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Bidirectional recovery patterns of Mojave Desert vegetation in an aqueduct pipeline corridor after 36 years: II. Annual plants

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ABSTRACT

We studied recovery of winter annual plants in a 97-m wide disturbed aqueduct corridor in the Mojave Desert 36 years after construction. We established plots at 0, 20, and 40 m from the road verge at the corridor center and at 100 m in undisturbed vegetation. We recorded 47 annual species, of which 41 were native and six were exotic. Exotic species composed from 64 to 91% of total biomass. We describe a bilateral process of recovery: from the road verge to the outward edge of the corridor and from undisturbed habitat into the corridor. Native annual plants significantly increased in richness from road verge to undisturbed vegetation, but not in density, biomass, or cover. In contrast, exotic annual plants increased in density, biomass, cover and richness with increasing distance from the road verge. The species of colonizing shrubs and type of canopy cover affected density, biomass, and richness of annuals. Species composition of native annuals differed significantly by distance, suggesting secondary succession. In general, native annuals were closer to achieving recovery on the 40-m plots than at the road verge. Recovery estimates were in centuries and dependent on location, canopy type, and whether considering all annuals or natives only.

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1. Introduction

Disturbances in deserts and to desert vegetation worldwide occur as a result of natural events such as flooding, wind erosion, or herbivory from rabbits, rodents, and other animals or as a consequence of anthropogenic activities (MacMahon, 1999). While the literature on disturbances, succession, and recovery of desert perennial plants has grown, a similar literature on annual plants has lagged (e.g., MacMahon, 1999; Abella, 2010), probably because annual plants are dependent on rainfall and less available for study. Frequency and abundance of annuals are affected by many factors, e.g., timing and level of precipitation (Brooks and Berry, 2006), microhabitats (Brown and Porembski, 2000), interference or competition from non-native or exotic species (El-Ghareeb, 1991; Brooks and Berry, 2006), and herbivory (Brooks et al., 2006; Sassi et al., 2009). The type, severity, and history of disturbances also are important and range from settlements and towns (Knapp, 1992; Webb et al., 2009), agriculture (El-Ghareeb, 1991), livestock grazing (Webb and Stielstra, 1979; Brown and Al-Mazrooei, 2003; Sassi et al., 2009), roads (Johnson et al., 1975), fires (Abella, 2010), military vehicles (Prose and Wilshire, 2000), and contamination (Brown and Porembski, 2000). Annual plants historically were described as early pioneers and colonizers of disturbed areas, based on research conducted in non-desert areas (e.g., Frenkel, 1970; Whittaker, 1975). Results of studies on successional stages of annuals have varied considerably and appear to be dependent on the aforementioned variables as well as length of time since disturbance, status of the seed bank, soil type and surficial geology, vegetation type, and presence of exotic plants.

We studied recovery of winter annual plants in a disturbance

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corridor created by construction of a buried aqueduct in the Mojave Desert. Transportation and utility corridors are common throughout North American deserts and elsewhere in the world, fragment landscapes, and may leave enduring impacts on vegetation. Impacts are especially noticeable in deserts where rainfall is low and variable, and regrowth of vegetation does not quickly erase signs of disturbance. Such corridors provide important opportunities to document natural recovery processes and to experiment with restoration techniques. In the Mojave and Sonoran deserts, botanists and ecologists have previously reported on responses of vegetation to disturbances along roads and from construction of roads, pipelines, transmission lines and aqueducts (Johnson et al., 1975; Vasek et al., 1975a, 1975b; Kay, 1979, 1988; Lathrop and Archbold, 1980; Brown and Porembski, 2000; Hessing and Johnson, 1982; Abella et al., 2007; Abella, 2010). The primary focus of these earlier papers was recovery of perennial shrubs and other perennial vegetation.

Germination and production of annuals may be affected by microhabitat, including the location (intershrub space or under a shrub canopy); the species, size, structure, and canopy type of the shrub; and whether the shrub is living or dead (Went, 1942; Muller, 1953; Muller and Muller, 1956; Halvorson and Patten, 1975; DeSoyza et al., 1997). Therefore, in disturbed areas, the species of colonizing perennial shrubs may in turn affect recovery of annual species. Ecologists and botanists have identified perennial plant species that colonize disturbed areas in the Mojave Desert. Most of these plants are shrubs. Shrubs can be categorized as short- or long-lived, and the short-lived species tend to be the colonizing or pioneer species (Vasek et al., 1975a, 1975b; Abella, 2010). Common short-lived species include *Ambrosia salsola*, *Eriogonum fasciculatum*, and *E. inflatum*. Two common long-lived species are *Larrea tridentata* and *Ambrosia dumosa* (Vasek et al., 1975a), both of which have also demonstrated pioneering capacities. Vasek (1983) presented evidence that succession occurs in perennial vegetation in the Mojave Desert and pointed out that pioneer species such as *A. salsola* invade, become established in disturbed areas, and represent early stages in succession (Vasek et al., 1975b). The question then arises whether recovery of annual plants parallels that of associated perennial shrubs or is on a separate trajectory.

Recovery of annual communities after disturbance and the potential for succession are other important topics. Abella (2010), in a review of the limited literature on recovery of annuals in Mojave and Sonoran deserts after disturbance, reported that annual communities "seem to reestablish fairly rapidly, and in moister years little difference may exist in cover and species composition between disturbed and undisturbed areas after disturbances." In a five-year study of revegetation of a powerline corridor in the Sonoran Desert, Hessing and Johnson (1982) reported that the herb community probably represented a seral stage. Vasek (1979/1980, 1983) suggested that the topic deserves in-depth exploration and noted that rich, dense annual vegetation was correlated with large old clones of *L. tridentata* in the southern Mojave Desert, a stable community persisting for several thousand years. He suggested that "some constellations of annual species may be members of stable old communities and therefore probably have evolved intricate highly integrated adaptations for long persistence in stable desert conditions" (Vasek, 1983).

We report here on our research on colonization and recovery of winter annual plants at a site along a severely disturbed aqueduct corridor in the Mojave Desert of California. Construction of the 219-km, second Los Angeles aqueduct was initiated in 1968 and completed in 1970 (Kay, 1979, 1988). The buried pipe of the aqueduct extends from the Great Basin Desert south through the western Mojave Desert to the Los Angeles Reservoir complex in southern California. Our general objectives were to characterize recovery of annual plants in the aqueduct corridor 36 years after disturbance. We addressed the following topics and questions:

1) Distance effects—How similar are composition, density, biomass, cover and richness of native and exotic annuals at different distances from the service road in the disturbed right-of-way of the aqueduct corridor to adjacent undisturbed desert? For example, does recovery of annuals follow a gradient from the center of the right-of-way (service road) to undisturbed habitat?
2) Effects of perennial shrub canopies and intershrub spaces—What effects do live and dead perennial plant species, specifically shrubs, have on annual plant composition, density, biomass, cover, and richness? Are the characteristics of annual plants similar under perennial shrub canopies compared to intershrub spaces for different species of perennial shrubs, and for different perennial canopy classes?
3) Evidence for succession in recovery of annual plants—Is there evidence for secondary succession in the recovery process within the aqueduct corridor? and
4) Recovery time—How many years might be required to achieve a composition of annual plants similar to adjacent undisturbed desert?

2. Methods

2.1. Study site

We selected a 1.17-km stretch of the Los Angeles aqueduct right-of-way in Kern County between UTM points 411260E, 3935144N and 412358E, 3935560 N (NAD 83, Zone 11N) at an elevation of 1048 m (Fig. 1A). The right-of-way for construction was 97-m wide with a dirt service road through the center. In 1970–1971, the City of Los Angeles, Department of Water and Power (LADWP), ripped the compacted soil (25 cm deep on 61 cm furrows) in much of the aqueduct corridor and then planted seeds of seven species of perennial shrubs at six experimental sites. We chose this site because Kay (1979, 1988) documented and photographed the aqueduct 9 and 12 years (in 1979 and 1988) after construction was completed, and he recorded the process of recovery of annual and perennial plants. He further identified the site as unseeded.

The site has uniform topography typical of large stretches of the aqueduct corridor in the Mojave Desert, is devoid of stream channels, and is on the broad alluvial fan of the Scodie Mountains in Indian Wells Valley. 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 and gravelly coarse sandy loam (depending on depth) and sand (U.S. Department of Agriculture, Natural Resources Conservation Service [NRCS] 2008). Vegetation is a *L. tridentata–A. dumosa* plant alliance (Sawyer et al., 2009), in a community dominated by *A. dumosa*. Average annual precipitation is 150 mm, most of which occurs in fall and winter months (U.S. Department of Agriculture, NRCS, 2008). Prior to and during the study, rainfall for the winter of 2005–2006 was 72% of the long-term average at the Inyokern weather station, 17 km northwest of the site and at a lower elevation, 743 m (National Oceanic Atmospheric Administration, 2005–2006, Inyokern weather station). However, at the study site in spring 2006, annual plants were common and below average winter precipitation (as recorded at the Inyokern weather station) did not appear to affect plant numbers.

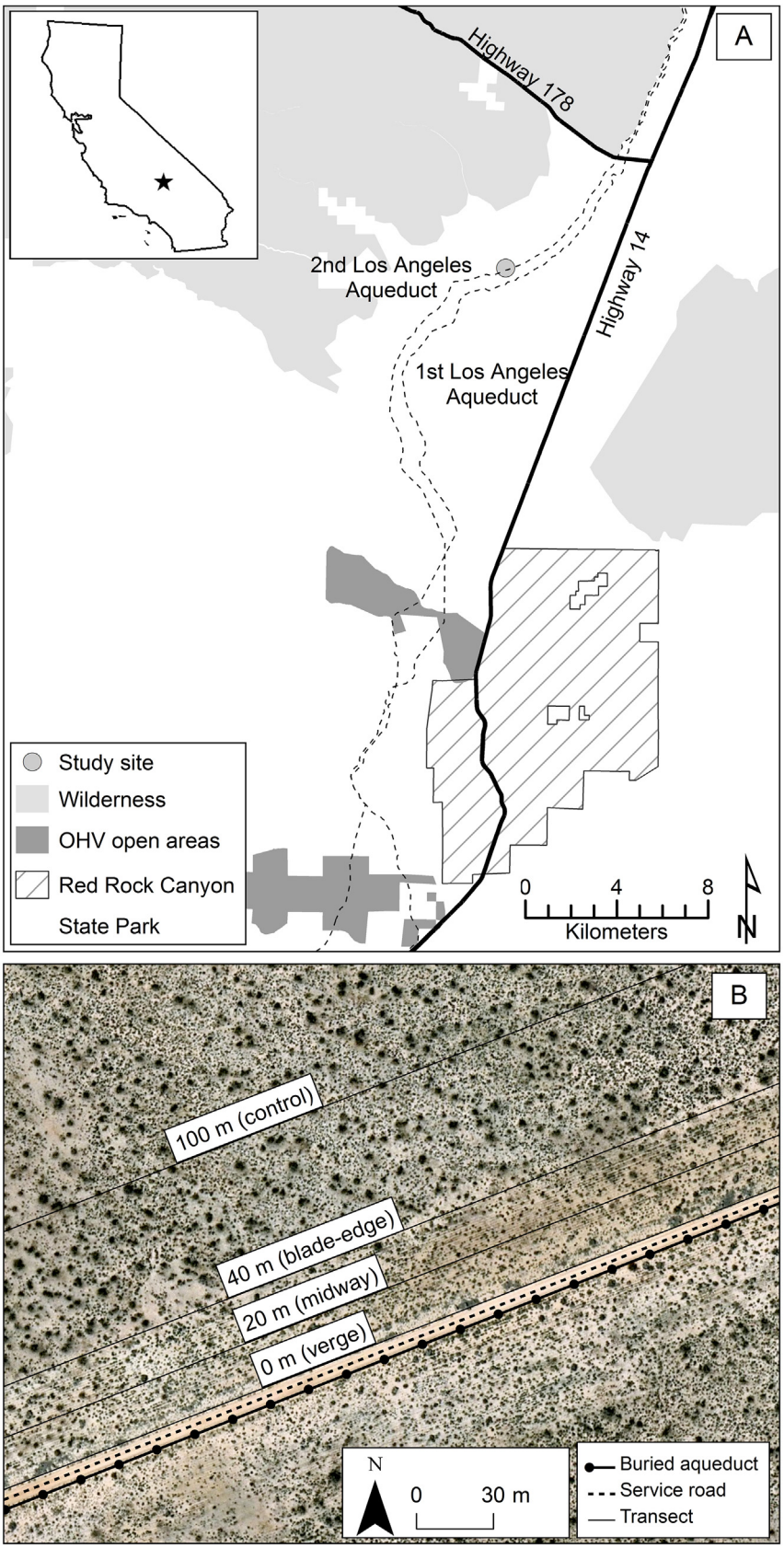

Fig. 1. A. Map of general location of the study site along the second Los Angeles aqueduct in the western Mojave Desert, California. OHV open areas = areas with unrestricted vehicle travel off road. B. Schematic drawing on an aerial photograph of the locations of the service road and the sampling distances within and adjacent to the second Los Angeles aqueduct disturbance corridor.

2.2. Land-use history

The study site and much of the aqueduct corridor 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 and the lands have been part of a livestock driveway between Tehachapi, California, and the Sierra Nevada high meadows (Wentworth, 1948; Fulwider, 1963; U.S. BLM, 1980). Other nearby anthropogenic uses are the first Los Angeles aqueduct, constructed between 1905 and 1913 (Nadeau, 1997), other travel and transportation corridors, and utility lines (Fig. 1A). The LADWP periodically maintains the service road with grading, and a low berm is often present at the road verge.

2.3. Data collection and sampling

We evaluated notes and photographs provided by Kay (1979, 1988) when he revisited the site nine and 18 years after construction of the aqueduct. We sampled annual vegetation present under the canopies of dominant perennial shrubs and within the intershrub spaces at four distances from the approximate center of the disturbance corridor starting with the road edge at 0 m and continuing at intervals of 20, 40, and 100 m (Fig. 1B). The 0-m plots were the closest to the buried aqueduct pipe and designated "verge" sites. Plots at 20-m and 40-m distances were within the disturbed right-of-way, hereafter disturbance corridor, and were termed the "midway" and "blade-edge" distances, respectively. The distance from the 0-m point to the undisturbed vegetation was 45 m. The 100-m plots comprised the undisturbed (except by livestock grazing) or control sites and were ~55 m from the bladed edge of the disturbed corridor.

Prior to sampling the annual vegetation, we characterized the perennial shrubs (Berry et al., 2015). Briefly, we established 14 randomly selected 20-m × 1-m plots at each of the four above-described distances for a total of 56 plots. Between July and November 2005, we collected data on distribution, species composition, and canopy cover of perennial shrubs and grasses. We divided shrub canopy into three classes: live (canopy >95% live vegetation), dead (canopy entirely dead), and mosaic (canopy consisting of live and dead components where the dead component is >5% of total canopy cover). We also measured greatest and smallest canopy diameters of each perennial plant to calculate cover (cm^2) by species, as well as total cover for each plot.

Three species of pioneer shrubs dominated the plots: *Ericameria nauseosa*, *A. salsola* and *A. dumosa* (Appendix A, see also Berry et al., 2015). The distribution patterns of the shrubs differed by distance from the road verge: *E. nauseosa* was the dominant species at verge sites, *A. dumosa* was dominant near the undisturbed vegetation, and *A. salsola* and *E. nauseosa* were rare or absent in undisturbed vegetation immediately outside the disturbance corridor. We then developed an experimental design for sampling annual plants based on the distribution and canopy cover of the dominant or co-dominant colonizing perennial shrubs within each of the four distances. First, we established 20 randomly placed 20-m × 1-m plots that were parallel to the road verge at each of four distances for a total of 80 plots. We used the following criteria to select the shrubs for sampling: (1) the shrub species was one of three dominant colonizing species (*E. nauseosa*, *A. salsola*, and *A. dumosa*); (2) the shrub was classified by target canopy class (live, dead, or mosaic); (3) the shrub was the first of the target species and canopy condition class to occur on the south end of the plot and within 1 m of either side of the plot; and (4) the shrub canopy covered >2000 cm^2. Second, at each of the four distances, specific species of shrubs and canopy classes were selected for sampling based on dominance and availability, and 20 samples each were collected under both north and south canopies of shrubs and in the intershrub spaces (Appendix A). The shrubs and sample totals for each distance were: (1) 0-m distance, live *E. nauseosa* and intershrub spaces (N = 60); (2) 20-m distance, *E. nauseosa* live and dead, *A. salsola* live and dead, and intershrub spaces (N = 180); (3) 40-m, *A. dumosa* live and dead and intershrub spaces (N = 100); and (4) 100-m distance (control), *A. dumosa* live, dead, and mosaic and intershrub spaces (N = 140). Third, for the sampling of annuals, we placed a semicircular sampling frame under the canopy and drip line of each selected shrub. The frames covered an area equal to 1000 cm^2, and were designed to fit under the canopy of larger, more mature shrubs. In addition to sampling under the shrubs, we also randomly placed one 50-cm × 20-cm (=1000 cm^2) quadrat in the intershrub spaces (open), with the longest side parallel to the aqueduct service road.

We sampled annual plants between April 25 and May 11, 2006, when annuals were at peak biomass (Jennings, 2001). Although we collected samples under both north and south canopies, sampling was less intensive under the south canopy since samples from north canopy and intershrub spaces were likely to provide the greatest range of variation (Brooks, 1999; Brooks and Berry, 2006). For all quadrats in the intershrub spaces and semicircles under the north canopy, we collected the following data for each annual species: numbers of individual plants per 1000 cm^2 (density), cover (cm^2), and biomass (g). For cover, we placed a transparency with a 1-cm × 1-cm grid over the sample area and estimated the number of square centimeters covered by each species. For biomass, we clipped individual annual plants rooted within each sampling area at ground level, air-dried them, and weighed them (Ohaus scale, Model Adventurer Pro AV53, Pine Brook, NJ). For the south canopy, we grouped counts of species in five categories based on numbers of individual plants: 1 = 1 plant, 2 = 2 to 3 plants, 3 = 4 to 9 plants, 4 = 10 to 19 plants, and 5 = ≥20 plants. We then calculated species richness as the total number of species, individually for both north and south samples. Plant names followed Baldwin et al. (2012; Appendix B).

2.4. Data analysis

We used a series of analysis of variance (ANOVA) tests to

Table 1
Resulting *P*-values of the ANOVA analyses for species richness of native and exotic annual plants at four distances from the service road verge in the Los Angeles aqueduct disturbance corridor to adjacent undisturbed land, Kern County, California.

Annual type	Source of variation	Distance (m)			
		0	20	40	100
Native	Plant species (An)		<0.001		
	Canopy class[a] (B)		0.053	0.015	0.998
	Aspect[b] (C)	0.108	0.037	0.010	<0.001
	An × B interaction		0.515		
	An × C interaction		0.398		
	B × C interaction		0.989	0.285	0.533
	An × B × C interaction		0.902		
Exotic	Plant (An)		0.001		
	Canopy class[a] (B)		0.016	0.621	0.591
	Aspect[b] (C)	0.899	0.065	0.012	0.718
	An × B interaction		0.114		
	An × C interaction		0.033		
	B × C interaction		0.256	0.912	0.783
	An × B × C interaction		0.188		

[a] Canopy classes: live, dead and mosaic.
[b] Aspect: north and south.

compare native and exotic annual vegetation characteristics (biomass, cover, density and richness) between sampling locations (Table 1). We used one-way ANOVA and Tukey's Honestly Significant Difference (HSD) post hoc test to compare the characteristics of intershrub annuals between distances (0, 20, 40 and 100 m). Within each distance, we used one-way ANOVA and Tukey's HSD post hoc test to compare the effects of canopy class (intershrub space, live, dead, or mosaic). At 20 m, we used an additional two-way ANOVA to investigate the effects of perennial species, canopy class and their interaction on native and exotic annual characteristics. We also tested for differences in richness between north and south canopies with a one-way ANOVA at 0 m, three-way ANOVA at 20 m and two-way ANOVA at 40 m and 100 m. We initially evaluated whether annual richness was different between samples under north and south canopies. The results showed that native annual richness was greater under north canopies at every distance except for 0 m (see Aspect, Table 1); these results supported previous findings on annuals (Brooks, 1999; Brooks and Berry, 2006). Therefore we focused subsequent analyses, results and discussion on data from the north canopy.

We performed a canonical discriminant analysis (CDA) to determine the linear combination of annual plants that maximize variance between the four distances, which was tested with a multivariate *F*-test (Wilks' Lambda *F*-test). The classification success of the CDA was checked using jackknifed cross-validation methods (i.e., leave-one-out methods). We then investigated the canonical coefficients for each species to quantify their contributions to the canonical functions and to identify the species best separating the sample distances. We conducted the analysis separately for annuals in the intershrub space, under shrub canopy, and with the two groups combined. Additionally, we conducted the analysis using only native annuals and with both native and exotic annuals combined.

We compared the annual plant community between distances with two additional metrics: Sørensen's similarity index (S_i) and Bray–Curtis index (BC_i). 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. We converted the index to percent similarity between distances by multiplying the index by 100. We then compared the results for comparisons between the undisturbed control site (100 m) and the three disturbed distances (0, 20, and 40 m) as a metric of recovery, to an estimate of recovery calculated by the linear model reported by Abella (2010): $y = 0.099x + 52.1$ where y is the predicted percent of recovery (i.e., percent similarity between disturbed and undisturbed samples) and x is the time since disturbance.

For the Bray–Curtis index, which incorporates measures of relative abundance, we used the annual 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. We then calculated the Bray–Curtis index: $BCi = 1 - BC_d$ where i is a comparison between distances. Similar to the Sørensen's similarity index, we converted the Bray–Curtis index to a percent and compared it to the Abella (2010) recovery estimate. We calculated a recovery rate by assuming a constant linear relationship between time and recovery and divided the percent recovery estimates by 36 years. We then estimated the time it would take to reach 100% recovery.

Prior to conducting the parametric statistical analyses (ANOVA and CDA), a constant (0.5) was added to all data and the data were log-transformed to conform to assumptions of normality and constant variance (Yamamura, 1999). All statistical analyses were performed in R 2.15.3 (R Development Core Team, 2013). Discriminant analysis was conducted using *lda* function in the *MASS* package (Ripley et al., 2013). Similarity indices were calculated using the *vegdist* function in the *vegan* package (Oksanen et al., 2013).

3. Results

3.1. Annuals in 1979, 1988, and 2005/06

The only information on annual plants prior to our 2005 surveys is from photographs and notes recorded in May 1979 and June 1988 (Kay, 1979, 1988). For the 1979 photograph, Kay (1979) wrote that the area "was very heavily grazed … Ground cover is annuals, mostly *Erodium* and *Schismus*." The June 1988 photograph had a similar description: "Understory is *Erodium* and *Schismus*." (Both *Erodium* and *Schismus* are exotic species.) Our paired re-photographs, taken in 2005 and 2006 showed the process of natural recovery of the unseeded area and the associated changes in distribution of annual and perennial plants (see Fig. 2 in Berry et al., 2015). In the 2005 plot surveys, we identified 47 species of annual forbs and grasses, of which 41 were native and 6 were exotic species (*Erodium cicutarium*, *Bromus berteroanus*, *Bromus rubens*, *Bromus tectorum*, *Schismus arabicus* and *Schismus barbatus*) (Appendix B). The two species of *Schismus* were treated as one taxon, since they were difficult to distinguish from each other, and some samples of *Festuca* were only identified to genus and likewise were not treated as separate species.

3.2. Annual vegetation in the intershrub spaces as a function of distance

Native and exotic species sampled in the intershrub space were examined separately for the effect of distance. For native annuals, biomass and cover did not differ between distances (ANOVA; biomass: $F_{3,76} = 1.45$, $P = 0.235$; cover: $F_{3,76} = 1.68$, $P = 0.178$; Fig. 2). Significant differences existed for density and richness (ANOVA; density: $F_{3,76} = 2.92$, $P < 0.05$; richness: $F_{3,76} = 5.52$, $P < 0.01$; Fig. 2). Density of natives was greater at 40 m compared to 0 m (Tukey's HSD post hoc test, $P = 0.043$), and richness of natives was greater at 40 m and 100 m than 0 m (Tukey's HSD post hoc test, 40 m: $P = 0.025$; 100 m: $P = 0.001$).

Exotic annuals exhibited significant differences between distances for all four measures (ANOVA; biomass: $F_{3,76} = 16.10$, $P < 0.001$; cover: $F_{3,76} = 18.35$, $P < 0.001$; density: $F_{3,76} = 18.68$, $P < 0.001$; richness: $F_{3,76} = 3.54$, $P < 0.05$; Fig. 2). Biomass, cover and density followed similar patterns and were greater at 20 m, 40 m and 100 m compared to 0-m (Tukey's HSD post hoc test, $P < 0.001$). Richness at 20 m and 100 m was greater than 0-m (Tukey's HSD post hoc test, 20-m: $P = 0.046$; 100 m: $P = 0.023$).

3.3. Characteristics of annual vegetation as a function of canopy class, shrub species, and distance

To evaluate the effects of shrub species and canopy class on annuals, we compared annuals in the intershrub space with combinations of annuals under shrub species and canopy classes at the four distances (Table 2). At the 0-m road verge, native annual biomass was significantly greater in the intershrub space than under live *E. nauseosa* (ANOVA; $F_{1,38} = 7.703$, $P < 0.01$). Cover, density and richness of native annuals were not different between the canopy and intershrub space (ANOVA; cover: $F_{1,38} = 1.63$,

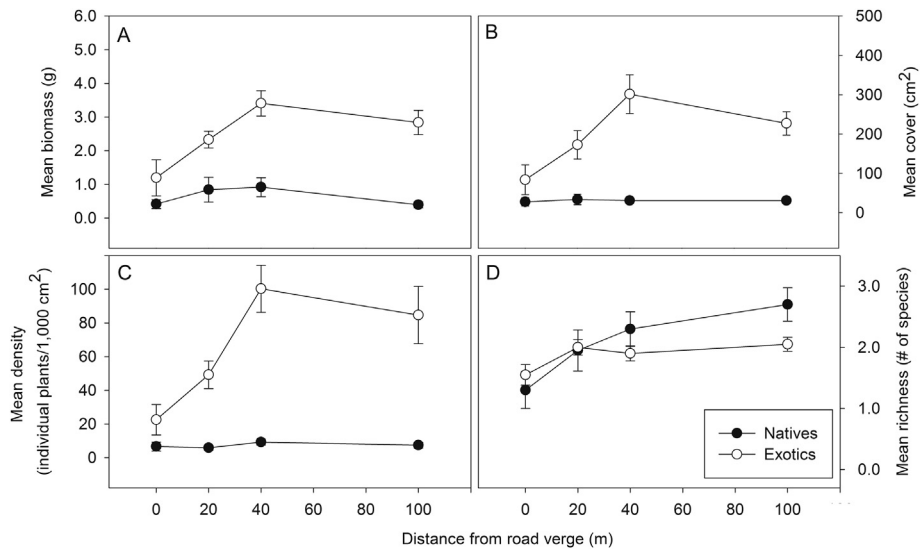

Fig. 2. The means and standard errors of biomass (A), cover (B), density (C), and richness (D) of exotic and native annual plants in the intershrub spaces at the service road verge (0-m), midway (20-m) and at the blade edge (40-m) of the disturbance corridor, and in the undisturbed or control area (100-m) of the second Los Angeles aqueduct corridor, western Mojave Desert, California.

Table 2
Results of Tukey's post hoc comparison test for native and exotic annual plants at four distances from the service road verge of the Los Angeles aqueduct disturbance corridor, Kern County, California. Samples were collected under canopies of *Ericameria nauseosa* (EN), *Ambrosia salsola* (AS), and *Ambrosia dumosa* (AD). Canopy conditions were live (L), dead (D), mosaic (M), and intershrub space (Is).

Distance (m)		Annual vegetation	
	Characteristic	Native	Exotic
0	Biomass	Is > EN[a]	NS
	Cover	NS	NS
	Density	NS	NS
	Richness	NS	NS
20	Biomass	ASD > ASL[b], ENL[b], END[a]; Is > ENL[a]	ASD > ENL[a], END[a], Is[a]; ASL > ENL[c]
	Cover	ASD > ENL[b], END[c]; Is > ENL[c]	ASD > ENL[c], END[a]
	Density	ASD > ENL[a], END[a]	ASD[c], ASL[c] > END
	Richness	ASD > ENL[c]	ASD > ENL[c], END[a]
40	Biomass	NS	NS
	Cover	NS	NS
	Density	NS	NS
	Richness	NS	ASD[b] > Is; ASL[a] > Is
100	Biomass	ADL[d], ADM[d] > Is	NS
	Cover	ADM > Is[b]	NS
	Density	NS	NS
	Richness	NS	NS

[a]$P < 0.01$.
[b]$P < 0.001$.
[c]$P < 0.05$.
[d]$P < 0.1$.

$P = 0.210$; density: $F_{1,38} = 1.42$, $P = 0.242$; richness: $F_{1,38} = 0.06$, $P = 0.805$). Exotic annual characteristics were not different between the canopy and intershrub space (ANOVA; biomass: $F_{1,38} = 0.41$, $P = 0.524$; cover: $F_{1,38} = 0.51$, $P = 0.478$; density: $F_{1,38} = 0.30$, $P = 0.590$; richness: $F_{1,38} = 0.92$, $P = 0.342$).

At 20 m from the road verge, native annuals were significantly different between shrub–canopy combinations for all four measures (ANOVA; biomass: $F_{4,95} = 8.52$, $P < 0.001$; cover: $F_{4,95} = 5.38$, $P < 0.001$; density: $F_{4,95} = 4.93$, $P < 0.01$; richness: $F_{4,95} = 3.94$, $P < 0.05$; see Table 2 for a list of significant post hoc comparisons). Consistently, native annual characteristics under dead *A. salsola* were higher than under live *E. nauseosa* (Tukey's HSD post hoc test; biomass: $P = 0.001$; cover: $P = 0.001$; density: $P = 0.002$; richness: $P = 0.017$). An additional two-way ANOVA that focused on perennial canopy cover showed a significant interaction for native biomass (Two-way ANOVA; $F_{1,76} = 5.45$, $P < 0.05$) where the biomass was higher under dead shrubs, but the effect was much stronger under *A. salsola* than under *E. nauseosa*.

Characteristics of exotic annuals at 20 m were also significantly different between shrub–canopy combinations (ANOVA; biomass: $F_{4,95} = 7.72$, $P < 0.001$; cover: $F_{4,95} = 4.64$, $P < 0.01$; density: $F_{4,95} = 3.37$, $P < 0.05$; richness: $F_{4,95} = 3.65$, $P < 0.01$). Similar to native annuals, the characteristics of exotic annuals were greater under dead *A. salsola* than under live *A. salsola*, or live or dead *E. nauseosa* (Table 2). The two-way ANOVA analyses showed no significant interactions, but had significant main effects for shrub species (*A. salsola* > *E. nauseosa*; all characteristics $P < 0.01$) and an

additional main effect for biomass for canopy class (dead > live; $P < 0.05$).

At 40 m from the road verge, no significant differences in characteristics of native annuals existed among the three combinations of shrub and canopy types: live *A. dumosa*, dead *A. dumosa*, and intershrub space (ANOVA; biomass: $F_{2,57} = 2.56$, $P = 0.086$; cover: $F_{2,57} = 1.96$, $P = 0.150$; density: $F_{2,57} = 2.39$, $P = 0.101$; richness: $F_{2,57} = 0.65$, $P = 0.528$). There was a significant difference for exotic annual richness (ANOVA; $F_{2,57} = 9.09$, $P < 0.001$), which was higher under live and dead *A. dumosa* canopy than in the intershrub space (Tukey's HSD post hoc test; live *A. dumosa*: $P = 0.001$; dead *A. dumosa*: $P = 0.002$).

At 100 m from the road verge, significant differences existed for native annual biomass and cover among the combinations of shrub and canopy types (ANOVA; biomass: $F_{3,76} = 3.00$, $P < 0.05$; cover: $F_{3,76} = 3.387$, $P < 0.05$), but post hoc analyses for biomass differences were inconclusive (Tukey's HSD post hoc test; $P \geq 0.062$). Native annual cover under mosaic canopies of *A. dumosa* was greater than in the intershrub space (Tukey's HSD post hoc test; $P = 0.034$). Exotic annual characteristics were not different between the canopy and intershrub space, however (ANOVA; biomass: $F_{3,76} = 0.60$, $P = 0.618$; cover: $F_{3,76} = 0.21$, $P = 0.890$; density: $F_{3,76} = 0.33$, $P = 0.804$; richness: $F_{3,76} = 0.50$, $P = 0.681$).

3.4. Distance effects, densities, and biomass of native and exotic annuals

Among the exotic species, *Schismus* spp. was the predominant species in densities (Appendix B), followed by the forb *E. cicutarium*. The species of bromes (*Bromus madritensis* ssp. *rubens*, *B. tectorum*, *Bromus berteroanus*) were less common. Overall, the exotic species were present in higher percentages in biomass compared to native species at all four distances (Table 3), whether in the intershrub spaces or under the canopies of shrubs.

3.5. Distance effects and species composition of annuals

Thirteen of the 47 species were present at all distances: 3 exotic species (*Schismus* spp., *B. madritensis* ssp. *rubens*, *E. cicutarium*), and 10 natives (*Amsinckia tessellata*, *Cryptantha nevadensis*, *Cryptantha pterocarya*, *Eriogonum gracillimum*, *Eriogonum maculatum*, *Malacothrix glabrata*, *Pectocarya linearis* ssp. *ferocula*, *Phacelia vallis mortae*, *Plagiobothrys arizonicus*, and *Stephanomeria exigua*). The numbers of taxa exclusively at a single distance increased with increasing distance from the road verge: none on the 0-m plots; three species on the 20-m plots (*Chorizanthe brevicornu* var. *brevicornu*, *Loeseliastrum matthewsii*, *Pectocarya platycarpa*); five species on 40-m plots (*Calyptridium monandrum*, *Cryptantha dumetorum*, *Eriogonum brachyanthum*, *Linanthus parryae*, *Mentzelia veatchiana*); and eight species on the 100-m plots (*Centrostegia thurberi*, *Eriophyllum pringlei*, *Eriogonum pusillum*, *Festuca octoflora*, *Festuca microstachys*, *Linanthus bigelovii*, *Lupinus sparsiflorus*, *Stylocline psilocarphoides*). The exotic species *B. tectorum* was only observed in the disturbed areas (0-m, 20-m and 40-m plots). In addition, there were species that appeared to be colonizing the disturbance corridor from the undisturbed habitat and were primarily at the 100-m distance but also found at 40-m and in some cases also at 20-m distances, e.g., *Acmispon strigosus*, *A. tessellata* var. *tessellata*, *Camissonia campestris* ssp. *campestris*, *Caulanthus cooperi*, *C. pterocarya*, *P. vallis-mortae* (Appendix B).

The canonical discriminant analysis model that combined all (i.e., native and exotic) intershrub and canopy annuals provided the greatest separation between distances (Table 4). This model was statistically significant (Wilk's Lambda = 0.141, approximate $F_{141,\ 647} = 4.597$, $P < 0.001$) and yielded three functions that together accounted for 85.9% of the variance. Of the variance explained by the three canonical functions, the first and second functions accounted for 90.6% of the total (66.9% and 23.7%, respectively; Fig. 3). The jackknifed cross-validation had an overall classification success of 64.5% and classified samples from the 0-m and 100-m plots with higher success (77.5% and 72.5%, respectively) than samples from 20-m and 40-m plots (63.0% and 45%, respectively).

The composition of annuals was most similar at the 20-m and 40-m plots, which was evident by the substantial overlap in Fig. 3, and most dissimilar for the 0-m and 100-m plots. Several species had more influence than others on the model and were more important in separating the sampling distances (structure coefficients, Appendix C). Species that had a strong positive loading on the first canonical function (i.e., more common in the 100-m plots) were *A. strigosus*, *C. cooperi*, *P. vallis-mortae*, and *Schismus* spp. There were no particular species that had a strong negative loading, but two species with moderate negative loadings and more common in the 0-m plots were *Cryptantha micrantha* and *P. arizonicus*. Several species influencing the first function were also relevant in the second function, including *P. arizonicus* and *Schismus* spp. Additional positive loading on the second function was from *Gilia brecciarum*, which was more common in the 0-m plots, and negative loading from *E. cicutarium*, which was more common in the 20-m and 40-m plots. Across both functions, *Schismus* spp., *C. cooperi*, *P. arizonicus* and *E. cicutarium* made sizeable contributions to the overall model (communality coefficient, Appendix C).

The Sørensen and Bray–Curtis indices differed by distances from disturbed to undisturbed habitats, by canopy class, and by whether natives were evaluated alone or with exotic species (Table 5). Both indices indicated that native annual plants showed approximately 2–8% similarity between the 0-m and 100-m distances, whether in the intershrub space or under the canopy. When similarity indices were applied to both native and exotic annual plants, similarities were higher between the 0-m and 100-m plots in the intershrub space (24–39%) and under the canopy of shrubs (13–34%). In all cases, similarity indices were higher between the 40-m and 100-m distances than the other distances.

3.6. Distance effects and recovery of annual vegetation

By treating similarity as a metric of recovery, the percent recovery for annual vegetation increased with increasing distance from the center of the disturbed area (0 m, the road verge) for native annuals and all (native and exotic) annuals (R_{100} in Table 5). Recovery was faster in the intershrub spaces compared to under perennial canopy cover and likewise the estimated time to 100%

Table 3
Percent of total biomass (mean ± SE) of annual plants, separated by native and exotic species, in the intershrub spaces and under canopy cover of perennial shrubs at four distances from the verge of the Los Angeles aqueduct disturbance corridor, Kern County, California.

Distance (m)	Intershrub space		Shrub canopy	
	Native	Exotic	Native	Exotic
0	36.2 (±8.1)	63.8 (±14.3)	13.2 (±3.0)	86.8 (±19.4)
20	17.6 (±3.9)	82.4 (±18.4)	9.5 (±1.1)	90.5 (±10.1)
40	17.4 (±3.9)	82.6 (±18.5)	15.0 (±2.4)	85.0 (±13.4)
100	15.6 (±3.5)	84.4 (±18.9)	25.9 (±3.3)	74.1 (±9.6)

Table 4
Mahalanobis distances and Wilks' F results for the canonical discriminant analysis of annuals sampled in intershrub space and under perennial canopy cover. Analyses were done for native annuals and native and exotic annuals combined. $P = 0.001$ for all Wilks' F values.

Location	Canopy (N = 200)		Intershrub (N = 80)		Canopy + intershrub (N = 280)	
	Natives	Natives + exotics	Natives	Natives + exotics	Natives	Natives + exotics
0 m–20 m	2.314	3.690	1.051	1.942	2.186	3.106
0 m–40 m	2.865	4.523	1.952	4.115	3.169	4.569
0 m–100 m	4.679	6.574	3.456	4.568	6.173	7.828
20 m–40 m	1.992	1.982	1.519	1.934	2.283	2.432
20 m–100 m	7.347	7.178	3.447	3.072	8.615	8.655
40 m–100 m	2.653	2.967	2.738	2.579	4.193	4.091
Wilks' F	3.429	4.055	2.164	2.793	4.090	4.597

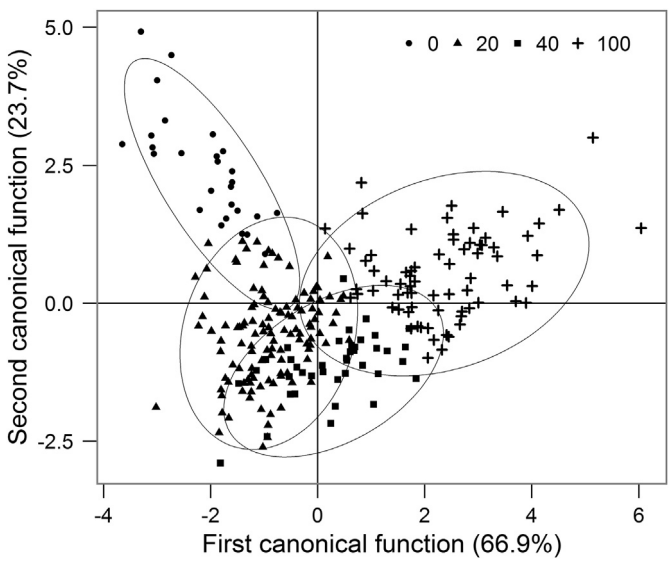

Fig. 3. Scatterplot of the first two canonical functions of the discriminant analysis for annual plant composition at 0 m, 20 m, and 40 m from the service road verge in the disturbance corridor of the second Los Angeles aqueduct corridor to the 100 m control in undisturbed habitat, western Mojave Desert, California.

Table 5
Average similarity indices (±SE) of annual species composition between disturbed (0, 20 and 40 m) and undisturbed plots (100 m) at the second Los Angeles aqueduct corridor, Kern County, California. As a metric of recovery, similarity indices were used to calculate the time (years) to 100% recovery (R_{100}).

Location		Sørensen		Bray–Curtis	
	Comparison	Natives	All species	Natives	All species
Intershrub	0 and 100	7.5 (±5.5)	39.4 (±4.2)	5.6 (±5.0)	23.5 (±4.4)
N = 80	R_{100}:	480	91	643	153
	20 and 100	12.4 (±5.3)	47.9 (±4.4)	6.0 (±2.8)	48.0 (±4.7)
	R_{100}:	290	75	600	75
	40 and 100	24.3 (±7.1)	54.5 (±4.3)	10.7 (±3.2)	57.2 (±4.8)
	R_{100}:	148	66	336	63
Canopy	0 and 100	4.7 (±1.6)	34.4 (±3.9)	2.0 (±0.8)	12.8 (±2.5)
N = 200	R_{100}:	766	105	1800	281
	20 and 100	7.2 (±1.4)	41.4 (±2.3)	4.4 (±1.1)	37.2 (±2.5)
	R_{100}:	500	87	818	97
	40 and 100	23.2 (±3.0)	50.2 (±2.5)	18.0 (±3.3)	45.6 (±2.8)
	R_{100}:	155	72	200	79

recovery was faster. These recovery trends were similar between the two indices, but overall the Bray–Curtis index was more conservative, estimating more years for recovery. Our estimates for years required for recovery were higher for all annual plants at the 0-m and 20-m locations in the disturbance corridor and were much higher at all locations for native annuals.

4. Discussion

4.1. Historical framework of land use and general effects on annual and perennial vegetation

The recovery of annual and perennial vegetation in the second Los Angeles aqueduct corridor should be viewed within the framework of historical and current land uses that influence vegetation. The study site and aqueduct corridor have a >130 year history of disturbance by numerous anthropogenic activities, including livestock grazing, transportation routes, utility corridors, and recreation (Fulwider, 1963; Nadeau, 1997). Livestock grazing, both by cattle and sheep, historically and during the study, was the predominant use (Wentworth, 1948; U.S. BLM, 1980). Kay (1979) noted that, "Grazing was particularly heavy, being by both cows and sheep in the early years and more recently only by cows, although for a prolonged season." Nine and 18 years after construction, Kay (1979, 1988) reported that ground cover was annuals, mostly *Erodium* and *Schismus*. The range condition, measured by grazing on and condition of perennial shrubs and bunchgrasses, was rated as fair (U.S. BLM, 1980). Livestock grazing has the potential to alter species composition of annual and perennial plants, reduce seed sources (especially of annual plants), thus altering and slowing the process of succession and recovery (Fowler, 1986), as well as the ultimate trajectory (MacMahon, 1999; Walker, 2012).

Anthropogenic impacts within the disturbance corridor differ in severity depending on location. The buried aqueduct and service road (0 m) are continually disturbed by vehicles and grading, whereas the 20-m, 40-m and 100-m plots have no vehicular disturbance. Repeated disturbance is typical of historically maintained dirt roads in the Mojave Desert (Johnson et al., 1975). The service road and runoff contribute to invasion of exotics (Frenkel, 1970; Johnson et al., 1975) and to the dense cover of *E. nauseosa*, which is typical of some desert dirt roads in the Great Basin and Mojave deserts (Kay, 1979, 1988; Lathrop and Archbold, 1980). In contrast, vegetation in the 40-m or blade-edge plots has experienced a lower level of disturbance over time: one-time clearance of vegetation followed by ripping to reduce compaction a few years later, creating parallel furrows. The lower level of disturbance and close proximity to the undisturbed, control area are reflected in a greater similarity in composition of annuals and potentially a more advanced stage of secondary succession (Fig. 3).

4.2. Exotic annuals and the aqueduct corridor

Exotics, which often thrive in disturbed places, have the potential to slow and change the trajectory of succession by sequestering nutrients, slowing the establishment of native species by pre-empting a site or ecosystem, and altering desert fire regimes (MacMahon, 1999; Walker, 2012). Our one-season study indicated that exotic annuals composed 12.5% of the flora and >60% of the

biomass, a finding compatible with research conducted elsewhere in the Mojave Desert. In the western, central, and southern Mojave Desert, exotics now compose >50% of the biomass (Brooks and Berry, 2006). During the last 30 years, several other scientists reported comparable high levels of *Schismus* spp. and *E. cicutarium* at sites in the Mojave Desert (Webb and Stielstra, 1979; Brooks, 1995, 1999; Brooks et al., 2006). Most of these studies were conducted in areas disturbed by livestock grazing or recreational use. In our study, the exotic annuals were more successful than the natives and had, in general, higher values of biomass, cover and density (Table 3, Fig. 2). The exotic grasses in particular may be suppressing the native annuals and limiting their potential for productivity (Brooks, 2000).

4.3. Effects of distance on annuals in the intershrub spaces

The responses of native annual characteristics in the intershrub space within the disturbance corridor showed remarkable similarity between the 40-m blade-edge and control area at 100 m in biomass, cover, density and richness (Fig. 2). However, native annuals showed statistically significant differences between the 0-m and the 100-m plots in richness, and the composition of native annual species differed significantly by distance. More species were present at the 100-m control than in the 0-m, 20-m, and 40-m plots, and some species present at the 100-m distance were also in low numbers at the 40-m blade edge distance.

4.4. Effects of distance, shrub species, and canopy class on annuals

The three species of shrubs we evaluated—*E. nauseosa*, *A. dumosa and A. salsola*—are widespread in the Great Basin, Mojave, and Sonoran deserts, and the distribution of *E. nauseosa* is even more extensive across the western United States. The responses of annuals to these shrub species varied substantially, differing by distance from the verge, shrub species, and canopy class. *E. nauseosa* does not appear to be as favorable or productive a location for native or exotic annuals as dead *A. salsola* or the intershrub space. Both species of shrub are colonizers that thrive in disturbed places, and *A. salsola* is a major shrub species in naturally and anthropogenically disturbed areas throughout the deserts, such as in stream channels and utility corridors (Vasek et al., 1975a, 1975b). The two species differ in longevity: *E. nauseosa* is long-lived, while *A. salsola* is short-lived. The variety of *E. nauseosa* in our study, *hololeuca*, is a major or predominant species at the road edge and within the disturbance corridors of both the first Los Angeles aqueduct (completed in 1913) and second Los Angeles aqueduct (Lathrop and Archbold, 1980). *E. nauseosa* has persisted as an important and dominant species on the first Los Angeles aqueduct for almost 100 years and is likely to follow a similar pattern for the second Los Angeles aqueduct, where it forms a dense line, similar to a hedge, at the verge.

Our findings indicate that dead shrubs (but not *E. nauseosa*) can be important sites for native annuals, supporting observations made by Went (1942) and Muller (1953) about dead shrubs and woody debris. Dead shrubs and wood from dead plants are used by restoration specialists to obscure trails and roads scheduled for closure (Weigand and Rodgers, 2009) and may also serve a dual purpose in enhancing recovery of annual plants in disturbed areas.

Over time, desert shrubs can develop coppice mounds or islands of fertility beneath their canopies, potentially providing a more mesic environment, nutrition, and protection from livestock for annual plants (e.g., Brown and Porembski, 2000; Bolling and Walker, 2002; Berry et al., 2015). Development of coppice mounds may contribute to more advanced seral stages and enhance recovery of annuals. We did not evaluate coppice mound development in this study and thus could not determine if coppice mounds and characteristics of annual plants varied by shrub species or canopy class.

4.5. Patterns of colonization of the aqueduct corridor by annual plants and succession

By species or groups of species, native annuals show patterns of colonization that may be important in understanding potential patterns of succession and thus restoration of disturbed areas. We placed native annuals in this study in six groups: 1) species found at all distances and may be generalists or colonizers; 2) species common at the service road verge and under *E. nauseosa*, and appear to be colonizing the disturbance corridor from the road to the interior of the disturbance corridor; 3) species present at the 20-m and 40-m distances but not at verge or control and thus appearing to tolerate disturbed habitats but perhaps not road edges or *E. nauseosa*; 4) species occurring only in the control area and not at the verge or in the aqueduct corridor; 5) species with highest densities in the control area and colonizing into the disturbance corridor from the control; and 6) species with insufficient information (Appendix B). The patterns we observed need to be further evaluated during multiple years, under different precipitation conditions, and replicated at other sites. If native annuals fall into groups similar to described above, e.g., species that are colonizers or species that are "members of stable old communities" (Vasek, 1983), then annuals may follow patterns similar to perennial species.

We compared the results of our study with a similar pipeline study by Johnson et al. (1975) on richness and density of annual plants; the latter study was conducted along an unpaved utility road 37 years after it was established in the southern Mojave Desert. In our study, richness increased significantly with increasing distance for natives and exotics, when evaluated separately. In the Johnson et al. (1975) study, richness was not significantly different between the road verge and the control or undisturbed sites. The two studies also differed in density or counts of individual plants/m^2 between the road edge and control. In our study, density increased significantly for exotic and native species between the road edge or 20-m distance and the 100-m control (Fig. 2), whereas Johnson et al. (1975) reported similarities in density between road edge and control sites (distance between road edge and control was not specified). The likely important differences in the studies were the widths of the disturbed area between the verge and control, sampling techniques, and the absence of *E. nauseosa* at the Johnson et al. (1975) site.

4.6. Estimated time for recovery of annuals

The time required for recovery of annual plants in severely disturbed areas, such as the Los Angeles aqueduct corridor, is dependent on many factors, including surficial geology and soil types, precipitation patterns, size and type of disturbance, and biological soil crusts (Webb et al., 2009; Abella, 2010). Recovery times can also be defined in terms of visual appearance, or specific metrics, such as density, biomass, and richness of species. We believe that composition of native annuals should be a critical variable, with a goal of achieving similarity or homogeneity with nearby undisturbed land. In our study, the composition of native annuals within the disturbance corridor differed significantly for the four distances and had not yet achieved similarity to that of the 100-m, undisturbed distance. The linear model provided by Abella (2010) predicted a 55.6% recovery at 36 years post-disturbance or 100% recovery at 65 years. The closest approximation for the Abella (2010) estimate was at the 40 m or blade edge of the disturbance, i.e., 66–72 years for recovery for all annuals using the Sørensen

index. Based on the Sørensen and Bray–Curtis similarity indices, we suggest that centuries are likely to be required for the composition of natives to become homogeneous with adjacent, undisturbed habitat (148–1800 years) with potentially less time if both native and exotic species are considered (63–281 years) (Table 5).

5. Management implications

Recovery of disturbed areas in deserts requires long periods of time, especially return of annual and perennial species to the previous composition or the composition in adjacent, undisturbed areas. Recovery to the pre-disturbance condition may not be possible. Therefore, limiting the amount of disturbances is a high priority. For linear corridors, reducing the width of disturbance could be beneficial. Another high priority is inhibiting invasion and establishment of new species of exotic plants. Aqueduct corridors and other utility corridors are important sites to monitor for arrival of new exotic annual plants (Brooks, 1999). The topic of whether and how invasive exotic plants inhibit or lower the rate and trajectory of recovery of annuals in disturbed areas, such as the Los Angeles aqueduct corridors, deserves consideration. Service roads are often associated with utility corridors and probably slow the long-term recovery of native annual as well as perennial vegetation (see Lathrop and Archbold, 1980; for perennial vegetation). Service roads, if maintained, continue to be sources of soil disturbances and, potentially, new invasive species.

Some utility corridors have well-established populations of *E. nauseosa*, while others do not. *E. nauseosa*, because of its longevity, size, and structure, may limit recovery of other plants. Some of the more pressing questions to be addressed include: under what conditions and in what regions of the Mojave Desert does *E. nauseosa* become established? Does variety of the species matter? Does *E. nauseosa* have negative or positive effects on populations of plants and animals? Would removal or reduction of *E. nauseosa* hasten recovery of other native vegetation at sites where it presently occurs? Are there other species of perennials that function similarly to *E. nauseosa* in other North American deserts and elsewhere in the world?

The in-depth evaluation of native annuals and their preferences for specific species of shrubs could provide beneficial information. Would, for example, removal of or reduction in density of *E. nauseosa* enhance recovery near the service road? Do *E. nauseosa*, *A. salsola*, *A. dumosa* and *L. tridentata* differ in the capacity to act as resource islands to accumulate nutrients or provide environmental protection for annuals? Does the development of coppice mounds and resource islands differ by shrub species and affect trajectories of recovery? Do these shrubs function as seed collectors and/or maintain seed banks? Do native annuals have an affinity for one species of shrub over another?

Halvorson and Patten (1975), in a Sonoran Desert study, reported that morphology of the shrub canopy plays a significant role because annual productivity was consistently higher under shrubs with tall, relatively loose-knit canopies, such as *L. tridentata*, than under shrubs with low, dense canopies, such as *A. dumosa*. DeSoyza et al. (1997) noted that richness and diversity of annual species was greater under hemispherical than conical *L. tridentata* bushes. Do canopy type and shape affect productivity of annuals, and if so, how can this information be used to enhance recovery of diverse native annuals at a disturbed site?

Our data indicate that native annual species have different response patterns to disturbances: some species may be colonizers and some may not thrive under disturbance regimes, even after many decades. Similarly, Prose and Wilshire (2000) reported that *Chaenactis fremontii* and *P. platycarpa* exhibited decreases in cover and density in compacted soils of tank tracks after > 40 years, whereas *Plantago insularis* and some native grass species showed increases in density. This topic deserves high priority in multi-year studies designed to include multiple sites throughout the deserts with different precipitation regimes, soil types, and on a variety of geological surfaces. Restoration specialists, using this information, may be able to enhance recovery rates of disturbed sites by seeding with appropriate annual species. Some annual plant species are important in diets of rare, threatened, and endangered animals, and these plant species need to be considered in restoration efforts too.

New methods to enhance recovery of vegetation in utility corridors and other large or linear scraped areas need to be explored, especially those dealing with native shrubs, nurse plants, plant islands, and fertile islands around shrubs (Bolling and Walker, 2002; Weigand and Rodgers, 2009). Testing hypotheses about the benefits of using woody plant material and debris can shed light on the species of wood, quantity of woody debris, and the type of placement (above, below ground) for enhancing reestablishment of native annuals.

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Appendix A. Canopy cover of perennial shrubs at the study site along the second Los Angeles aqueduct corridor, Kern County, California. We selected *Ambrosia dumosa*, *Ericameria nauseosa*, and *Ambrosia salsola* as dominant shrub species for the study based on canopy cover at the four distances from the service road verge in the corridor and adjacent.

Distance (m)	Percent canopy cover														
	Ambrosia dumosa			*Ericameria nauseosa*			*Ambrosia salsola*			*Larrea tridentata*			Other species		
	Live	Dead	Total	Live	Dead	Total	Live	Dead	Total	Live	Dead	Total	Live	Dead	Total
0	0.04	0.00	0.04	82.93[a]	7.38	90.31	4.35	0.03	4.38	0.00	2.99	2.99	2.22	0.07	2.29
20	5.45	2.52	7.97	27.80[a]	19.00[a]	46.80	25.69[a]	12.05[a]	37.74	0.00	0.00	0.00	6.81	0.67	7.48
40	14.88[a]	14.42[a]	28.43	2.96	0.68	3.64	7.54	4.15	11.69	22.90	0.00	22.90	28.06	5.40	34.46
100	14.35[a]	8.83[a]	23.18	0.00	0.00	0.00	0.85	0.62	1.47	41.46	4.73	46.19	18.37	10.78	29.15

[a]Perennial species-canopy class combinations that were sampled in this study.

Appendix B. Mean density (number/1000 cm^2; ±SE) of native and exotic annual plants at four distances from the service road verge of the second Los Angeles aqueduct disturbance corridor, Kern County, California. The means include intershrub and canopy samples. All plants listed are native forbs unless noted with an *. * = native annual grass; ** = exotic forb; * = exotic annual grass.**

Species	Mean density (±SE) of annual plants at four distances (m) from the verge			
	0	20	40	100
Acmispon strigosus	0.00	0.01 (±0.01)	0.10 (±0.03)	0.46 (±0.1)
Amsinckia tessellata var. *tessellata*	0.05 (±0.03)	0.14 (±0.07)	0.26 (±0.09)	0.28 (±0.1)
Calyptridium monandrum	0.00	0.00	0.02 (±0.01)	0.00
Camissonia campestris ssp. *campestris*	0.00	0.00	0.05 (±0.03)	0.19 (±0.09)
Caulanthus cooperi	0.00	0.11 (±0.06)	1.62 (±0.45)	4.14 (±0.63)
Caulanthus lasiophyllus	0.00	0.46 (±0.25)	0.02 (±0.01)	0.00
Centrostegia thurberi	0.00	0.00	0.00	0.09 (±0.04)
Chaenactis fremontii	0.00	0.01 (±0.01)	0.02 (±0.01)	0.00
Chorizanthe brevicornu var. *brevicornu*	0.00	0.05 (±0.05)	0.00	0.00
Chorizanthe watsonii	0.00	0.08 (±0.03)	0.23 (±0.1)	0.10 (±0.04)
Cryptantha dumetorum	0.00	0.00	0.05 (±0.05)	0.00
Cryptantha micrantha	2.35 (±1.29)	0.33 (±0.16)	0.72 (±0.36)	0.00
Cryptantha nevadensis	0.25 (±0.18)	0.03 (±0.01)	0.13 (±0.08)	0.12 (±0.06)
Cryptantha pterocarya	0.10 (±0.04)	0.26 (±0.1)	0.32 (±0.14)	0.54 (±0.15)
Descurainia pinnata	0.00	0.00	0.02 (±0.01)	0.02 (±0.01)
Eriogonum brachyanthum	0.00	0.00	0.03 (±0.03)	0.00
Eriogonum gracillimum	0.02 (±0.02)	0.12 (±0.04)	0.13 (±0.08)	0.08 (±0.05)
Eriogonum maculatum	0.05 (±0.03)	0.07 (±0.04)	0.37 (±0.19)	0.10 (±0.05)
Eriogonum nidularium	0.00	0.01 (±0.01)	0.12 (±0.11)	0.00
Eriogonum pusillum	0.00	0.00	0.00	0.02 (±0.01)
Eriophyllum pringlei	0.00	0.00	0.00	0.81 (±0.38)
*Festuca microstachys**	0.00	0.00	0.00	0.02 (±0.02)
*Festuca octoflora**	0.00	0.03 (±0.02)	0.00	0.02 (±0.02)
Festuca spp.	0.00	0.00	0.00	0.01 (±0.01)
Gilia brecciarum ssp. *neglecta*	0.15 (±0.06)	0.00	0.00	0.01 (±0.01)
Lasthenia californica	0.00	0.17 (±0.08)	0.05 (±0.05)	0.00
Layia glandulosa	0.10 (±0.05)	0.00	0.02 (±0.01)	0.22 (±0.09)
Linanthus bigelovii	0.00	0.00	0.00	0.04 (±0.02)
Linanthus parryae	0.00	0.00	0.03 (±0.03)	0.00
Loeseliastrum matthewsii	0.00	0.12 (±0.07)	0.00	0.00
Lupinus sparsiflorus	0.00	0.00	0.00	0.02 (±0.02)
Malacothrix glabrata	0.35 (±0.16)	0.25 (±0.06)	0.20 (±0.07)	0.24 (±0.11)
Mentzelia veatchiana	0.00	0.00	0.02 (±0.01)	0.00
Pectocarya linearis ssp. ferocula	0.05 (±0.03)	0.08 (±0.04)	0.17 (±0.08)	0.16 (±0.1)
Pectocarya penicillata	0.00	0.02 (±0.01)	0.12 (±0.07)	0.11 (±0.06)
Pectocarya platycarpa	0.00	0.01 (±0.01)	0.00	0.00
Phacelia fremontii	0.00	0.00	0.02 (±0.01)	0.01 (±0.01)
Phacelia vallis-mortae	0.02 (±0.02)	0.01 (±0.01)	0.08 (±0.04)	1.07 (±0.28)
Plagiobothrys arizonicus	0.28 (±0.1)	2.19 (±0.35)	3.15 (±0.69)	0.34 (±0.09)
Stephanomeria exigua	0.02 (±0.02)	0.14 (±0.05)	0.07 (±0.03)	0.01 (±0.01)
Stylocline psilocarphoides	0.00	0.00	0.00	0.01 (±0.01)
Tropidocarpum gracile	0.00	0.01 (±0.01)	0.00	0.10 (±0.05)
Uropappus lindleyi	0.52 (±0.25)	0.08 (±0.03)	0.00	0.00
*Erodium cicutarium***	1.75 (±1.03)	4.59 (±0.58)	5.00 (±0.6)	2.58 (±0.38)
*Bromus berteroanus****	0.00	0.62 (±0.43)	0.02 (±0.01)	0.06 (±0.04)
Bromus madritensis ssp. *rubens****	2.67 (±0.64)	8.12 (±1.64)	5.08 (±1.19)	3.79 (±1.24)
*Bromus tectorum****	0.98 (±0.72)	0.08 (±0.05)	0.10 (±0.07)	0.00
Schismus barbatus or *S. arabicus*, or both***	11.43 (±4.03)	50.85 (±5.18)	70.93 (±7.67)	64.47 (±6.61)

Appendix C. Results of the canonical discriminant analysis of annual plants at four distances from the service road verge of the second Los Angeles aqueduct disturbance corridor, Kern County, California. Displayed are the standardized canonical function coefficient (Coef), structure coefficient (r_s), squared structure coefficient (r_s^2), and communality coefficient (h^2). For emphasis, structure coefficients above |0.30| and communality coefficients above 30% were underlined.

Species	Function1 Coef	r_s	r_s^2(%)	Function 2 Coef	r_s	r_s^2(%)	h^2
Acmispon strigosus	0.538	0.436	19.04	0.158	0.074	0.55	19.59
Amsinckia tessellata var. *tessellata*	0.146	0.160	2.57	0.056	−0.088	0.77	3.34
Calyptridium monandrum	0.098	0.006	0.00	−0.134	−0.115	1.32	1.32
Camissonia campestris ssp. campestris	0.152	0.218	4.76	−0.155	0.025	0.06	4.82

(*continued on next page*)

(*continued*)

Species	Function1 Coef	r_s	r_s^2(%)	Function 2 Coef	r_s	r_s^2(%)	h^2
Caulanthus cooperi	0.723	0.631	39.84	−0.094	−0.006	0.00	39.84
Caulanthus lasiophyllus	−0.133	−0.149	2.21	0.018	−0.132	1.74	3.95
Centrostegia thurberi	0.010	0.236	5.56	0.064	0.101	1.02	6.58
Chaenactis fremontii	0.017	−0.036	0.13	−0.219	−0.112	1.24	1.38
Chorizanthe brevicornu var. *brevicornu*	−0.022	−0.057	0.32	0.094	−0.043	0.18	0.51
Chorizanthe watsonii	0.070	0.060	0.36	−0.042	−0.179	3.20	3.56
Cryptantha dumetorum	0.098	0.006	0.00	−0.134	−0.115	1.32	1.32
Cryptantha micrantha	0.147	0.006	0.00	−0.207	−0.115	1.32	1.32
Cryptantha nevadensis	−0.170	−0.200	4.00	0.285	0.116	1.35	5.36
Cryptantha pterocarya	0.062	0.038	0.15	0.034	0.096	0.93	1.07
Descurainia pinnata	−0.095	0.190	3.62	0.152	0.021	0.05	3.66
Eriogonum brachyanthum	0.068	0.127	1.61	−0.037	−0.014	0.02	1.63
Eriogonum gracillimum	0.011	0.006	0.00	0.113	−0.115	1.32	1.32
Eriogonum maculatum	−0.036	−0.032	0.10	−0.077	−0.117	1.37	1.48
Eriogonum nidularium	0.078	0.039	0.15	−0.289	−0.136	1.85	2.00
Eriogonum pusillum	−0.135	−0.016	0.03	0.123	−0.123	1.50	1.53
Eriophyllum pringlei	0.348	0.287	8.24	0.289	0.123	1.51	9.75
*Festuca microstachys**	0.180	0.107	1.14	0.060	0.046	0.21	1.35
*Festuca octoflora**	−0.033	0.007	0.00	0.028	−0.017	0.03	0.03
Festuca spp.*	0.232	0.151	2.28	−0.053	0.065	0.42	2.70
Gilia brecciarum ssp. *neglecta*	−0.157	−0.123	1.51	0.373	0.404	16.32	17.84
Lasthenia californica	−0.141	−0.120	1.44	0.005	−0.138	1.90	3.35
Layia glandulosa	0.002	0.203	4.11	0.144	0.224	5.03	9.13
Linanthus bigelovii	0.098	0.148	2.20	0.021	0.064	0.40	2.61
Linanthus parryae	0.084	0.006	0.00	−0.152	−0.115	1.32	1.32
Loeseliastrum matthewsii	−0.089	−0.110	1.21	−0.108	−0.082	0.67	1.88
Lupinus sparsiflorus	−0.003	0.107	1.14	0.022	0.046	0.21	1.35
Malacothrix glabrata	−0.131	−0.060	0.36	0.124	0.028	0.08	0.44
Mentzelia veatchiana	0.142	0.006	0.00	−0.098	−0.115	1.32	1.32
Pectocarya linearis ssp. *ferocula*	−0.079	0.030	0.09	0.030	−0.057	0.32	0.41
Pectocarya penicillata	0.062	0.124	1.53	−0.065	−0.096	0.93	2.46
Pectocarya platycarpa	−0.025	−0.057	0.32	0.037	−0.043	0.18	0.51
Phacelia fremontii	0.063	0.079	0.63	−0.132	−0.049	0.24	0.87
Phacelia vallis-mortae	0.531	0.438	19.16	0.114	0.158	2.48	21.65
Plagiobothrys arizonicus	−0.184	−0.223	4.96	−0.469	−0.568	32.24	37.20
Stephanomeria exigua	−0.082	−0.121	1.47	−0.079	−0.150	2.26	3.73
Stylocline psilocarphoides	0.140	0.107	1.14	0.084	0.046	0.21	1.35
Tropidocarpum gracile	0.122	0.175	3.06	0.151	0.069	0.47	3.54
Uropappus lindleyi	−0.152	0.148	2.20	0.132	0.224	5.03	7.23
*Erodium cicutarium***	−0.163	0.025	0.06	−0.309	−0.589	34.64	34.70
*Bromus berteroanus****	0.041	−0.004	0.00	−0.110	−0.045	0.20	0.20
Bromus madritensis ssp. *rubens****	−0.167	−0.180	3.25	−0.042	−0.173	3.00	6.25
*Bromus tectorum****	−0.089	−0.147	2.15	0.161	0.144	2.07	4.21
Schismus barbatus or *S. arabicus*, or both***	0.501	0.387	15.00	−0.429	−0.605	36.62	51.61

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