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Long-term impacts of dam construction on plant succession and survival of an endangered species

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Abstract. This study was conducted to determine what changes have occurred in an arid alluvial riparian shrub habitat in the upper Santa Ana River basin over a 20+-yr period beginning prior to the completion of the Seven Oaks Dam in San Bernardino County, California and continuing until 8 yr after the completion of the dam in 2000 to assess the implications any changes may have on the persistence of the short-lived Santa Ana River Woolly Star (*Eriastrum densifolium* ssp. *sanctorum*, Polemoniaceae). Small-scale habitat changes were determined by comparing non-native annual plant data from 1989 to 2008. Large-scale habitat changes were determined by comparing perennial plant data from 1987 to 2008. The results of this study suggest that annual species, lichen crust, and dead shrubs are increasing, and that bare ground and live shrubs are decreasing. The older sites are also increasing in annual grass cover. Successional changes have occurred since the last significant flood event in 1969 although these changes are gradual and on a continuum, precluding a sharp distinction between different age stages. The data support previously predicted rates of succession indicating ultimate maturity within at least 100 yr. The continuation of these habitat changes will likely contribute to the decline of the Woolly Star population, particularly during future drought periods.

Key words: *Eriastrum densifolium* ssp. *sanctorum*; floodplain; rare and endangered species; Santa Ana River Woolly Star; Seven Oaks Dam; succession.

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Introduction

Ecosystems are often resilient to changing conditions (Holling 1973, Walker et al. 2004). Such resilience is determined by the degree and amount of disturbance a system can sustain without shifting to an alternative state (Holling 1973, Hanes 1984, Gunderson 2000). Normally, riparian plant communities found in arid alluvial river systems are resilient because they persist under highly variable ecological conditions related to periodic flooding events (White and Stromberg 2011). Such periodic flooding can maintain the resilience of these ecosystems by redistributing resources and inhibiting competitive exclusion (Huston 1994). However, the installation of a dam may result in a significant modification of normal disturbance events of periodic flooding that is sufficient to promote a shift to an alternative state (Baxter 1977, Poff et al. 1997, Nilsson and Berggren 2000, Beisner et al. 2003, Burk et al. 2007, Stromberg et al. 2007). Such flooding events that rejuvenate the habitat for early successional species, such as the endangered Santa Ana River Woolly Star, will no longer be possible with the installation

of the Seven Oaks Dam located in the Upper Santa Ana River floodplain in San Bernardino County, California and may result in the extinction of this taxon unless artificial means of rejuvenating the habitat are instituted.

The Santa Ana River Woolly Star and its habitat

The Santa Ana River Woolly Star, *Eriastrum densifolium* ssp. *sanctorum*, (Benth.) Mason, Polemoniaeae (hereafter referred to as *Eds*), is a federal and state endangered subshrub now restricted to a single geographic area—the Upper Santa Ana River floodplain (United States Fish and Wildlife Service 1987). It is one of the twelve most endangered taxa in California (York 1987). The only suitable habitat for this short-lived species is newly deposited alluvial sand within the floodplain of the river (Burk et al. 1988). *Eds* does not persist at older sites that have experienced ecological succession and have become dominated by weedy exotics, non-native annual grasses, and larger perennial plants and woody shrubs. These species compete with *Eds* for resources such as space, light, and water (United States Fish and Wildlife Service 1987; Wheeler 1991, Ryan 1995, Wendel 2003, Burk et al. 2007).

Under natural conditions, the floodplain would receive new alluvial material during major flood events, thus maintaining suitable habitat for *Eds* by removing non-native annual grasses and some of the larger shrubs while depositing new sand. However, due to the construction of the Seven Oaks Dam further upstream that was completed in 2000, future flood events will be severely limited or completely eliminated (Burk et al. 2007). This means that the available *Eds* habitat will gradually decrease over time as no new sand will be deposited, and the habitat will undergo ecological succession (Burk et al. 2007). Loss of habitat as a result of this succession threatens the viability of the population, which has already shown a substantial decline and may become extinct within the next 20 yr (Moskovitz 2003), particularly in the event of a drought lasting 10 yr or more (Atallah et al. 2016*a*).

Habitat succession and mechanisms

One of the many theoretical mechanisms for succession is the resource-ratio hypothesis, whereby the timing of establishment by certain plant species is dictated by their specific requirements for limiting resources (e.g., soil nutrients, water, light), the availability of which change over time (Tilman 1988). As these limiting resources fluctuate over time, total plant biomass increases; however, if the rate of accumulation of these resources is slow, succession occurs as a slowly shifting trajectory for plant communities, which is determined by the resource availability at that point in time (Tilman 1988).

In arid floodplain environments, the limiting resources are soil nutrients and water availability. This is due, in part, to high temperatures and low precipitation, as well as porous sandy soil (Atallah et al. 2016*b*). Sand and gravel are deposited by dynamic, high velocity flood events. Due to its relative large particle size and the porosity of sand, it is generally devoid of nutrients and has a low moisture retaining capacity. In addition, the high reflectivity of the sand may also increase surface temperatures (Ryan 1995). During a young successional stage pioneer plant species are present, which are tolerant of the poor soil conditions of the newly deposited alluvial sand (Smith 1980, Wheeler 1991, Ryan 1995). Plants that require more resources in the form of moisture and nutrients, such as non-native annual plant species and larger woody shrubs, are limited by the harsh, resource-poor environment of the early successional stage.

Over time, however, soil conditions change due to an increase in fine soil particles (clay and silt). These soil changes are largely attributed to Aeolian dust deposition, which is the process whereby fine soil particles (silts, clays, and organics) are picked up by the wind from a local source and blown into the area (McTainsh and Strong 2007, Muhs et al. 2008). Aeolian dust deposition is thought to be a regionally important soil development process in coastal Southern California (Muhs et al. 2008). Most of the soil development on the fluvial terraces within the Cajon Pass area of Southern California is due to increases in silt and clay from Aeolian dust deposition, likely from the Mojave Desert to the east (McFadden and Weldon 1987).

This increase in fine soil particles increases the water-holding capacity of the soil (Dorronsoro and Alonso 2006), as in addition to increasing

Table 1. Species generally associated with young, intermediate and old successional stages in the Upper Santa Ana River floodplain.

Young successional sites	Intermediate successional sites		Old successional sites
Bebbia juncea var. *aspera*	*Acmispon glaber*	*Salvia apiana*	*Adenostoma fasciculatum*
Encelia farinosa	*Ericameria linearifolia*	*Senecio flaccidus*	*Artemisia californica*
Eriastrum densifolium ssp. *sanctorum*	*Eriogonum fasciculatum*	*Hesperoyucca whipplei*	*Cylindropuntia californica* var. *parkeri*
Heterotheca sessiliflora	*Gutierrezia californica*	Dead shrubs	*Eriodictyon trichocalyx* var. *trichocalyx*
Lepidospartum squamatum	*Juniperus californica*	Lichen crust	*Stephanomeria pauciflora*
	Opuntia littoralis		Annual grasses

minerals and nutrients, which are eventually responsible for succession (Olson 1958, McBride and Stone 1976, Danin 1978, Smith 1980, Fearnehough et al. 1998, Ravi et al. 2007). This increase in vegetation contributes further to soil nutrients and fine soil particle deposition due to entrainment, when airborne particles are intercepted by above-ground leaves and stems (Fearnehough et al. 1998, Ravi et al. 2007). The establishment and growth of lichen crusts also aid in the accumulation of fine soil particles, moisture, and nutrients (Danin 1978, Belnap 2003, Veluci et al. 2006).

Successional stages in the Upper Santa Ana River Floodplain

Succession within Southern California arid alluvial floodplain ecosystems, along the San Gabriel and Santa Ana Rivers, has been demonstrated as progressing from early to late-successional stages in the absence of flooding, each with a suite of plant species and soil conditions (Smith 1980, Hanes 1984, Ryan 1995, Burk et al. 2007). Early successional sites were created during the last large flood event in the Santa Ana River in 1969 (Burk et al. 2007). These sites are indicated by the presence of stress-tolerant species such as *Lepidospartum squamatum* and/or *Heterotheca sessiliflora* and other species commonly occurring in this stage include *Encelia farinosa, Bebbia juncea* var. *aspera,* and *Eriastrum densifolium* ssp. *sanctorum* (Ryan 1995, Burk et al. 2007) (Table 1). Ruderal and annual species are generally absent at young sites.

Intermediate stage sites are associated with terraces last disturbed by the floods of 1938, and are indicated by the presence of species capable of competing for resources, including coastal scrub species and non-native grasses (Ryan 1995, Burk et al. 2007). Perennial coastal shrub species include *Acmispon glaber, Ericameria linearifolia, Eriogonum fasciculatum, Gutierrezia californica, Hesperoyucca whipplei, Juniperus californica, Opuntia littoralis, Salvia apiana,* and *Senecio flaccidus* (Table 1). Intermediate sites also commonly support dead shrubs, cryptograms (lichen crust), and herbaceous annuals are associated with the transition phase between the intermediate and oldest successional stages.

The oldest sites exist on terraces that were last disturbed during 19th-century flood events in either 1862 or 1891 (Burk et al. 2007). Late-successional sites are indicated by the presence of *Adenostoma fasciculatum, Artemisia californica, Eriodictyon trichocalyx, Cylindropuntia californica* var. *parkeri,* and *Stephanomeria pauciflora* (Table 1). Annual grasses are also present in this stage.

Implications of succession on the Santa Ana River Woolly Star

Habitat succession in the absence of flooding events is detrimental to the persistence of *Eds* (Burk et al. 1988). As described above, succession results in an increase in annual grasses and perennial species, which compete with *Eds* for resources such as soil moisture (Knoop and Walker 1985, Wendel 2003). In drought years, the effect of annual grasses on soil moisture can be even more dramatic, by increasing stress on *Eds* seedlings and adults that are known to suffer high mortality due to drought conditions (Wendel 2003, Atallah et al. 2016*a*).

The timing of rains within a single season can contribute to *Eds* mortality, as the seeds require at least 3.5 cm of precipitation in October or November to germinate, and seedlings require steady rains accumulating at least 20 cm between

January and March to survive (Wheeler 1991, Atallah et al. 2016*a*). If the first significant rains occur late into the season, *Eds* seeds will usually germinate, but the late start relative to the germination of annual species, usually results in the death of these seedlings (Burk et al. 2007).

Given the detrimental effects that habitat succession can have on *Eds*, and given the overall decline in this taxon and its tenuous prospects for persistence in the long term, if the current rate of succession were known such information could be useful for recovery efforts. This study seeks to determine whether predicted changes in habitat have actually occurred over the 20+ yr that *Eds* has been studied.

Methods

Nomenclature

The nomenclature included in this study follows the Jepson eFlora (Jepson Flora Project 2015).

Study area

The study area is located in the Upper Santa Ana River floodplain, north of the City of Redlands and south of the City of Highland, San Bernardino County, California. The study area has been the focus of numerous studies and master's theses on *Eds* and its habitat since 1987. The four study sites used in this study (Sites 1, 2, 3, and 5) are located within the 764-acre habitat reserve, which was established as mitigation for the Seven Oaks Dam, constructed upstream from the study area in the late 1990s and completed in 2000 (Fig. 1).

The study area is dominated by the alluvial fan sage scrub plant community, which is similar to coastal sage scrub except that it has a greater variety of evergreen shrubs, some chaparral, riparian, and desert species, much more *Lepidospartum squamatum*, and a greater cover of spring wildflowers (Burk et al. 2007). Previous studies have found that, due to the historic flooding regime in the floodplain, sites tend to represent various ages and stages of habitat succession. The youngest sites were created during the massive disturbance associated with the last substantial flood event occurring in 1969 (Wheeler 1991, Ryan 1995, Burk et al. 2007). The intermediate-aged sites were created during the 1938 floods, and the mature sites were created during the large floods in 1862 or 1891 (Ryan 1995, Burk et al. 2007).

Data were collected at four of the same five sites as those used in previous studies by Burk et al. (1988) and Wheeler (1991) to allow for direct comparison between historic (1987 and 1989, respectively) and later (2008) vegetation data. In these earlier studies, the sites were numbered 1, 2, 4, and 5, which have since been renumbered to be called 2, 3, 5, and 1, respectively; these latter site numbers will be used henceforth throughout the remainder of this document. Two of these sites (1 and 2) represent younger successional sites, and the other two sites (3 and 5) represent intermediate successional sites (Wheeler 1991, Ryan 1995, Burk et al. 2007, Lucas 2009). Data were not collected at the former Site 4 (now Site 5) because no hoops were established there by Wheeler (1991), and this site is no longer considered to represent suitable habitat for *Eds*. Site 1 (now Site 2) was also not used as none of the original permanent circular hoops placed at the site over 20 yr ago could be found in 2008 (Lucas 2009).

Sampling methodology

Both hoops and transacts were used in previous and current studies to gather data. The primary purpose of these transects was to gather shrub and perennial cover information, not annuals; the hoops were designed to assess annual cover. The hoop data collection method is designed to capture individuals of annual species because it is based on a random pin-drop intercept, not on whether the individual species occupies a certain minimum area. Therefore, the hoop method is more accurate in determining actual, fine-scale annual cover values than the transect method.

Hoops

Over 100 hoops were installed in 1987 at the four sites, each near an adult and encompassing *Eds* seedlings, consisting of black drip irrigation tubing to create a 0.56 m diameter hoop (with an area of 0.25 m^2). The same methodology used by Wheeler (1991) was utilized in all studies to collect the annual vegetative cover at Sites 2, 3, and 5. A varying number of the original hoops were located at sites 2, 3, and 5, some with their original identity tags and some without; those with original identity tags were used in the paired *t*-test analyses described below. Specifically, only 15 hoops were found in 2008

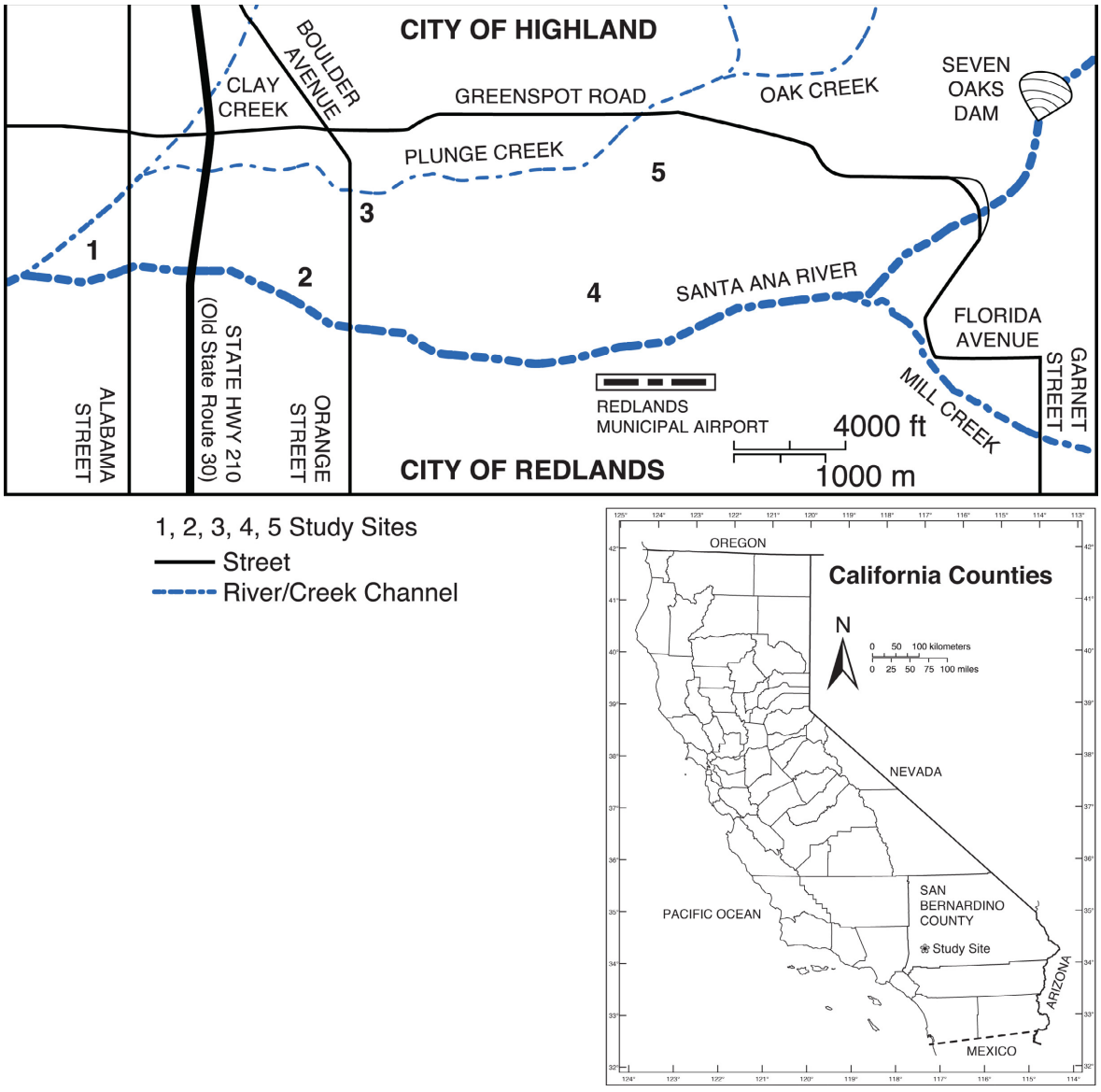


Fig. 1. Location of study area and study sites.

among the five sub-transects in Site 2 and only five were found at Site 5.

At each of these hoops, the following methodology was used to determine percent cover for annual plant species, bare ground, and vegetative litter. Cover was determined with a point-intercept frame that vertically lowered 20 pins (wire flags) spaced exactly one inch apart. A meter stick was placed along the edge of the hoop, and the frame was lowered perpendicular to this stick at three random points within the hoop, resulting in a total of 60 pin drops within each hoop. At each pin drop, the plant species touching the pin was recorded; if no plants were touched, then bare ground or litter was recorded. Percent cover per species was calculated by the following equation:

$$\%\ \text{cover (species A)} = \frac{(\text{No. pin contacts for species A})}{(\text{total no. pins})} \times 100$$

Every species present within each hoop was recorded, regardless of whether it was contacted

by one of the 60 pins using the point-intercept frame, to assess the changes in the presence or absence of each species.

Although species cover data were collected at these hoops in 1988, 1989, and 1990, only the data from 1989 were used in this analysis, as this was the only year that percent cover values were recorded by Wheeler (1991).

Transects

The same methodology used by Burk et al. (1988) was used to collect the transect vegetation data to allow for maximum comparability between the current conditions (in 2008) and the previous data collected in 1987. Although vegetation data were collected at subsites within each of the four study sites (subsite "a" for areas supporting *Eds* and subsite "b" for those areas not supporting *Eds*), data were only collected at the "a" sites to associate any vegetation or soil changes with the *Eds* population at each site.

In 2008, the end points of the original 100-m long baseline transect at each site were located; these transects had been marked in 1987 with permanent orange stakes (John Wheeler, personal communication). Each baseline transect was oriented east-west, with the starting point at the eastern end. From each baseline transect, five 30-meter-long subtransects were established perpendicular to the baseline at the same meter marks randomly chosen in 1987 (using a random number table); these meter marks are given in Table 2.

Table 2. Locations of subtransects along baseline transects at each site.

Site (old numbers)	Site (new numbers)	Meter mark locations for subtransect placement along baseline transect
1	2	20, 54, 68, 76, 94
2	3	17, 29, 43, 61, 88
4	5	12, 34, 39, 49, 72
5	1	34, 54, 83, 91, 94

The starting point for these subtransects was located at their intersection with the baseline transect, and was oriented south-north from the baseline continuing. Along each subtransect, the length that was intercepted by plants or substrate (to the nearest dm) was recorded according to the following categories: bare ground, rock (>10 cm), dead shrubs/litter, perennials (by species), and annuals (herbs and grasses combined; Table 3).

Table 3. Unpaired hoop averages per general cover type per site, 1989 and 2008 and annual grasses are non-natives.

Site	Cover type	1989	SD	2008	SD	% change
Site 2 (1989, n = 31 2009, n = 15)	Annuals	5.91%	3.89%	12.00%	5.57%	6.09%
	Annual grass	0.86%	1.82%	0.89%	1.53%	0.03%
	Bare/rock	81.40%	7.47%	61.22%	21.74%	−20.18%
	Lichen crust	0.00%	0.00%	7.22%	15.44%	7.22%
	Litter	12.53%	6.19%	12.78%	14.69%	0.25%
	Moss	0.32%	1.52%	0.00%	0.00%	−0.32%
	Vegetation	6.24%	3.78%	18.89%	19.53%	12.65%
Site 3 (1989, n = 26 2009, n = 17)	Annuals	20.51%	9.02%	75.59%	19.83%	55.08%
	Annual grass	14.17%	7.47%	29.79%	21.41%	15.63%
	Bare/rock	49.49%	11.65%	19.48%	13.03%	−30.01%
	Lichen crust	0.00%	0.00%	12.65%	13.59%	12.65%
	Litter	31.22%	8.75%	7.27%	6.68%	−23.95%
	Moss	2.44%	6.11%	0.00%	0.00%	−2.44%
	Vegetation	20.90%	8.92%	75.59%	19.83%	54.69%
Site 5 (1989, n = 25 2009, n = 10)	Annuals	5.07%	5.52%	26.33%	15.09%	21.27%
	Annual grass	4.60%	5.14%	19.83%	14.71%	15.23%
	Bare/rock	64.20%	18.63%	38.50%	19.17%	−25.70%
	Lichen crust	0.00%	0.00%	6.17%	9.69%	6.17%
	Litter	31.53%	17.70%	22.50%	20.75%	−9.03%
	Moss	0.40%	1.38%	3.17%	10.01%	2.77%
	Vegetation	5.47%	5.66%	39.17%	24.46%	33.70%

Data analysis

Raw data were grouped into cover type categories: bare/rock (bare ground including large rocks—for hoops and transacts), annual grass (for hoops only), vegetated (hoops only), live shrub (transects only), and dead shrub (transects only). Analyses were also run on individual species observed for hoops and transects.

For hoops, the total number of "hits" per species/cover type was divided by 60, which is the total number of possible hits per hoop, to determine the percent cover by that species/cover type in each hoop.

For transects, the total length of each subtransect occupied per species/cover type (in decimeters) was divided by 300, which is the total number of decimeters per 30-m long subtransect, to determine the percent cover by that species/cover type along each subtransect.

Sites 1, 2, 3, and 5 (Table 1) had five paired subtransects. Site 2 had 15 paired hoops, and Site 5 had five paired hoops that were located in 2008. Paired *t*-tests were conducted in Microsoft Excel for the each paired set of subtransects and hoops per site, comparing the previous data (1987 for transects, 1989 for hoops) to data (2008). The null hypothesis for these *t*-tests was that there would be no change in the percent cover of each species/cover type between the first sampling period (1987 for transects, 1989 for hoops) and the second sampling period in 2008. Significance was determined by a two-tailed $P \leq 0.05$, indicating that the null hypothesis should be rejected and that the percent cover had changed significantly.

Since some sites included hoops which were not located (and therefore could not be part of the paired *t*-test analysis), mean percent cover values for each species/cover type were also determined for each site by averaging the values for all hoops sampled per site. However, significance tests could not be conducted for those hoops with missing identity tags; therefore, since none of the hoops at Site 3 could be found, no significance tests could be conducted on data for this site.

McNemar's test was conducted for the paired hoops collectively (all 20 together) on presence/absence data to determine if a particular species or cover type had changed significantly since 1989 (Elzinga et al. 1998). (Calculations for McNemar's test were conducted using a calculator at http://faculty.vassar.edu/lowry/propcorr.html). A *P* value of 0.05 or less was also considered significant, indicating that the presence or absence of a species had changed significantly.

Results

Hoops—percent cover

Unpaired hoop averages.—Based on the average cover values of each site using the unpaired hoop data, all three sites (2, 3, and 5) showed an increase in annuals and annual grass, lichen crust and overall vegetation cover, and a decrease in bare/rock and litter (Table 3). These changes were the most pronounced for Site 3, followed by Site 5, especially for annuals, vegetation, and litter. While all three sites showed similar reductions in bare/rock (−20.18%, −30.01%, and −25.7% for Sites 2, 3, and 5, respectively), the increase in annuals differed among sites. Site 2 showed only a small increase in annuals (6.09%), whereas Sites 3 and 5 showed substantial increases in annuals (55.08% and 21.27%). Sites 3 and 5 showed similar increases in annual grasses (15.63% and 15.23%), whereas Site 2 showed a very minor increase (0.03%).

Paired hoop averages.—Using only the data from the paired hoops at Sites 2 and 5 (with 15 and 5 hoop pairs, respectively), both sites generally showed the same trends for % change and decreases shown using the unpaired hoop averages (Tables 3 and 4). However, using the paired hoop data, the increase in overall vegetation and annuals was greater for Site 5 (+33.67% and +20%, respectively) than for Site 2 (+13.44% and +6.89%, respectively), but these increases were only found to be significant at Site 2. The increase in annuals at Site 5 is likely due, in part, to the increase in annual grasses (+10.67%), although this increase was not found to be significant.

When the paired hoops for both Sites 2 and 5 were combined (N = 20), cover type changes were found to be significant, including an increase in annuals (10.17%), a decrease in bare/rock (−20.33%), and increase in lichen crust (8.08%), and an increase in overall vegetation (18.5%) (Table 4). Cover types were also found to have a significant change at Site 2 (all except for lichen crust), which may mean that this data set

Table 4. Paired hoop averages per general cover type per site, 1989 and 2008, percent change values with an asterisk (*) were significant at the 0.05 level, and annual grasses are non-natives.

Site	Cover type	1989	SD	2008	SD	% change
Site 2 (n = 15)	Annuals	5.11%	3.30%	12.00%	5.57%	6.89%*
	Annual grass	0.78%	1.39%	0.89%	1.53%	0.11%
	Bare/rock	81.22%	6.89%	61.22%	21.74%	−20.00%*
	Lichen crust	0.00%	0.00%	7.22%	15.44%	7.22%
	Litter	13.33%	6.67%	11.79%	14.71%	−1.55%
	Moss	0.56%	2.15%	0.00%	0.00%	−0.56%
	Vegetation	5.44%	3.30%	18.89%	19.53%	13.44%*
Site 5 (n = 5)	Annuals	7.33%	5.08%	27.33%	18.66%	20.00%
	Annual grass	7.00%	5.06%	17.67%	18.77%	10.67%
	Bare/rock	60.33%	21.93%	40.67%	18.32%	−19.67%
	Lichen crust	0.00%	0.00%	10.67%	12.11%	10.67%
	Litter	31.00%	21.72%	12.33%	7.03%	−18.67%
	Moss	1.00%	2.24%	6.33%	14.16%	5.33%
	Vegetation	7.33%	5.08%	41.00%	29.76%	33.67%
Site 2 and 5 (n = 20)	Annuals	5.67%	3.80%	15.83%	11.94%	10.17%*
	Annual grass	2.33%	3.80%	5.08%	11.46%	2.75%
	Bare/rock	76.42%	15.01%	56.08%	22.41%	−20.33%*
	Lichen crust	0.00%	0.00%	8.08%	14.45%	8.08%*
	Litter	17.50%	13.96%	12.67%	13.02%	−4.83%
	Moss	0.67%	2.12%	1.58%	7.08%	0.92%
	Vegetation	5.92%	3.76%	24.42%	23.75%	18.50%*

is driving the analysis, especially given its larger sample size of 15 hoop pairs (compared to five at Site 5). Interestingly, although the percent change of lichen crust increases at Sites 2 and 5 were not significant, when both sites were combined the increase was significant.

The percent change from 1989 to 2008 for most individual species was not significant, which may be due to the low cover per species in the hoops (Table 5). Only two species exhibited more than 5% cover (*Crassula connata* at Site 2 (5.56%) and Site 5 (5.33%) and *Bromus madritensis* at Site 5 (10.67%), and these only occurred in 2008; no species exhibited more than 5% cover in 1989. However, two species did show significant changes in percent cover between 1989 and 2008. *Crassula connata* showed a significant increase at both Sites 2 and 5 (by 5.56% and 5.33%, respectively), and *Logfia filaginoides* also showed a significant increase at Sites 2 and 5 (by 2.22% and 1.33%, respectively) (Table 5).

Percent cover changes for paired and unpaired hoop averages per cover type for Sites 2 and 5 are in Table 6. Given that the differences between the paired and unpaired average cover values for Sites 2 and 5 were minimal (especially for Site 2, which had a large sample size similar to Site 3), it is possible that the significant cover changes observed at Sites 2 and 5 (annuals, vegetation, *Crassula connate* and *Logfia filaginoides*, and lichen crust for Sites 2 and 5 together—Table 4) would be similarly significant at Site 3.

Presence/absence

Based on a two-tailed McNemar's test of the presence/absence data for all paired hoops combined (20 hoops for Sites 2 and 5 together combining data in Table 5), of the 26 species found during both sampling years only four showed a significant change from 1989 to 2008: *Bromus madritensis* (decrease), *Crassula connata* (increase), *Schismus barbatus* (decrease), and lichen crust (increase).

The significant increase in the presence of *Crassula connata* is consistent with the significant increase in the percent cover of this species at both Sites 2 and 5. The significant increase in presence of lichen crust is also consistent with the significant increase in its percent cover at Sites 2 and 5, when these sites were combined.

Table 5. Paired hoop percent cover averages per species, 1989 and 2008 where only species where the percent cover changed by more than 5% in at least one hoop are included and percent change values with an asterisk (*) were significant at the 0.05 level.

Site	Species	1989	SD	2008	SD	% change
Site 2 (n = 15)	*Bromus madritensis*	0.56%	0.00%	0.11%	0.43%	−0.44%
	Bromus tectorum	0.00%	0.00%	0.33%	0.93%	0.33%
	Chaenactis glabriuscula	0.00%	0.00%	0.00%	0.00%	0.00%
	Crassula connata	0.00%	0.00%	5.56%	5.37%	5.56%*
	Croton californicus	0.00%	0.93%	3.44%	13.34%	3.44%
	Eriastrum densifolium ssp. *sanctorum*	0.33%	0.00%	0.11%	0.43%	−0.22%
	Eriogonum fasciculatum	0.00%	3.27%	0.00%	0.00%	0.00%
	Erodium cicutarium	4.11%	0.59%	2.11%	3.05%	−2.00%
	Logfia filaginoides	0.22%	0.00%	2.44%	1.98%	2.22%
	Gutierrezia californica	0.00%	0.00%	3.33%	12.91%	3.33%
	Hesperoyucca whipplei	0.00%	0.00%	0.00%	0.00%	0.00%
	Vulpia myuros	0.00%	0.00%	0.00%	0.00%	0.00%
Site 5 (n = 5)	*Bromus madritensis**	4.67%	2.74%	10.67%	11.28%	6.00%
	Bromus tectorum	0.67%	1.49%	4.00%	4.80%	3.33%
	Chaenactis glabruiscula	0.00%	0.00%	1.33%	2.98%	1.33%
	*Crassula connata**	0.00%	0.00%	5.33%	4.92%	5.33%
	Croton californicus	0.00%	0.00%	0.00%	0.00%	0.00%
	Eriastrum densifolium ssp. *sanctorum*	0.00%	0.00%	4.67%	10.43%	4.67%
	Eriogonum fasciculatum	0.00%	0.00%	5.00%	11.18%	5.00%
	Erodium cicutarium	0.33%	0.75%	0.00%	0.00%	−0.33%
	*Lofia filaginoides**	0.00%	0.00%	1.33%	1.39%	1.33%
	Gutierrezia californica	0.00%	0.00%	0.00%	0.00%	0.00%
	Festuca myuros	0.67%	1.49%	3.00%	4.47%	2.33%
	Hesperoyucca whipplei	0.00%	0.00%	4.00%	8.94%	4.00%

However, the significant decrease in the presence of *Bromus madritensis* contradicts the substantial, although not significant, increase in the percent cover of this species at Site 5 by 6%. There was a total lack of *Schismus barbatus*, in any hoops in 2008; however, in 1989, it exhibited only 1.7% cover in two hoops and 5% cover in one hoop.

Table 6. Percent cover changes for paired and unpaired hoop averages per general cover type for Sites 2 and 5 where annual grasses are non-natives.

Site	Cover type	% change unpaired	% change paired	Difference
Site 2	Annuals	6.09	6.89	0.80%
	Annual grass	0.03	0.11	0.08%
	Bare/rock	−20.18	−20.00	0.18%
	Lichen crust	7.22	7.22	0.00%
	Litter	0.25	−1.55	1.80%
	Moss	−0.32	−0.56	0.24%
	Vegetation	12.65	13.44	0.79%
Site 5	Annuals	21.27	20.00	1.27%
	Annual grass	15.23	10.67	4.56%
	Bare/rock	−25.70	−19.67	6.03%
	Lichen crust	6.17	10.67	4.50%
	Litter	−9.03	−18.67	9.64%
	Moss	2.77	5.33	2.56%
	Vegetation	33.70	33.67	0.03%

Table 7. Paired subtransect percent cover averages for all sites combined, 1987 and 2008 and percent change values with an asterisk (*) were significant at the 0.05 level.

Cover type	1987	SD	2008	SD	% change
Bare/rock	33.55%	3.34%	54.27%	4.25%	20.72%*
Annuals	21.63%	13.75%	16.97%	14.83%	−4.67%
Live shrub	33.59%	17.02%	25.88%	16.29%	−7.71%
Dead shrub	4.92%	3.90%	11.83%	8.30%	6.92%*
Acmisspon glaber	0.00%	0.00%	0.52%	1.50%	0.52%
Croton californicus	3.72%	4.39%	0.98%	1.74%	−2.73%*
Eriastrum densifolium ssp. *sanctorum*	5.43%	5.30%	1.38%	1.90%	−4.04%*
Ericameria linearifolia	3.68%	4.81%	0.13%	0.46%	−3.55%*
Eriodictyon trichocalyx var. *trichocalyx*	10.35%	12.13%	3.83%	5.67%	−6.52%*
Eriogonum fasciculatum	5.68%	7.82%	6.52%	8.39%	0.83%
Juniperus californica	1.42%	5.67%	3.57%	9.08%	2.15%
Lepidospartum squamatum	3.68%	5.12%	5.12%	7.42%	1.43%
Hesperoyucca whipplei	0.42%	1.64%	0.77%	1.58%	0.35%

Although the change in the presence or absence of *Eds* was not found to be significant, it is worth noting that of the two hoops that had *Eds* in 1989 only one also had *Eds* in 2008, and four hoops showed new *Eds* in 2008 which were previously unoccupied by any *Eds* in 1989. All 20 paired hoops compared contained *Eds* when they were originally established in 1987, so the presence of *Eds* in five hoops in 2008, although an improvement over the two hoops in 1989, still represents a loss of *Eds* in 75% of the hoops over the past 22 yr.

Transects

When all 20 paired subtransects were analyzed together (Sites 1, 2, 3, and 5 combined), the only cover types showing significant change were increases in bare/rock (20.72%) and dead shrub (6.92%) (Table 7). Annual cover showed a slight decrease (−4.67%), but was not significant. Several species also showed significant decreases in percent cover: *Croton californicus* (−2.73%), *Eriastrum densifolium* ssp. *sanctorum* (−4.04%), *Ericameria linearifolia* (−3.55%), and *Eriodictyon trichocalyx* var. *trichocalyx* (−6.52%).

Table 8. Paired subtransect percent cover averages for general cover types per site, 1987 and 2008 and percent change values with an asterisk (*) were significant at the 0.05 level.

Site	Cover type	1987	SD	2008	SD	% change
1	Bare/rock	50.67%	7.25%	65.80%	14.52%	15.13
	Annuals	17.00%	3.10%	5.33%	4.30%	−11.67*
	Live shrub	18.00%	6.17%	20.27%	8.09%	2.27
	Dead shrub	2.13%	0.69%	9.07%	7.69%	6.93
2	Bare/rock	45.07%	8.28%	69.27%	10.39%	24.20*
	Annuals	14.80%	4.15%	2.80%	1.56%	−12.00*
	Live shrub	30.20%	9.56%	17.53%	8.48%	−12.67
	Dead shrub	2.67%	1.25%	11.40%	3.29%	8.73*
3	Bare/rock	13.13%	2.44%	49.73%	10.00%	36.60*
	Annuals	43.53%	5.97%	36.33%	7.19%	−7.20
	Live shrub	40.37%	17.90%	30.60%	28.11%	−9.77
	Dead shrub	3.93%	0.55%	8.80%	6.74%	4.87
5	Bare/rock	25.33%	10.32%	32.27%	9.10%	6.93
	Annuals	11.20%	3.86%	23.40%	5.63%	12.20*
	Live shrub	45.80%	19.70%	35.13%	8.43%	−10.67
	Dead shrub	10.93%	2.72%	18.07%	11.91%	7.13

Table 9. Average percent cover of species for young and intermediate successional stages using transect data with stages assigned based on Ryan (1995) and/or Burk et al. (2007).

Young stage (Sites 1 and 2)	Young	Intermediate	Old	1987	SD	2008	SD
Acmispon glaber		X		0.00%	0.00%	1.03%	2.05%
Croton californicus	X			2.17%	4.05%	1.30%	1.73%
Eriastrum densifolium ssp. sanctorum	X			4.23%	3.49%	1.37%	1.48%
Ericameria linearlifolia		X		7.00%	4.80%	0.20%	0.63%
Eriogonum fasciculatum		X		6.73%	9.24%	6.30%	8.58%
Gutierrezia californica		X		0.17%	0.53%	0.53%	0.86%
Hesperoyucca whipplei		X		0.00%	0.00%	0.57%	1.47%
Lepidospartum squamatum	X			5.83%	6.13%	8.90%	8.99%
Phacelia sp.		X		0.00%	0.00%	0.03%	0.11%
Senecio flaccidus var. douglasii		X		0.13%	0.42%	0.00%	0.00%
Stephanomeria virgata			X	0.00%	0.00%	0.13%	0.42%
Total % Young				12.23%		11.57%	
Total % Intermediate				14.03%		8.67%	
Total % Old				0.00%		0.13%	

Intermediate stage (Sites 3 and 5)	Young	Intermediate	Old	1987	SD	2009	SD
Croton californicus	X			5.27%	4.35%	0.67%	1.78%
Cylindroputia californica			X	0.20%	2.60%	0.00%	0.00%
Eriastrum densifolium ssp. *sanctorum*	X			6.62%	6.63%	1.40%	2.34%
Ericameria linearlifolia		X		0.37%	1.16%	0.07%	0.21%
Eriodictyon trichocalyx var. trichocalyx			X	20.70%	8.53%	7.67%	5.93%
Eriogonum fasciculatum		X		4.63%	6.41%	6.73%	8.65%
Gutierrezia californica		X		1.40%	1.59%	1.77%	2.42%
Hesperoyucca whipplei		X		0.83%	2.31%	0.97%	1.72%
Juniperus californica		X		2.83%	7.96%	7.13%	12.08%
Lepidospartum squamatum	X			1.53%	2.71%	1.33%	1.94%
Opuntia littoralis		X		0.40%	0.86%	0.00%	0.00%
Salvia apiana		X		0.00%	0.00%	0.33%	1.05%
Senecio flaccidus var. *douglasii*		X		0.73%	1.26%	0.00%	0.00%
Stephanomeria virgata			X	0.40%	0.77%	0.23%	0.74%
Total % Young				13.42%		3.40%	
Total % Intermediate				11.20%		17.00%	
Total % Old				21.30%		7.90%	

There were no changes in a particular cover type or species that were significant at all four sites (Table 8). Changes in annual cover were significant at three of the four sites (1, 2, and 5), showing a decrease at the first two (−11.67% and −12.00%, respectively) and an increase at Site 5 (12.20%). Bare/rock showed a significant increase at Sites 2 and 3 (24.20% and 36.60%, respectively). Dead shrub only showed a significant increase at Site 2 (8.73%).

Only three species showed any significant change in cover based on transect data (Table 9). *Eriogonum fasciculatum* showed a significant increase at Site 1 (11.6%) and a significant decrease at Site 2 (−12.5%). *Ericameria linearifolia* also showed significant changes at Sites 1 and 2, decreasing at both sites (−9.7% and −3.9%, respectively). The only other significant species change occurred at Site 3 for *Eriodictyon trichocalyx* var. *trichocalyx,* which exhibited a decrease (−13.0%). No other species showed significant changes, and no species changed in percent cover by more than 6%. *Eriastrum densifolium* ssp. *sanctorum* showed decreases at all sites (by 4.07%, 1.67%, 6.03%, and 4.4%, respectively, for Sites 1, 2, 3, and 5), but none were found to be significant.

Discussion

Hoops—microhabitat analysis

The original intent of the hoops established by Wheeler (1991) was to monitor the survivorship of *Eds* seedlings as well as to characterize the microhabitat (all annual species) associated with these seedlings and to help determine the successional age of each study site. Given that the hoops were established in 1987 specifically to encompass *Eds* seedlings and plants, they represent known occupied, or formerly occupied, habitat for this species. By using the species cover and presence data collected in 1989 and comparing it to data collected in 2008, it is possible to document the changes in *Eds* microhabitat over a 20-yr period, and to evaluate what kind of effects these changes may have on current and future *Eds* individuals. The successional ages of the sites studied in 1989 and 2008 are as follows. Sites 1 and 2 represent early successional sites established as a result of the 1969 flood event; whereas, sites 3 and 5 represent intermediate successional sites established as a result of the 1938 flood event. Site 4, which no longer supports a population of *Eds*, and was not included in this study, was probably established during either the 1862 or the 1891 flood events.

Change in all annual species cover and presence

A comparison of the 1989 and 2008 data clearly shows that the percent cover of all annual species is increasing at the study sites (Tables 3 and 4); the decrease in percent cover of bare/rock is likely due to this increase in annual cover. Changes are expected, as numerous studies have shown that annual vegetation cover increases in arid floodplain habitats with successional age, mainly due to the increase in fine soil particles (clay and silt) which increases the nutrients and water-holding capacity of the soil (Olson 1958, McBride and Stone 1976, Danin 1978, Wheeler 1991, Ryan 1995, Fearnehough et al. 1998, Dorronsoro and Alonso 2006, Ravi et al. 2007).

Contrary to the studies showing and increase in soil fines over time, a recent study conducted by Atallah et al. (2009) evaluating changes in soil textures at Sites 2 (an early successional site) and 3 (an intermediate successional site), did not show a consistent increase in fine soil particles. Statistical analyses of the soil composition in the upper two centimeters of soil of both sites combined showed there was no significant change in the percent of clay, silt, or sand between 1989 and 2008. However, there was a significant increase in clay at Site 3. It would be expected that if succession is occurring equally at both sites, then both sites should show increases in clay. Perhaps Site 3 exhibits an increase because it is closer to gravel operations than Site 2, or because it has a higher cover of lichen crust, which has been shown to possibly aid in the accumulation of fine particles (Belnap 2003, Chen et al. 2009).

The increase in percent cover of annuals *Crassula connata* and *Logfia filaginoides*, and the significant increase in the presence of *Crassula connata* at Site 2, may be related to an increase in soil fines and associated increases in soil moisture and/or nutrients. *Crassula connata* is characterized by Clarke et al. (2007) as occurring "often at the edges of ponds and wetlands," indicating its preference for areas with higher soil moisture.

Biological crusts (normally including lichens and mosses among other organisms) have also been shown to increase soil moisture, minerals, and nutrients, such as 369 carbon and nitrogen (Belnap 2003, Veluci et al. 2006, Chen et al. 2009). Su et al. (2009) have shown that lichen crust, particularly a complex crust including moss, increases the germination rate of annual non-native grasses compared to germination on bare soil. The observed increase in lichen crust may be due, in part, to the lack of physical surface soil disturbance in the area since its designation as a habitat reserve. Human and livestock activities that disturb soil surfaces have been shown to destroy crust, and it can take at least 20 yr for such crusts to recover after the disturbance is removed (Belnap 2003).

Change in non-native annual grass cover and presence

Interestingly, although annuals increased at both Sites 2 and 5, non-native annual grasses only increased substantially at Site 5, although not significantly (Tables 3 and 4). This difference could be directly due to the increase in soil nutrients or moisture over time, which may be partially due to increased moss cover. Moss cover only increased substantially at Site 5, but decreased at Site 2 and 3 (both not significantly

Tables 3 and 4). Deines et al. (2007) found that lichen crust inhibited the germination of annual grasses, but when moss was present with lichen crust it resulted in less inhibition and germination was more comparable to soils with no crust. Su et al. (2009) found similar results such that moss crust resulted in more germination than lichen crust without mosses for some species.

The significant decrease in the presence of the non-native annual grass species *Bromus madritensis* is not due to a general decrease in annual species or non-native annual grasses, as the data show an increase in the percent cover at Site 5 (Table 5). Rather, the decrease in the presence of this grass species may be due to a shift in the composition of annual species over time. For example, although *Bromus madritensis* was not found in 12 of the 20 paired hoops between 1989 and 2008, *Bromus tectorum* appeared in 8 of the 20 hoops in 2008 where it was not present in 1989. Further, while *Schismus barbatus* was not found in 12 of the 20 paired hoops, *Poa annua* appeared in 6 of the 20 hoops.

Rainfall and temperature

Given the extreme variability in germination and growth that annual species can exhibit based on differences in temperature and precipitation patterns (Figs. 2 and 3), a comparison of climate data from 1989 and 2009 to determine whether the observed increase in annual species may simply be attributed to large differences in climates during those years was completed. Although both years were considered drought years, below the normal average of 34.60 cm, total rainfall was similar for the 1988–89 season (21.03 cm) and the 2008–09 season (21.87 cm) (Western Regional Climate Center 2009). However, the timing of precipitation can also have a substantial effect on germination and survival of annual species.

Early precipitation gives annual seeds a head start on germination, and regularly occurring rains throughout the winter and spring result in considerable growth of those germinated seeds (Pitt and Heady 1978). Late onset of rains (not occurring until after December) means that annuals have less time during the winter/spring

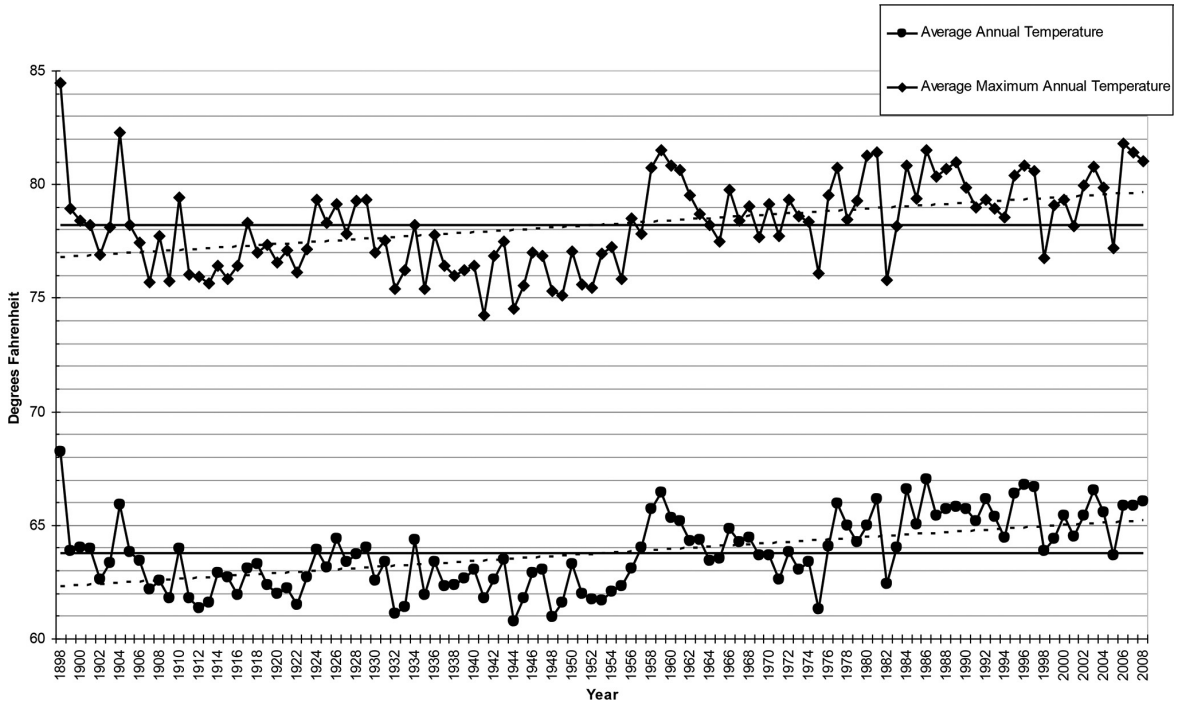


Fig. 2. Average annual and average maximum temperatures for Redlands, California, from 1898 to 2009. Solid black lines represent the average temperatures over the entire period, and dotted lines represent the general trend in temperatures over the entire period.

season to germinate and mature before the dry, hot summer months. Prolonged periods of dry weather during the spring can retard the growth of germinated annual plants, or result in the death of the seedlings as temperatures rise.

Since the pattern of rain events was similar in the 1988–89 and the 2008–09 seasons, with rains beginning in November, substantial storms occurring in December and February, and dry periods occurring during January and from March forward, the increase in annuals observed in this study cannot be attributed to major differences in either the total precipitation or the pattern of rain events between these two seasons.

However, rainfall data do show an overall reduction in total annual precipitation by approximately 5 cm since 1898 (Fig. 3). Since 1987, the percent of drought years is 65–70%, whereas the percent of years with normal rainfall is 30–35%.

Temperature can also affect the germination and growth of annual species. Growing Degree Days (GDD) are used to measure the time available for a plant to germinate and grow and GDD facilitates comparison with other species, using a known minimum temperature for germination as the basis for the calculation. For this study, a base temperature of 45° Fahrenheit was used. A daily GDD value is calculated by the following formula: *Average Daily Temperature—Minimum Germination (Base) Temperature = GDD.*

Temperature data from the Western Regional Climate Center (recorded at the Redlands airport adjacent to the study areas) indicate a trend of increased average and maximum temperatures (average maximum temperature over this period is 78.2°F) by nearly three degrees over the period of record (since 1898) (Fig. 2). Since 1976, the average and maximum annual temperatures have been at or above average every year but three (1982, 1998, and 2005). This is higher than the preceding period, from 1957 through 1976, where temperatures fluctuated mostly around the average. Prior to 1957, most temperatures were at or below the average (except for 1898 and 1904).

Macrohabitat analysis

Transects established by Burk et al. (1988) to characterize the community-scale habitat (focused on perennial species) associated with *Eds* habitat. Given that transects were established in areas containing *Eds*, the 1987 data (Tables 7 and 8) represent the composition of the perennial plant

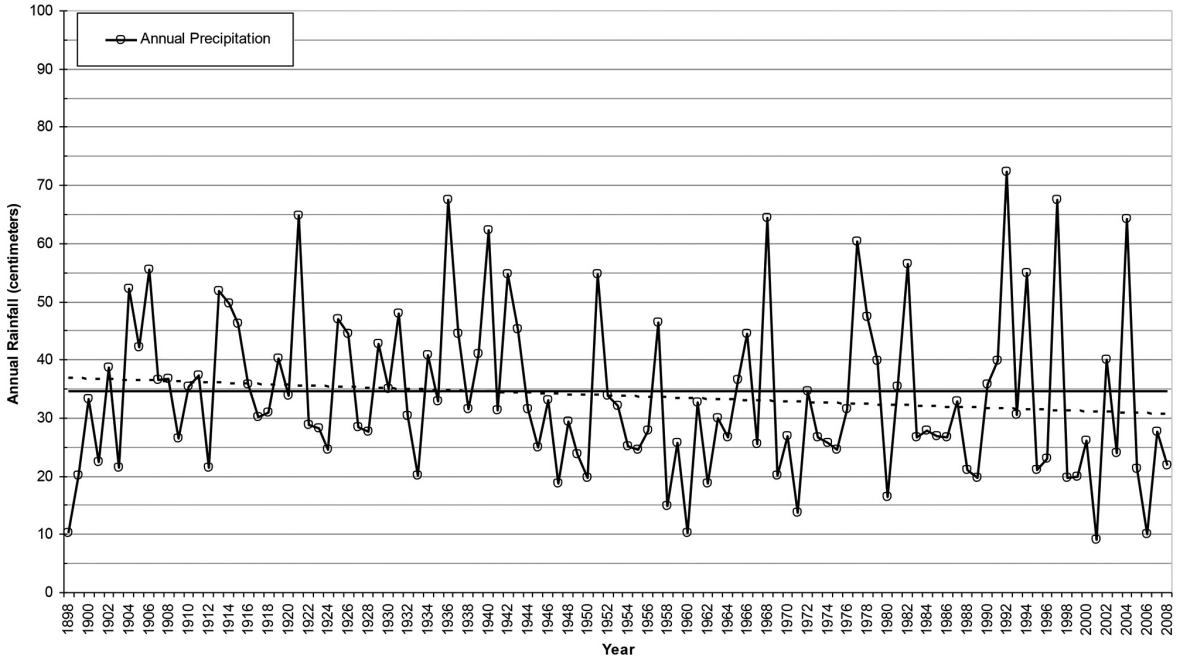


Fig. 3. Annual rainfall totals for Redlands, California, from 1898 to 2009. The solid bold black line represents the average annual rainfall over the entire period, and the dotted line represents the general trend in annual rainfall over the entire period.

community occupied by *Eds* at that time (although annuals were also recorded as a general cover type). By comparing data collected in 1987 to data collected in 2008, it is possible to document the changes on a macrohabitat scale for occupied *Eds* habitat over a 22-yr period, and to evaluate what kind of effects these changes may have on the continued suitability of this habitat for *Eds*.

Transect data generally showed a decrease in annual cover, an increase in bare/rock, an increase in dead shrub, and a decrease in live shrubs. Based on these data, it is likely that the increase in bare/rock may be related to the decrease in annual cover (particularly for Sites 1 and 2) and/or to the increase in dead shrubs, and that the increase in dead shrubs may be related to the decrease in live shrubs. However, if one assumes habitat succession, the opposite would be expected, such that annuals and live shrubs would be expected to increase and bare/rock to decrease. Possible reasons for these unexpected changes, such as sampling methodology or climate variability are discussed below.

Changes in annual species cover

The increase of annuals, using hoop data (Tables 3 and 4), contradicts the apparent decrease of annuals at three of the four sites using the transect data (Table 8). This may be due, in part, to the differences between the two sampling methods. The sampling unit for the transect data collection was one decimeter; therefore, any plants occupying less than that unit were not counted. Given the small size of individual annual plants, they were only counted as a general cover type "annuals" where they occurred in patches that occupied at least one decimeter along each transect.

The seemingly opposing trend in annual cover between the hoop and transect data could be attributed to climate patterns and not sampling methods. The climate patterns between the hoop sampling years (1989 and 2008) were very similar; therefore, the increase in annuals using hoop data cannot be attributed to differences in climate. This same analysis can also be used to compare 1987 and 2008 climate patterns and determine whether the apparent decrease in annual cover using the transect data is attributable to climate.

Although the 1986–87 and 2008–09 rainy seasons were also considered drought years, their total rainfall amounts differed by nearly 5 cm, (1986–87 = 26.70 cm; 2008–09 = 21.87 cm). Rains began earlier in 1986–87 and continued regularly through March, giving the annuals a head start coupled with reliable rains into the spring. The annuals in 2008–09, germinated in November, then had a large gap in rainfall during their prime growing period (January), and had a truncated precipitation period (rains ending in February) (Fig. 3).

Analysis of transect data indicates that the differences between rainfall patterns in 1986–87 and 2008–09 are likely responsible for the observed decrease in annual vegetation at Sites 1, 2, and 3, and the apparent increase in bare/rock at all sites. The variation in precipitation and its effect on annual vegetation may be tempered at the intermediate sites, as they tend to have higher amounts of clay and silt, which can hold water for longer periods of time. This may be why, despite the lower rainfall of 2008–09 compared to 1986–87, Site 5 showed a significant increase in annuals (Table 4), and why the decrease at Site 3 was only slight and not significant (Table 8).

Given the advantages of the hoop sampling method and the similar climate patterns between the sampling years, it appears that the actual trend for annual cover is increasing, with a larger increase at intermediate-aged sites.

Changes in shrub cover

All sites showed a decrease in live shrub cover and an increase in dead shrub cover. Although most of were not significant, when all site transects were combined the increase in dead shrub was found to be significant (Table 7). It is possible that this is due to the gradually increasing temperatures and longer and more frequent drought periods, which can have a detrimental effect on shrubs, resulting in abnormal shrub death (Bowers 2005, Hamerlynck and McAuliffe 2008).

Dead shrubs have been found to be associated with the intermediate stage of succession in the *Eds* habitat (Ryan 1995, Burk et al. 2007). Thus, it is possible that the increase in dead shrub cover may simply be due to succession, whereby individual shrubs that initially became established following the last flood disturbance have now reached natural senescence and are being replaced by other

species. Coastal sage scrub and chaparral species generally have life spans of at least 50 to 60 yr (Keeley, 1992; 2006), suggesting that the observed increase in dead shrubs, although not significant, would be more likely at the intermediate stage sites (3 and 5; Table 8), as the shrubs that first colonized these sites after the floods of 1938 would now be over 70 yr old. However, an increase in dead shrubs was also observed at the early successional sites (1 and 2); those that colonized these sites after the 1969 floods would only be 46 yr old, although the 1969 flood probably was not sufficient to remove all of the existing shrubs so the ones observed to be dead may have been a lot older.

Successional trends

Several studies of the vegetation within the upper Santa Ana River watershed determined the species composition of the three successional stages, and each stage is indicated by the presence of certain species (Ryan 1995, Burk et al. 2007). By comparing the percent cover of the young, intermediate, and old stage species in 1987 to their cover in 2009, changes in the successional stage of each may be evident (Table 9).

Based on transect data collected in 1987, Sites 1 and 2 (young - early successional sites) supported approximately equal cover of young stage species (12.23%) and intermediate successional stage species (14.03%), and supported no species characteristic of old sites (Table 9). In 2009, the cover of young stage species was nearly the same at 11.57%, the intermediate stage species cover decreased to 8.67%, and the percent cover of old stage species was 0.13%. The combined transect data also show an increase in dead shrubs at Sites 1 and 2 (Tables 7 and 8) and the paired hoop data show an increase lichen crust (at Site 2 – Table 4), categories which are more typically associated with intermediate stages. The hoop data also show an increase in annuals and a small increase for annual grasses at Site 2 (Table 4), categories that are associated with later successional stages.

In 1987, Sites 3 and 5 (intermediate successional stage sites) exhibited a high % cover of old stage associated species (21.30%), due to the prevalence of *Eriodictyon trichocalyx* var. *trichocalyx*, with the second highest proportion from species typically associated with young sites (13.42%), and the lowest proportion from intermediate stage species (11.20%). These relative proportions shifted in 2009, such that the highest cover is by intermediate stage species at 17.00% (which increased since 1987), followed by old stage species cover at 7.90% (which decreased substantially since 1987, again due to *Eriodictyon trichocalyx* var. *trochocalyx*), with the lowest cover by young stage species at 3.40% (which has decreased substantially since 1987). Similar to the young sites, the combined transect data show an increase in dead shrubs for Sites 3 and 5 (Tables 7 and 8) and the hoop data show an increase lichen crust for Site 5 (Table 4), both of which are associated with intermediate stages. The hoop data also show an increase in all annuals (Table 3 and 5), which are associated with intermediate successional stages.

This analysis suggests that a slight shift in vegetative composition may have occurred in the past 22 yr, indicating a possible, but gradual, successional trend. This is attributed, in part, to the apparent decrease in early successional stage species at the intermediate-aged sites, although the cover at young sites did not decrease (see Table 1 for species characteristic of each successional stage). Succession is also indicated by the general increase in dead shrubs, lichen crust, and annuals. However, the cover of intermediate successional stage species decreased at the young successional sites and increased at the intermediate sites. The possible reason for the substantial decrease in old successional stage species at the intermediate stage sites is unknown, but may reflect the general decrease in live shrubs and increase in dead shrubs observed at all sites. This suggests that compositional changes are occurring on a continuum whereby specific stages cannot be readily distinguished. Ryan (1995) found that these stages (early and intermediate) are in a continuous succession without large breaks between stages, and that although early stage species composition is very different from old stage composition, species turnover is gradual. This is consistent with the resource-ratio hypothesis of succession, whereby changes occur on a gradient over time relative to the changing availability of limiting resources at the soil surface (Tilman 1988). This gradient is evidenced by the fact that some species occur in several stages, such as *Eriogonum fasciculatum, Senecio flaccidus* var. *douglasii,* and *Salvia apiana,* which occur in both young and intermediate stages (Ryan 1995) and *Acmispon glaber* and *Juniperus*

californica, which occur in both intermediate and old stages (Burk et al. 2007). This heterogeneity is common throughout the floodplain.

Despite the possible slight shift in successional composition between 1987 and 2009, it does not appear that 22 yr is enough time for these sites to undergo a substantial shift from one successional stage to another. This finding is inconsistent with Smith (1980), who suggested that, based on shrub ring counts in different aged stands within the San Gabriel River floodplain, successional time to reach the old (mature) stage was 40 to 50 yr, and that the intermediate stage was reached by 25 to 30 yr. Rather, the findings of this study appear to be more consistent with a recent study by Burk et al. (2007), which suggests that the young successional stage may be complete after 40 yr, and that the intermediate stage may last at least 100 yr. Danin (1978) also hypothesized that succession on sandy soils could take dozens to hundreds of years. This study shows that the youngest sites (1 and 2), although created 40 yr ago during the last large floods of 1969, have not reached the old stage, but rather appear to be transitioning toward the intermediate stage. This study also shows that the intermediate stage sites (3 and 5), created over 70 yr ago during the floods of 1938, have not reached the old stage and instead, represent an intermediate stage of succession.

Habitat changes relative to the Santa Ana River Woolly Star

This study suggests that succession may be occurring within the upper Santa Ana River floodplain, but at a slow rate similar to that suggested by Burk et al. (2007). Succession is a threat to the continued existence of *Eds*, because suitable sandy soil habitat will be eliminated in the absence of large flood events that would normally deposit new sand and remove competitive vegetation. Based on a recent analysis of *Eds* demographic trends, the absence of future flood events downstream of the Seven Oaks Dam is compounded by the adverse effects of extreme seasonal temperatures and annual rainfall variability (Atallah et al. 2016*b*). In years where sufficient rains do not occur (at least 3.5 cm in October or November, and at least 20 cm spread out from January through March), *Eds* mortality can reach as high as 85% (Atallah et al. 2016*b*). In normal circumstances, when an *Eds* population begins to recover from periods of high mortality, it needs enough suitable habitat to allow the population to recover in preparation for the next drought period. However, in the study area, over time, habitat will become less available downstream of the Seven Oaks Dam due to the invasion of non-native annual grasses and succession. In addition, annual non-native grasses have been shown to have an adverse effect on *Eds* not only due to competition for space and water (Wendel 2003).

This study has shown a general increase in non-native annual species as well as lichen crusts and, if these two factors are correlated, then efforts to reduce lichen crust may result in a decrease in annual species. Previous restoration experiments have focused on the removal of above-ground vegetation, the excavation of soil (20 cm), the placement of new sand, or the construction of berms in an effort to determine the best strategy for rejuvenating *Eds* habitat (Thomey 2003). Soil studies have shown that the percent of sand increases substantially and the percent of silt decreases substantially below the upper 2 cm of the soil surface (Table 10). Removal or disturbance of the upper few centimeters of soil would remove the lichen crust, which may also slow the accretion of fine soil particles.

Several studies have shown that surface disturbance such as grazing can minimize the biological crust and its soil stabilization and nitrogen contribution functions (Sperry et al. 2006, Liu et al. 2009). Grazing within the preserve was eliminated when the preserve was established and that alone could account for the increase in non-native annuals. We suggest that grazing, if timed appropriately, would also help to reduce competitive annual plant cover. Such

Table 10. Average percent composition of sand, silt and clay particles in soils associated with *Eds* at varying depths.

Particle type	Upper 2 cm (Atallah et al. 2009)	Upper 10 cm (Burk et al. 1988)	Subsurface – 10–25 cm (Burk et al. 1988)
Sand	88%	97%	98%
Silt	12%	2%	1%
Clay	<1%	<1%	<1%

methods would likely be more cost effective and should be investigated further; however, caution should be used to ensure that any restoration efforts do not jeopardize the survival of *Eds* or the other rare and endangered species inhabiting this area, including the slender-horned spineflower (*Dodecahema leptoceras*) and the San Bernardino Kangaroo Rat (*Dipodomys merriami* ssp. *parvus*).

Along with the increase in non-native annuals, succession will also ultimately result in an increase in shrub cover, which will also compete with *Eds* for space, light, nutrients, and especially water (Knoop and Walker 1985). Our study also shows a general decrease in live shrubs.

An analysis of historic climate data indicates a gradual increase in average temperatures and a gradual decrease in annual precipitation, as well as an increase in frequency and duration of drought periods. If these climate trends continue, it could result in increased shrub mortality, which could result in reduced competition for *Eds*. If the climate continues to have increased temperatures and droughts, this would compound the effects that non-native annual species have already been shown to have on available soil moisture for *Eds* (Wendel 2003).

Although it is predicted that site-specific successional changes would have a detrimental effect on the survival of *Eds* at each site, these changes may not tell the entire story. Site 5, an intermediate stage site, has had the second lowest *Eds* population size since 2003 (Atallah et al. 2016*a*,*b*). However, Site 3, also an intermediate stage site, and considered to be the oldest site (Burk et al. 2007), currently supports the largest population of *Eds*. In addition, Site 3 also showed the largest recovery after the drought period in the early 2000s, and it has one of the lowest overall mortality rates (along with Site 2) (Atallah et al. 2015). Therefore, there are probably other site-specific factors that play an important role in facilitating *Eds* recovery and persistence, such as a lower seed predation rate or genetic variability. For example, Brunell (1991) found through a genetic analysis of *Eds* that individuals at Site 3 exhibited a rare allele which could contribute to the genetic diversity of this subpopulation and, therefore, its increased fitness to respond to environmental variability. Atallah (2003) found that predation of *Eds* seeds was the lowest at Site 3 at 2.9%, compared to the other sites which ranged from 12.9% to 62.5%.

Conclusion

The results of this study indicate that changes have occurred within habitat occupied by *Eds* over the last 20+ yr. Based on the species-specific percent cover changes per successional stage, it appears that succession is occurring, although slowly and on a gradual continuum without clear delineation between stages. In the absence of large flood events rejuvenating the habitat for *Eds*, the micro- and macro-habitat changes observed will reduce the available habitat for *Eds* over time, as well as result in increased competition for resources such as water. Climatic and normal successional stresses in the absence of significant flooding events because of the Seven Oaks Dam could compound the already declining *Eds* population, particularly during drought years. In the absence of habitat rejuvenation or restoration efforts, and assuming that current climate and precipitation patterns persist, it is possible that *Eds* populations at the intermediate stage sites may face a loss of suitable habitat due to succession toward the oldest stage beginning in at least 30 yr.

The results of this study indicate that successional changes in the Santa Ana River floodplain due to the construction of the Seven Oaks Dam has had a deleterious impact on the potential long-term survival of *Eds.* No matter how well intended the installation of the Seven Oaks Dam was, this study suggests that it is having effects that adversely effect *Eds* and its ecosystem, including other rare and endangered species and their habitats.

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