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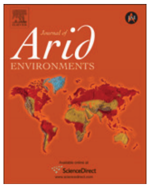

Factors affecting exotic annual plant cover and richness along roadsides in the eastern Mojave Desert, USA

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ABSTRACT

Roads are often considered a critical point of entry for invasive exotic plant species. We evaluated the cover and richness of exotic plants relative to road type (gravel or paved) and distance from roads in the eastern Mojave Desert where exotic annual species are increasing the flammability of the desert. Exotic and native annual plant cover and richness were sampled from five to 45 m from roads in three prevalent microsite types for this system: *Larrea tridentata* microsites, *Ambrosia dumosa* microsites, and interspaces between shrubs. Six exotic and 58 native annual species were detected during sampling. There was no distinction between the behavior of exotics and natives relative to road type or distance from the roads. *A. dumosa* and *L. tridentata* microsites had more exotic cover than interspaces. Likewise, exotic richness was significantly higher in the shrub microsites. A taxonomically controlled analysis involving three plant families revealed no significant differences in cover of native or exotic species relative to their distance from the road. Our results suggest that exotic plant species in the Mojave Desert are not necessarily more prevalent near roadsides than in adjacent undisturbed desert. Therefore, roadside surveys alone may not be adequate to detect exotic species presence.

1. Introduction

Transportation corridors, such as roadsides, are considered the primary vectors of exotic plant species dispersal (Gelbard and Belnap, 2003; Hansen and Clevenger, 2005; Trombulak and Frissell, 2000; Tyser and Worley, 1992). Furthermore, the extent to which roads facilitate exotic plants may be a function of road type (Gelbard and Belnap, 2003) and physical climate. Roads in the Mojave Desert exhibit elevated diversity and ground cover of both perennial and annual natives as well as exotics along their verges (Johnson et al., 1975), and areas with high road density tend to have more exotic species than areas with low road density (Brooks and Berry, 2006; Dark, 2004). In deserts, road verges may host relatively greater native-plant biomass because of increased water collection at road edges (Starr and Mefford, 2002). Consequently, monitoring programs for exotic plants have focused on roadside surveys in the Mojave Desert (Abella et al., 2009) even though there are no published documents indicating that distributions of exotic species in the Mojave Desert are limited to roadsides.

Although it is accepted that disturbances created by roadways often facilitate the establishment of exotic plants within verges, the role of roads as invasion corridors has been questioned (Christen and Matlack, 2006; Harrison et al., 2002; Kalwij et al., 2008). Road verges may merely host alien species that are dispersing from multidirectional sources (Kalwij et al., 2008). Exotic species presence is affected by factors other than road presence. Higher numbers of exotic plant species have been correlated with low elevation and high native-plant species richness (Dark, 2004), but the importance of transportation corridors relative to these other factors remains unclear. Disturbed roadsides appear to be susceptible to exotic invasion, but there are notable exceptions. In the Mojave Desert, some of the most devastating species are those that easily spread into relatively undisturbed areas. *Bromus rubens* L. has shown this capacity (Beatley, 1966). Moreover, this grass, along with *Schismus* spp., is fueling more frequent and intense wildfires, thus altering entire ecosystem processes (D'Antonio and Vitousek, 1992).

The spread of exotic species from roadsides into undisturbed adjacent areas also varies according to the details of the system. In mesic communities, level of invasion decreases as distance from the corridor edge increases (Flory and Clay, 2006; Fowler et al., 2008; Hansen and Clevenger, 2005; Tyser and Worley, 1992). However, different community types exhibit different rates of exotic species declines as distance from roads increases (Hansen and Clevenger,

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2005) and some exotic species do not follow this generalized trend (Fowler et al., 2008).

In Mojave Desert systems, microsite characteristics may be an important determinant of system invasibility. One of the most conspicuous phenomena found in desert scrub is the fertile island effect (e.g., Garcia-Moya and McKell, 1970; Thompson et al., 2005; Titus et al., 2002). Substrates under desert shrubs contain significantly higher nitrogen, organic matter, and moisture than surrounding interspaces (Thompson et al., 2005), providing a more fertile habitat for native and exotic annual plant species. Several studies have further examined interactions between desert annuals and shrub species (e.g., Holzapfel and Mahall, 1999; Shmida and Whittaker, 1981; Tielbörger and Kadmon, 1997, 2000). However, interactions between shrubs and annuals are difficult to predict because they depend on annual precipitation (Tielbörger and Kadmon, 2000), complex indirect species interactions mediated through resource competition (Booth et al., 2003), and/or direct interactions such as allelopathy (Muller, 1966). Native desert annual plant species are sensitive to variations in microhabitat provided by the presence or absence of different desert shrub species (Muller, 1953; Went, 1942). There is some evidence that exotics have similar responses. For example, Brooks and Berry (2006) reported that *B. rubens* abundance was higher in moist environments, such as under shrubs, while *Schismus* spp. and *Erodium cicutarium* were more prevalent in exposed interspaces and at lower elevations. Despite the known importance of shrub microsites to desert annuals, few studies have examined the role of microsites as opposed to disturbance in regard to exotic establishment. One study reported that exotic annual richness and biomass were more strongly associated with microhabitat features such as shrub canopies and lower topographic positions (i.e. washes) than disturbance (i.e. grazing and OHV use) (Brooks, 1999).

In the Mojave Desert, a small proportion of annual plant species are exotic, yet invasive exotics may constitute a large percentage of the total annual plant biomass (Beatley, 1969; Brooks, 1998). Studies have alluded to the roles of either roads or microsite conditions in exotic annual plant invasions in the Mojave Desert; however, none have examined the two synchronously. The goal of this study is to understand the pattern of exotic as opposed to native species richness and cover relative to roads and microsites. Specifically, we will compare the patterns of natives and exotics as groups, and then perform taxonomically paired analyses to explore the behavior of confamilial native and exotic species in the same habitat. Our results will help us better understand the distinctions between native and exotic species distributions relative to roadside disturbance and microsites in a desert environment. Understanding the relationship of exotic species richness and cover with respect to roads and microsites may offer insight to the value of monitoring programs already in place. In this study, we expect that exotic species richness and cover will decrease with distance from road and vary significantly between road types, and among three microsites consisting of interspaces, and canopies of *Ambrosia dumosa* and *Larrea tridentata*.

2. Methods

2.1. Study area

We conducted our study in Lake Mead National Recreation Area (LMNRA) and on adjacent Bureau of Land Management (BLM) land in Clark County, Nevada and Mohave County, Arizona in the eastern Mojave Desert, USA. We used a Geographic Information System (GIS) to stratify the study area into three polygons to evenly distribute our sampling points throughout the park region. Within selected polygons, we used a GIS to randomly select points along both gravel and paved road corridors that had a $\leq 5°$ slope. From these random points, we established sampling sites along a total of 12 roadsides, including six gravel and six paved surface roads. Average distance between sites was 47 km, minimum distance was 5 km, and maximum was 113 km.

Some current roads in the park were former trails that date back to the 1860s; however, since most have undergone improvements and course changes, categorizing them by age would be difficult. Today, park visitation at LMNRA is relatively high, with over 7.6 million recreational visits in both 2007 and 2008 compared to Yellowstone National Park, which had approximately 3.1 million visits in those same years (NPS Stats, 2009).

Precipitation in the eastern Mojave Desert varies widely both spatially and temporally; however, most effective precipitation occurs during the cool-season months of October–April even though the far eastern Mojave receives some monsoon-season precipitation in July–September. Average annual precipitation for nearby Las Vegas, Nevada is 106 mm while monthly temperatures range from an average low of 1.3 °C in January to an average high above 40 °C in July (Western Regional Climate Center, Reno, NV).

Although Las Vegas reported receiving 47% of normal precipitation during the 2008 growing season (i.e., October 2007–April 2008), areas closer to study sites in LMNRA reported substantially higher levels. In December 2008, two locations within LMNRA, Echo Bay and Callville Bay, reported precipitation approximately three times higher than normal (Western Regional Climate Center, Reno, NV). The dominant plant community within LMNRA is creosote-scrub which is typical for much of the Mojave Desert below 1200 m in elevation (Rundel and Gibson, 1996). Soils of the area are basalt and gypsum derived (Lato, 2006).

2.2. Sampling methods

Sampling was conducted in March 2008 when winter annuals were near peak bloom. Five 100-m transects were positioned parallel to each road starting at 5 m and extending at 10-m intervals out to 45 m from the road edge. Within each distance, two plots containing each of the microsite types (*A. dumosa*, *L. tridentata*, and interspace) were randomly located within each half of the transect. The first *L. tridentata* and *A. dumosa* encountered within 1 m of the transect starting at the zero-meter point represented one sub-plot while the other was located beyond the 50-m point using the same criteria. Each shrub microsite had to be an independent unit (i.e. no overlapping canopies with other dominant shrubs) and greater than 1 m from other selected shrubs within that transect. One interspace microsite was randomly located along each half of each transect for a total of 10 per site. Interspaces were determined as area which was not under the canopy of any shrub. For perennial shrub microsites, percent cover of all understory plant species was recorded using cover categorizations (0–1, 1–2, 2–5, 5–10, 10–25, 25–50, 50–75, 75–95 and >95%) within a 0.25-m^2 frame around the center of the shrub. Interspaces were sampled using the same cover categorizations within a 0.25-m^2 frame. Mid-points of each category were used for analysis.

2.3. Data analysis

The study design was a split–split plot consisting of the whole plot factor road type (levels: gravel or paved) where the 'subject' was each individual road. The design also included the sub-plot factor 'distance' from roadside (five levels: 5, 15, 25, 35, and 45 m) which was applied to each road but harbored multiple sampling transect points within each distance, and the sub-sub-plot factor 'microsite' type (three levels: below *L. tridentata*, below *A. dumosa*, and interspace) which was nested within road and distance. This design was analyzed using an analysis of variance (PROC MIXED) in the software SAS (SAS Institute, 1999). Percent cover of annual species was calculated from the mid-point of the cover category, $\log_{10}$ transformed and modeled with fixed effects of road type, distance, and microsite, along with all possible interactions. Site within road type and its two-way interaction terms with fixed effects were treated as random effects. Natives and exotics were analyzed separately; they were not placed in the same analysis due to concerns about lack of independence. For significant effects ($\alpha = 0.05$), post-hoc pair-wise comparisons were Tukey adjusted to maintain the family-wise error rate at 0.05. Back-transformed least-squares means and SE are reported from the minimum adequate model, determined using the Akaike Information Criterion corrected for small sample size (AICC).

Species richness was modeled using a model with the same fixed and random effects (and expected mean squares) as above, but relative effects rather than parametric quantities based on the raw data were used to estimate significance (Brunner et al., 2002). Tukey post-hoc tests were used to conduct pair-wise tests for significant effects. Relative treatment effects and their associated error and the medians for each treatment are reported.

Distribution of native and exotic species was quite patchy, with some species highly abundant in one site and absent entirely in another. In order to study the behavior of individual exotic species compared to confamilial species within the same site, we created three data sets which contained one exotic species and at least one native in at least three sites (Table 2). Sites were included for the within-family comparison only if they contained all of the species together. A nonparametric ANOVA based on rank-derived relative effects rather than means (Brunner et al., 2002) was employed to analyze the resulting comparisons. Species was a fixed effect in the model under the assumption that the species were unlikely to be competitively excluding one another given the low percentage cover of each individual species considered. This assumption was less tenable in the analysis for overall cover. The nonparametric ANOVA included fixed effects of distance (whole plot), microsite, and species (both sub-plot), along with all of their two- and three-way interactions. Site within road type was modeled as a random effect, along with all two- and three-way interactions with fixed effects. Each point (distance and site combination) was treated as the subject. Post-hoc Tukey tests were applied in the case of significant effects ($\alpha = 0.05$). Effect sizes are reported based on the minimum adequate model determined by AICC, and the relative effects along with median values from the raw data are provided.

3. Results

We identified 64 annual plant species, and six of these (9.4%) were exotics. The exotic species encountered were *Schismus* spp., *B. rubens*, *E. cicutarium*, *Brassica tournefortii*, *Sisymbrium irio*, and *Malcolmia africana*. *Schismus* spp. occurred most frequently (12 of 12 sites) of any exotic followed by *E. cicutarium* (7 of 12 sites). Combined, these two species accounted for 82% of all exotic occurrences at the microsite level. *B. tournefortii* occurred at four sites while *B. rubens*, *M. africana* and *S. irio* each occurred at two sites. Frequently encountered native annuals included *Plantago ovata* (12 of 12 sites), *Pectocarya recurvata* (12 of 12 sites), *Eriophyllum lanosum* (11 of 12 sites), *Cryptantha nevadensis* (11 of 12 sites), and *Chorizanthe rigida* (10 of 12 sites). Frequency data for species are available in Appendix A.

3.1. Percent cover

Both natives and exotics varied by microsite, where annual plant cover was higher under shrubs than in interspaces (Table 1, Fig. 1).

Table 1
Analysis of variance results for overall cover and species richness of exotic and native annual plants in relation to distance from roads and microsite types in the eastern Mojave Desert. Degrees of freedom (df) are reported as numerator, denominator.

Effect	Exotics			Natives		
	df	*F*	*p*-value	df	*F*	*p*-value
Cover (%)						
Road type	1, 10	0.23	0.6449	1, 10	0.14	0.7117
Distance	4, 40	1.94	0.1220	4, 40	0.64	0.6366
Road type × Distance	4, 40	0.16	0.9563	4, 40	0.25	0.9097
Microsite	2, 20	3.80	**0.0399**	2, 20	6.80	**0.0056**
Road type × Microsite	2, 20	0.10	0.9084	2, 20	1.19	0.3237
Microsite × Distance	8, 80	1.31	0.2513	8, 80	1.95	0.0644
Road type × Microsite × Distance	8, 80	0.69	0.6952	8, 80	3.09	**0.0044**
Richness						
Road type	1.0, 8.9	0.13	0.7226	1.0, 9.0	0.24	0.6380
Distance	4.0, 20.6	0.56	0.6941	4.0, 26.2	0.34	0.8479
Road type × Distance	4.0, 20.6	1.63	0.2045	4.0, 26.2	0.14	0.9642
Microsite	1.9, inf[a]	3.06	**0.0491**	1.9, inf	5.77	**0.0039**
Road type × Microsite	1.9, inf	0.21	0.8030	1.9, inf	0.41	0.6483
Microsite × Distance	7.2, inf	1.65	0.1141	7.4, inf	1.76	0.0848
Road type × Microsite × Distance	7.2, inf	1.30	0.2418	7.4, inf	1.09	0.3637

[a] inf = infinite.

We observed no other significant main or two-way effects in the ANOVA involving overall cover of exotics and natives. There was a significant three-way interaction among road type, microsite, and distance for natives but not exotics (Table 1). Post-hoc comparisons revealed only one significant difference in means: paved *L. tridentata* at 15 m (mean = 4.1, lower and upper back-transformed SE bounds = 3.0–5.6) from the road had significantly less native cover than paved *L. tridentata* at 45 m (9.9, 6.9–14.5). Based on this result, the minimum adequate model included microsite as the only fixed effect.

3.2. Richness

Microsite was the most important factor affecting species richness (Table 1; Fig. 2). Because of the marginally significant microsite by distance interaction, richness effect sizes are reported for this interaction (Fig. 3), and it was included in the minimum adequate

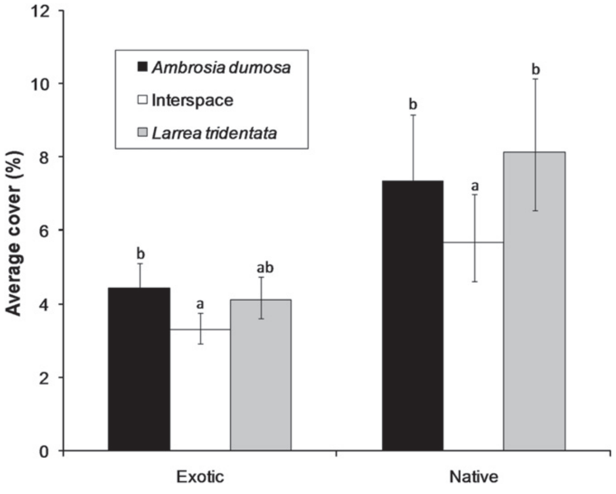

Fig. 1. Back-transformed means and SE for microsite effects in exotic and native annual plant cover in the eastern Mojave Desert. Letters denote significant pair-wise differences after Tukey adjustment ($\alpha = 0.05$).

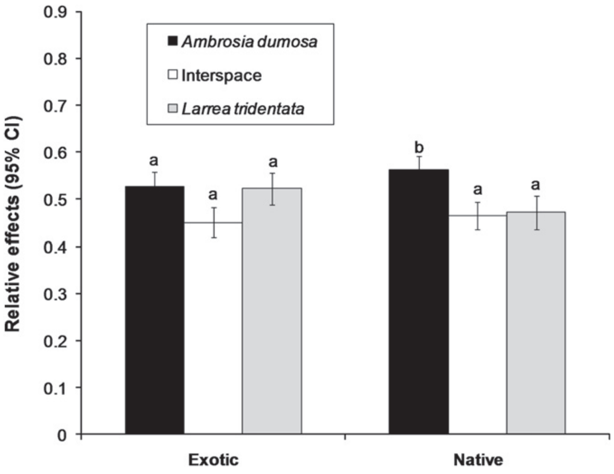

Fig. 2. Relative treatment effects of microsite for exotic and native annual plant species richness. Letters denote significant differences ($\alpha = 0.05$).

Table 2

Nonparametric ANOVA results for confamilial native and exotic species comparisons of cover, eastern Mojave Desert. Degrees of freedom (df) denote numerator degrees of freedom; denominator degrees of freedom were infinite. For Brassicaceae, natives were *Guillenia lasiophylla* and *Lepidium lasiocarpum* while the exotic was *Brassica tournefortii* (3 sites). For Geraniaceae, the native was *Erodium texanum* and the exotic was *Erodium cicutarium* (4 sites). For Poaceae, the native was *Vulpia octoflora* and the exotic was *Schismus* spp. (3 sites).

Effect	df	*F*	*p*-value
Brassicaceae			
Distance	3.8	1.21	0.3037
Microsite	2.0	2.79	0.0613
Distance × Microsite	7.7	0.50	0.8483
Species	2.0	0.39	0.6788
Distance × Species	7.4	1.33	0.2297
Microsite × Species	3.9	2.17	0.0708
Distance × Microsite × Species	14.6	0.59	0.8777
Geraniaceae			
Distance	3.9	0.24	0.9134
Microsite	2.0	0.04	0.9584
Distance × Microsite	7.7	0.24	0.9823
Species	1.0	1.96	0.1617
Distance × Species	3.9	0.02	0.9994
Microsite × Species	2.0	0.17	0.8462
Distance × Microsite × Species	7.7	0.09	0.9993
Poaceae			
Distance	3.9	0.40	0.8030
Microsite	2.0	0.31	0.7370
Distance × Microsite	7.7	0.20	0.9890
Species	1.0	28.36	**0.0000**
Distance × Species	3.8	0.56	0.6857
Microsite × Species	2.0	0.18	0.8317
Distance × Microsite × Species	7.4	0.40	0.9128

model. None of the pair-wise comparisons were significant after family-wise error rate adjustment (data not shown). The richness in interspaces appeared to trend lower further from the road, while the shrub microsites did not show this general trend. There was an apparent interaction between microsite and plant origin, as richness of natives was highest under *A. dumosa* compared to *L. tridentata* and interspaces; richness of exotics was high under both shrub species (Fig. 2). The differences between natives and exotics should be interpreted cautiously because of the limited number of exotic species (six) compared to natives (58). Raw species richness data are provided in Appendix B.

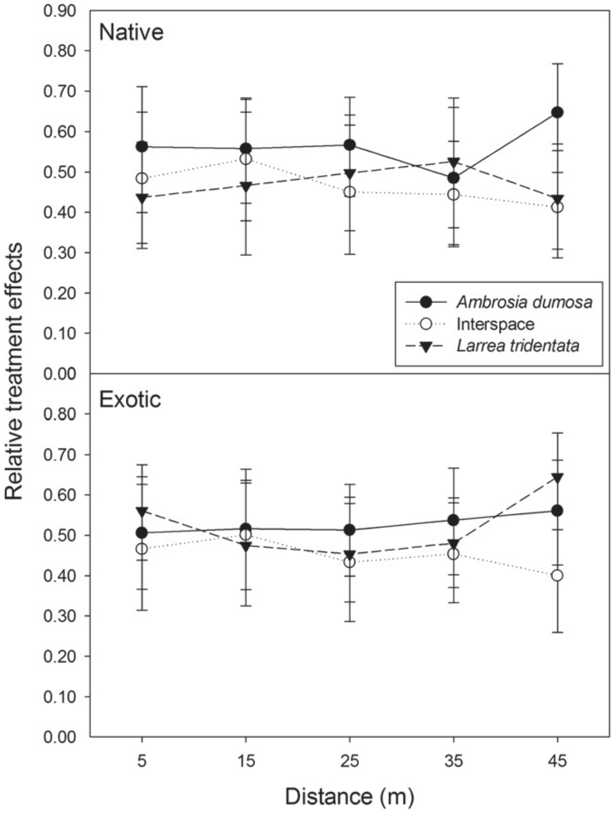

Fig. 3. Relative treatment effects and 95% CI for microsite by distance interaction of species richness.

3.3. *Confamilial comparisons*

None of the confamilial comparisons suggested significant differences between native and exotic species cover relative to their distance from the road (Table 2). There was a marginally significant difference in microhabitat use among species in Brassicaceae (Table 2). Although post-hoc tests did not yield any significant differences (statistical power was likely quite low), qualitatively *B. tournefortii* and *Guillenia lasiophylla* were more abundant under either type of shrub than in interspaces. *Lepidium lasiocarpum* was highly abundant under *A. dumosa*, but was rarer under *L. tridentata* and interspaces (Fig. 4).

4. Discussion

Roads are special relative to other disturbances for three reasons: their overall spatial extent on the landscape, their heavy use by people for transportation of themselves as well as plant and animal agricultural products (all of which can provide the source material for an invasion), and that their shape is both continuous and maximizes the amount of edge abutting undisturbed habitat. Roads could therefore be the ‘incubator’ which allows newly arrived exotics to increase numbers to the point that they become invasive. Looking at species richness tests this role, and looking at plant abundance can be construed as an effort to study the patterns associated with more established invasive exotics relative to roadways.

Our results suggest that native and exotic species are quite similar in cover and richness patterns with respect to roads and microsites. We found little evidence to suggest that proximity to the road edge dictates the richness or cover of native or exotic plant

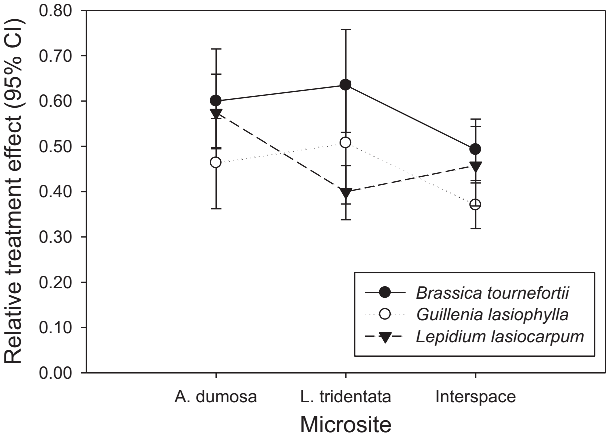

Fig. 4. Relative treatment effects and 95% CI for native and non-native species of Brassicaceae by microsite interaction of species richness.

species. Thus, the invasibility of areas at 45 m from the road appears to be similar to those at 5 m. There were some slight differences in overall native compared to exotic plant cover relative to the species of shrub involved in creating the microsite, but the general patterns were identical. The three confamilial groups that were available for analysis supported the conclusions from the grouped native and exotic species, where we observed little distinction in distribution based on plant origin.

The six exotic species observed in this study are of Eurasian origin, and they include the most common and widespread of all exotic annual species in the Mojave Desert (Kemp and Brooks, 1998). The relatively small number of exotics relative to natives has also been previously reported (Brooks, 1999). In the study by Brooks (1999), five of the 52 annual plants observed were exotic. Since many of the exotic species occurrences in this study were from the common and widespread species *Schismus* spp. and *E. cicutarium*, one could argue that these species would not exhibit the same patterns as newer invaders. However, if roadside habitat is suggested to be prime habitat and a source of exotic propagules invading the greater landscape, one could also argue that the source should have greater abundance than the sink. Yet, our data did not support our expectation that all species, especially successful invaders that capitalize on disturbance to spread, would be more prevalent near roads. Our study is not unique in finding unexpected patterns associated with exotics of varying establishment times. Harrison et al. (2002) expected the long-established exotic species to have consistent densities moving from the base to the tip of a peninsular reserve, but it was the opposite pattern where newer noxious invaders remained consistent and long-established species declined. It is likely that many exotic plant species introductions do not strictly invade new areas along roadways. In fact, *E. cicutarium* has been in North America long before the prevalence of roads (Mensing and Byrne, 1998).

Disturbance takes on many forms other than roads. A phenomenon observed in the Mojave Desert is disturbance around shrubs created by burrowing animals. Thus, where desert is said to be "undisturbed," it might actually have enough disturbance for exotic species to establish. Schiffman (1994) suggested a mutualistic relationship occurs between a burrowing rodent and exotic annuals such as *B. rubens* and *E. cicutarium* since rodent 'precincts' were dominated by weeds more than relatively undisturbed adjacent areas. Other natural disturbance-prone areas might include desert washes. Many of the gravel roads in the study tended to follow natural washes.

Road edge management may also have effects on the invasibility of the roadside habitat. Brooks (2009) reported that roads with berms exhibit higher productivity of *B. tournefortii* at the edge; however, soil type was a stronger factor in the success of *B. tournefortii* with increasing distance from roads. Therefore, underlying microsite characteristics may be the more powerful driver of invasibility. As seen in this study, microsites vary in the amount of exotic and native-plant cover they support. This could have implications for management decisions such as perennial species selection, plant spacing, and how the local exotic species will interact with microsites. For example, if a particular shrub species exhibits a tendency to facilitate exotics more than other shrubs, planting it in a restoration project may enhance exotic establishment.

It is possible that this study did not sample far enough from the road to observe a decrease in annual plant cover and species richness. Exotic cover patterns could change at distances beyond 45 m from roads. In addition, incorporating more shrub species, and including measurements of shrub size and spacing would also be important to examine in future research. Future research could also employ measures such as biomass and seed production of exotics since simple cover measures may not accurately account for the potential exotic pressure on a site. For example, as Trader et al. (2006) found, lower plant density of *B. tournefortii* meant higher biomass and seed production, indicating an inverse relationship between density and individual reproductive output.

5. Conclusions

Some exotic species established in our parks and natural areas over a century ago, while new species regularly threaten to invade. Managers face many difficulties in deciding which species to target and how they should try to control the species (Westman, 1990). In this study, we examined the impacts of roads and shrub/interspace microsites on exotic annual plant cover and richness in the eastern Mojave Desert. Our findings suggest that exotic annual plant distributions along roadsides do not always follow predictable patterns where distance from roadways and surface types are factors. Microsite characteristics may be more prognostic of the invasibility of an area and distributions of exotic plants. Although roadside surveys provide one way to detect incipient exotic populations, these are not suitable for all exotic species, especially those dispersed independently of roads and those that exploit natural disturbances well away from roads.

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Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2009.10.012.

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