as *Artemisia californica*, *Malosma laurina*, *Salvia leucophylla*, and native grasses, such as *Elymus condensatus*, *Stipa pulchra*, and *Stipa lepidota*, increased. Finally, after canopy closure (age class C > 23 yr), analysis showed native species diversity declined slightly while non-native species almost disappeared.

Results thus suggest that *B. pilularis* invasion of exotic grasslands can facilitate the reestablishment of other CSS species, as well as native bunch grasses, over time. We found a relatively high level of native species richness distributed across all eleven transects. Natives accounted for 12 of the 29 species identified. These results show *B. pilularis* stands are associated with native species richness. This diversity included a substantial native grass population as well as several species of shrubs, trees, and surprisingly the endangered *Astragalus brauntonii* Parish, where 11 of 15 individuals encountered occurred in stands older than 23 yr of age (age class C). Native grasses accounted for 108 of the 1218 individual plants encountered (9% of all vegetation). Non-native grasses were more abundant overall than native grasses. There were 284 non-native grass individuals encountered (23% of all vegetation), considerably more than native grasses. The native grasses,

however, increased in class B, while non-native grasses declined steadily from class A to class C.

Our results support those of Zavaleta and Kettley (2006) who also found that over time, native species colonized the area beneath the *B. pilularis* canopy and that exotic cover gradually declined with time in the San Francisco Bay Area. However, in northern Californian cases, where precipitation is notably higher than in the Santa Monica Mountains, *B. pilularis* invasion of grasslands led to a shift to woodland cover with low native species richness (Hobbs and Mooney 1986; Williams et al. 1987; Russell and McBride 2003; Zavaleta and Kettley 2006) while, in our southern California context, coyote brush invasion increased native shrub and grass species richness over time, a phenomenon which has not been documented in prior studies on coyote brush.

The frequency of native and non-native species within each age class revealed stark differences. Portions of shrub stands less than 12 yr of age contained the highest percentage of non-native species, while also having the lowest percentage of native species. Nearly every data collection point (95%) in age class A contained a non-native plant, while far fewer (38%) contained a native plant. This suggests that while the vegetation composition in this age class consisted primarily of non-native annuals, native species can co-exist under specific circumstances.

The high percentage of non-native species in age class A may reflect increased stress or intense competition. When considering portions of transects that are at least 12 yr of age but less than 23 (class B), however, a reversal of vegetation dominance transpires. The percentage of data collection points having a native plant nearly doubles (from 39% to 74%). Surprisingly, native grasses increased despite increased shrub cover—only 10 individuals were found in age class A (3% of data points in this class), followed by 59 in age class B (14% of data).

When analyzing portions of transects at least 23 yr of age, the data suggest that an ecological threshold has been breached, and that a transition to a new state of shrubland is occurring. This is supported by the fact that native species were found in 80% of all age class C data points, while non-native grasses were found in just 9%. In addition, native grasses remained relatively high with 39 individuals identified in age class C (12% of all age class C data collection points). The vegetation composition in age class C indicates that a transition to a CSS/grassland mix is underway. This finding is also consistent with Zavaleta and Kettley (2006), who used a similar methodology to document the role of coyote brush in facilitating the conversion of exotic grasslands to woodlands in the San Francisco Bay Area.

As documented, the rapid establishment of coyote brush canopy can inhibit some species, especially annual grasses, from establishing. This canopy effect was measured in the field by the attribute of no

change. While the majority of no change values followed *B. pilularis* individuals, other less encountered species in the no change category included *Artemisia californica* and *Malosma laurina*. Considering that *B. pilularis* stands were singled out for this study, an expectation would follow that over time, increasing shrub canopies would shade out lower stature vegetation regardless of being native or non-native. In addition, nearly monospecific stands of *B. pilularis* or other CSS shrub species would come to dominate the landscape over time. However, when analyzing the frequency of *B. pilularis* with all other native species, there was minimal effect with stand age (see Table #). Although *B. pilularis* stands appear as a monoculture when viewed from the stand edge or using aerial imagery (Figs. 1 and 5), when observed *in situ* or from within a shrub stand, a broad mix of native species becomes apparent.

Importantly, the process of facilitation can be observed where portions of the shrub canopy are no longer contiguous. As noted previously, at approximately nine yr of age, most *B. pilularis* individuals begin the process of senescence. These relatively older shrubs begin to break down physically, creating gaps in the canopy that permit other species to germinate. This continual breakdown of *B. pilularis* individuals over time may partially explain the non-monotonic increase of native vegetation across all age classes, from 125 through 322 to 262 in classes A, B, and C, respectively. *Baccharis pilularis*, meanwhile, is a relatively static element of the vegetation mix throughout, its share of the native species varying only from 30% to 26% to 35% in those age classes.

The classification of transects into age classes revealed considerable variations in individual extents. The fact that all age classes did not appear uniform across the eleven transects illustrates the diverse trajectories of recovery that shrub stands are experiencing in the Santa Monica Mountains. These variations may be reflective of past land use issues, such as the type and severity of disturbance and time since disturbance or variations in edaphic conditions or a combination. Research has shown that following the release from grazing, CSS shrub recovery in the Santa Monica Mountain region was most rapid in locations not previously disturbed mechanically, which tend to be located on steeper, or rockier, slopes (Laris et al. 2017). Many areas where intensive mechanical disturbance occurred experience very slow shrub recovery and have remained covered by non-native annual grasslands for decades (Engelberg et al. 2013). This study finds that the presence of coyote brush tends to counteract the impact of past mechanical disturbances and to facilitate native plant recovery.

Conclusion

Large areas of southern California remain under exotic annual grass cover, while areas under native

vegetation continue to decline or remain threatened. Although there have been, and are, numerous efforts to restore these areas and replace the exotics with native species, there remain key questions as to the nature of the original plant cover. Notions of the native plant cover of the foothills and valleys of southern California have been heavily influenced by Clements' "bunch-grass hypothesis," which assumes that areas currently dominated by exotic annual grasses were at one point covered in native bunch grasses (Clements 1934). The influence of this theory is quite apparent for the La Jolla Valley, a focus of this study, which was established as a preserve in 1972 to encourage native grassland recovery (Goode 1981; Gale 1983). As noted, however, recent evidence casts considerable doubt on the notion that bunch grasses covered large areas of southern California (Hamilton 1997; Schiffman 2005; Minnich 2008). Nonetheless, the impression that the exotic grasslands must have been native "grasslands" in the past is a difficult one to shake, especially given the fact that few areas of native grasses remain in the southern part of the state (Minnich 2008). As such, it is important to consider the findings of this study within the broader context of these theories and ideas.

This study finds that coyote brush is currently advancing into well-established exotic grasslands in the Santa Monica Mountains. Although in some areas the shrub appears to form a contiguous monotypic stand, at least in the short term, the long term results suggest that coyote brush gradually gives way to, or facilitates, the establishment of a mix of native plants. In the southern Californian foothills and valleys studied here, young coyote brush stands contain a high percentage of exotic species, primarily grasses, and few native ones. Conversely, mature stands of coyote brush support a wide variety of both native shrubs and grasses beneath the canopy, while exotics are reduced to less than 10% of the cover.

While it is possible that the species recovering beneath the coyote brush canopy reflect what existed pre-disturbance (at least pre-European contact), we are cautious when interpreting the results in this manner. First, our previous research suggests that disturbance intensity plays a critical role in determining current vegetation cover in southern Californian coastal valleys and hillsides and that the intensity of disturbance was also a function of various factors including elevation, slope, and soil rockiness (Engelberg et al. 2013; Laris et al. 2017). Therefore, although the results presented here indicate that coyote brush stand age is a critical determinant of native species presence, the stands we studied were advancing downhill and thus the findings may be subtly influenced by other factors, such as soil type or disturbance regime history. When considering La Jolla Valley, for example, while it is quite clear that coyote brush has rapidly advanced into areas on slopes where previously mechanical disturbance has been used to remove shrubs, it is not



FIG. 8. A mix of CSS shrubs recovering three yr after the 2013 Spring fire on a site formerly dominated by coyote brush. Note the large burned stems of dead coyote brush shrubs, lack of dense exotic grass cover and presence of bare soil (Photograph by Paul Laris).

clear whether coyote brush will continue to advance onto the valley floor which is still dominated by grasses. We do not doubt the facilitating role played by coyote brush; rather, we suggest caution when interpreting the results suggesting that CSS shrubs will continue to be dominant in the understory as the coyote brush advances into lower elevations with more gradual slopes and deeper soils, areas where, it has been argued by some, that native grasses and forbs would have been the dominant cover (Wells 1962; Callaway and Davis 1993; Keeley 2005). It should be noted, however, that Zavaleta and Kettley (2006) documented that coyote brush facilitated the conversion of previously disturbed level valley floors from grassland to woodland at Stanford University's Jasper Ridge Biological Preserve in San Mateo County, northern California.

Thus, whether coyote brush is advancing into areas that were once dominated by native shrubs or areas that were historically covered by grasses and forbs is difficult to determine from our results at this point in time at this site. As has been argued elsewhere, shrubland/grassland boundaries, disturbance regimes, and edaphic conditions often overlap, making it difficult to determine original vegetation cover in coastal California (Wells 1962; Laris et al. 2017). Moreover, it may well be the case that cycles of disturbance and recovery (whether human- or climate-induced) have long caused shifting of grassland/shrubland boundaries in California. Coyote brush may simply be an opportunistic species that has caused a temporary landscape cover shift that may eventually lead to yet more change over time. Indeed, if the current post-fire recovery pattern in the la Jolla Valley, for example is indicative of more general processes of change, coyote brush is not recovering on the upper-slopes (although it is on the lower ones), suggesting that the specific set of conditions that led to its invasion have now changed.

The vegetation on the upper slopes has shifted to a mix of predominantly native shrubs after the 2013 fire (Fig. 8). The current vegetation pattern might be explained by the fact that coyote brush is known to be fire-sensitive and able to resprout from light canopy fire but not from more intense fires that burn the base of the plant (Steinberg 2002) or that coyote brush is most successful on moist soils.

In closing, the results of this study might prove useful for restoration biologists who seek to speed-up the recovery of native species in areas long dominated by exotic grasses in southern California coastal areas. Our findings support the "*Baccharis* hypothesis" put forth by DeSimone and Zedler (2001) that coyote brush can facilitate recovery of a more diverse mixture of species on the landscape by removing or damping the competition from exotic grasses. Our results suggest that it is probable that establishing a stand or belt of coyote brush at the up-wind edge of an area of exotic grasses might be effective at facilitating the recovery of a wide variety of CSS and native grass species over time, at least in some settings, especially in southern California where annual precipitation is low and variable. Although the process of recovery may take up to 20 yr or more, many areas dominated by exotic grasses today have remained devoid of native shrubs or grasses for a century or more; as such, coyote brush may well be effective at speeding the restoration process.

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