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Bidirectional recovery patterns of Mojave Desert vegetation in an aqueduct pipeline corridor after 36 years: I. Perennial shrubs and grasses

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ABSTRACT

We studied recovery of 21 perennial plant species along a severely disturbed aqueduct corridor in a *Larrea tridentata-Ambrosia dumosa* plant alliance in the Mojave Desert 36 years after construction. The 97-m wide corridor contained a central dirt road and buried aqueduct pipeline. We established transects at 0 m (road verge), 20 m and 40 m into the disturbance corridor, and at 100 m in undisturbed habitat (the control). Although total numbers of shrubs per transect did not vary significantly with distance from the verge, canopy cover of shrubs, species richness, and species diversity were higher in the control than at the verge and other distances. Canopy cover of common shrubs (*Ericameria nauseosa, Ambrosia salsola, A. dumosa, L. tridentata, Grayia spinosa*) and perennial grasses (*Elymus elymoides, Poa secunda*) also varied significantly by location. Discriminant analysis clearly separated the four distances based on plant composition. Patterns of recovery were bidirectional: secondary succession from the control into the disturbance corridor and inhibition from the verge in the direction of the control. Time estimated for species composition to resemble the control is dependent on location within the disturbance corridor and could be centuries at the road verge. Our findings have applications to other deserts.

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1. Introduction

The Mojave, Sonoran, and Chihuahuan deserts of North America and the Monte Desert of South America have many similarities, including several genera of trees, shrubs, and perennial grasses (Turner et al., 1995; Roig et al., 2009; Baldwin et al., 2014). One genus of shrubs (*Larrea*, family Zygophyllaceae) is represented by four species, one in North America (creosote bush, *Larrea tridentata*) and three in South America (*Larrea divaricata, Larrea cuneifolia*, *Larrea nitida*) (Laport et al., 2012). *L. tridentata* is the predominant and widespread shrub of North American deserts (Turner et al., 1995) and *Larrea* spp. characterize the Monte Desert in South America (Roig et al., 2009). *Larrea* spp. are part of many simple and complex vegetation associations and communities (e.g., McAuliffe, 1988; Turner et al., 1995; Guevara et al., 2009). The deserts of North and South America also share some commonalities in historic and current land uses and disturbance regimes: settlements and urbanization, occupation of riparian areas, development of agriculture, livestock grazing, extraction of wood, and fire (e.g., Gibbens et al., 2005; Lovich and Bainbridge, 1999; Guevara et al., 2009; Villagra et al., 2009). Degradation and desertification from the accumulation of anthropogenic land uses are widespread in these New World deserts.

The recovery of disturbed lands has been an important topic in ecology for the last century (Walker, 2012). Desert ecologists have focused on identifying and describing anthropogenic disturbances, succession and recovery of vegetation and soils, time required for recovery, and whether recovery could be enhanced by remediation (e.g., Lovich and Bainbridge, 1999; Weigand and Rodgers, 2009; Guevara et al., 2009). In North America, vegetation alliances with *L. tridentata* have received considerable attention. Severe disturbances result after vegetation and surface layers of soil are scraped away, trenches are dug for pipelines, town sites are abandoned, or fires have consumed vegetation. Several authors have described

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early stages of succession and noted that the Mojave Desert is slow to recover after disturbance (Vasek, 1979/1980; Lathrop and Archbold, 1980a, 1980b; Webb et al., 2009; Abella, 2010). Estimates for perennial plant species to re-occupy disturbed areas range from decades to centuries, depending on severity and extent of disturbance, precipitation patterns, soil types, landforms, surficial geology, and other factors. Further, estimated times for recovery depend on whether the objective is to attain a desired perennial plant density, biomass, canopy cover, or floristic composition similar to adjacent, undisturbed lands. The longest times projected for recovery are for floristic composition (Vasek et al., 1975a, 1979/1980; Lathrop and Archbold, 1980b; Bolling and Walker, 2002; Webb et al., 2009; Abella, 2010). Most studies of recovery have involved examples of secondary succession; however, Vasek and Lund (1980) described an example of primary succession at the edges of a dry lake bed in the Mojave Desert.

Linear corridors of disturbance, specifically utility rights-of-way for pipelines, aqueducts, and transmission lines, are special cases. These rights-of-way, often hundreds of kilometers in length and widespread throughout North American deserts, are narrow in width and often have associated unpaved access roads. Ecologists and botanists have documented plant succession and partial recovery from linear disturbances in the Mojave Desert (Vasek et al., 1975a, 1975b; Kay, 1979, 1988; Lathrop and Archbold, 1980a, 1980b; Abella et al., 2007).

We designed a study to determine the status of recovery of perennial vegetation in a *L. tridentata* alliance along the second Los Angeles aqueduct 36 years after construction. Construction of the second Los Angeles aqueduct created a severe linear disturbance traversing 219 km of Great Basin and Mojave deserts and the San Gabriel Mountains (Kay, 1979, 1988; Baldwin et al., 2014). The disturbance involved removing soil and vegetation sufficient to bury the aqueduct pipe, construction of a dirt service road, breaking up compaction after construction, and continuously maintaining the road through the middle of the 97-m wide corridor (Kay, 1979, 1988). Few studies are available describing natural recovery of vegetation for similar linear disturbances for the Mojave Desert (Johnson et al., 1975; Lathrop and Archbold, 1980a; Abella et al., 2007; Webb et al., 2009). Most studies (summarized in Webb et al., 2009; Abella, 2010) on natural recovery of vegetation have dealt with large and irregularly-shaped disturbances (towns, fires, military maneuvers) or roads and are not necessarily applicable to the unique characteristics of an aqueduct right-of-way corridor with a maintained dirt road at the center.

Our objectives were to address topics that would provide basic information on succession and the recovery process of perennial plants in the *L. tridentata-Ambrosia dumosa* vegetation alliance (Sawyer et al., 2009) under these types of disturbance scenarios and to provide information for abbreviating the recovery process. Our focus was not only on the two more common and well-known species of shrubs but also on the other perennial species and their potential inter- and intra-specific associations. Our questions were: 1) Do perennial plants differ in total numbers, canopy cover, or canopy types (live, dead, or a combination of live and dead) within the disturbed right-of-way of the aqueduct corridor and between the corridor and adjacent undisturbed vegetation? 2) Do species composition, richness, and diversity vary with distance from the disturbance at the road verge of the right-of-way? 3) Do patterns of contagion within and between species exist? 4) Which species serve as nurse shrubs for other perennials? and 5) How much time might be required for perennial vegetation in the disturbed right-of-way corridor to recover to conditions similar in adjacent undisturbed habitat? These questions are important to address because hundreds of square kilometers of Mojave, Sonoran, and Great Basin deserts require restoration of degraded habitat from solar and wind development and other activities (e.g., California Energy Commission, 2014) Similarly, habitats of rare and threatened plant and animal species require restoration if the species are to thrive, e.g., the Mohave ground squirrel (*Xerospermophilus mohavensis*), a species endemic to the western Mojave Desert, and Agassiz's desert tortoise (*Gopherus agassizii*) (California Department of Fish and Wildlife (2015a), 2015b). Both species require cover of shrubs to protect them from temperature extremes and predators.

2. Methods

2.1. Site description

The site is a 1.17-km stretch of the second Los Angeles aqueduct right-of-way in Kern County between 35° 33′ 32″ N, 117° 58′ 22″ W, 1048 m (Fig. 1A). The topography is uniform and typical of large stretches of aqueduct corridor and *L. tridentata* vegetation in the Mojave Desert, is devoid of desert washes, and is on a broad alluvial fan. Soils are from the Dovecanyon–Koehn association on 2–8% slopes and are characterized as alluvium derived from granite with loamy sand, coarse sandy loam, gravelly coarse sandy loam (depending on depth), and sand (U.S. Department of Agriculture, Natural Resources Conservation Service [USDA NRCS], 2008). *L. tridentata* is a canopy-emergent shrub in a *L. tridentata-A. dumosa* alliance with 19 other species of perennial shrubs, grasses and cactus (Table 1). The arid climate has an average annual precipitation of ~150 mm with most precipitation occurring in fall and winter months (USDA NRCS, 2008). We selected the site because Kay (1979, 1988) documented and photographed site treatment and recovery of perennial shrubs twice after construction, once in 1979 (Fig. 2A) and again in 1988 (Fig. 2B), and because the site is typical of about 70% of the aqueduct corridor.

In 1968, the Department of Water and Power for the City of Los Angeles (LADWP) bulldozed the right-of-way for the aqueduct and removed all vegetation from the 97-m wide corridor. When completed, the right-of-way corridor contained the aqueduct and dirt service road in the center with adjacent disturbed land. In 1971–1972, after completion of the aqueduct, much of the construction zone adjacent to the service road was ripped to a depth of 25 cm on 61-cm centers to reduce soil compaction and to facilitate seedling growth of naturally colonizing shrubs (Kay, 1979, 1988, Fig. 2A). Although a few parts of the aqueduct corridor were seeded with *A. dumosa*, *Ambrosia salsola*, *Atriplex canescens, Atriplex polycarpa, Ephedra nevadensis, L. tridentata*, and *Lepidospartum squamatum*, the study site we selected had not been seeded. The LADWP maintains the service road by grading, and a low berm is often present at the road verge.

The study site and much of the aqueduct corridor in the Mojave Desert are on public land administered by the U.S. Department of the Interior, Bureau of Land Management (BLM). Livestock have grazed the area since the 1870s (Wentworth, 1948; U.S. BLM, 1980). Other nearby anthropogenic uses include the first Los Angeles aqueduct, constructed between 1905 and 1913 (Nadeau, 1997).

2.2. Sample design for vegetation

The disturbance corridor at the sampling site was approximately 90 m wide with a 7-m wide graded dirt service road in the center. We established fourteen 20-m × 1-m randomly selected transects at each of four distances (0, 20, 40, and 100 m) parallel to the north verge of the service road into undisturbed habitat for a total of 56 transects (Fig. 1B). The 0-m transects were next to the road berm but not on it, were the closest to the buried aqueduct, and were designated as “verge” sites. Transects at 20-m and 40-m distances

were within the disturbed right-of-way and were termed the midway and blade-edge distances, respectively. The distance from the 0-m point and undisturbed vegetation was 45 m. The 100-m transects comprised the undisturbed or control sites and were 55 m from the bladed edge of the disturbed corridor.

Between July and November of 2005, we collected data on distribution, species composition, and canopy cover of perennials by distance from the road verge. The SE corner of each transect was located using a GeoExplorer 3 (Trimble Navigation Limited, Sunnyvale, California), and data were recorded in UTMs (NAD 83, Zone 11N) for a geographic information system (GIS) layer. A compass and tape measure were used to mark transect corners. We then measured locations of individual shrubs (using the single basal stem) from the SE corner of the transect and converted data on centers of shrubs to UTM coordinates. *L. tridentata*, which usually has multiple stems, was measured from the center of the ring of basal stems. Perennials were identified to species, and shrub canopies were placed in one of three classes: live (canopy >95% live vegetation), dead (canopy entirely dead), or mosaic (canopy consisting of live and dead components where the dead component is >5% of total canopy cover). We also measured the greatest length and width of each perennial species to calculate cover (m^2) by species, as well as total cover for each transect. We report cover as percent cover, calculated for each species as cover divided by transect area. Species richness (total number of species) and Simpson's diversity index ($D = 1 - \sum[n_i(n_i - 1)/N(N - 1)]$, where n_i is the number of the ith species and N is the number of all individual plants on the transect [Pielou, 1969]) were calculated for each transect. The number of shrub islands (≥2 individual shrubs with intersecting canopies) and the number and species of shrubs composing the islands were recorded for each transect. We also collected data on perennial shrubs and grasses serving as nurses (Padilla and Pugnaire, 2006; Filazolla and Lortie, 2014) by recording the number and species of seedlings and small shrubs growing within the understory of each shrub or perennial grass. Plant names and abbreviations followed Baldwin et al. (2014, Table 1).

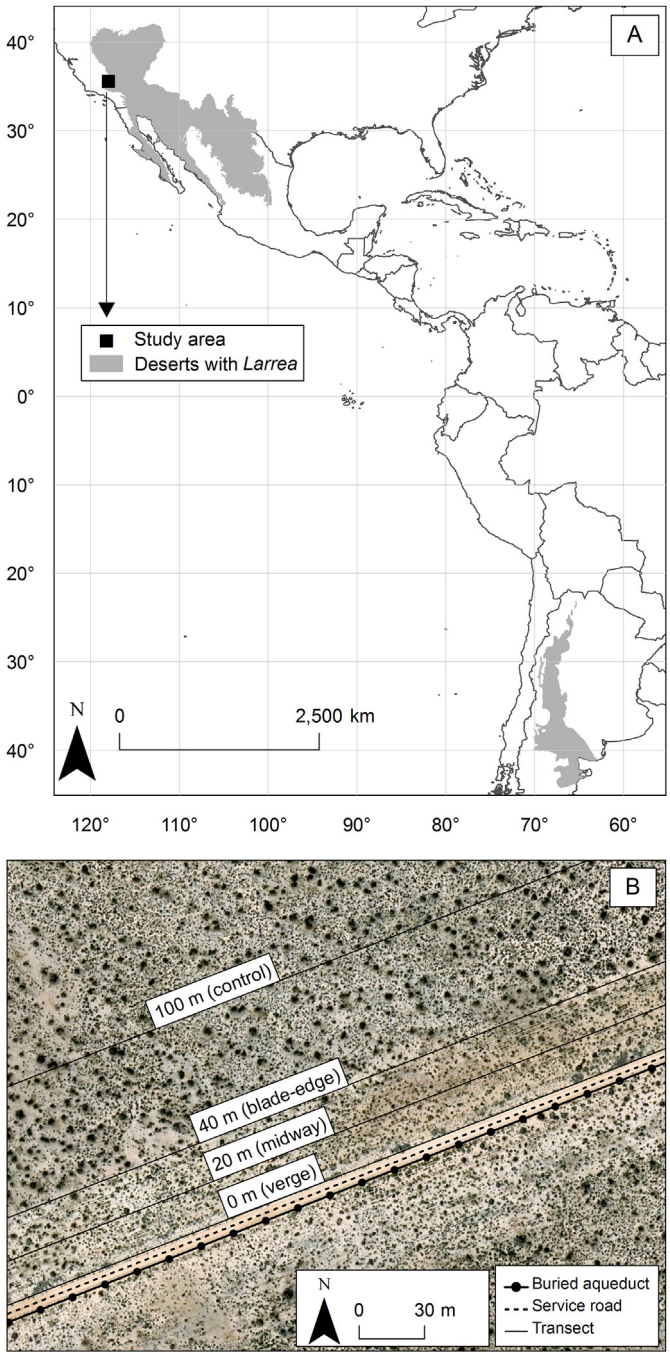

Fig. 1. (A) Location of the study area in the second Los Angeles aqueduct corridor, Mojave Desert, California, in relationship to other deserts with *Larrea* vegetation alliances: the Mojave, Sonoran, and Chihuahuan deserts of North America and the Monte Desert of South America. (B) Schematic of the second Los Angeles aqueduct corridor with the buried pipe, service road, the four distances (0, 20, 40, and 100 m) from the edge of the service road, and undisturbed land.

2.3. Data analysis

We assigned potential life spans to the perennial species using published data from the Mojave Desert, when available (Table 1; Frenkel, 1970; Johnson et al., 1975; Vasek et al., 1975a, 1975b, 1979/1980; Lathrop and Archbold, 1980a; Bowers et al., 1997; Lauenroth and Adler, 2008). For two species (*Acamptopappus sphaerocephalus, Eriogonum fasciculatum*), life span estimates varied and may have been dependent on desert region, surficial geology, elevation, and vegetation alliance. We also noted distributional affinities of each species in the North and South American deserts (Benson and Darrow, 1981; Turner et al., 1995; Baldwin et al., 2014).

We compared total number of shrubs and one species of cactus, total shrub cover (live and dead canopies), total live canopy cover, total dead canopy cover, and number of mosaic shrubs (defined as having both live and dead canopies) by distance from the road verge (0, 20, 40, and 100 m) using linear mixed-effects models (with distance from the road verge as a fixed effect and transect identification as a random effect) and post hoc Tukey's Honestly Significant Difference (HSD) test. We used this method of analysis to account for relatedness of measurements made on the same transect. We similarly compared canopy cover (total canopy cover, total live and dead canopy cover) by distance from the road verge for four perennial grass species (*Elymus elymoides, Poa secunda, Stipa speciosa, Stipa hymenoides*) using linear mixed-effects models. We also compared live canopy cover for six individual shrub species of interest (*Ericameria nauseosa, A. salsola, A. dumosa, L. tridentata, Ericameria cooperi, Grayia spinosa*), species richness, Simpson's diversity index, number of shrub islands, number of shrubs per shrub island, and species richness of shrub islands among the four distances from the road verge using linear mixed-effects models and Tukey's HSD test.

To examine contagion patterns in the vegetation, we used a GIS layer containing locations of each perennial shrub and grass species to determine the nearest species with the “near proximity” tool in

Table 1
Abundance of perennial shrubs and grasses at each distance band at the second Los Angeles aqueduct site, western Mojave Desert, California. Estimated longevity (references in Methods): SL = short-lived, ML = mid-lived, LL = long-lived, VLL = very long-lived, and ? = longevity unknown or suspected from limited data. Life form: PG = perennial grass, PS = perennial shrub, and HPS = herbaceous perennial shrub.

Species abbrev.	Scientific name	Estimated longevity	Life form	Desert affinity[a]	Number of plants, all transects			
					0 m	20 m	40 m	100 m
ACSP	*Acamptopappus sphaerocephalus*	SL, ML	PS	Great Basin, Mojave, Sonoran	0	3	40	42
AMDU	*Ambrosia dumosa*	VLL	PS	Great Basin, Mojave, Sonoran	2	73	188	292
AMSA	*Ambrosia salsola*	SL	PS	Great Basin, Mojave, Sonoran	22	119	26	10
ATCA	*Atriplex canescens*	ML, LL	PS	Great Basin, Mojave, Sonoran, Chihuahuan	1	2	0	0
CYEC	*Cylindropuntia echinocarpa*	LL	Cactus	Great Basin, Mojave, Sonoran	0	0	0	1
ELEL	*Elymus elymoides*	SL?	PG	Great Basin, Mojave, Sonoran, Chihuahuan	29	3	1	0
ERCO	*Ericameria cooperi*	LL	PS	Great Basin, Mojave	6	12	61	136
ERNA	*Ericameria nauseosa*	LL	PS	Great Basin, Mojave, Chihuahuan	373	175	5	0
ERTE	*Ericameria teretifolia*	?	PS	Great Basin, Mojave	0	3	1	0
ERFA	*Eriogonum fasciculatum*	SL, LL	PS	Great Basin, Mojave, Sonoran	0	0	0	1
GRSP	*Grayia spinosa*	LL	PS	Great Basin, Mojave, Sonoran	0	4	10	11
KRLA	*Krascheninnikovia lanata*	LL	PS	Great Basin, Mojave, Sonoran, Chihuahuan	0	0	0	8
LATR	*Larrea tridentata*	VLL	PS	Mojave, Sonoran, Chihuahuan	3	0	8	31
LESQ	*Lepidospartum squamatum*	SL?	PS	Mojave, Sonoran	0	1	0	0
LYAN	*Lycium andersonii*	VLL, LL	PS	Great Basin, Mojave, Sonoran, Chihuahuan	0	0	2	0
MILA	*Mirabilis laevis*	SL	HPS	Mojave, Sonoran	1	0	10	0
POSE	*Poa secunda*	?	PG	Many desert plant communities, N.A., S.A.	0	0	1	53
STPA	*Stephanomeria pauciflora*	SL	PS	Great Basin, Mojave, Sonoran	40	37	1	15
STHY	*Stipa hymenoides*	LL?	PG	Many plant communities	5	2	6	0
STSP	*Stipa speciosa*	SL	PG	Many plant communities, N.A.,S.A.	4	3	4	4
TEST	*Tetradymia stenolepis*	SL	PS	Great Basin, Mojave	0	0	0	2
Other[b]					3	11	8	32

[a] Not shown: several plant species have non-desert affinities.
[b] Other perennial plants were unidentifiable to species and were usually dead shrubs. N.A. = elsewhere in North America; S.A = South America.

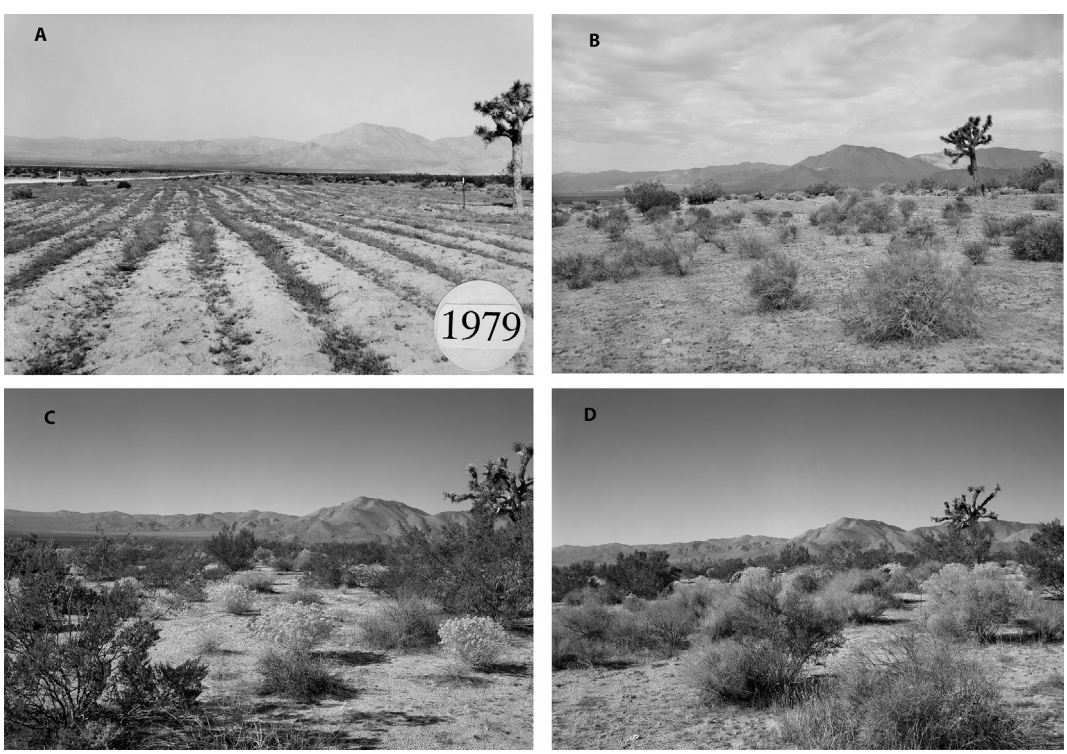

Fig. 2. Two sets of photographs of the study area, each taken at a different location, within the Los Angeles aqueduct corridor, western Mojave Desert, California. (A) 1979, taken ~10 years after the right-of way was cleared of vegetation, the pipeline was buried, and the right-of-way was ripped to decompact the soil. Note the rarity of shrubs and the presence of annuals in the furrows. (B) 1988, taken 19 years after construction. Although the furrows are still evident, shrubs (e.g., *Ambrosia salsola*) were present. (C) A re-photograph of (A), taken in 2005, 26 years after (A) and 36 years after construction. (D) A re-photograph of (B), taken in 2006, taken 37 years after construction. In both (C) and (D), the cover of shrubs has become well-established. Burgess Kay took photographs A and B (Kay, 1979, 1988); Dominic Oldershaw took C and D. In the 2005 and 2006 photographs, the service road is still present but obscured by shrubs.

ArcGIS Vers. 9.2 (ESRI, Redlands, California). We then constructed a contingency table of the more common species (N = 9) with the species identity of the nearest perennial plant to examine contagion patterns using chi-square statistics. Finally, we constructed a contingency table to analyze associations between the more common nurse shrubs (N = 8) and the perennial plants growing within their understory, also using chi-square statistics.

We performed a discriminant function analysis to determine whether the four distances represented distinct plant communities based on species composition. For this analysis, we used frequency counts of all perennial shrubs and perennial bunch grasses as predictor variables to characterize each distance from the road verge. We also compared the similarity of the perennial plant community between distances with two additional metrics: Sørensen's similarity index (S_i) and Bray–Curtis index (BC_i). These indices provide a measure of similarity where 0 represents no similarity between communities (i.e., distances) and 1 represents identical communities.

For Sørensen's similarity index, we converted our dataset to presence/absence data and calculated indices between sampling distances: $S_i = 2C/(2C + A + B)$ where i is a comparison between distances, C is the number of species shared by two distances, A is the number of species exclusive to distance A, and B is the number of species exclusive to distance B. For the Bray–Curtis index, which incorporates measures of relative abundance, we used the perennial density data to first calculate a Bray–Curtis distance (BC_d): $BC_d = \sum_i^n |x_{ij} - x_{ik}| / \sum_i^n x_{ij} + x_{ik}$ where d is a comparison between distances, x_{ij} is the density of species i at distance j, x_{ik} is the density of species i at distance k, and n is the total number of species (Pekas and Schupp, 2013). We then calculated the Bray–Curtis index: $BC_i = 1 - BC_d$. For these analyses, we combined perennial species with different canopy states (live and dead).

We converted similarity indices to percent similarity by multiplying the index by 100. We then calculated a recovery rate by assuming a constant linear relationship between time and recovery and divided the percent recovery estimates by 36 years. For each distance comparison, we used the recovery rates to estimate time required to reach 100% recovery. We also compared the recovery rates after 36 years to estimates of recovery calculated by two linear models reported by Abella (2010): $y = 0.285x + 38.6$ and $y = 0.295x + 44.7$, where y is the predicted percent of recovery (i.e., percent similarity between disturbed and undisturbed samples) and x is the time since disturbance. The former equation was developed from a meta-analysis of 31 studies, each with one year of data. The latter equation was developed with data collected by Bolling and Walker (2000) from a series of abandoned roads in the Mojave Desert.

Linear mixed-effects models were fitted in R v.2.11.1 (R Development Core Team, 2010) using the *nlme* package (Pinheiro and Bates, 2013) and Tukey's HSD tests were conducted with the *multcomp* package (Hothorn et al., 2008). Similarity indices were calculated using the *vegdist* function in the *vegan* package (Oksanen et al., 2013). All other statistical tests were performed with SYSTAT v.13 (SYSTAT Software, Inc., 2009) and considered significant at $P < 0.05$.

3. Results

The photograph taken by Kay (1979) approximately 10 years after construction indicates that few shrubs had colonized the aqueduct corridor; none was evident in the foreground of the study area (Fig. 2A). In a second photograph taken 19 years after construction, *A. salsola* was common in the fore- and mid-ground and *L. tridentata* was occasional (Kay, 1988, Fig. 2B). At the time of our study 36 years after construction in 2005, 16 species of perennial shrubs, one species of cactus, and four species of perennial grasses were present on all transects, including the control (Table 1, Fig. 2C and D). The species found within the disturbance corridor were, with several exceptions (*E. nauseosa, Ericameria teretifolia, E. elymoides, Atriplex canescens, L. squamatum, Lycium andersonii, Mirabilis laevis*; Table 1), the same species found on control transects outside the disturbance corridor; all species were part of the local *L. tridentata-A. dumosa* vegetation alliance. Within the study site, 11 species were long-lived, eight species were short-lived, and the longevity of two species was unknown (Table 1). All species occur in two or more North American deserts, and three of the grass species occur in many plant communities, including those in South America.

Within the study site, five species were present at all distances: four shrubs (*A. dumosa*, *A. salsola*, *Stephanomeria pauciflora*, and *E. cooperi*) and one perennial bunch grass (*S. speciosa*). The number of species exclusive to each distance varied with distance to the road verge: none on the 0-m transects; one species on the 20-m transects (*L. squamatum*); one species on the 40-m transects (*Lycium andersonii*); and four species on the 100-m transects (*Cylindropuntia echinocarpa, E. fasciculatum*, *Krascheninnikovia lanata*, and *Tetradymia stenolepis*). *G. spinosa* and *A. sphaerocephalus* were never observed on 0-m transects, *P. secunda* was never observed on 0-m or 20-m transects, *Atriplex canescens* was never observed on 40-m or 100-m transects, and *E. nauseosa*, *E. elymoides* and *S. hymenoides* were never observed on 100-m transects. Three species of perennial grass (*S. hymenoides, S. speciosa*, *E. elymoides*) were rare: each species composed <2% of the total number of individual perennial species recorded. Six shrub species (*E. fasciculatum*, *E. teretifolia, K. lanata, L. squamatum*, *L. andersonii, T. stenolepis*), one cactus species (*C. echinocarpa*), and one herbaceous perennial plant (*Mirabilis laevis*) comprised <1% of the total number of individual perennial species recorded.

3.1. Numbers, distribution, and canopy cover of common species

The total number of shrubs and the single cactus (not including grasses) per transect did not vary significantly with distance from the road verge ($F_{3,39} = 1.94$, $P = 0.139$). However, total live and dead shrub cover varied with distance from the road verge ($F_{3,39} = 19.08$, $P < 0.001$). Tukey's HSD test revealed that total cover was greater at 100 m than all other distances ($P < 0.007$), greater at 20 m than 40 m ($P = 0.001$), and no differences existed between 0 m and 20 m ($P = 0.144$) or 0 m and 40 m ($P = 0.266$). Overall, long-lived perennial plants composed 42% of individuals and 75% of cover within the disturbance corridor (Table 1). Of the long-lived species, *E. nauseosa* composed 59% of individuals and 67% of cover.

Live canopy cover varied with distance from the road verge ($F_{3,39} = 8.55$, $P < 0.001$), with significantly more cover at 100 m than other distances ($P < 0.03$). Dead canopy cover also varied with distance from the road verge ($F_{3,39} = 13.89$, $P < 0.001$), with more dead cover at 100 m or 20 m than at 40 m or 0 m ($P < 0.001$). At 0 m, dead shrubs formed 10.5% of the canopy cover, peaking at 20 m with 34.2% of canopy cover, and declining to 23.6% and 25.2% at 40 m and 100 m distances, respectively (Table 2). Additionally, the number of shrubs with mosaic canopies increased with increasing distance from the road verge ($F_{3,39} = 31.75$, $P < 0.001$), with significantly more shrubs with mosaic canopies at 100 m than all other distances ($P < 0.001$).

The cover of individual live shrub species also varied with distance to the road verge. Cover of live *E. nauseosa* decreased with

Table 2
Percent cover of live and dead perennial plants at distances of 0 m, 20 m, 40 m, and 100 m from the road verge at the second Los Angeles aqueduct site, western Mojave Desert, California.

Scientific name	Mean (±SE) percent cover							
	0 m	0 m	20 m	20 m	40 m	40 m	100 m	100 m
	Live	Dead	Live	Dead	Live	Dead	Live	Dead
Acamptopappus sphaerocephalus	0	0	<0.1 (±0.1)	<0.1 (±0.1)	3.7 (±1.2)	0.4 (±0.2)	1.3 (±0.6)	2.2 (±0.8)
Ambrosia dumosa	<0.1 (±0.1)	0	3.4 (±1.3)	1.6 (±1.2)	5.5 (±1.8)	4.9 (±1.1)	11.9 (±1.8)	7.3 (±1.4)
Ambrosia salsola	2.1 (±1.1)	<0.1 (±0.1)	15.9 (±4.0)	7.5 (±2.3)	2.8 (±1.1)	1.5 (±0.8)	0.7 (±0.4)	0.5 (±0.3)
Atriplex canescens	<0.1 (±0.1)	0	<0.1 (±0.1)	0.1 (±0.1)	0	0	0	0
Cylindropuntia echinocarpa	0	0	0	0	0	0	0	<0.1 (±0.1)
Elymus elymoides	0.2 (±0.1)	0	<0.1 (±0.1)	0	<0.1 (±0.1)	0	0	0
Ericameria cooperi	0.2 (±0.2)	0	1.8 (±1.3)	0.1 (±0.1)	4.7 (±2.6)	1.2 (±0.6)	7.6 (±2.4)	5.2 (±1.4)
Ericameria nauseosa	40.4 (±4.3)	3.6 (±1.2)	17.2 (±4.1)	11.8 (±3.2)	1.1 (±0.9)	0.3 (±0.3)	0	0
Ericameria teretifolia	0	0	0.2 (±0.2)	0	0.4 (±0.4)	0	0	0
Eriogonum fasciculatum	0	0	0	0	0	0	0.1 (±0.1)	0.1 (±0.1)
Grayia spinosa	0	0	0.9 (±0.5)	0.1 (±0.1)	1.1 (±0.7)	0	3.2 (±1.6)	0.3 (±0.2)
Krascheninnikovia lanata	0	0	0	0	0	0	0.3 (±0.3)	<0.1 (±0.1)
Larrea tridentata	0	1.5 (±1.0)	0	0	8.4 (±4.1)	0	34.3 (±7.9)	3.9 (±2.1)
Lepidospartum squamatum	0	0	0.1 (±0.1)	0	0	0	0	0
Lycium andersonii	0	0	0	0	0.3 (±0.3)	<0.1 (±0.1)	0	0
Mirabilis laevis	<0.1 (±0.1)	0	0	0	<0.1 (±0.1)	0.3 (±0.1)	0	0
Poa secunda	0	0	0	0	<0.1 (±0.1)	0	0.8 (±0.4)	0
Stephanomeria pauciflora	0.5 (±0.2)	0	1.1 (±0.7)	0	<0.1 (±0.1)	0	0.1 (±0.1)	0
Stipa hymenoides	0.2 (±0.1)	0	<0.1 (±0.1)	0	<0.1 (±0.1)	<0.1 (±0.1)	0	0
Stipa speciosa	<0.1 (±0.1)	0	0.1 (±0.1)	0	<0.1 (±0.1)	0	1.1 (±0.8)	<0.1 (±0.1)
Tetradymia stenolepis	0	0	0	0	0	0	0.8 (±0.8)	0.2 (±0.5)
Other	0	<0.1 (±0.1)	0	0.1 (±0.1)	0	0.1 (±0.1)	0	0.9 (±0.5)
Total shrub and grass cover	43.3 (±4.0)	5.1 (±1.9)	40.7 (±3.5)	21.2 (±3.3)	28.1 (±5.0)	8.7 (±1.3)	61.9 (±7.2)	20.8 (±3.0)

increasing distance from the road ($F_{3,39} = 52.40$, $P < 0.001$; Fig. 3A), with significantly more cover at 0 m than all other distances ($P < 0.001$) and more cover at 20 m than 40 m ($P < 0.001$) and 100 m ($P < 0.001$). Cover of live *A. salsola* varied with distance to the road verge ($F_{3,39} = 11.63$, $P < 0.001$), with significantly more cover at 20 m than all other distances ($P < 0.001$; Fig. 3B). Patterns of increased canopy cover with increasing distance from the road verge were apparent for both live *A. dumosa* ($F_{3,39} = 14.67$, $P < 0.001$; Fig. 3C) and live *L. tridentata* ($F_{3,39} = 12.01$, $P < 0.001$; Fig. 3D). More live cover of *A. dumosa* occurred at 100 m than all other distances ($P < 0.002$) and cover was also greater at 40 m than 0 m ($P < 0.05$). Live cover of *L. tridentata* was absent at 0 m and 20 m but was significantly greater at 100 m than all other distances ($P < 0.001$). Similarly, cover of live *E. cooperi* was significantly greater at 100 m ($F_{3,39} = 4.61$, $P = 0.007$) than 0 m and 20 m ($P < 0.02$). Cover of live *G. spinosa* also increased with increasing distance from the road verge ($F_{3,39} = 3.00$, $P = 0.042$), with significantly more cover at 100 m than 0 m ($P = 0.025$).

Cover of individual dead shrub species also showed corresponding patterns across the disturbance corridor, reflecting

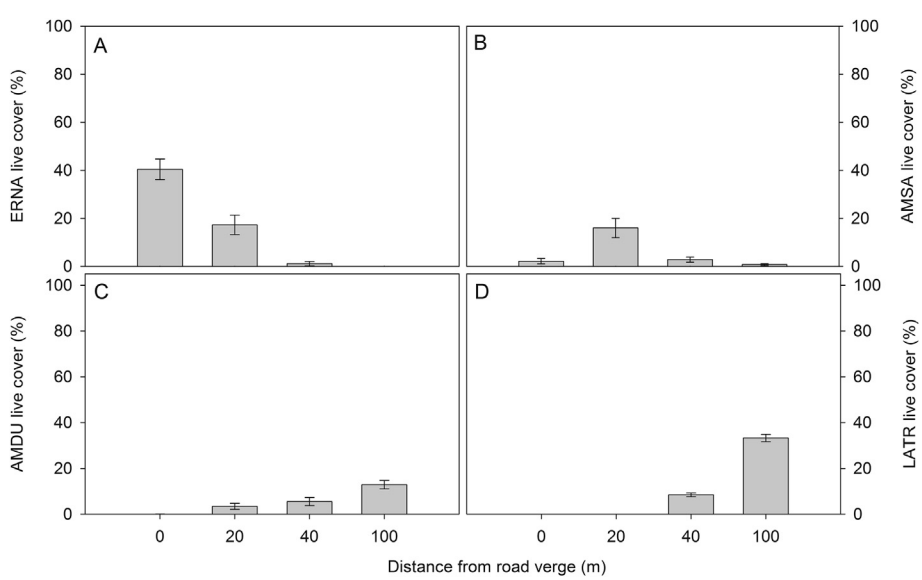

Fig. 3. Percent live cover of *Ericameria nauseosa* (A), *Ambrosia salsola* (B), *Ambrosia dumosa* (C), and *Larrea tridentata* (D) at the service road verge (0 m), midway (20 m) and at the blade edge (40 m) of the right-of-way, and in the undisturbed or control area (100 m) of the second Los Angeles aqueduct corridor, western Mojave Desert, California.

recovery and succession (Table 2). Dead *E. nauseosa,* for example, composed 8.2% of cover for the species at 0 m vs. 40.6% at 20 m. By 100 m, neither live nor dead *E. nauseosa* were present on transects. Dead *A. salsola*, in a pattern similar to *E. nauseosa*, formed 0.4% of cover at 0 m vs 31.9% and 35.5% at 20-m and 40-m distances, respectively. Only dead *L. tridentata* occurred at 0 m.

Total cover of the four species of perennial grasses varied significantly by transect distance ($F_{3,39} = 4.32$, $P = 0.010$), with greater cover at the 100-m distance than at 40 m or 20 m ($P < 0.05$; Table 2). When evaluated by individual species of perennial grass, cover of live and dead *E. elymoides* combined decreased with increasing distance from the road ($F_{3,39} = 3.59$, $P < 0.022$), and cover was significantly greater at 0 m than all other distances ($P < 0.05$). In contrast, cover of live and dead *P. secunda* increased with increasing distance from the road ($F_{3,39} = 3.41$, $P = 0.027$), with significantly greater cover at 100 m than all other distances ($P < 0.05$). The live and dead cover for *S. speciosa* and *S. hymenoides* did not vary significantly by distance, although *S. speciosa* cover tended to be higher at the 100-m distance than at other distances ($F_{3,39} = 2.06$, $P = 0.12$), and counts of *S. hymenoides* cover tended to be highest at the verge and lowest at the 100-m distance ($F_{3,39} = 2.77$, $P = 0.055$). The results did not change when only the live bunch grasses were analyzed.

3.2. Species richness, diversity and composition

Indices of species richness and diversity varied with distance from the road verge. Species richness increased with increasing distance from the road verge ($F_{3,39} = 4.25$, $P = 0.011$), with significantly more species on 100-m transects (4.4 species per transect) and 40-m transects (4.3 species per transect) than on 0-m transects (2.9 species per transect; $P < 0.02$). Simpson's diversity index also increased with increasing distance from the road verge ($F_{3,52} = 4.32$, $P < 0.009$), with significantly greater species diversity at 100 m and 40 m than at 0 m ($P < 0.021$) and a trend for greater diversity at 20 m than at 0 m ($P = 0.059$).

Species composition differed significantly among the four distances based on perennial plant composition (Wilk's Lambda = 0.001, approximate $F_{90,\ 63} = 6.834$, $P < 0.001$; Fig. 4) and classified 100% of the transects to the correct distance. Transects at 20 m and 40 m were more similar in terms of species composition, while transects at 100 m were most distinct (Fig. 4). Three discriminant functions explained 87.6%, 7.1%, and 5.3% of the variation in the dataset, respectively. Function coefficients of each perennial species with these three discriminant functions are shown in Appendix A; species that were important in separating the four distances were *E. nauseosa, A. salsola, A. dumosa, L. tridentata, E. cooperi,* and *E. elymoides*.

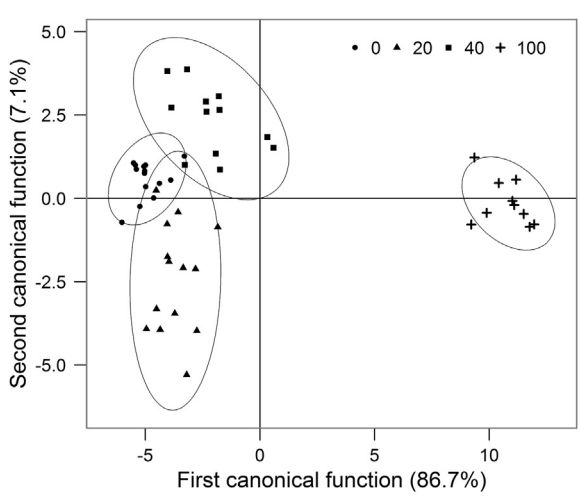

Fig. 4. Scatterplots of discriminant analysis functions for perennial plant composition at 0 m (road verge), 20 m, and 40 m distances within the disturbance corridor of the second Los Angeles aqueduct, and at 100 m (control) on adjacent undisturbed habitat, western Mojave Desert, California.

The four distances from the road verge contained distinct groupings or associations of plants. Even though the discriminant analysis correctly classified all 56 transects, there was notable overlap between 0-m, 20-m, and 40-m transects in species composition (Table 2, Fig. 4). These results imply that reestablishment of perennial plants has occurred along a transitional gradient of disturbance from the road verge to the control, with control transects representing the most distinct plant community (Fig. 4), with the greatest species diversity and dominated by the long-lived *A. dumosa* and *L. tridentata*. The lack of overlap in the discriminant analysis between the control sites with the three disturbance distances shows that none of the distances within the disturbance corridor has achieved the original species composition observed at the control.

3.3. Shrub islands

Shrub islands reflected the common species present at the four transect distances. At 0 m, most shrub islands consisted of only *E. nauseosa*, followed in descending order by *E. nauseosa* and *A. salsola*, *E. nauseosa* and *S. pauciflora*, and *E. nauseosa* and *E. cooperi*. At 20 m, *E. nauseosa* and *A. salsola* were again the most frequent components of shrub islands, and *A. dumosa* appeared in low numbers. At 40 m, *A. dumosa* was the predominant species and co-occurred with *E. cooperi*, *A. sphaerocephalus*, and *G. spinosa* in shrub islands. At 100 m, most shrub islands were composed of only *A. dumosa*, followed by only *E. cooperi*, and combinations of *A. dumosa* with *E. cooperi*, *Acamptopappus spherocephalus*, and *L. tridentata*. Although species composition of shrub islands differed at the four distances, the number of shrub islands per transect and the number of shrubs per shrub island did not vary significantly with distance from the road verge ($F_{3,39} = 2.78$, $P = 0.054$; $F_{3,39} = 0.01$, $P = 0.999$, respectively). Number of species (1–4) composing a shrub island also did not vary with distance from the road verge ($F_{3,39} = 1.73$, $P = 0.177$).

3.4. Patterns of association: nearest neighbors and nurse plants

The nearest species analysis revealed that individual perennial species varied in their patterns of association with other species. All perennials showed strong positive associations with conspecifics (Table 3). *A. salsola* showed negative associations with *A. dumosa* and all heterospecifics, and *E. nauseosa* and *S. pauciflora* showed negative associations with all heterospecifics except for the perennial grass *E. elymoides*. In contrast, *L. tridentata, A. dumosa, A. spherocephalus,* and the perennial bunch grasses *E. elymoides* and *P. secunda* each showed positive associations with multiple heterospecifics (Table 3).

We evaluated the eight more common species of shrubs that acted as nurse plants (Table 4: *A. sphaerocephalus*, *A. dumosa*, *A. salsola*, *E. cooperi, E. nauseosa, Grayia spinosa, L. tridentata*, and *Stephanomeria pauciflora*). Dead and live shrubs were equally as likely to serve as nurse shrubs to other perennials ($\chi^2 = 0.15$, df = 1, $P = 0.701$). Nurse plants occurred at all distances within the site and composed 7.9% of all plants measured, in proportions that varied little by distance: 9.0% at 0 m, 8.0% at 20 m, 8.3% at 40 m, and 6.8% at 40 m (Appendix B). Nurse species differed by distance, with *E.*

Table 3
Summary of the most common perennial plant species with counts and Pearson residuals of their nearest perennial plant species occurring at the second Los Angeles aqueduct site, western Mojave Desert, California. Pearson residuals were calculated as (Observed − Expected)/√Expected. *All Pearson residuals >2 indicated strong positive associations and a significant departure at the 95% level. **All Pearson residuals > − 2 indicated strong negative associations and a significant departure at the 95% level. Plant abbreviations are given in Table 1.

Counts of nearest perennial plant species (standardized deviates)										
Species	ACSP	AMDU	AMSA	ELEL	ERCO	ERNA	LATR	POSE	STPA	Total
ACSP	12 (6.35)*	31 (2.62)*	5 (−0.46)	1 (−0.61)	4 (−1.09)	0 (−4.45)**	1 (−0.20)	8 (3.67)*	2 (−1.01)	64
AMDU	28 (2.39)*	338 (15.37)*	21 (−3.82)**	4 (−2.69)**	47 (−0.80)	19 (−10.81)**	10 (0.20)	21 (0.66)	5 (−4.68)**	493
AMSA	6 (−0.11)	24 (−3.94)**	95 (19.27)*	4 (−0.42)	7 (−2.68)**	25 (−3.90)**	1 (−1.26)	2 (−1.73)	9 (−0.58)	173
ELEL	0 (−1.11)	3 (−2.28)**	1 (−1.25)	6 (5.10)*	1 (−1.38)	17 (2.00)*	2 (1.68)	0 (−1.12)	4 (1.27)	34
ERCO	6 (−0.30)	52 (−0.64)	5 (−3.05)**	1 (−1.88)	99 (17.65)*	7 (−6.69)**	4 (0.23)	9 (0.80)	4 (−2.27)**	187
ERNA	0 (−4.45)**	24 (−11.01)**	28 (−3.35)**	24 (2.14)*	9 (−6.46)**	429 (20.06)*	3 (−2.29)**	0 (−4.48)**	28 (−1.09)	545
LATR	2 (0.32)	17 (0.99)	0 (−2.05)**	2 (0.66)	6 (0.59)	5 (−2.33)**	10 (10.01)*	0 (−1.27)	2 (−0.47)	44
POSE	5 (2.22)*	17 (0.22)	3 (−0.92)	0 (−1.23)	6 (0.14)	0 (−4.05)**	0 (−1.00)	22 (14.34)*	0 (−1.83)	53
STPA	2 (−0.67)	5 (−4.21)**	3 (−1.87)	6 (2.20)*	1 (−2.74)**	18 (−1.77)	1 (−0.52)	0 (−1.80)	52 (19.72)*	88
Total	61	511	161	48	180	520	32	62	106	1681

nauseosa composing 95% of nurse species at 0 m, compared with 51% at 20 m, and 3% at 40 m. In contrast at 40-m and 100-m distances, three species—*A. dumosa, Ericameria cooperi* and *A. sphaerocephalus*—that had minor or no presence at 0-m and 20-m distances, composed 83% and 92% of nurses, respectively.

Shrub species differed in their ability to act as nurse shrubs for particular species (Table 4). For example, *E. nauseosa* was an important nurse shrub to other *E. nauseosa*, and *A. salsola* was an important nurse shrub to other *A. salsola*, but the other nurse shrubs were not important to their conspecifics. *E. nauseosa* acted as a nurse shrub to six other species, two of which were congenerics (*E. cooperi, E. teretifolia*), and four that were common in the 0-m and 20-m distances (*E. elymoides, A. salsola, S. pauciflora, S. hymenoides*). However, the only significant positive relationships for *E. nauseosa* were with other *E. nauseosa* and *E. elymoides. E. cooperi*, in contrast, had significant positive nurse relationships with *A. sphaerocephalus, A. dumosa*, *G. spinosa,* and *K. lanata* (Table 4). Some nurse shrubs, e.g., *A. sphaerocephalus*, acted as nurse for species typically at the 100-m distance, e.g., *A. sphaerocephalus* nursed *A. dumosa, M. laevis*, and *P. secunda*. The role of *L. tridentata* as a nurse was marginal, and then only for *A. dumosa*.

About one-third of the plants observed to be nursed were perennial grasses (35%, 65/186; Table 4). A different species of shrub or array of shrubs served as nurse plants for each of the four perennial grass species. Only two grass species had significant positive relationships: *E. elymoides* was nursed only by *E. nauseosa* and *P. secunda* was nursed by *A. sphaerocephalus*. Significant negative relationships were also recorded: *A. dumosa* and *E. cooperi* with *E. elymoides* and *E. nauseosa* with *P. secunda*.

3.5. Distance effects and recovery of perennial vegetation

The percent similarity between distances within the disturbance corridor and undisturbed perennial vegetation increased with increasing distance from the road verge and center of the disturbed area (Table 5). Likewise, the estimated time to 100% recovery was faster with increased distance (R_{100} in Table 5). The Sørensen and Bray–Curtis indices showed similar patterns, but the Bray–Curtis index was more conservative, especially at 0-m, with an estimate of 600 years. The linear models from Abella (2010) provided similar estimates of percent recovery after 36 years and time to 100% recovery (Table 5).

We estimate that the time for composition of perennial plants to return to values observed at the undisturbed control will be dependent on location within disturbance corridor, and may require from 176 to 600 years at the verge, versus 63–90 years at the 40-m or blade edge portion of the corridor (Table 5). Recovery at the blade edge will be much more rapid, because the 40-m distance is only 5 m from undisturbed lands, compared with the 0-m distance, which is 45 m away. The 0-m distance at the road verge is also in an area of frequent disturbance.

4. Discussion

4.1. Colonization and succession within the disturbance corridor

Colonization of the aqueduct corridor is bidirectional and has occurred from two directions: from the control into the disturbance corridor and from the verge of the central road into the disturbance corridor. The three distances within the disturbance corridor represent three different stages of colonization and secondary succession that are still underway in a gradient between the road and control. The first and more advanced stage, from the control into the disturbance corridor, appears in the 40-m transects, 5 m from the blade edge of the disturbance with the control and is an example of secondary succession. Several long-lived species (e.g., *A. dumosa, E. cooperi, G. spinosa, L. tridentata*) and at least one mid-lived species, *A. sphaerocephalus*, are present, further decrease in numbers and canopy cover at the 20-m, or are absent at the verge (Tables 1 and 2). The single *L. tridentata* occurring at the verge is dead. In this case, long-lived species are acting as pioneers and colonizing the adjacent disturbed area, similar to Vasek's (1979/1980) description *of L. tridentata* succession at a barrow pit. Species diversity and richness, highest in the control, decreases progressively from the 40-m transects to the verge.

The second colonization and successional pattern, initiated at the verge, extends across the disturbance corridor to the 40-m transects. The road verge represents a continually disturbed ruderal site. The successional pattern appears to be a variation of the Connell and Slatyer (1977) inhibition model, in which early occupant(s) somehow secure the site and exclude, inhibit, suppress or modify the environment so that it subsequently is less suitable for recruitment of late successional species. In our case, *E. nauseosa*, a long-lived species, and *A. salsola, S. pauciflora*, and *E. elymoides*, three short-lived species, dominate the verge (Tables 1 and 2). *E. nauseosa* occurs in decreasing numbers in 20-m and 40-m transects and is absent from the control. The proportions of live to dead cover of *E. nauseosa* at the verge (11:1) decrease markedly (1.5:1) at 20 m, a potential indicator that *E. nauseosa* has failed to thrive away from the verge. In contrast, *A. salsola* and *S. pauciflora* peak in numbers

Table 4
The more common perennial shrubs that acted as nurse plants, with counts and Pearson residuals of perennials growing in their understory at the second Los Angeles aqueduct site, western Mojave Desert, California. Pearson residuals were calculated as (Observed − Expected)/√Expected. *All Pearson residuals >2 indicated strong positive associations and a significant departure at the 95% level. **All Pearson residuals > −2 indicated strong negative associations and a significant departure at the 95% level. Plant abbreviations are given in Table 1.

	Counts of understory perennial plant species (standardized deviates)															
Nurse	ACSP	AMDU	AMSA	ELEL	ERCO	ERNA	ERTE	GRSP	KRLA	MILA	POSE	STHY	STPA	STSP	None
ACSP	0 (−0.94)	4 (2.20)*	0 (−0.92)	0 (−1.21)	0 (−0.21)	0 (−0.68)	0 (0.21)	0 (−0.21)	0 (−0.21)	1 (2.44)*	3 (2.23)*	0 (−0.41)	1 (−0.21)	0 (−0.46)	70
AMDU	6 (−0.19)	13 (0.88).	0 (−2.49)**	4 (−2.07)**	0 (−0.56)	0 (−1.84)	0 (−0.56)	0 (−0.56)	0 (−0.56)	2 (1.11)	11 (1.77)	0 (−1.11)	1 (−2.66)**	4 (1.97)	534
AMSA	5 (1.96)	1 (−1.29)	9 (4.89)*	2 (−0.83)	0 (−0.32)	0 (−1.06)	0 (−0.32)	0 (−0.32)	0 (−0.32)	0 (−0.55)	3 (0.59)	0 (−0.64)	3 (0.03)	0 (−0.71)	166
ERCO	8 (3.47)*	9 (2.55)*	1 (−0.90)	0 (−2.04)**	0 (−0.35)	0 (−1.15)	0 (−0.35)	1 (2.55)*	1 (2.55)*	0 (−0.60)	4 (0.94)	1 (0.76)	7 (1.90)	0 (−0.77)	190
ERNA	2 (−1.80)	5 (−1.67)	9 (1.08)	28 (5.11)*	1 (1.22)	11 (4.05)*	1 (1.22)	0 (−0.56)	0 (−0.56)	0 (−0.97)	0 (−2.57)**	3 (1.55)	15 (1.94)	1 (−0.46)	510
GRSP	0 (−0.53)	0 (−0.67)	1 (1.41)	0 (0.69)	0 (0.12)	0 (−0.39)	0 (−0.12)	0 (−0.12)	0 (−0.12)	0 (−0.20)	0 (−0.53)	0 (−0.23)	1 (0.98)	0 (−0.26)	23
LATR	0 (−0.66)	1 (0.37)	0 (−0.65)	0 (−0.86)	0 (−0.15)	0 (−0.48)	0 (−0.15)	0 (−0.15)	0 (−0.15)	0 (−0.25)	0 (−0.66)	0 (−0.29)	0 (−0.78)	0 (−0.32)	38
STPA	0 (−1.03)	0 (−1.29)	0 (−1.00)	1 (−0.57)	0 (−0.22)	0 (−0.74)	0 (−0.22)	0 (−0.22)	0 (−0.22)	0 (−0.39)	0 (−1.03)	0 (−0.45)	0 (−1.20)	0 (−0.50)	92
Unk	0 (−0.77)	0 (−0.96)	0 (−0.75)	0 (−0.99)	0 (−0.17)	0 (−0.56)	0 (−0.17)	0 (−0.17)	0 (−0.17)	0 (−0.29)	0 (−0.77)	0 (−0.33)	1 (0.21)	0 (−0.37)	51
Total	21	33	20	35	1	11	1	1	1	3	21	4	29	5	1674

Table 5
Average percent similarity (±SE) of perennial species composition between disturbed (0, 20 and 40 m) and undisturbed transects (100 m) at the second Los Angeles aqueduct study area, western Mojave Desert, California. Percent similarity was estimated using two indices: Sørensen and Bray–Curtis. As a metric of recovery, percent similarity was used to calculate the time (years) to 100% recovery (R_{100}). Two linear models provided by Abella (2010) were used to calculate additional estimates of percent similarity and R_{100}.

Comparison between plots	Similarity index	
	Sørensen	Bray–Curtis
0–100	20.5 (±) 5.4	6.0 (±1.9)
R_{100}:	175.6	600.0
20–100	31.7 (±4.0)	18.6 (±3.9)
R_{100}:	113.6	193.6
40–100	57.6 (±) 4.2	40.0 (±4.8)
R_{100}:	62.5	90.1
Abella 2010[a]	48.9	
R_{100}:	215	
Abella 2010[b]	55.3	
R_{100}:	187	

[a] Data from 31 studies, 1 year of data each, time since disturbance: 1–74 years.
[b] Data from Bolling and Walker (2000), time since disturbance: 5–88 years.

and cover at the 20-m and 40-m transects and are present in low numbers and cover values in the control. In addition to *E. nauseosa*, *E. elymoides* is also absent from the control.

E. nauseosa appears to be a highly successful dominant at the road edge in this part of the Mojave Desert, potentially influencing the trajectory of succession, not only here but at the first Los Angeles aqueduct corridor constructed between 1905 and 1913 (Lathrop and Archbold, 1980a). In the first Los Angeles aqueduct corridor, *E. nauseosa* is entrenched and remains dominant along the road verge and within the corridor after 100 years (Lathrop and Archbold, 1980a; observations of authors). This deeply-rooted species is widespread across North American deserts, and is "particularly common on degraded range lands where is replaces the more valuable perennial grasses" (Benson and Darrow, 1981). It has limited value for livestock and is associated with poor range management (Enloe et al., 2009). *E. nauseosa* is difficult to control and herbicides have been used to manage it elsewhere (Enloe et al., 2009).

The dominance of *E. nauseosa* at our site differs from results of two other studies on recovery of vegetation along unpaved access roads adjacent to transmission line corridors in the southern Mojave Desert (Johnson et al., 1975; Vasek et al., 1975a). The transmission lines and roads were 33 and 37 years old at the time of the studies. In both studies, *L. tridentata* was the dominant perennial shrub at the road edge. *E. nauseosa* was uncommon in the region where Johnson et al. (1975) and Vasek et al. (1975a) conducted research (Baldwin et al., 2014). Johnson et al. (1975) also reported that perennial shrubs showed a pronounced increase in density, cover, biomass, and diversity along the verge of unpaved roads compared to undisturbed controls, in contrast to our findings. We found significantly higher densities, cover, and diversity of perennials in the control plots.

4.2. Spatial patterns of perennial species and potential roles of shrub islands and nurse plants

Spatial patterns of perennial shrubs and interspecific competition are topics of interest in arid and semi-arid environments (e.g., Fowler, 1986) and may play a role in succession and recovery of damaged habitats (Padilla and Pugnaire, 2006). In our study, strong patterns of contagion with conspecifics were evident for all species

(Table 3). Without exception, the nearest neighbor of each species was most likely to be one of its own, a result for *Larrea* and *Ambrosia* noted previously by Phillips and MacMahon (1981). Positive but less so were interspecific relationships between *A. dumosa* and *A. sphaerocephalus*; between *A. sphaerocephalus* and *P. secunda;* between *E. elymoides* and *E. nauseosa*; and between *S. pauciflora* and *E. elymoides* (Table 3). Both positive and negative relationships between *A. sphaerocephalus* and *A. dumosa* have been reported previously (Schenk and Mahall, 2002). Some species of shrubs and grasses were less likely to be in close proximity and thus potentially exhibited aversion: *E. nauseosa* vs *A. dumosa, E. cooperi, P. secunda, A. sphaerocephalus,* and *L. tridentata; A. dumosa* vs *S. pauciflora, A. salsola*, and *E. elymoides*; and *E. cooperi* vs *A. salsola* and *S. pauciflora*. *E. nauseosa* appeared to have negative associations with other long-lived species, while *A. dumosa* had negative associations with the short-lived species. Many factors affect spatial distribution and neighbors. In our study, spatial patterning and inter- and intra-specific relationships may be related to location within the disturbance corridor and the undisturbed habitat. With the exception of *E. nauseosa* at the verge, long-lived species were less likely to be near short-lived species.

Over time, shrub islands contribute to nutrient cycling in soils and development of islands of fertility. Shrub islands within the disturbance corridor represent potential sites for development of islands of fertility and thus may be an integral part of succession and the recovery process (e.g., Schlesinger and Pilmanis, 1998; Bolling and Walker, 2002; Titus et al., 2002). Shrub islands accumulate litter, windborne sand, seeds, and mineral nutrients; and provide protection for animal burrows (Walker et al., 2015), fragile annual plants, and plants sensitive to grazing from domestic livestock.

Nurse plants also may play important roles in recovery of degraded lands. The concept of nurse plants is well-developed in the literature for shrubs, trees, and cacti in the Mojave, Sonoran and Chihuahuan deserts (e.g., Fowler, 1986; Padilla and Pugnaire, 2006). However, for many species, the mechanisms and resulting advantages and disadvantages of growing under a nurse plant are not known or understood and in some cases may be negative (McAuliffe, 1988; Walker et al., 2001; Flores and Jurado, 2003; Padilla and Pugnaire, 2006). The verge and 20-m transects were dominated by *E. nauseosa* and *A. salsola*, species most likely to nurse their own species but less likely to nurse other perennial plant species (Table 5). The long-lived *E. nauseosa* appears to have a self-perpetuating cycle, and where it dominates, low diversity of perennial plants is likely. When acting as a nurse plant for other species, *E. nauseosa* generally nursed con-generics (*E. cooperi, E. teretifolia*) and short-lived species (*S. hymenoides, S. pauciflora, A. salsola*). In contrast, sites with *A. dumosa* and *E. cooperi* were more likely to contain nurse plants that nursed multiple species, including long-lived species (e.g., *S. speciosa, A. dumosa, G. spinosa, K. lanata, P. secunda*). These sites had higher species diversity.

4.3. Estimates of recovery

The first Los Angeles aqueduct, constructed in 1913, parallel to and ~0.5 km downslope of our site, provides valuable insight on the potential time span for recovery. Lathrop and Archbold (1980a) measured recovery of perennial vegetation along the 1913 and 1970 aqueducts 65 and 8 years after construction, respectively. Using biomass data from several sites, they estimated 57 years until recovery for the rights-of-way and 61 years for the road edges. However, they noted that time to pre-disturbance composition would require at least three times that of biomass recovery (~180 years). Abella (2010) estimated similar lengths of time for recovery to pre-disturbance composition of 215 and 187 years (Table 5).

Our recovery estimates were also higher or lower, depending on the similarity index used to calculate recovery. For example, after 36 years, estimates from the Sørensen index at 0 m and 20 m were lower (20.5% and 31.7%, respectively) than the Abella models (48.9% and 55.3%), at 40 m were above (57.6%). The estimates from the Bray–Curtis indices were lower for all three distances (Table 5). The Sørensen index may perform poorly in communities that contain rare species (Pekas and Schupp, 2013), whereas the Bray–Curtis index, which accounts for abundance species-by-species, may be more realistic.

4.4. Factors affecting recovery times

The history of land uses are important considerations in estimating recovery of vegetation. Herbivory, for example, can influence the rate or trajectory of succession by affecting, arresting or delaying successional stages (Connell and Slatyer, 1977; Walker, 2012). At our study area, interactions between livestock and the assemblage of perennial plant species continue to be an important dynamic in the long-term capability for the disturbance corridor to recover. The entire study area was grazed and has been grazed for >100 years (Wentworth, 1948). In 1980, the U.S. BLM rated the grazing allotment as in fair condition (U.S. BLM, 1980). Kay (1988) reported excessive pressure from cattle grazing and effects on palatable plants in the aqueduct corridor and adjacent lands, and we made similar observations in August 2005. Cattle and sheep do not browse on *E. nauseosa, E. cooperi, E. teretifolia, L. tridentata*, and *A. salsola* (U.S. BLM, 1980; our observations). Instead, they favor forbs, perennial grasses (*S. hymenoides, S. speciosa, P. secunda*), and chenopod shrubs *(G. spinosa*, *K. lanata*, *A. canescens*), which have high forage importance indices (U.S. BLM, 1980; Kay and Graves, 1983). Livestock grazing also can affect spatial distribution and succession (e.g., Fowler, 1986) by suppressing establishment and growth of palatable, long-lived species such as *K. lanata*, *G. spinosa,* and *P. secunda* both in the undisturbed habitat and the disturbance corridor and thus may retard recovery within the disturbance corridor. Both *K. lanata* and *G. spinosa* are important forage plants for the threatened Mohave ground squirrels (California Department of Fish and Wildlife, 2015b).

Species palatable to livestock, in turn, may escape browsing in shrub islands and within canopies of unpalatable species. *E. cooperi*, for example, a species not consumed by livestock and that nursed several species, may have protected other, smaller shrubs under its canopy from grazing, thus contributing to perennial species diversity within the 40-m and the 100-m distance transects.

The combined effects of grazing and drought are likely to extend the time required for recovery of the perennial vegetation (e.g., Verwijmeren et al., 2014). Increasing droughts and aridity, predicted for the American Southwest (Seager et al., 2007; Ault et al., 2014), are additional stressors. Although many of the desert shrubs are drought-tolerant, germination of seeds and growth of plants will be negatively affected under a climate regime of lower rainfall and warmer temperatures. We may expect to see elevated mortality in perennial vegetation with increasing and longer droughts (e.g., Turner, 1990; McAuliffe and Hamerlynck, 2010) and a shift to species more tolerant of drier and hotter conditions. However, at the study site, the current composition of perennial species reflects a wide array of physical and biotic tolerances: most of the species occur in both hot and cold deserts (Table 1). Therefore, some of the species may be less vulnerable to prolonged droughts than others, e.g., 13 shrub species have affinities in the Sonoran Desert and may be more resilient to drier conditions.

Other species, typical of the Mojave and Great Basin deserts, may shift their distributions northward or upward in elevation over time.

Active intervention may accelerate recovery of vegetation in old disturbances. For example, at the second Los Angeles aqueduct corridor, *E. nauseosa* is entrenched and probably inhibiting recovery. Mechanical removal, girdling, or burning the undesirable shrub, followed by planting *A. dumosa* and *L. tridentata* along the verge, and irrigating the new shrubs may hasten the trajectory for recovery (Lathrop and Archbold, 1980a; Kay, 1988). The result may be a shrub alliance that better approximates the natural diversity and composition of the control sites. Herbicides are another tool deserving of consideration (Enloe et al., 2009). Seeding or planting long-lived species such as *E. cooperi* may also shorten recovery time to achieve the plant composition typical of adjacent, undisturbed lands. Additionally, the efficacy of using dead shrubs or stems of dead shrubs ("vertical mulching") as nurses could be explored (Weigand and Rodgers, 2009). Livestock grazing, if reduced or eliminated, may have a positive effect (Kay, 1979), if soil amendments are added and perennial grasses are planted in the open spaces before shrubs can take hold (Gibbens et al., 2005).

The time required for recovery after disturbance can be modulated through initial planning, specifically by minimizing the amount and severity of disturbance. Recovery time can be lessened in *L. tridentata-A. dumosa* plant alliances if topsoil, islands of fertility, and crowns of shrubs remain intact when a site is cleared of vegetation (Schlesinger and Pilmanis, 1998; Bolling and Walker, 2002; Gibson et al., 2004). At sites where projects result in severe disturbance, soil amendments and planting of long-lived species and their nurses may accelerate recovery.

5. Summary and implications for the future

At a severely disturbed site in the Mojave Desert where recovery had been underway for 36 years, we identified two types of succession: secondary succession from undisturbed land to within the disturbance corridor and inhibition at the road verge. We estimated that for the disturbed area the time for recovery to a composition of perennial species similar to the adjacent undisturbed area may require as long as 600 years, and potentially longer with climate change and continued livestock grazing.

To learn more about the recovery process, we evaluated 21 species of shrubs, grasses, and one cactus—species common in vegetation alliances of North American deserts—for their respective roles. We found that several long- and short-lived species act as pioneers, depending on proximity to the source, to undisturbed land, or continued disturbances. We also examined nearest neighbor associations and nurse relationships quantitatively for several species. We learned that the nearest perennial plant species were most likely to be of the same species and that each species had positive relationships with one to three heterospecifics and potentially negative relationships with several other species. We identified nurse roles for eight perennial shrubs, and observed that of the eight shrub species examined, only three nursed their own species. *E. nauseosa*, a long-lived species of degraded environments, acted as nurse for more species than any other species of nurse, and appears to inhibit recovery to predisturbance perennial plant composition. The information we compiled on inter- and intraspecific associations is preliminary and could be followed in the field over time, replicated, and tested experimentally as well. Responses may vary considerably from site to site and by desert. Plants that act as nurses or receive the benefits of nursing in one situation may be negatively affected in another. In the meantime, data about pioneering roles of species, inter- and intraspecific associations, successional stages, and recovery times can be applied to potentially truncating recovery processes in damaged *Larrea* and other vegetation alliances in the Mojave, Great Basin, Sonoran, and Chihuahuan deserts. The information is also likely to be of value in *Larrea* alliances in the Monte Desert.

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Appendix A. Discriminant analysis function coefficients of perennial plant species in the second Los Angeles aqueduct corridor, western Mojave Desert, California. Plant abbreviations are given in Table 1.

Species	Function 1	Function 2	Function 3
ACSP live	−1.31	−0.95	−0.61
ACSP dead	0.27	0.37	0.11
AMDU live	2.19	1.14	0.80
AMDU dead	0.10	−0.59	−0.71
AMSA live	0.06	0.91	−0.11
AMSA dead	−0.07	0.14	−0.27
ATCA live	−0.11	−0.15	0.38
ATCA dead	−0.11	0.43	−0.34
CYEC dead	−4.52	−0.92	−1.05
ELEL	0.04	−0.09	0.48
ERCO live	1.28	0.37	0.25
ERCO dead	0.32	−1.13	−0.95
ERFA live	0.91	0.05	0.05
ERNA live	−0.16	0.06	0.70
ERNA dead	−0.32	0.78	−0.49
ERTE live	0.24	−1.14	−0.77
GRSP live	−1.26	−0.42	−0.60
GRSP dead	−0.11	0.43	−0.34
KRLA live	4.81	0.84	0.96
KRLA dead	0.49	1.17	1.00
LATR live	2.45	0.34	0.13
LATR dead	−0.03	−0.07	0.26
LESQ live	−0.02	1.28	0.20
LYAN live	−1.43	−0.21	−0.11
LYAN dead	−1.43	−0.21	−0.11
MILA live	0.44	−0.25	−0.01
POSE	1.35	0.39	0.28
STHY	−0.33	0.42	0.01
STPA live	−0.29	0.07	0.63
STSP	2.04	0.16	0.30
TEST live	1.78	0.51	0.42
TEST dead	1.78	0.51	0.42
Other	1.34	0.21	0.37

Appendix B. Species of nurse plants and counts occurring at each distance in the disturbance corridor and in the control (100-m distance) at the second Los Angeles aqueduct study site, western Mojave Desert, California. The proportion of each nurse species comprising the total for each distance is shown. Abbreviations are shown in Table 1.

Transect distance	Perennial species	Nurse plant?			Proportion of species that nurse		Proportion of nurses at each distance
		Yes	No	Total	Yes	No	
0	ERNA	39	346	385	0.10	0.90	0.95
	AMSA	1	21	22	0.05	0.95	0.02
	STPA	1	39	40	0.03	0.98	0.02
	AMDU	0	2	2	0.00	1.00	0.00
	ERCO	0	6	6	0.00	1.00	0.00
20	ERNA	18	160	178	0.10	0.90	0.51
	AMSA	10	111	121	0.08	0.92	0.29
	AMDU	4	69	73	0.05	0.95	0.11
	ERCO	2	11	13	0.15	0.85	0.06
	GRSP	1	3	4	0.25	0.75	0.03
	ACSP	0	3	3	0.00	1.00	0.00
	STPA	0	37	37	0.00	1.00	0.00
	UNK	0	11	11	0.00	1.00	0.00
40	AMDU	11	177	188	0.06	0.94	0.38
	ERCO	7	53	60	0.12	0.88	0.24
	ACSP	6	35	41	0.15	0.85	0.21
	AMSA	3	25	28	0.11	0.89	0.10
	ERNA	1	4	5	0.20	0.80	0.03
	LATR	1	7	8	0.13	0.88	0.03
	GRSP	0	10	10	0.00	1.00	0.00
	STPA	0	1	1	0.00	1.00	0.00
	UNK	0	8	8	0.00	1.00	0.00
100	ERCO	17	120	137	0.12	0.88	0.44
	AMDU	16	286	302	0.05	0.95	0.41
	ACSP	3	32	35	0.09	0.91	0.08
	AMSA	1	9	10	0.10	0.90	0.03
	GRSP	1	10	11	0.09	0.91	0.03
	UNK	1	32	33	0.03	0.97	0.03
	LATR	0	31	31	0.00	1.00	0.00
	STPA	0	15	15	0.00	1.00	0.00

References

Abella, S.R., 2010. Disturbance and plant succession in the Mojave and Sonoran deserts of the American Southwest. Int. J. Environ. Res. Public Health 7, 1248–1284.

Abella, S.R., Newton, A.C., Bangle, D.N., 2007. Plant succession in the eastern Mojave desert: an example from Lake Mead National recreation area, southern Nevada. Crossosoma 33 (2R), 45–55.

Ault, T.R., Cole, J.E., Overpeck, J.T., Pederson, G.T., Meko, D.M., 2014. Assessing the risk of persistent drought using climate model simulations and paleoclimate data. J. Clim. 27, 7529–7549.

Baldwin, B.G., Keil, D.J., Markos, S., Mishler, B.D., Patterson, R., Rosatti, T.J., Wilken, D.H., 2014. Jepson Flora Project. Jepson eFlora. http://ucjeps.berkeley.edu/IJM.html (accessed 15.12.14.).

Benson, L., Darrow, R.A., 1981. Trees and Shrubs of the Southwetern Deserts, third ed. University of Arizona Press, Tucson.

Bolling, J.D., Walker, L.R., 2000. Plant and soil recovery along a series of abandoned desert roads. J. Arid Environ. 46, 1–24.

Bolling, J.D., Walker, L.R., 2002. Fertile island development around perennial shrubs across a Mojave Desert chronosequence. West. N. Am. Nat. 62, 88–100.

Bowers, J.E., Webb, R.H., Pierson, E.A., 1997. Succession of desert plants on debris flow terraces, Grand Canyon, Arizona, U.S.A. J. Arid Environ. 36, 67–86.

California Department of Fish and Wildlife, 2015a. State and Federally Listed Endangered and Threatened Animals of California, January 2015. http://www.dfg.ca.gov/wildlife/nongame/t_e_spp/ (accessed 12.01.15.).

California Department of Fish and Wildlife, 2015b. California Rare and Endangered Mammals, Species Accounts: Mohave Ground Squirrel. http://www.dfg.ca.gov/wildlife/nongame/t_e_spp/ (accessed 12.01.15.).

California Energy Commission, California Department of Fish and Wildlife, U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, 2014. Desert Renewable Energy Conservation Plan (DRECP) and Environmental Impact Report/Environmental Impact Statement. http://www.drecp.org/ (accessed 14.01.15.).

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111, 1119–1144.

Enloe, S.F., Kniss, A., Ferrell, M., Lafantasie, J., Aagard, S.D., 2009. Black greasewood (*Sarcobatus vermiculatus*), gray rabbitbrush (*Ericameria nauseosa*), and perennial grass response to Chlorsulfuron and Metsulfuron. Invasive Plant Sci. Manag. 2, 247–252.

Filazolla, A., Lortie, C.J., 2014. A systematic review and conceptual framework for the mechanistic pathways of nurse plants. Glob. Ecol. Biogeogr. 23, 1335–1345.

Flores, J., Jurado, E., 2003. Are nurse-protégé interactions more common among plants from arid environments? J. Veg. Sci. 13, 911–916.

Fowler, N., 1986. The role of competition in plant communities in arid and semiarid regions. Annu. Rev. Ecol. Syst. 17, 89–110.

Frenkel, R.E., 1970. Ruderal Vegetation along Some California Roadsides, vol. 20. University of California Publications in Geography, pp. 1–163.

Gibbens, R.P., McNeely, R.P., Havstad, K.M., Beck, R.F., Nolen, B., 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. J. Arid Environ. 61, 651–668.

Gibson, A.C., Sharifi, M.R., Rundel, P.W., 2004. Resprout characteristics of creosote bush (*Larrea tridentata*) when subjected to repeated vehicle damage. J. Arid Environ. 57, 411–429.

Guevara, J.C., Grünwaldt, E.G., Estevez, O.R., Bisigato, A.J., Blanco, L.J., Biurrun, F.N., Ferrando, C.A., Chirino, C.C., Morici, E., Fernández, B., Allegretti, L.I., Passera, C.B., 2009. Range and livestock production in the Monte Desert, Argentina. J. Arid Environ. 73, 228–237.

Hothorn, T., Bretz, F., Westfal, P., 2008. Multcomp:Simultaneous Inference in General Parametric Models. R Package Version 1.3-8. http://www.R-project.org (accessed 05.12.14.).

Johnson, H.B., Vasek, F.C., Yonkers, T., 1975. Productivity, diversity and stability relationships in Mojave Desert roadside vegetation. Bull. Torrey Bot. Club 102, 106–115.

Kay, B.L., 1979. Summary of Revegetation Attempts on the Second Los Angeles Aqueduct. University of California, Davis, Agronomy and Range Science. Mojave Revegetation Notes No. 22:1–23.

Kay, B.L., 1988. Artificial and Natural Revegetation of the Second Los Angeles Aqueduct. University of California, Davis, Agronomy and Range Science. Mojave Revegetation Notes No. 24:1–32.

Kay, B.L., Graves, W.L., 1983. Revegetation and stabilization techniques for disturbed desert vegetation. In: Webb, R.H., Wilshire, H.G. (Eds.), Environmental Effects of Off-road Vehicles. Impacts and Management in Arid Regions. Springer-Verlag New York Inc., New York, pp. 325–340.

Laport, R.G., Minckley, R.L., Ramsey, J., 2012. Phylogeny and cytogeography of the North American creosote bush (*Larrea tridentata*, Zygophyllaceae). Syst. Bot. 37, 153–164.

Lathrop, E.W., Archbold, E.F., 1980a. Plant response to Los Angeles aqueduct construction in the Mojave Desert. Environ. Manag. 4, 137–148.

Lathrop, E.W., Archbold, E.F., 1980b. Plant responses to utility right of way construction in the Mojave Desert. Environ. Manag. 4, 215–226.

Lauenroth, W.K., Adler, P.B., 2008. Demography of perennial grassland plants: survival, life expectancy and life span. J. Ecol. 96, 1023–1032.

Lovich, J.E., Bainbridge, D., 1999. Anthropogenic degradation of the Southern California desert ecosystem and prospects for natural recovery and restoration. Environ. Manag. 24, 309–326.

McAuliffe, J.R., 1988. Markovian dynamics of simple and complex desert plant communities. Am. Nat. 131, 459–490.

McAuliffe, J.R., Hamerlynck, E.P., 2010. Perennial plant mortality in the Sonoran and Mojave deserts in response to severe, multi-year drought. J. Arid Environ. 74, 885–896.

Nadeau, R.A., 1997. The Water Seekers, fourth ed. Crest Publishers, Santa Barbara, California.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. Vegan: Community Ecology Package. http://CRAN.R-project.org/web/packages/vegan/index.html (accessed 15.08.13.).

Padilla, F.M., Pugnaire, F.I., 2006. The role of nurse plants in the restoration of degraded environments. Front. Ecol. Environ. 4, 196–202.

Pekas, K.M., Schupp, E.W., 2013. Influence of aboveground vegetation on seed bank composition and distribution in a Great Basin Desert sagebrush community. J. Arid Environ. 88, 113–120.

Phillips, D.L., MacMahon, J.A., 1981. Competition and spacing patterns in desert shrubs. J. Ecol. 69, 97–115.

Pielou, E.C., 1969. An Introduction to Mathematical Ecology. Wiley-Interscience, New York.

Pinheiro, J., Bates, D., 2013. nlme: Nonlinear Mixed-effects Models. R Package Version 3.1-113. http://www.R-project.org (accessed 05.12.14.).

R Development Core Team, 2010. R: a Language and Environment for Statistical Computing. The R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (accessed 15.08.11.).

Roig, F.A., Roig-Juñent, S., Corbalán, V., 2009. Biogeography of the monte desert. J. Arid Environ. 73, 164–172.

Sawyer, J.O., Keeler-Wolf, T., Evens, J., 2009. A Manual of California Vegetation, second ed. California Native Plant Society, Sacramento, California.

Schenk, H.J., Mahall, B.E., 2002. Positive and negative plant interactions contribute to a north-south patterned association between two desert shrub species.

Oecologia 132, 402–410.
Schlesinger, W.H., Pilmanis, A.M., 1998. Plant-soil interactions in deserts. Biogeochemistry 42, 169–187.
Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H., Hrnik, N., Leetmaa, A., Lau, N., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316, 1181–1184.
SYSTAT Software, Inc, 2009. SYSTAT 12.02 Software Package. California, Richmond.
Titus, J.H., Nowak, R.S., Smith, S.D., 2002. Soil resource heterogeneity in the Mojave Desert. J. Arid Environ. 52, 269–292.
Turner, R.M., 1990. Long-term vegetation change at a fully protected Sonoran Desert Site. Ecology 71, 465–477.
Turner, R.M., Bowers, J.E., Burgess, T.L., 1995. Sonoran Desert Plants, an Ecological Atlas. University of Arizona Press, Tucson.
U.S Department of Agriculture (USDA), Natural Resources Conservation Service (NRCS), 2008. Soil Survey of Jawbone-Butterbredt ACEC Area, California. http://soildatamart.nrcs.usda.gov/Manuscripts/ca682/0/Kern_CA.pdf (accessed 20.09.11.).
U.S Department of the Interior, Bureau of Land Management (U.S. BLM), 1980. The California Desert Conservation Area Plan, 1980. U.S. Department of the Interior, Bureau of Land Management, Desert District, Riverside, California (Appendix XIII: Livestock Grazing).
Vasek, F.C., 1979/1980. Early successional stages in Mojave Desert scrub vegetation. Israel J. Bot. 28, 133–148.
Vasek, F.C., Lund, L.J., 1980. Soil characteristics associated with a primary plant succession on a Mojave Desert dry lake. Ecology 61, 1013–1018.
Vasek, F.C., Johnson, H.B., Eslinger, D.H., 1975a. Effects of pipeline construction on creosote bush scrub vegetation of the Mojave Desert. Madroño 23, 1–12.
Vasek, F.C., Johnson, H.B., Brum, G.D., 1975b. Effects of power transmission lines on vegetation of the Mojave Desert. Madroño 23, 114–129.
Verwijmeren, M., Rietkerk, M., Bautista, S., Mayor, A.G., Wassen, M.J., Smit, C., 2014. Drought and grazing combined: contrasting shifts in plant interations at species pair and community level. J. Arid Environ. 111, 53–60.
Villagra, P.E., Defossé, G.E., del Valle, H.F., Tabeni, S., Rostagno, M., Cesca, E., Abraham, E., 2009. Land use and disturbance effects on the dynamics of natural ecosystems of the Monte Desert: implications for their management. J. Arid Environ. 73, 202–211.
Walker, L.R., 2012. The Biology of Disturbed Habitats. Oxford University Press, Inc., New York.
Walker, L.R., Thompson, D.B., Landau, F.H., 2001. Experimental manipulations of fertile islands and nurse plant effects in the Mojave Desert, USA. West. N. Am. Nat. 61, 25–35.
Walker, L.R., Vrooman, S.S., Thompson, D.B., 2015. Rodent mounds facilitate shrubs and shrubs inhibit seedlings in the Mojave Desert, USA. J. Arid Environ. 113, 95–113.
Webb, R.H., Belnap, J., Thomas, K.A., 2009. Natural recovery from severe disturbance in the Mojave Desert. In: Webb, R.H., Fenstermaker, L.F., Heaton, J.S., Hughson, D.L., McDonald, E.V., Miller, D.M. (Eds.), The Mojave Desert: Ecosystem Processes and Sustainability. University of Nevada Press, Reno, pp. 343–377.
Weigand, J., Rodgers, J., 2009. Active restoration for the Mojave Desert. In: Webb, R.H., Fenstermaker, L.F., Heaton, J.S., Hughson, D.L., McDonald, E.V., Miller, D.M. (Eds.), The Mojave Desert: Ecosystem Processes and Sustainability. University of Nevada Press, Reno, pp. 378–409.
Wentworth, E.N., 1948. America's Sheep Trails. The Iowa State College Press, Ames, Iowa.