# **Assessment of topsoil salvage and seed augmentation in the restoration of coastal sage scrub on Santa Catalina Island, California**

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 ABSTRACT.—The Catalina Island Conservancy manages over 22,000 acres of coastal (California) sage scrub (CSS) habitat off the coast of Southern California, including much of the infrastructure, roads, and recreation associated with habitat disturbance. Restoration trials were initiated to establish best management practices for roadside and disturbed site revegetation under local site conditions. Site treatments compared excavated native subsoil and surface soil (**+–**20 cm) reapplication practices with and without seed augmentation. Evaluation of native and nonnative germinants indicated that salvaged surface soil alone may not be sufficient to restore native cover. Seeding improved native cover and reduced establishment of nonnative species on unirrigated sites. Evaluation of water potential of seedlings indicated that high-frequency irrigation may favor establishment of nonnative annual grasses. Most compelling for land managers is the indication that CSS habitats may contain a significant nonnative seed bank in spite of the composition of aboveground vegetation, such that disturbance may facilitate habitat-type conversion without seed augmentation or weed control.

 RESUMEN.—El programa de Conservación de la Isla Catalina, administra un hábitat de más de 22,000 acres de matorrales de salvia costeros de California (CSS, por sus siglas en inglés), cerca de la costa del sur de California. Incluyendo gran parte de la infraestructura, los caminos y los usos recreativos asociados a la perturbación del hábitat. Se iniciaron pruebas de restauración para establecer mejores métodos de gestión en los bordes de las carreteras y reforestación de las áreas perturbadas, por condiciones locales. El tratamiento de áreas comparó el uso de subsuelo nativo excavado, con los métodos de re-aplicación de suelo superficial (**+–**20 cm), con y sin aumento de semillas. La evaluación de semillas germinantes nativas y no nativas indicó que el suelo superficial rescatado, por sí solo, no es suficiente para restaurar la cobertura nativa. La siembra mejoró la cobertura nativa y redujo el establecimiento de especies no nativas en sitios no irrigados. La evaluación del potencial hídrico de las plántulas sugirió que el riego de alta frecuencia puede favorecer el establecimiento de pastos anuales no nativos. Lo más esclarecedor para los gestores de las tierras, es indicarles que los hábitats de CSS pueden contener un importante banco de semillas no nativas, a pesar de la composición de la vegetación superficial, de tal forma que, su perturbación puede facilitar la transformación del tipo de hábitat, sin tener que aumentar la cantidad de semillas o controlar las malezas.

 Coastal sage scrub, also described as California sagebrush scrub (CSS), is a shrubland vegetation community with a limited range typically defined as coastal, central, and southern California and northwestern Baja California. The community is characterized by associations of low-growing, perennial shrubs including typical genera *Artemisia, Salvia,* and *Eriogonum.* This vegetation alliance has been described as a number of unique subassociations (Sawyer et al. 2009), and throughout its range it is known for high rates of floristic endemism (Kraft et al. 2010). These include alliances of the California Channel Islands, whose vegetation may be defined by insular endemic species such as the *Deinandra clementina–Eriogonum giganteum* Shrubland Alliance (Island tar plant–Island buckwheat scrub), which is found only on the California Channel Islands (Johnson and Rodriguez 2001, Sawyer et al. 2009).

 In *Terrestrial Vegetation of California,* Rundel (2007) cites the widespread loss and fragmentation of CSS habitats, with only about 10% of the original extent remaining, due to urbanization, recreational development, and

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alteration of natural disturbance regimes. As many as 36 plant species known from CSS are federally or state listed as threatened or endangered, and at least 3 species are presumed to be extinct or extirpated from the California Channel Islands (CNPS 2017). Advancement in the understanding of restoration ecology related to coastal scrub habitats is increasingly important for species conservation and the efficacy of mandated mitigation measures related to development disturbance (Feldman and Jonas 2000).

 Coastal sage scrub is adapted to episodic disturbance from fire and may be highly resilient under the right conditions, for example, where native soil seed banks are intact and belowground root material persists, allowing vegetation to resprout (Malanson and O'Leary 1982, Westman and O'Leary 1986, Keeley 1991). It has been demonstrated, however, that agricultural disturbance such as grading, tilling, and compaction, which alter soil seed banks and remove root material, may render habitats highly degraded and unable to recover even after decades (Stylinski and Allen 1999, Holl et al. 2000). Salvaged topsoil has been shown to improve revegetation outcomes on semiarid disturbed sites (Tormo et al. 2007; J. Belnap, personal communication, 2012); however, many studies indicate that soil disturbance itself is not the most influential factor contributing to degradation of habitats, but rather exotic species invasion, which contributes the most severe negative outcomes to loss of biodiversity (Keeley et al. 2005, Fleming et al. 2009, Cox and Allen 2011, Keeley and Brennan 2012). A factor contributing to the establishment of exotic forbs and grasses may be water availability during the germination and establishment phase (Lauenroth et al. 1978, Padgett et al. 2000). Among semiarid shrublands of Southern California, coastal sage scrub is particularly at risk of exotic species invasion due to differences in water availability (Pratt et al. 2008, Jacobsen et al. 2009). Additionally, the resilience of species or habitats may be severely threatened due to increasing variability in precipitation and climatic factors at the regional and the site scale (Riordan and Rundel 2009, Anacker et al. 2013).

 The Catalina Island Conservancy (CIC) manages over 22,000 acres of CSS habitat off the coast of Southern California, including much of the infrastructure, roads, and recreation associated with habitat disturbance. The CIC has a mandate to conserve biological resources through a balance of conservation, education, and recreation, and has stated goals for the preservation of biodiversity. However, needed functioning roads and other infrastructure often come at the expense of habitat integrity. The establishment of best management practices that consider local site conditions may be a critical step in avoiding increased fragmentation and degradation of habitats. All of the common challenges facing revegetation projects are variably influenced by local site conditions. These challenges include the difficulty of restoring native biodiversity following disturbance (Allen et al. 1993), the latent threat posed by exotic species in the soil seed bank (Cox and Allen 2008a, Fleming et al. 2009), and variable water availability.

 This study was intended to provide understanding of the role of soil seed banks in vegetation recovery following roadside and development disturbance under local site conditions with a goal of establishing best management practices. Trials were designed to (1) assess the efficacy of existing soil seed banks, salvaged during construction, in restoring native cover and species richness, (2) assess the efficacy of seed augmentation on various soil reapplication treatments in restoring native cover and species richness, and (3) understand the role of drought and water availability in the germination and establishment of native and nonnative species. Iterative restoration trials were installed over 2 years and monitored to assess the performance of several topsoil salvage and seed augmentation treatments. Concurrent germination trials in a controlled nursery setting explored the physiological drought stress tolerance of species representing different functional groups at the seedling stage.

#### **METHODS**

### Site Description

 The site located at Middle Ranch on Catalina Island (Los Angeles County, California) was the proposed location for construction of a 16,000-gallon water tank, which would involve significant excavation, grading, compaction, and displacement of native vegetation over one acre. Initial vegetation surveys were

completed to determine a baseline condition in the spring of 2013. Total vegetative cover was approximately 60%, with about 40% native cover dominated by *Artemisia californica* (15%) and 20% nonnative cover that was primarily exotic annual grasses such as *Hordeum murinum, Bromus madritensis,* and *Brachypodium distachyon;* bare soil constituted the remaining fraction. Forty species were recorded from the site, including several species of limited distribution such as *Crossosoma californicum, Eriogonum giganteum* var. *giganteum, Galium nuttallii* subsp. *insulare,* and *Malacothamnus fasciculatus* var. *catalinensis* (Baldwin et al. 2012, CNPS 2017).

 Construction was initiated in 2013 by removing all aboveground vegetation succeeded by topsoil salvage following 2 protocols: (1) surface soil (TS1) was scraped using a bulldozer to a depth of **+–**20 cm and (2) subsoil (Reg) was excavated to an average depth of 1.8 m and homogenized (topsoil and subsoil). Subsoil could also be characterized as mineral soil, acknowledging that it contained some organic material and seed, albeit at much reduced density relative to surface soil. Soils were stored for 5–16 months in piles <2.5 m in height and covered with tarps to maintain dryness. Subsoil was used as backfill on the site and compacted to a minimum of 95% of the maximum dry density based on the ASTM D1557-07 (ASTM International 2012) test method. Soil is characterized as Nauti-Flyer-Marpol complex, which is well-drained, silty clay loam, with a shallow depth to weathered diorite bedrock (USDA 2008). Soils were reapplied to the construction site following grading and construction as described in methods for the field trials.

 Precipitation during the period of the study (2013–2015) was below average for Catalina Island, which averages between 30 and 35 cm (11–14 inches) annually (WRCC 2015). The total precipitation in the 2014 water year (October 2013 to September 2014) was 9.12 cm (3.59 inches), and in the 2015 water year it was 19.02 cm (7.39 inches; values are an average of data from weather stations across the island). An initial precipitation event in November 2013 occurred over 3 days and totaled 3.15 cm (1.24 inches), followed by several weeks of drought. In the 2015 water year, precipitation was slightly more consistent but still characterized by light rain events followed by extended periods of winter drought.

## Field Trials

 Seeds from 20 common species (Table 1) of CSS were collected from adjacent watersheds in the 3 years preceding the construction work. Seeds were processed and held in cold storage and tested for purity and viability by Ransom Seed Laboratory (Carpinteria, CA). Pure Live Seed (PLS) was calculated per industry standards as

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 purity  $\times$  % germ)/100.

Seeding rates were estimated based on PLS per m2, assuming

(target seedling density per m2 / estimated  $\%$  survival)  $\times$  target  $\%$  cover by species.

The ultimate seed weight per acre was calculated to be approximately 9821 g/acre (21 lbs./acre).

 Installation of site treatments occurred in November 2013 and October 2014 and each installation was followed by 3 years of subsequent monitoring. Soil reapplication treatments on all sites were graded to a uniform 2:1 slope ranging in aspect from 120° to 300° (SE–NW). Subsoil and surface soil were spaced alternately across 3 sites in the first year and on a fourth site in the second year, with each soil reapplication area averaging about 200 m2. Surface soil was reapplied to an approximate depth of 20 cm immediately preceding seed and erosion-control installations. Seed was broadcast at 9821 g/acre (21 lbs./acre) and covered with jute erosion-control blankets (Earthsavers, Woodland, CA). Seeded sites and no-seed controls were paired within each of the soil reapplication areas. Thirty 1-m2 plots were deployed across the site and monitored for percent cover, species richness, and number of germinants. Ten plots each were established on seeded sites with either surface soil or subsoil. Five plots each were established on unseeded sites with either surface soil or subsoil. Data were averaged across each treatment type in each year and plotted using spreadsheet functions.

# Physiology Studies

 Concurrent germination trials of species expected to occur on the field sites were





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conducted in a controlled nursery setting. These trials were designed to observe physiological drought stress tolerance of different functional groups at the seedling stage. Six taxa were selected to represent functional groups, including native forb *Deinandra fasciculata,* nonnative forb *Mesembryanthemum crystallinum,* nonnative grasses *Hordeum murinum* and *Bromus diandrus,* and native perennial shrubs *Artemisia californica* and *Eriogonum giganteum.* A specific weight of seed was measured for each of 6 taxa and sown into  $10.5 \times 10.5 \times 2.25$ -inch-deep trays. Trays were weighed to determine dry weight of the potting media and irrigated to initiate germination. Trays were allowed to dry to the initial weight and then subjected to either 0, 3, 9, or 27 days of drought before irrigation was resumed. Each species was sown individually to 2 replicate trays (control), and 6 replicates were sown with species combined for each of the 4 drought treatments. Germinants were noted as they emerged or as mortality was observed. Data for each species were averaged across each treatment type and plotted using spreadsheet functions.

# **RESULTS**

# Field Trials

 Germination and establishment of seeded species in the field varied from the PLS values, with about 40% of the taxa nonperforming across most sites in the first 2 years (Table 2). Evaluation of percent cover without seed augmentation indicated that salvaged surface soil (TS1) alone may not be sufficient to restore native cover (Fig. 1). Seeding improved native cover and reduced the establishment of nonnative species. Native species richness was improved with surface soil (TS1) application (Fig. 2) but was offset by comparable increases



 Fig. 1. Percent cover of field plots in year 1 (2014 water year) and year 2 (2015 water year). Reg = subsoil treatment, TS1 = surface soil treatment.



 Fig. 2. Species richness of field plots in year 1 (2014 water year) and year 2 (2015 water year). Reg = subsoil treatment, TS1 = surface soil treatment.



Fig. 3. Number of germinants per m<sup>2</sup> in field plots in year 1 (2014 water year) and year 2 (2015 water year). Reg = subsoil treatment, TS1 = surface soil treatment.

in nonnative cover. Surface soil also had significant nonnative cover compared to subsoil (Reg). Contrary to our hypothesis that surface soil would be most effective at restoring native cover and species richness, subsoil and surface soil with the addition of seed performed very similarly. Another measure that may indicate percent cover over time, or the trajectory of the plot, is offered by the inventory of the number of germinants. In this measure (Fig. 3), subsoil with seed augmentation showed the optimal proportion of native to nonnative germinants between the site treatments. Some of the species overperformed based on their PLS values. This may be attributable to variation in the seed mix or broadcast methods; however, the results across multiple sites indicate that certain species are effective colonizers following disturbance (Table 2). These include *Artemisia californica, Encelia californica, Eriogonum giganteum,* and *Deinandra fasciculata. Deinandra fasciculata* was the only native annual herb deployed on the site that proved to be extremely effective at establishment, rapid growth, and seed dispersal in disturbed ground.

# Physiology Studies

 Results from similar studies (Dixon unpublished data) indicate that irrigation may not be necessary or beneficial on seeded restoration sites in semiarid shrublands. It is likely that timing, in addition to total volume of irrigation, may affect cover and species richness. Nursery-based germination trials that were subjected to increasing drought once a baseline dry weight of the media was reached showed differences in the response of native shrubs and nonnative forbs and grasses. *Bromus diandrus* and *Deinandra fasciculata* failed to germinate or provided insufficient data to be included in the results. The nonnative annual grass *Hordeum murinum* was particularly susceptible to drought and showed a clear pattern of mortality with increasing drought (Fig. 4). The nonnative forb *Mesembryanthemum crystallinum* was extremely resistant to drought, showing little mortality after 27 days of drying (Fig. 5). Native shrubs *Eriogonum giganteum* and *Artemisia californica* at the seedling stage were only moderately drought resistant, but typically exhibited secondary germination from dormant seed bank reserves under drought conditions (Figs. 6, 7).



Fig. 4. Germination of *Hordeum murinum* following days of drought.



**M. crystallinum**

Fig. 5. Germination of *Mesembryanthemum crystallinum* following days of drought.

The physiological differences between annual grasses and perennial shrubs in this case are likely to be expressed on the field site depending on frequency and abundance of precipitation or irrigation. It is possible therefore that frequent irrigation may contribute to increased cover by nonnative annual grasses, which may lead to decreased native cover or species richness due to competition and slower establishment rates of native shrubs.

#### **DISCUSSION**

 As with any applied restoration effort, particularly those employed on construction sites, it may be impossible to control for the myriad variables that affect outcomes. Rather, results developed over multiple iterations under local site conditions may be assumed to be useful in informing best management practices and contributing to accepted norms within the field. This study highlighted challenges common to



Fig. 6. Germination of *Eriogonum giganteum* following days of drought.



Fig. 7. Germination of *Artemisia californica* following days of drought.

restoration practitioners that are well documented in literature. Restoration projects on disturbed sites in semiarid shrublands may fail to recover from the alteration of successional processes as a result of exotic species invasion (Stylinski and Allen 1999, Allen et al. 2000, Montalvo et al. 2002, Cox and Allen 2008b, Fleming et al. 2009). Succession of the disturbed site may result in a new vegetation type, either consisting of exotic species or new combinations of native species that were not formerly part of the late-seral landscape (Davis et al. 1994). Local site experiments that include evaluation of soil seed banks prior to expected development disturbance may be an effective way to address latent threats posed by exotic species. Another challenge is the variable establishment success of particular taxa which are to be restored by seed. Here again, localized site experiments may be useful in identifying limitations not indicated through lab-based germination tests. California sage scrub and chaparral shrublands include many species known to be rare (making it difficult to acquire seed) or slow to establish, and some may have prolonged seed dormancy patterns which limit success in the field. In order to restore floristic diversity to a site, it is likely that a suite of propagation techniques (seed, vegetative propagation, tissue culture), establishment methods (seed drilling, imprinting, container planting), and timing will be required to represent the varying life history syndromes of the target flora.

 This study indicated that surface soil alone may not be sufficient to restore native cover and moreover that surface soils (where predisturbance cover was approximately 2:1 native to nonnative) may be less suitable than seeded subsoils due to the high density of exotic species following disturbance. Although not considered in this study, surface soil treatments exhibited much faster growth rates and higher density of vegetation overall, presumably due to more available soil nitrogen. This assumption would be in line with research that indicates that increased soil nitrogen may have a positive effect on exotic species invasion in arid environments (Padgett and Allen 1999, Abraham et al. 2009, Schneider and Allen 2012). However, the assertion that seeded subsoils perform better in this study does not take into account the slower growth rate and increased gap space which may allow for exotic species invasion over time. Likewise, the results of the surface soil treatment may have had much more favorable outcomes had exotic species been controlled, as would be typical of most restoration projects. These results can be assumed to be specific to this particular site; however, these findings are consistent with many studies and applied projects devoted to the restoration and management of semiarid shrublands. Further examination of diverse revegetation techniques following disturbance will help us refine best practices for the conservation of biodiversity and the restoration of native habitats.

## **CONCLUSIONS**

 This study indicated that CSS habitats may contain a significant nonnative seed bank in spite of the composition of aboveground vegetation, and that disturbance may facilitate habitattype conversion without seed augmentation or weed control. Reapplication methods using salvaged surface soil (0–20 cm) were not sufficient to restore native cover. Seeding improved native cover and reduced the establishment of nonnative species on unirrigated sites. Certain irrigation regimes particularly high-frequency irrigation—may favor nonnative species such as annual grasses. When planning projects with a goal of restoring biodiversity, managers should anticipate variable establishment success across species and accommodate with effective establishment methods.

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### LITERATURE CITED

- ABRAHAM, J., J. CORBIN, AND C. D'ANTONIO. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. Plant Ecology 201:445–456.
- ANACKER, B., M. GOGOL-PROKURAT, K. LEIDHOLM, AND S. SCHOENIG. 2013. Climate change vulnerability assessment of rare plants in California. Madroño 60: 193–210.
- ALLEN, E.B., S.A. ELIASON, V.J. MARQUEZ, G.P. SCHULTZ, N.K. STORMS, C.D. STYLINSKI, T.A. ZINK, AND M.F. ALLEN. 2000. What are the limits to restoration of coastal sage scrub in southern California? Pages 253–262 *in* J.E. Keeley, M. Baer-Keeley, and C.J. Fotheringharn, editors, 2nd Interface Between Ecology and Land Development in California. Open-File Report 00-62, U.S. Geological Survey, Western Ecological Research Center, Sacramento, CA.
- ALLEN, E.B., B.I. HEINDL, AND J.P. RIEGER. 1993. Trajectories of succession on restored roadsides in southern California. Fifth Annual Conference, Society for Ecological Restoration, 16–20 June, Irvine, CA.
- ASTM INTERNATIONAL. 2012. D1557-12, Laboratory standards for soil compaction. ASTM International, 100 Barr Harbor Drive, Box C700, West Conshohocken, PA 19428-2959.
- BALDWIN, B.G., D.H. GOLDMAN, D.J. KEIL, R. PATTERSON, T.J. ROSATTI, AND D.H. WILKEN, EDITORS. 2012. The Jepson manual: vascular plants of California. 2nd edition. University of California Press, Berkeley, CA.
- [CNPS] CALIFORNIA NATIVE PLANT SOCIETY, RARE PLANT PROGRAM. 2017. Inventory of rare and endangered plants [online edition, v8-02]. California Native Plant Society, Sacramento, CA; [accessed 26 February 2017]. http://www.rareplants.cnps.org
- COX, R., AND E. ALLEN. 2008a. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. Plant Ecology 198:37–46.
- COX, R., AND E. ALLEN. 2008b. Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. Journal of Applied Ecology 45:495–504.
- COX, R., AND E. ALLEN. 2011. The roles of exotic grasses and forbs when restoring native species to highly invaded southern California annual grassland. Plant Ecology 212:1699–1707.
- DAVIS, F., P. STINE, AND D. STOMS. 1994. Distribution and conservation status of coastal sage scrub in southwestern California. Journal of Vegetation Science 5:743–756.
- FELDMAN, T.D., AND A.E.G. JONAS. 2000. Sage scrub revolution? Property rights, political fragmentation, and conservation planning in southern California under the Federal Endangered Species Act. Annals of the Association of American Geographers 90:256–292.
- FLEMING, G., J. DIFFENDORFER, AND P. ZEDLER. 2009. The relative importance of disturbance and exoticplant abundance in California coastal sage scrub. Ecological Applications 19:2210–2227.
- HOLL, K., H. STEELE, M. FUSARI, AND L. FOX. 2000. Seed banks of maritime chaparral and abandoned roads: potential for vegetation recovery. Journal of the Torrey Botanical Society 127:207–220.
- JACOBSEN, A., R. PRATT, AND L. MOE. 2009. Plant community water use and invasibility of semi-arid shrublands by woody species in southern California. Madroño 56:213–220.
- JOHNSON, L., AND D. RODRIGUEZ. 2001. Terrestrial vegetation monitoring, Channel Islands National Park 1996–2000 report. Technical Report 01-06, National Park Service, Channel Islands National Park, Ventura, CA.
- KEELEY, J. 1991. Seed germination and life history syndromes in the California chaparral. Botanical Review 57:81–116.
- KEELEY, J., M. BAER-KEELEY, AND C. FOTHERINGHAM. 2005. Alien plant dynamics following fire in Mediterraneanclimate California shrublands. Ecological Applications 15:2109–2125.
- KEELEY, J., AND T. BRENNAN. 2012. Fire-driven alien invasion in a fire-adapted ecosystem. Oecologia 169: 1043–1052.
- KRAFT, N., B. BALDWIN, AND D. ACKERLY. 2010. Range size, taxon age and hotspots of neoendemism in the California flora. Diversity and Distributions 16: 403–413.
- LAUENROTH, W., J. DODD, AND P. SIMS. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36:211–222.
- MALANSON, G., AND J. O'LEARY. 1982. Post-fire regeneration strategies of Californian coastal sage shrubs. Oecologia 53:355–358.
- MONTALVO, A.M., P.A. MCMILLAN, AND E.B. ALLEN. 2002. The relative importance of seeding method, soil ripping, and soil variables on seeding success. Restoration Ecology 10:52–67.
- PADGETT, P., AND E. ALLEN. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. Plant Ecology 144:93–101.
- PADGETT, P., S. KEE, AND E. ALLEN. 2000. The effects of irrigation on revegetation of semi-arid coastal sage scrub in southern California. Environmental Management 26:427–435.
- PRATT, R., A. JACOBSEN, R. MOHLA, R. EWERS, AND S. DAVIS. 2008. Linkage between water stress tolerance and life history type in seedlings of nine chaparral species (Rhamnaceae). Journal of Ecology 96: 1252–1265.
- RIORDAN, E., AND P. RUNDEL. 2009. Modelling the distribution of a threatened habitat: the California Sage Scrub. Journal of Biogeography 36:2176–2188.
- RUNDEL, P.W. 2007. Sage scrub. Pages 208–228 *in* M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr, editors, Terrestrial vegetation of California. University of California Press, Berkeley, CA.
- SAWYER, J.O., T. KEELER WOLF, AND J.M. EVENS. 2009. A manual of California vegetation. 2nd edition. California Native Plant Society, Sacramento, CA.
- SCHNEIDER, H., AND E. ALLEN. 2012. Effects of elevated nitrogen and exotic plant invasion on soil seed bank composition in Joshua Tree National Park. Plant Ecology 213:1277–1287.
- STYLINSKI, C., AND E. ALLEN. 1999. Lack of native species recovery following severe exotic disturbance in southern Californian shrublands. Journal of Applied Ecology 36:544–554.
- TORMO, J., E. BOCHET, AND P. GARCÍA-FAYOS. 2007. Roadfill revegetation in semiarid Mediterranean environments. Part II: topsoiling, species selection, and hydroseeding. Restoration Ecology 15:97–102.
- [USDA] UNITED STATES DEPARTMENT OF AGRICULTURE, NATURAL RESOURCES CONSERVATION SERVICE. 2008. Soil Survey of Santa Catalina Island, California.
- [WRCC] WESTERN REGIONAL CLIMATE CENTER. 2015. Western U.S. Climate Historical Summaries— Weather. Desert Research Institute, Reno, NV; [accessed 27 September 2015]. https://wrcc.dri.edu/ Climate/summaries.php
- WESTMAN, W., AND J. O'LEARY. 1986. Measures of resilience: the response of coastal sage scrub to fire. Vegetatio 65:179–189.

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