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A dam in the drylands: Soil geomorphic treatments facilitate recruitment of the endangered Santa Ana River woolly star

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Citation: Hernandez, R. R., and D. R. Sandquist. 2019. A dam in the drylands: Soil geomorphic treatments facilitate recruitment of the endangered Santa Ana River woolly star. Ecosphere 10(3):e02621. 10.1002/ecs2.2621

Abstract. The long-term management of aridland riparian ecosystems impacted by dams is crucial to reduce losses of biodiversity, reduce extinction risks for species, and restore ecosystem services. When dams preclude natural flow, safeguarding aridland riparian ecosystems adapted to infrequent, catastrophic floods poses additional challenges owing to the need to consider biological and pattern legacies. Seven Oaks Dam (California, USA) eliminated the occurrence of flooding, scouring, and deposition across the rare plant community downstream. This Riversidian alluvial fan sage scrub or alluvial scrub includes one of the most endangered plants in California, *Eriastrum densifolium* spp. *sanctorum* (Santa Ana River woolly star, hereafter called woolly star). In this study, we evaluated the impact of six soil geomorphic treatments on alluvial scrub and woolly star re-establishment after 5, 7.5, and 13 yr. We implemented a complete randomized block design, with each block incorporating six treatments: cleared, diked, cut, filled-10 (10 cm soil), filled-20 (20 cm), and filled-30 (30 cm), mimicking one or more physical disturbances (pattern legacy) occurring after a natural flood event. We performed plant community surveys (cover, abundance, maturity, invasibility, diversity) on full plots in 2006, representing 7.5 yr of response from the original 1999 treatment, and on half-plots in 2012, representing 5 yr of response following re-disturbance in 2007, and 13 yr of response on half-plots left intact since 1999. We found very limited recruitment of woolly star into control plots (1.2% cover). By contrast, the cut treatment showed consistently higher cover of woolly star (25.3%, 53.4%, 14.3%), after 5, 7.5, and 13 yr, respectively. Other treatments showed responses ranging between these extremes. Similar results were found for total native cover and diversity. Woolly star cover was inversely related to alien grass cover, suggesting that exotic grass invasions inhibit early recovery of the perennial. The re-establishment of base flows and flood pulses or soil geomorphic disturbances that mimic pattern legacies associated with infrequent, catastrophic flooding could be implemented to sustain downstream ecosystems that include woolly star populations. In the absence of such actions in the Santa Ana River floodplain, the persistence of woolly star as a species appears unlikely.

Key words: alluvial scrub; aridland ecosystems; biological legacies; disturbance; endangered species; *Eriastrum densifolium* spp. *sanctorum;* exotic annual grasses; floodplain; pattern legacies; restoration; riparian ecosystems; succession.

Received 4 September 2018; revised 3 January 2019; accepted 15 January 2019. Corresponding Editor: Gregory S. Okin.
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Introduction

Dams are one of the major drivers of global change on Earth owing to their size and proliferation, with over one million dams constructed across the world (Lehner et al. 2011). Research is limited, however, on the long-term restoration and management of dam-impacted terrestrial (e.g., downstream) ecosystems within arid environments, and even more so for the riparian corridors therein. Restoration activities within riparian ecosystems facilitate increased biodiversity, reduce biological invasions, restore ecosystem services, and provide an improved understanding of management actions (Rey Benayas et al. 2009, González et al. 2015). Thus, such activities may facilitate recovery of an ecosystem that has been degraded, damaged, or destroyed by dams, and hopefully lead to a self-sustaining ecosystem (SER 2004). Broadly, these actions can support ecosystem function to redress losses in biodiversity or ecosystem services where success can be measured by the differences in outcomes across different types of treatments (and/or compared to a control or reference site, when possible).

Although such actions have not been adequately studied within aridlands (Millennium Ecosystem Assessment 2005; Rey Benayas et al. 2009), it is recognized that restoration and management activities in highly dynamic and variable ecosystems, like aridlands, may not follow or respond to successful conventional approaches demonstrated elsewhere (Kondolf 1998, Feng et al. 2001, Hughes et al. 2005, Kondolf et al. 2007). For example, mediterranean ecosystems with high inter-annual and seasonal precipitation variability coupled with complicated patterns of biotic and abiotic heterogeneity pose unique problems for maintaining species populations and restoration (Maestre et al. 2006, Valladares and Gianoli 2007, Cooper et al. 2012). Further, the restoration of ecosystems adapted to natural disturbances—especially those ecosystems with natural disturbances that occur over relatively longer timescales (e.g., 100-yr floods, volcanoes)—confers additional complexity and challenges in delineating goals associated with mitigating anthropogenic disturbances (Acreman et al. 2014). In these cases, restoration can be something of a misnomer in that natural disturbances are critical editing processes, allowing biological legacies (changes in biological elements and processes, e.g., downed wood, sterilization of soil fungi, removal of seed banks) and pattern legacies (changes in physical elements and processes, e.g., scouring of top soil, reduction of soil fertility) that usher the ecosystem through important successional stages of recovery (Franklin 1990).

Eriastrum densifolium spp. *sanctorum* (Milliken) Mason (Santa Ana River woolly star, hereafter referred to as woolly star) is a short-lived perennial that colonizes recently deposited alluvium—deposits of clay, silt, sand, and gravel left by lotic systems—following infrequent, catastrophic floods in the Santa Ana River floodplain of mediterranean southern California (Fig. 1A–C; Thomey et al. 2003, Burk et al. 2007, Sandquist 2013). Due to urban development and flood control measures that significantly reduced woolly star habitat, the plant was classified as an endangered species in 1987 under the Federal Endangered Species Act of 1973. Although the species is emblematic of the more general case of the fate of early-successional species during succession, it has been considered among the top 12 most endangered plants in California (York 1987). Between flood events, it persists in open microhabitats typically having low-fertility soils or having experienced subsequent disturbance (e.g., animal burrowing).

Restoration and management actions in mediterranean floodplains are poorly understood (Martin et al. 2012, Murphy and Romanuk 2016) as demonstrated by numerous proposals to generally restore habitat without consideration of biological and pattern legacies after large floods. Such catastrophic floods create biological and pattern legacies including floodplain scour, sediment deposition, and the re-colonization of vegetation (Franklin 1990, Kondolf 1998, Hughes et al. 2005). In systems where such legacies are created and initiate a series of successional stages, these ecosystems face additional global-change-type threats beyond the cessation of natural flooding events. Across southern California aridlands broadly, exotic species invasions are facilitated by disturbance, but in the case of alluvial sage scrub habitat, alien plants, particularly exotic annual grasses, may ensue when soils have become more stable and nutrient supplies increase. This poses a different threat for woolly

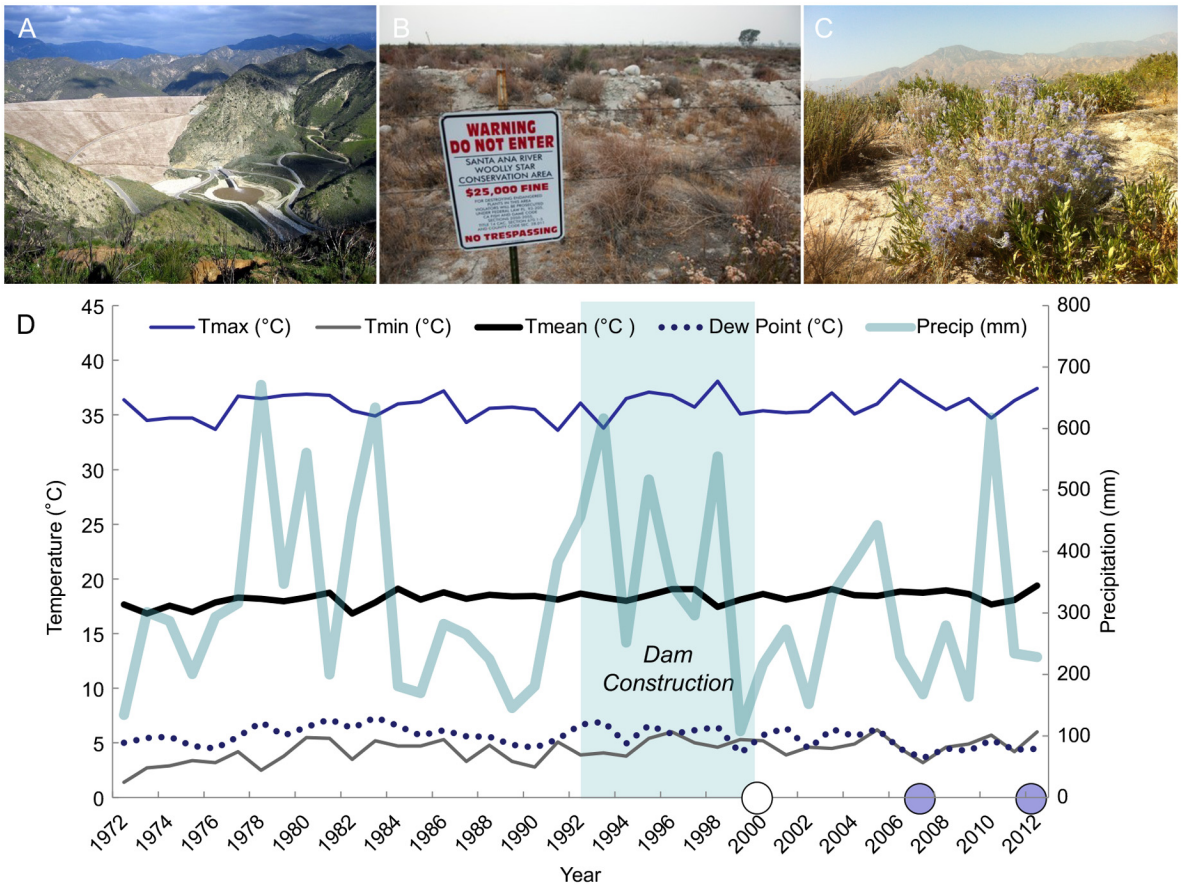


Fig. 1. (A) The Seven Oaks Dam (170 m), the 10th largest earth and rock fill embankment dam in the world, across the Santa Ana River in the San Bernardino Mountains (6.4 km NE of Redlands, California, USA; photograph: Steve Shumaker, WikiMedia Creative Commons) where floods last inundated in 1867; (B) "No Trespassing" sign showing the Santa Ana River Woolly Star Conservation Area and Riversidian alluvial scrub habitat (background; photograph: Joel Sartore); (C) *Eriastrum densifolium* ssp. *sanctorum,* (maturity stage 5) endemic species to the Santa Ana River drainage listed endangered in 1987 (photograph: Darren R. Sandquist). (D) The Long-Term Alluvial Sage Scrub Experimental Site is characterized by a mediterranean climate of hot, dry summers and cool, wet winters with highly variable inter-annual rainfall. Years (1993–2000) of dam construction and completion (2000) are denoted by the light teal polygon; experimental plots establishment (white) and surveys (purple) are denoted by points along the *x*-axis.

star as an early-successional species, whereby it may become competitively inferior over time as ecosystem development causes an increase in soil water and nutrient retention related to increasing soil organic material (Burk et al. 1988). Lastly, conservation here is also challenging in that the ecosystem is, as Askins (2001) describes, unpopular. Open-habitat-type ecosystems, like shrublands and scrublands, are often mistakenly characterized by humans as unappealing—perceptions that can adversely impact conservation priorities for early-successional species (Askins 2001).

The construction of the Seven Oaks Dam in 2000—the 10th largest earthen dam in the world (Fig. 1A)—altered the natural hydrology and disturbance regime of the Santa Ana River floodplain, thus limiting the normal scouring and deposition processes that confer favorable habitat for woolly star and two other endangered species: the slender-horned spineflower (*Dodecahema leptoceras*) and the San Bernardino kangaroo

rat (*Dipodomys merriami parvus*; Lucas et al. 2016). Such alterations ultimately preclude natural succession of this alluvial scrub habitat and may result in altered plant communities and species extinction.

Traditional restoration of river ecosystems occurs along riverbanks or floodplains and may include hydrological actions (or treatments), active plant introduction, exotic species removal, and grazing and herbivory control (González et al. 2015). Specifically, hydrologic actions include dam removal (e.g., converting land back to floodplain; Poff and Hart 2002) or modulating flow regimes at a specific duration and intensity as aligned with restoration goals (Acreman et al. 2014), or in some cases, to simply explore restoration potential (e.g., Grand Canyon flooding of 1996, Schmidt et al. 2001). The management of pattern legacies includes geomorphic actions that may include the recreation of micro-, meso-, or macro-habitat—for example, construction of floodplain terraces, surface profiling or leveling, soil disturbance, and bank stabilization—to facilitate vegetation establishment and development. Unfortunately, rarely are two or more restoration/management approaches compared with each other. Further, González et al. (2015) found that biotic factors (e.g., vegetation, invertebrates) are only used in approximately half (52%) of restoration assessments owing to laborious field-based efforts needed for monitoring (SER 2004). When monitoring of restoration activities has occurred in riparian systems, it rarely continues longer than six years (González et al. 2015).

Objectives and hypothesis

The absence of information about restoration of alluvial scrub riparian systems adapted to infrequent, catastrophic floods and their legacies, coupled with the need for realistic management that will sustain woolly star populations, led to the development of a long-term experimental site downstream of the Seven Oaks Dam. Here, our goal was to elucidate the effectiveness of novel soil treatments on vascular plant recovery within the Riversidian alluvial sage scrub plant community. Specifically, we sought to (1) quantify how six different soil geomorphic treatments impact re-establishment of a Riversidian alluvial fan sage scrub plant community, (2) determine if these soil geomorphic modifications facilitate recruitment of woolly star (as measured by plant cover, abundance, and maturity), and (3) understand the impact of time-since-treatment and treatment frequency on the alluvial sage scrub plant community properties (i.e., invasibility and diversity). We hypothesized that soil geomorphic treatments mimicking infrequent, catastrophic floods characteristic of the Santa Ana River floodplain will facilitate the establishment of woolly star while the absence of such treatments will facilitate the establishment of exotic plant species. Such findings have implications for decision-making on conservation policy and managed water-flow alternatives in this rare ecosystem and provide insights into the use of pattern legacy-based restoration in aridland riparian ecosystems elsewhere (Thomey et al. 2003, Sandquist 2013).

Methods

Study area

This study was located in the upper Santa Ana River floodplain (34.099283°N, 117.180667°W; 391 m) in southwestern San Bernardino County, California (Figs. 1 and 2). Here, the rare California plant community Riversidian alluvial fan sage scrub or alluvial scrub forms along ephemeral river edges and the floodplain where the lack of perennial water precludes riparian woodland development (Fig. 1B; Burk et al. 1988, 2007). This area is characterized by a Mediterranean-type climate of hot, dry summers and cool, wet winters with highly variable interannual rainfall. Precipitation averages 320 mm annually, and approximately 90% of total rainfall occurs between November and April. Mean daily temperatures are lowest from November through January (minimum temperatures, 5.6° ± 1.7°C standard deviation (SD), 1972–2002, PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA) and peak from June through August (maximum temperatures, 33.6° ± 2.5°C SD) with an annual average of 18.3°C (monthly averages; Fig. 1D).

We established the long-term alluvial sage scrub (hereafter called LOTUS) experimental site within a 20-km^2 area that supports, in part, the remaining population of woolly star. This area includes fluvial terraces of three general successional stages, early, intermediate, and mature,

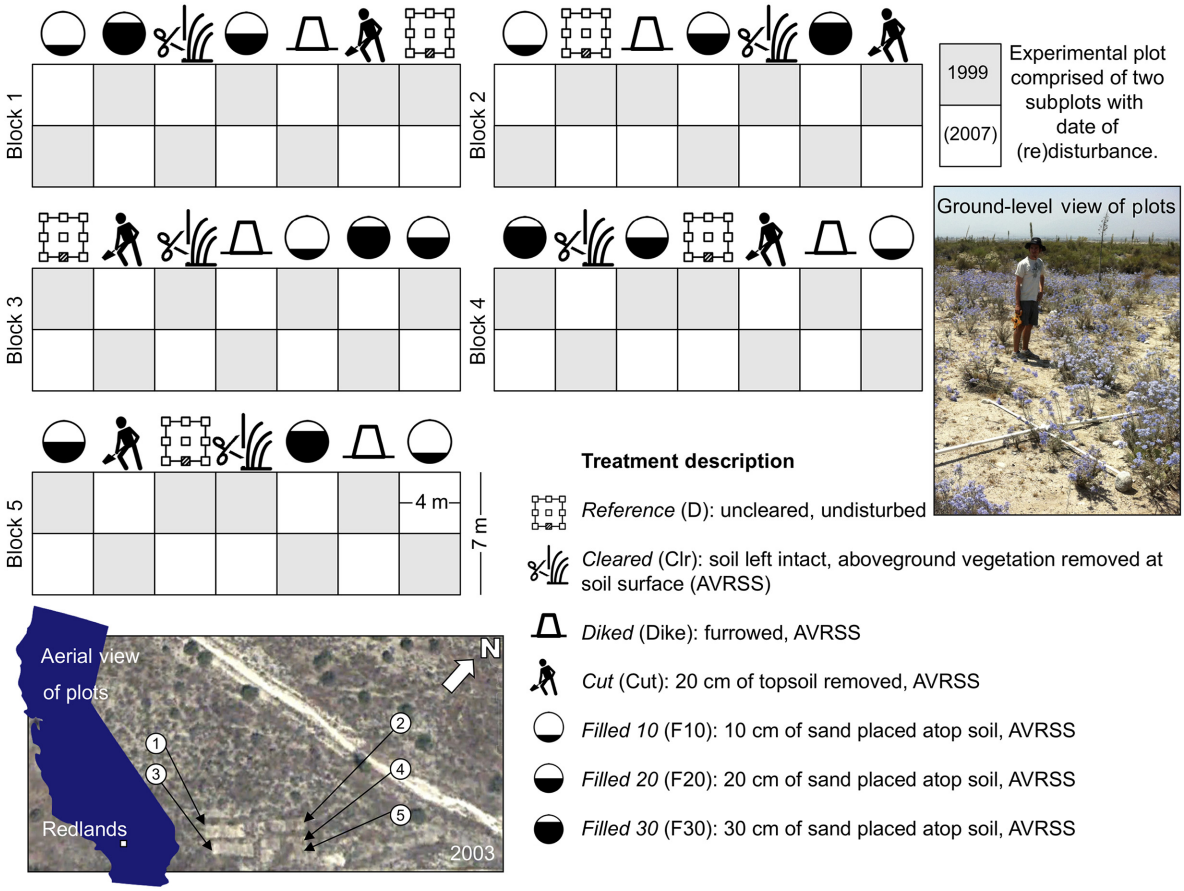


Fig. 2. The Long-Term Alluvial Sage Scrub Experimental Site (~20 km^2) in Redlands (California, USA) that supports, in part, the remaining population of woolly star on a mature successional terrace (scale = local [< meander]), last inundated by floods in 1862 and 1867. Here, we established a randomized complete block design (n = 5) comprised of six different soil geomorphic treatments. Each plot is comprised of two subplots: gray (disturbed in 1999) and white (re-disturbed in 2007). Photographs: Darren R. Sandquist.

that coincide with major floods dating to 1969, 1938, and 1862 (Agua Mansa flood), respectively. The early stage is an open-canopy, pioneer stage that contrasts with the mature sere, which supports a diverse plant community including large evergreen shrubs and some trees. We conducted this study on a mature successional terrace, last inundated by floods in 1862 and 1867 (Burk et al. 2007). This habitat represents a site in which woolly star is slowly being replaced by larger shrubs and weedy annuals that appear to outcompete species of earlier successional alluvial scrub seres (Hanes et al. 1989). Prior to the study's inception, dominant vascular plant species within the LOTUS experimental site included *Eriodictyon trichocalyx* (hairy yerba santa), *Croton californicus*, *Senecio flaccidus* var. *douglasii*, *Gutierrezia bracteata*, *Juniperus californica*, *Opuntia parryi*, and *Opuntia littoralis*. Other species included *Bebbia juncea*, *Eriastrum densifolium* subsp. *sanctorum*, *Ericameria pinifolia*, *Eriogonum fasciculatum*, *Lepidospartum squamatum*, *Acmispon glaber* (formerly *Lotus scoparius*), *Rhus ovata*, *Sambucus neomexicana*, and *Hesperoyucca whipplei*.

Habitats within and surrounding the study area have been heavily impacted by human activities, notably during the twentieth century. Such activities include fragmentation by urban and agricultural development, changes in the local surface hydrology and drops in the local

water table, sand and gravel mining activities, and channelization of the main Santa Ana River drainage. In 2000, the completed construction of the Seven Oaks Flood Control Dam, obstructing the flow of the main Santa Ana River channel from the San Bernardino Mountains, eliminated downstream flooding, scouring, and deposition across the study area. The LOTUS study area and impacts of the dam on alluvial scrub vegetation and soils are described in further detail in Burk et al. (2007).

Treatments

The experiment at the LOTUS site commenced in January of 1999 with the establishment of a complete randomized block design of five blocks, each incorporating seven 4 × 7 m experimental plots (i.e., 35 total; Fig. 2). In a single block, all experimental plots were randomly assigned one of six novel geomorphic treatments or left as a control, with no replication within a single block. Plot designations included (1) control (abbreviated, Dam): the soil and vegetation left undisturbed, representing approximately 100 yr since flood-related disturbances; (2) cleared (Clr): Aboveground vegetation was removed manually at the soil surface while disturbance of the soil was avoided; (3) cut (Cut): Aboveground vegetation and the top 20 cm of soil were manually removed, thereby eliminating the physical and biological soil crust (Hernandez and Sandquist 2011, Hernandez and Knudsen 2012), litter, micro-organics, silts, and clays and exposing sand; (4) diked (Dike): Aboveground vegetation was removed from the entire plot, and soil was removed to create four parallel trenches (each measuring 70 cm wide and 50 cm deep) evenly spaced across the long axis of each plot; (5) sand-fill to 10 cm (F10): Aboveground vegetation was cleared and sand was placed atop the plots to a depth of 10 cm thereby mimicking natural sand deposition that would occur following a major flood event; (6) sand-fill to 20 cm (F20): procedure same as above but to a depth of 20 cm; and (7) sand-fill to 30 cm (F30): procedure same as above but to a depth of 30 cm. All sand used (0.5–2.0 mm particle size) was obtained from a nearby sand mine and washed prior to use.

Treatments Clr, Cut, Dike, F10, F20, and F30 were implemented to mimic pattern legacies that likely occur after a natural flood event, including aboveground canopy removal (treatments Clr, Cut, Dike, F10, F20, and F30), soil scouring (treatments Cut and Dike), and sediment deposition (treatments F10, F20, and F30). To study the impact of time-since-treatment and greater disturbance frequency on the alluvial sage scrub plant community, in September of 2007 we re-disturbed half of each plot with the same treatment (excluding Dam), thereby creating an age sequence of disturbance.

Thomey et al. (2003) measured soil texture and macronutrients across each LOTUS treatment plot at three of four plot corners (9.7 cm diameter, 7 cm depth) and aggregated into one sample bag. All sand-fill treatments (F10, F20, F30) contained a significantly higher percentage of gravel and lower percentage of silt and clay when compared to Dam. The Cut treatment was also significantly lower than Dam in clay. Thomey et al. (2003) found no significant difference in magnesium, calcium, and phosphorus across treatment plots; however, nitrogen, an essential limiting resource for plant growth and reproduction (Bazzaz et al. 1987), was significantly lower in all sand-fill treatments compared to Dam.

Plant cover, diversity, and invasibility

Plant community surveys were done on full plots in summer 2006, representing 7.5 yr of recovery from the 1999 soil geomorphic treatment, and on half-plots in fall 2012—one half-plot representing 13 yr of recovery from the 1999 treatment and the other half representing 5 yr of recovery from the 2007 treatment. The surveys quantified percent cover of all species along six, evenly spaced (60 cm apart) transects parallel to the long axis (NW to SE) that ran through each subplot. Plant cover as a metric is used to represent growth—one of three (reproduction, defense) essential plant functions that may differ across individuals when resource availability varies within or among environments (Bazzaz et al. 1987).

Transects were not surveyed within 0.5 m of the plot border to avoid edge effects. Plant cover was measured independently for each perennial species observed. Dominant shrubs were subclassified as either living or dead: dead woolly star identified by the gray stems and the absence of leaves and seed heads, and dead *E. trichocalyx*

identified by black-to-blackish stems and the absence of leaves and flower stalks. Such remains of dead plants were intact and could be easily used for identification and cover estimates. Dead cover measurements of dominant woody shrubs provide supplemental information about aboveground biomass cover and recruitment dynamics (i.e., retention of individual skeletons) from previous cohorts (e.g., 3- to 4-yr-old), which may serve an ecological role (e.g., shade, wildlife habitat). Additionally, dead cover measurements may capture recruitment dynamics for older cohorts from previous years (~ 3 to 4 yr) or when mortality occurs for younger plants (~ 1 to 2 yr; e.g., drought, disease). Annual plants were combined into a single group for cover measurements. These were predominantly exotic, annual grasses of Mediterranean origin (e.g., *Bromus* sp., *Avena* sp.).

Plant abundance and maturity

A corollary metric to that of plant cover is maturity. Measuring the maturity of a focal plant species across different soil geomorphic treatments may reveal differences in the maturity stages leading toward reproduction. Reproduction is an essential plant function where allocation of resources for reproduction creates tradeoffs for growth and defense and thus is an indicator for fitness where timing is a crucial factor (Bazzaz et al. 1987, Kozlowski 1992). Reproductive traits are typically measured at the end of the growing season, as we did here, or at plant maturity (Bazzaz et al. 1987). Within each subplot, we counted the number (i.e., abundance) of all plants and classified living woolly star and *E. trichocalyx* plants according to size-class (i.e., maturity) to determine if potential differences in resources available among treatments correspond to differences in fitness. We use maturity as a proxy for fitness under the assumption that stress will delay or prevent growth and flowering in perennials. We acknowledge that extreme stress may promote flowering, which could confound observations (Bazzaz et al. 1987), but in such cases, growth will likely be reduced.

Plant maturity of woolly star was recorded as one of five development stages: Stage I (seedling, unbranched), Stage II (juvenile, singly branched, usually not yet reproductive), Stage III (adult, flowers present, ≤30.0 cm in height), Stage IV (adult, flowers present, 30.1 cm < height ≤ 60.0 cm), and Stage V (adult, flowers present, height > 60.0 cm). Maturity of *E. trichocalyx* was recorded as one of five development stages: Stage I (seedling, ≤2 branches, no wood), Stage II (juvenile, >2 branches), Stage III (adult small, ≤0.5 m in height), Stage IV (adult medium, 0.5 < height ≤ 2.0 m), and Stage V (adult large, height > 2.0 m). Long-term monitoring plots show that mean woolly star lifespan is approximately 2–2.5 yr and rarely do they live more than five years (D. R. Sandquist, *personal observation*). Observations of *E. trichocalyx* lifespan at the LOTUS site have not been made.

Climate data for the site were calculated from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) over 40 yr from January 1972 to December 2012. Annual precipitation and air temperatures (minimum, maximum, mean) were calculated from 800-m-resolution raster data, and dew point from 4000-m data. Modeled weather data were compared to nearest weather stations to confirm accuracy (Fig. 1).

Statistics

The effects of soil surface treatments on vegetation response measures were tested using a randomized complete block design (RCBD) analysis of variance (ANOVA) within each time-since-treatment. All response variables were tested against the main effects of treatment and block, with data from Dam (control) plots statistically excluded, as this did not represent a restoration measure, and thus provided focus of the analysis only on vegetation properties following surface treatments. In cases where the main effect of treatment was found to be significant ($P < 0.05$), a Tukey's HSD post hoc test was used to identify significant ($P < 0.05$) differences among individual treatments. The response variables tested were as follows: living woolly star cover, living + dead woolly star cover, exotic annual grass cover, and total perennial/native plant cover.

To determine the relationship between exotic annual plant cover and woolly star cover (across all treatments, including control plots), we ran linear regressions where exotic annual and woolly star plant cover were the independent and dependent variables, respectively. We

conducted regressions for datasets from 7.5 yr, 5 yr (re-disturbed), 13 yr, and across all yr in RStudio (version 0.99.473, RStudio, Boston, Massachusetts, USA). Multiple R^2 values and associated *P*-values were used to determine explanatory power and significance, respectively. Data were tested to ascertain that assumptions of linear regression models were met including those related to linearity, homoscedasticity, and the mean and autocorrelation of residuals.

A two-way full-factorial ANOVA was used to evaluate effects of treatment (excluding control), size-class, and treatment-by-size-class interaction on frequency of woolly star and the other dominant shrub, yerba santa (*Eriodictyon trichocalyx*), separately. Analyses were done independently for each year-since-disturbance, because the sequence is not a true time series owing to re-disturbance in 2007. Significant frequency differences among treatments represent more- and less-favorable geomorphic treatments for re-establishment of woolly star or *E. trichocalyx*, whereas frequency differences among size-classes indicate variability of establishment, survival, or growth across all treatments—interpreted as underlying demographic-related population processes, probably based on climate effects (e.g., recent drought would result in few small recruits and favor survival of more-deeply rooted large plants). A significant interaction effect would indicate that establishment, survival, or growth processes that affect size-class distribution differ among treatments, a result likely due to an interaction between climate (namely precipitation) and soil properties that affect water availability.

We enumerated species richness (living + dead) within each individual (sub)plot and reported species richness as the total number of species across all (sub)plots by treatment. We calculated mean species richness by calculating the average species richness of (sub)plots by treatment. To elucidate patterns of species richness and evenness of their abundance across treatments, we selected the Shannon diversity index ($H' = -\Sigma p_i \times \ln(p_i)$, where p_i = proportion population made up of species *i*; Shannon and Weaver 1949) as it is more sensitive to rare species than Simpson's. As a measure of rarity, we also examined if the frequency of species occurring only once (i.e., singletons) or more times (i.e., 2, 3, 4, or 5) across sampling units was more likely to do so in a specific treatment more than others (after Hernandez and Knudsen 2012).

Results

Impact of soil geomorphic treatments on plant cover

Santa Ana River woolly star.—Surveys done on full plots in summer 2006, representing 7.5 yr of recovery from the 1999 treatment, showed significant differences of woolly star cover among treatments (live cover, $F_{(5,20)} = 5.54$, $P < 0.002$; Fig. 3A). The Cut treatment had the most living woolly star cover (26.0 ± 11.4%; mean ± SE), significantly greater than that for Clr, Dike, and F30 treatments ($P < 0.05$; Tukey's HSD). Cover of woolly star was sequentially next greatest in the F10 and F20 treatments, which were not different from Cut. On half-plots re-disturbed in 2007 and sampled in 2012, representing 5 yr of recovery, we also found that woolly star cover was significantly different among treatments (live cover, $F_{(5,20)} = 10.38$, $P < 0.001$; Fig. 3B); however, Cut plots had significantly greater living cover (24.5 ± 2.9%) than all other treatments ($P < 0.05$; Tukey's HSD), with no differences in cover among the other five treatments. On half-plots representing 13 yr of recovery from the 1999 treatment and sampled in 2012, cover of live woolly star was greatest in the F10 treatment (11.7 ± 5.4%) followed by the Cut treatment (10.0 ± 4.4%; Fig. 3C), but the mean values were not statistically different among any treatments at this point of recovery (live cover, $F_{(5,20)} = 1.715$, $P < 0.117$).

Across all surveys, Dam plots were consistently lowest for total woolly star cover regardless of treatment age, that is, never exceeding 3%. Likewise, Dike plots also showed very little total woolly star cover (<4.8%) across the three treatment ages (Fig. 3).

Dead woolly star plants contributed little (range 0.03–4.18%) to total woolly star cover within each treatment and did not significantly affect differences among treatments within any sampling date. Living woolly star accounted for nearly all (90.0%) woolly star cover in the recently disturbed (5 yr) half-plots, and the 7.5-yr plots (89.0%), but as would be expected with

time, dead cover increased after 13 yr to 24.5% across all treatments.

Exotic annual cover.—No alien shrubs were encountered within the plots, but a low-lying layer of annuals, composed primarily of non-native, annual grasses of Mediterranean origin, was present in most plots. There were few, if any, native annuals evident within these grasses. Alien annuals dominated the vegetative cover of most treatments, but rarely exceeded 50% overall (Fig. 4). In both the 7.5- and 5-yr post-treatment surveys, annual cover was significantly different among treatments (7.5 yr: $F_{(5,20)} = 5.14$, $P < 0.004$; 5 yr: $F_{(5,20)} = 3.10$, $P < 0.004$). In the plots representing 7.5 yr of recovery from the 1999 treatment, annuals were present in greatest abundance within the Clr (65.8 ± 31.0%; mean ± SE) and Dike (49.9 ± 25.5%) treatments. The F20 (23.7 ± 17.3%), F10 (26.9 ± 15.4%), and Cut (27.3 ± 29.3%) treatments showed the lowest percent cover of annuals at 7.5 yr of recovery. Statistically, the Clr treatment had significantly more annual cover than the Cut, F10, and F20 treatments ($P < 0.05$; Tukey's HSD). On half-plots re-disturbed in 2007 and sampled in 2012, representing 5 yr of recovery, the percent cover of annuals was statistically different between only the treatment with the lowest mean, Cut (18.2 ± 8.9%), and that with the greatest, Clr (54.1 ± 7.1%; $P < 0.05$; Tukey's HSD). On half-plots representing 13 yr of recovery from the 1999 treatment and sampled in 2012, annual cover was not statistically different among treatments ($F_{(5,20)} = 0.13$, $P = 0.983$).

Across all surveys, patterns of annual cover were similar among treatments with Clr plots always being among the highest and Cut being among the lowest, along with F10 and F20. The Dam plots, having no vegetation removal, consistently had the highest annual cover at 57.3%, exceeded by only one other mean, that of the Clr treatment after 7.5 y (65.8%).

Native perennial cover.—Besides woolly star, eight other native perennial plant species were found within the LOTUS experimental site (Fig. 5). Mean perennial native plant cover (hereafter native plant cover) differed significantly among treatments after 7.5 yr of recovery from the 1999 treatment ($F_{(5,20)} = 7.29$, $P < 0.001$). The greatest percent cover of native plants was found in the Cut plots (48.9 ± 6.3%; living + dead mean + SE) and F10 plots (45.5 ± 7.3%), which were significantly greater than the F30 and Dike treatments ($P < 0.05$, Tukey's HSD; Fig. 5A). On

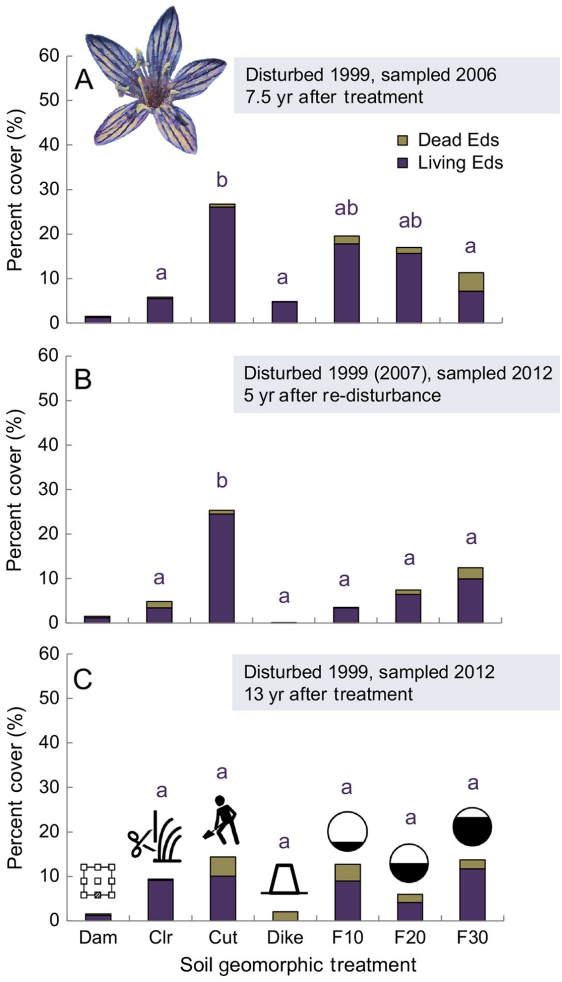


Fig. 3. Total percent cover (%) of *Eriastrum densifolium* ssp. *sanctorum* (living = purple bars [Living Eds]; dead = light brown bars ['Dead Eds']) as a function of treatment: reference plots (Dam); cleared (Clr); cut (Cut); furrowed (Dike); sand-fill to 10 cm (F10); sand-fill to 20 cm (F20); and sand-fill to 30 cm (F30); and by time since disturbance: (A) representing 7.5 yr of recovery from the 1999 disturbance (sampled in 2006), (B) representing 5 yr of recovery from 2007 re-disturbance (first disturbance occurring in 1999, sampled in 2012), and (C) representing 13 yr of recovery from the 1999 disturbance (sampled in 2012). Reference (Dam) plots were last disturbed in the 1860s floods. Letters above treatments designate significant differences ($P < 0.05$; Tukey's HSD) among means for Living Eds within sampling year.

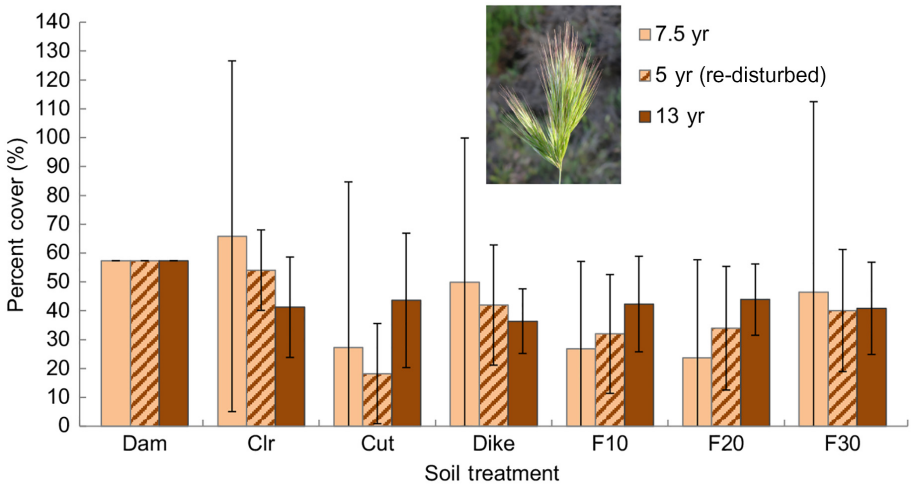


Fig. 4. Total percent cover (%; mean ± 95% CI) of exotic annual grasses as a function of treatment: reference plots (Dam); cleared (Clr); cut (Cut); furrowed (Dike); sand-fill to 10 cm (F10); sand-fill to 20 cm (F20); and sand-fill to 30 cm (F30); and by time since disturbance: (light orange-brown) representing 7.5 yr of recovery from the 1999 disturbance (sampled in 2006), (striped) representing 5 yr of recovery from 2007 re-disturbance (first disturbance occurring in 1999, sampled in 2012), and (dark orange-brown) representing 13 yr of recovery from the 1999 disturbance (sampled in 2012). Reference (Dam) plots were last disturbed in the 1860s floods.

half-plots re-disturbed in 2007 and sampled in 2012, representing 5 yr of recovery, we also found significant differences among treatments ($F_{(5,20)}$ = 3.42, P = 0.02), influenced mostly by the high percent cover of native plants in the Cut treatment (52.9 ± 9.3%), compared to means of all other soil geomorphic treatments (Fig. 5B), albeit statistically greater than only the Dike treatment (P < 0.05, Tukey's HSD; Fig. 5B). Similarly, on half-plots representing 13 yr of recovery from the 1999 disturbance and sampled in 2012, we observed that a significant difference among treatments ($F_{(5,20)}$ = 3.43, P = 0.02) was due to a higher percent cover of native plants in the Cut treatment (67.8 ± 8.9%) versus the F20 and F30 treatments (P < 0.05, Tukey's HSD; Fig. 5C).

Impact of soil geomorphic treatments on plant maturity (Santa Ana River woolly star and E. trichocalyx*)*

Size-class frequency distribution significantly differed for both woolly star and *E. trichocalyx* within each year-since-disturbance, with only one exception (*E. trichocalyx*, 5 yr; Appendix S1: Table S1). Medium-sized plants (class 4) were statistically the most common in each of these analyses. Treatment had a significant effect on woolly star frequency at 5 and 7.5 yr of recovery, and on *E. trichocalyx* at 5 yr. In both species at 5 yr, the Cut treatment had the highest frequency of plants, but the pattern did not hold through 7.5 and 13 yr, with no significant differences in plant frequency among treatments for either species in the latter (Appendix S1: Table S1). Across both species and years-since-disturbance, only one treatment-by-size-class interaction had a significant effect on plant frequency, that in the 5-yr woolly star sample (Appendix S1: Table S1).

Invasibility and diversity

Invasibility.—Across all sample years and treatments, we found a significant negative relationship between woolly star cover (living) and exotic annual grasses, where exotic annual plant cover explained 48.4% of the variability in woolly star cover (P-value = <0.001, multiple R^2 = 0.484, F-stat = 17.82; Fig. 6). At 7.5 yr after treatment, exotic annual plant cover was significantly negatively related to woolly star cover (living), explaining 74.1% of the variability in woolly star cover (P-value = 0.013, multiple R^2 = 0.741, F-stat = 14.330). At 5 yr (re-treated subplots), exotic annual plant cover was negatively related to woolly star cover (living), explaining 55.4% of the variability in woolly star cover albeit at a

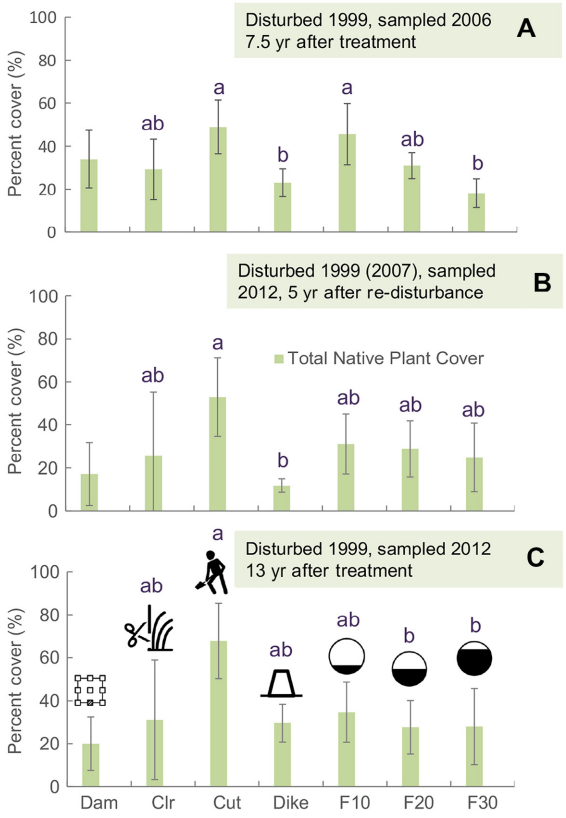


Fig. 5. Total native plant cover (%; mean ± 95% CI) per treatment: reference plots (Dam); cleared (Clr); cut (Cut); furrowed (Dike); sand-fill to 10 cm (F10); sand-fill to 20 cm (F20); and sand-fill to 30 cm (F30); and by time since disturbance, (A) representing 7.5 yr of recovery from the 1999 disturbance (sampled in 2006), (B) representing 5 yr of recovery from 2007 re-disturbance (first disturbance occurring in 1999, sampled in 2012), and (C) representing 13 yr of recovery from the 1999 disturbance (sampled in 2012). Reference (Dam) plots were last disturbed in the 1860s floods. Letters above treatments designate significant differences ($P < 0.05$; Tukey's HSD) among means for total native plant cover within sampling year.

slightly higher *P*-value (*P*-value = 0.055, multiple $R^2 = 0.554$, *F*-stat = 6.215). After 13 yr, we found no significant relationship between exotic annual plant cover and (living) woolly star cover (*P*-value = 0.781, multiple $R^2 = 0.017$, *F*-stat = 0.086).

Diversity.—Across all years, total species richness (R) across (sub)plots by treatment was greatest in the Dike treatment (5 yr) at seven species. Six species were observed in Cut, Dike, and F30 (5 yr, 13 yr; Appendix S1: Fig. S1). Mean species richness was greatest (3.6) in F30 (13 yr), and also high (3.4) in Cut (13 yr) and Dike (7.5 yr, 13 yr). Shannon diversity index (*H'*), which increases with increasing diversity and evenness, exceeded 1.5 for treatment type Dike (subplots) after 5 yr of a re-disturbance and for treatment type Cut 13 yr after treatment. The lowest *H'* (0.75) was observed in Dam subplots representing 5 yr after re-disturbance. Across all survey years, we observed 30 instances where species were only observed in one (sub)plot across a single treatment (singletons; Appendix S1: Fig. S2), the plurality of which was observed in the Dike treatment (27%, $n = 8$ subplots). The most common singleton species were *E. fasciculatum*, *S. neomexicana*, *H. whipplei*, and *E. pinifolia.*

Discussion

The restoration of aridland riparian ecosystems is of global concern to reduce losses of biodiversity and restart, partially or in full, ecosystem services that humans depend upon. Since 1960, the amount of water held by dams has quadrupled (Vörösmarty et al. 2000, Millennium Ecosystem Assessment 2005). As of 2011, over one million dams have been constructed and are in operation globally (Lehner et al. 2011). The restoration of aridland riparian ecosystems adapted to infrequent and sometimes catastrophic floods creates exceptional challenges owing to highly variable abiotic conditions and environmental heterogeneity, the existence of sensitive species, and notably, the importance of restoring pattern legacies of soils to which early-successional native plants are adapted.

The surveys reported here are the first to examine recovery of alluvial sage scrub native plant populations—in particular the federally endangered Santa Ana River woolly star (*Eriastrum densifolium* spp. *sanctorum*)—for more than two years after various soil geomorphic legacy-based restoration treatments. These treatments were intended to emulate natural processes (e.g., floodplain scour, sediment deposition) that revitalize woolly star habitat in this endangered species' home range and to determine the feasibility and long-term efficacy of such treatments. Such treatments are likely to play an important role in

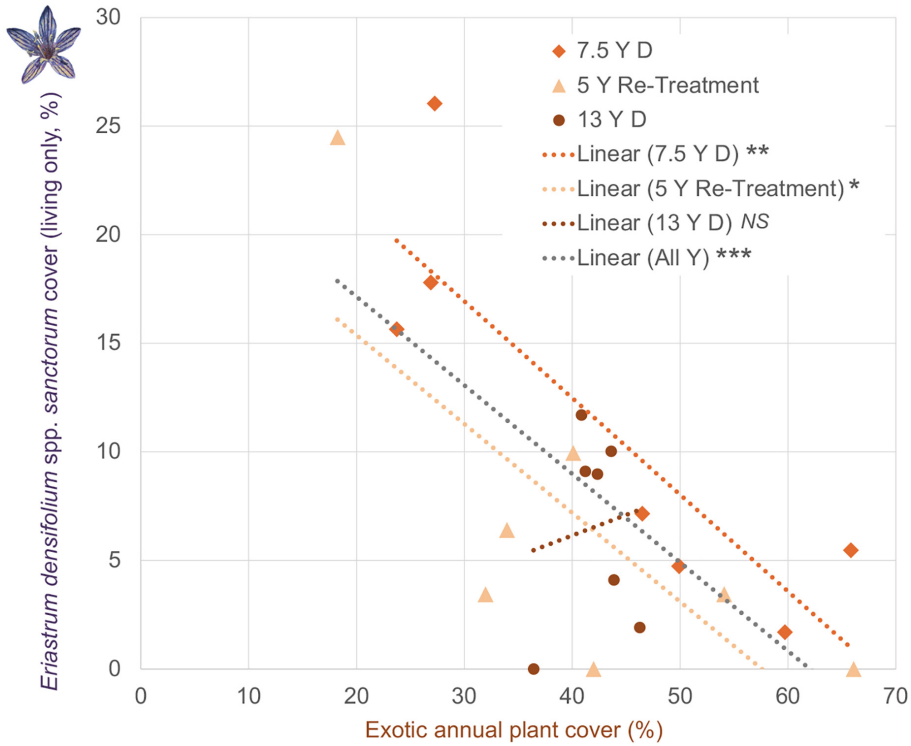


Fig. 6. *Eriastrum densifolium* spp. *sanctorum* cover (living, %; Santa Ana River woolly star) as a function of exotic annual plant cover (%) and linear regressions for relationships at 7.5 yr, 5 yr (re-treated subplots), 13 yr, and all years, after treatment (all plots, including Dam). We found a significant negative relationship between woolly star cover (living) and exotic annual grasses, across all years (All Y), 7.5 yr (7.5 Y D), and 5 yr (re-treated subplots, 5 Y Re-Treatment) where exotic annual plant cover explained 48.4%, 74.1%, and 55.4% of the variability in Santa Ana River woolly star cover, respectively. After 13 yr (13 Y D), we found no significant relationship between exotic annual plant cover and Santa Ana River woolly star cover. Statistical significance is denoted by *($P < 0.05$), **($P < 0.01$), ***($P < 0.001$), and NS for no significance.

sustaining vestige populations of alluvial scrub endemics and endangered species, such as the Santa Ana River woolly star, an early-successional species whose numbers have declined continuously since installation of the Seven Oaks Dam (York 1987, Sandquist 2017). Earlier studies by Thomey et al. (2003) and Psomas and CSUF (2009) followed recovery processes for two years after treatment, but their findings were slightly contradictory. These authors conceded, however, that climate conditions during their respective experiments were less than ideal for germination and seedling recruitment. Despite these studies, there have been no thorough investigations, either short-term or long-term, of the efficacy of legacy-based restoration for the federally endangered woolly star and its companion species. The following are critical ecological discussion points summarizing our findings and their implications for the persistence of woolly star and the alluvial sage scrub community broadly:

Not all legacy-based soil geomorphic treatments are functionally similar

Our results reveal that different soil geomorphic treatments mimicking pattern legacies of floods may alter physiochemical properties of the seedbed environment that affect plant germination, establishment, and reproductive traits of woolly star. Mechanisms of this response include changes in soil texture, organic matter and nutrients, and altered soil water content and hydrological processes. For example, removing or burying the existing soil surface, as done in the Cut and the Fill treatments, appears to be the most

important driver for expediting re-establishment by woolly star. Additionally, the Cut treatment may facilitate water run-on critical for germination and plant establishment of not only woolly star but also other associated native plant species, as shown by the significant response of native plant cover to the Cut treatment. At 5 and 7.5 yr following treatment, full removal of surface soil (Cut) yielded highest woolly star cover, followed by sand-fill (surface burial) treatments (Fig. 3). Leaving surface soils intact, with or without vegetation (Dam and Clr treatments, respectively), or even partially intact (Diked), constrains recruitment of woolly star, at least through the first 7.5 yr. Results from the diversity indices and the high number of singletons (i.e., species only observed once across treatments) suggest that some species may be rare in the community and that treatments on community diversity may benefit from additional long-term observations and comparisons, particularly those emphasizing community observations within the Dike, Cut, and F30 treatments.

Exotic grasses inhibit early recovery of native plants

Shrub establishment in early recovery years is negatively correlated with exotic annual grass cover (Fig. 5). This implies some level of competition between native plants and exotic annuals. Thus, the soil treatments that best facilitate shrub recovery may do so, in part, by limiting alien grass productivity. The Cut treatment had the greatest woolly star and native plant cover and also had the least cover of annual plants. This negative relationship appears to be a general pattern among all treatments when considered together, and as such suggests that annuals plants, which are largely non-native grasses, negatively affect recruitment of native perennials. This negative impact on plant community structure and composition is commonly found where alien grasses have invaded arid ecosystems (Gordon et al. 1989), but a definitive study to confirm this hypothesis for woolly star has not yet been done. Interestingly, soil disturbances, similar to treatments done in this study, typically increase annual grass cover in nearby non-riparian communities (Hernandez and Sandquist 2011), but on deep sandy soils such as those of the Riversidian alluvial scrub, years of stabilization and nutrient accumulation may be required to support an abundance of exotic annuals.

Across soil geomorphic treatments, biogeochemical properties may converge after a decade

Native vegetation composition and cover (including that of the endangered woolly star) show no significant differences after 13 yr of recovery (Figs. 3 and 5), and even annual grass cover becomes similar across treatments after this period (Fig. 4). Such homogenization appears related to redistribution of soil particles, gradual soil stabilization, and vegetation establishment (accelerated by annual grasses). Biogeochemical mechanisms leading to a convergence of effects should be explored in greater detail in follow-up studies.

Climate drives demography of dominant shrubs during recovery

Although geomorphic surface treatments had an effect on shrub frequencies during early recovery, the absence of treatment-by-size-class effects in five of six analyses indicates that underlying drivers of size-class frequency distribution (e.g., precipitation) probably overwhelm any differences in substrate that might affect establishment, survival, and growth. That underlying factors, likely climate-related, more strongly affect size-class distributions than substrate affects can also be seen in near-ubiquitous dominance of stage 4 (medium-sized) plants across all datasets (years-since-disturbance and both species); however, assessment of these patterns should include a stronger understanding of growth limitations for both woolly star and *E. trichocalyx*.

Another notable result of the 5-yr woolly star size-class analysis was that the Cut treatment had many more plants than all other treatments, reinforcing the finding we observed for woolly star cover and total plant cover (i.e., that Cut is a more favorable soil treatment for most recovery responses). However, as also observed for cover analyses, the significant differences of woolly star frequency among treatments at 5 and 7.5 yr were absent after 13 yr of recovery, inferring that biogeochemical differences across treatments converge after this time span.

Soil geomorphic disturbances are required for population viability

Our results confirm the expectation that periodic, intentional soil treatments are necessary for long-term persistence of the endangered woolly star and associated native vegetation of the Riversidian alluvial scrub community. Fortunately, our results also demonstrate that certain treatments provide more favorable conditions for re-establishment without significantly greater effort. Such findings have implications for managed water-flow alternatives in these rare ecosystems and provide insight into legacy-based restoration of Mediterranean riparian ecosystems elsewhere.

Mediterranean riparian ecosystems dependent on catastrophic flooding: implications for management and policy

Reservoirs impounded by dams are distinct from natural lakes in several ways but notably for the modification of their catchments and flows (via outflow structures) that are often actively managed to benefit human populations (e.g., flood control, drinking water access). Reservoirs (with or without outflow structures) impose twice the management stress (i.e., human resources and decision-making) of natural lakes and often exacerbate global-change-type threats, including habitat loss and degradation (Hayes et al. 2017). Mitigation of economic and environmental losses may be achieved through the establishment and management of environmental flows from impounded catchments that mimic natural flows, including their magnitude, frequency, timing, duration, and predictability (e.g., droughts, floods), to sustain freshwater and riparian ecosystems and their goods and services (Arthington et al. 2006).

For example, management may include selective release from reservoirs to rivers that emulate natural system complexity (e.g., frequency, duration) and, in reservoirs with outlet gates at different heights, to induce unique catchment and/or floodplain effects (e.g., bottom outlets can flush deposited sediments out of the reservoir via scouring; Arthington et al. 2006, Hayes et al. 2017). In 2011, federal engineers released water via two 18-ft outlet gates within the Seven Oaks Dam for the purpose of hydraulic testing but, to date, no subsequent controlled releases have occurred. In 2016, three environmental groups—the Center for Biological Diversity, the California Native Plant Society, and the Tri-County Conservation League—filed a federal lawsuit accusing the Army Corps of Engineers of violating the Endangered Species Act and failing to provide consultation with the U.S. Fish and Wildlife Service to define and execute mitigation options to protect the three endangered species dependent on biological and pattern legacies incurred from flooding. The plaintiffs argued for consultation to lessen the impact of the dam via buying additional land to protect the species' habitat and/or facilitating the release of water from the dam (Center for Biological Diversity 2016).

Our long-term results (>10 yr) in the Santa Ana River floodplain show that the persistence of woolly star as a species is unlikely without targeted soil geomorphic treatments—restoration actions that emulate pattern legacies and may steer ecosystems through natural successional stages to support alluvial scrub. Without the targeted re-establishment of flows and flood pulses that artificially mimic impacts associated with infrequent, catastrophic flooding, woolly star populations and the ecosystem services of this Riversidian alluvial scrub ecosystem are unlikely to endure.

Acknowledgments

We thank Drs. Michelle Thomey, Jack Burk, and C. Eugene Jones for establishing the plots adopted for this long-term study. Dr. Carmen Cortez and many CSUF undergraduates were instrumental in data collection and site maintenance over the years. Plot establishment and continued access was provided by the San Bernardino County Flood Control District. Funding was provided by The Sandquist Laboratory for Physiological Plant Ecology and the Department of Biological Science, California State University, Fullerton, to DRS. Additional support was made possible by the Society of Woman Geographers Evelyn L. Pruitt National Minority Fellowship, the CSU Sally Casanova Pre-Doctoral Fellowship, the California Garden Club, UC President's Postdoctoral Fellowship, and the United States Department of Agriculture (USDA), National Institute of Food and Agriculture (NIFA), through Hatch Formula Grant Funding for RRH. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the authors and do not necessarily reflect the views of the USDA or NIFA.

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