

# Effects of an invasive plant on a desert sand dune landscape

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**Abstract** Given the abundance of non-native species invading wildland habitats, managers need to employ informed triage to focus control efforts on weeds with the greatest potential for negative impacts. Our objective here was to determine the level of threat Sahara mustard, *Brassica tournefortii*, represents to meeting regional goals for protecting biodiversity. Sahara mustard has spread throughout much of the Mojave and lower Sonoran Deserts. It has occurred in southern California's Coachella Valley for nearly 80 years, punctuated by years of extremely high abundance following high rainfall. In those years the mustard has clear negative impacts on the native flora. Using mustard removal experiments we identified reductions in native plant reproduction, shifting composition increasingly toward Sahara mustard while decreasing the fraction of native species. High between-year variance in precipitation may be a key to maintaining biodiversity as the mustard is less abundant in drier years. Sahara mustard impacts to the native fauna were much less evident. Of the animal species evaluated, only the

Coachella Valley fringe-toed lizard, *Uma inornata*, demonstrated a negative response to mustard abundance; however the impacts were short-lived, lasting no more than a year after the mustard's dominance waned. Without control measures the long-term impacts to desert biodiversity may rest on the changing climate. Wetter conditions or increased periodicity of high rainfall years will favor Sahara mustard and result in reduced biodiversity, especially of native annual plants. Drier conditions will keep the mustard from becoming dominant but may have other negative consequences on the native flora and fauna.

**Keywords** Sahara mustard · *Brassica tournefortii* · Weed management · Native biodiversity · Natural communities

## Introduction

Exotic species invasions are second only to habitat destruction as a threat to biodiversity (Wilcove et al. 1998; Ludsin and Wolfe 2001; Simberloff 2004). Simberloff's (2003) pragmatic call to remove exotic species before they become established, rather than conduct research to determine their potential impacts, may seem prudent, but fails to address the fact that not all plant invasions result in negative effects (Brown and Sax 2005; Ricciardi and Cohen 2007). An emphasis on predicting the relative invasiveness of species and

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invasibility of landscapes has contributed to a lag in research on the relative impact of invaders (Thomson 2005). The focus on early detection and eradication also does not address the myriad of exotic species already ensconced in otherwise protected habitats worldwide (Usher 1988). Is an exotic species benign, does it directly compete with native species, does it alter ecosystem processes, or does it have potentially desirable effects? Answering these questions has direct implications for the magnitude of response resource managers need to marshal to address each exotic invasion. For those established invaders, management triage is the prudent path, which requires insight into their relative levels of impact (Simberloff 2004; Ricciardi and Cohen 2007; Rinella and Luschi 2007).

While invasive species can have overwhelming negative impacts on native species (Elton 1958), for an exotic species to have broad community impacts, it will likely have to alter ecosystem processes (Vitousek 1986). A number of studies have demonstrated that ecosystem properties would be different in the absence of an invader (Vitousek 1986; Walker and Smith 1997; Gordon 1998; Ehrenfeld 2003). Ecosystem-level changes are most likely when the introduced species possesses characteristics that are divergent from native species (Chapin et al. 1996; Ehrenfeld 2003). Where research has demonstrated invasions of exotic plants having impacts to ecosystem processes, such as nitrogen cycles (Pickart et al. 1998), and fire regimes (Brooks et al. 2004), there have been broad negative impacts to biodiversity. The impacts of invaders can be particularly acute when both the amplitude and frequency of disturbance regimes are altered (Brooks et al. 2004).

It should be noted that not all exotic species invasions result in the loss of species or ecosystem function (Simberloff 1981; Williamson 1996; Brown and Sax 2005). For example, in Hawaii, 4,600 exotic plant species have become established. Of those alien species, 800 are considered invasive and 86 species represent a serious threat to native species or ecosystems (Smith 1985; Vitousek 1990). More specific to the current study, Barrows (1997) reported that adult Coachella Valley fringe-toed lizards (*Uma inornata*), a federally threatened species, did not seem to be affected by the presence of exotic tumbleweed (*Salsola tragus*) on desert sand dunes, whereas hatchling lizards had a positive response, using the tumbleweeds as cover to avoid predation. It is possible that persistent

drought typical of the Coachella Valley never allows *Salsola* to reach densities where floristic diversity or ecosystem functions are negatively impacted. These examples highlight why it should not be assumed that all plant invasions threaten biodiversity, and emphasize the need for reliable and comprehensive information on their effects.

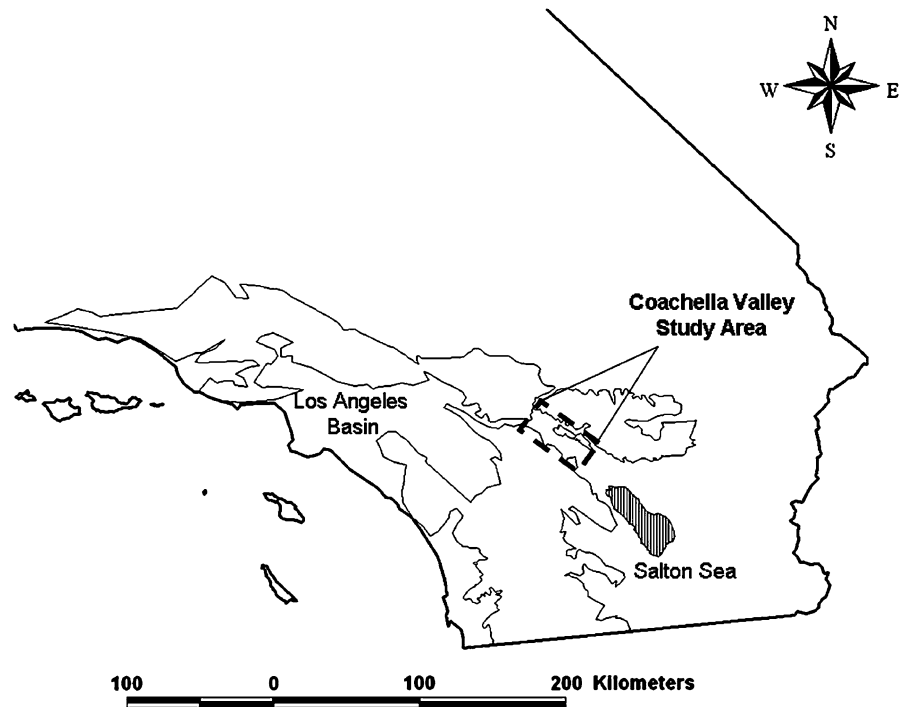
Our objective here was to document the establishment and environmental impacts of the invasive species Sahara mustard, *Brassica tournefortii*, across an aeolian sand landscape. Rather than focus on the effects of this invasion on a single conservation target, we evaluated the impacts at various scales including populations, communities and ecosystem processes. We describe the abundance of Sahara mustard varying with respect to precipitation and responses of the native biota across multiple aeolian sand community types. Through mustard removal experiments we were able to partition impacts of mustard abundance on native plant and animal species and ecosystem processes from otherwise typical community dynamics. Sahara mustard initially invaded the Coachella Valley aeolian sand habitats as early as 1927 and has since expanded over much of the Mojave and lower Sonoran Deserts (Sanders and Minnich 2000). While continuously present in the Coachella Valley since its introduction, this species has been a conspicuous component of the region's flora only in years when annual precipitation has been in excess of long-term means, such as in 1977–1983 (Sanders and Minnich 2000), 1994–1995 and again in 2005 (Barrows, unpubl. data). The ephemeral “explosions” of this exotic species have created an opportunity to examine short and long-term impacts to individual taxa as well as to environmental variables those taxa depend on. Such episodic periods of numerical dominance allowed us to address conditions that promote establishment of an exotic species and to consider how changes in those conditions may impact native species.

## Methods

### Study sites

We analyzed fluctuations of Sahara mustard and native species in the Coachella Valley near Palm Desert, Riverside County, California, from 2002 to 2008 (Fig. 1). The Coachella Valley is a shrub desert with a west to east mean annual rainfall gradient of

**Fig. 1** Study area with respect to southern California, USA. Gray-shade outlined areas represent mountain ranges



125–79 mm (most recent 60 year means, Western Regional Climate Center, Palm Springs and Indio reporting stations). The lowest rainfall years occurred in 2002 and 2007, with just 7–4 mm respectively recorded across the valley floor. In contrast, in 2005 326–210 mm of rainfall was measured, the largest annual rainfall total recorded in the past 50 years for some Coachella Valley locations. Temperatures are also extreme, ranging from a low approaching 0°C in the winter to highs exceeding 45°C commonly recorded during July and August. All precipitation data reported here are based on a July–June rain year.

The experimental mustard removal portion of our study was conducted in the eastern portion of the valley, within the Thousand Palms Preserve (33°47' N, 116°20' W). Additional data, not associated with mustard removal, were collected within the entire rainfall gradient of the valley's available aeolian habitats. The Preserve includes approximately 1,300 ha of contiguous aeolian sand habitats characterized by two primary communities (Barrows and Allen 2007): (1) active sand dunes (low shrub density, high levels of sand movement, high topographic relief); and (2) stabilized sand fields (relatively high shrub density, low hummock topographic relief and low to moderate sand movement). Survey plots in the

western end of the Coachella Valley included a third aeolian community type, ephemeral sand fields. Ephemeral sand fields occurred only near the wetter, windier portion of the valley where there was relatively high perennial shrub density and hummock topography, but also a high degree of sand movement (Holland 1986; Barrows and Allen 2007).

#### Study design

One hundred and twelve 10 m × 100 m (0.1 ha) study plots were established during 2002 to evaluate correlations with rainfall and aeolian community type on the abundance and species composition of annual plants, including Sahara mustard, and associated wildlife species. Eighty-six of those plots were within the Thousand Palms Preserve and 36 occurred at more western locations within the valley. Each plot was marked along its long axis with a short wooden stake at the beginning, middle and end. Study plots were located in a stratified random manner within the three aeolian community types.

Thirty of the study plots in the stabilized sand fields on the Thousand Palms Preserve were selected to conduct mustard removal experiments during 2005. Fifteen of the plots were selected for mustard

removal treatment and 15 were retained as non-weeded control plots. Treatment and control plots alternated across the landscape, with approximately 50 m between paired treatment–control plots. The arrangement of the overall 112 plots was random, however the selection of treatment–control plot pairs was regular-alternating; this allowed for paired plot analyses, minimizing between plot differences that could otherwise confound results. Treatment plots were cleared by hand of Sahara mustard; entire mustard plants, including taproots, were removed from weeded plots and from a 5 m buffer around each plot. Mustard plants germinated after each major rain event in the fall of 2004, and plots were weeded once in late January 2005 when there were at least three age/size classes of mustard seedlings present; no further mustard germination occurred that season. The objective was to weed the sites as early in the growing season as possible in order to minimize any effects (either from the mustard or the weeding effort) on native species germinating at the same time, but late enough so that all mustard plants could be removed in one effort. The tap-rooted mustard seedlings were readily pulled from the loose sand without disturbing adjacent plants. Mean effort required to remove mustard plants was 9.1 person hours/0.1 ha plot, and varied depending on the mustard density (range 3.75–17.5 person hours). Weeded mustard plants were placed outside the experimental areas and were allowed to decompose there.

The distribution of Sahara mustard on the active dune community was patchy compared to the more continuous distribution on the stabilized sand fields. In order to assess its impacts on the endangered Coachella Valley milkvetch, *Astragalus lentiginosus* var. *coachellae*, a plant restricted to communities with more dynamic aeolian sand transport such as the active dunes, paired plots (one weeded, one adjacent control) were selected non-randomly here to capture both high density mustard as well as the occurrence of the sensitive native plants. These plots were smaller than those described previously (5 m × 10 m, 0.005 ha). Initial weeding occurred in mid February 2005, using the same technique as described above. To assess impacts to sensitive fauna on active dunes, paired 2.5 ha sites were selected (again one weeded, one control). Within those sites, six 10 m × 100 m plots were randomly located and surveyed.

## Vegetation and soil measurements

Vegetation density and species composition were measured on each of the 112 plots, including those used in the mustard removal experiments, each year in March–April from 2002 to 2008. Annual plants were also sampled on experimental treatment and control plots in November 2005 after October rains resulted in early plant germination that year. Perennial shrub density was recorded within the entire 10 m × 100 m treatment plot. Annual plant density and cover were measured within a 1 m<sup>2</sup> sampling frame placed at 12 locations along the midline of the plot. Four frames were sampled on alternating sides of the center line leading into the plot from both the beginning and ending stakes; an additional four frames were sampled at the center point (two on each side of the stake) of each plot. In each frame all individual plants were counted by species to determine their densities, and each species was estimated for its percent cover. For frames with mustard present, an estimate of mustard cover to the nearest 1% was made first, and then the mustard was removed so that cover estimates could be made for those plant species occurring below the mustard canopy within the same frame. These values were then averaged for each species for the 12 frames of each plot.

Soil seedbank composition in the mustard removal experiment was measured from samples collected in the fall of 2006. Approximately 300 g soil surface samples (from a depth of roughly 2 cm and an area of 400 cm<sup>2</sup>) were collected at the center stake and at each end of the 30 plots used in the mustard removal experiment. A ½ cup (111 cm<sup>3</sup>) portion was grown in a greenhouse during winter 2006–2007 following methods adapted from Brenchley and Warrington (1930) and modified by Young and Evans (1975). Seed bank density and species richness were measured by counting the number of germinated seedlings for each species.

Sand compaction has been described as a key habitat variable for Coachella Valley fringe-toed lizards (Barrows 1997) and serves as a quantitative measure of sand stabilization. Sand compaction was measured at 25 points, approximately 4 m apart, along the midline of each plot, each year, using a hand-held pocket penetrometer with an adapter foot for loose soils (Ben Meadows Company, Janesville, WI, USA).

### Vertebrate measurements

Vertebrates were sampled during May–July 2002–2007. The fine aeolian sand of the Thousand Palms Preserve created an opportunity unique to sand dunes to quantify the occurrence and abundance of all terrestrial species occurring within plots with equal detectability. Each vertebrate species and many arthropods that traversed the sand surface could be identified to species and age class by their diagnostic tracks left in the sand. Ground-based species left easily identifiable tracks, and so their ability to avoid detection by differences in activity times, cryptic coloration, or stealthy behavior was nullified. Because late afternoon and evening breezes would “wipe the sand clean” the next day’s accumulation of tracks could not be confused with those from the previous day. Vertebrate surveys began each morning after the sand surface temperature had risen sufficiently so that diurnal reptiles were observed to be active. In this way surveys documented tracks that occurred during the previous night and the current early morning. Surveys often did not include tracks created mid-day through early evening, because afternoon and evening breezes typically removed evidence of them prior to surveys conducted the following morning. Surveys continued until late morning when the high angle of the sun reduced the observer’s ability to distinguish and identify the tracks across the sand. One or two observers working in tandem completed a survey on a given plot in 10–15 min, recording all fresh tracks observed within the plot. Tracks were followed off the plot if it was necessary to confirm a species’ identification and to ensure that the same individual was not crossing the same plot repeatedly, thus avoiding an inflated count of the individuals active on that plot. Each plot was re-surveyed six times between May and July each year from 2002 to 2007. Data from the repeated samples were then summarized as means per plot per year.

### Invertebrate measurements

Arthropods were sampled using dry pitfall traps in April of 2003–2007, and again in September of 2005. Pitfall traps, cups with an 11 cm diameter mouth and 14 cm deep, were placed at both ends and at the middle of each plot for a total of three pitfalls/plot for

each of the 112 plots. All arthropods were identified to the species level. Arthropod data are presented here as the total individuals/plot (combined counts for the three pitfall traps).

### Data analyses

Our data did not conform to a normal distribution and so nonparametric statistics were used throughout. For analyses not based on paired plots, Mann–Whitney *U* tests were employed to detect between treatments or between year differences (Zar 1974). For analyses that were based on paired plots (i.e. experimental mustard removal), a Wilcoxon Signed Ranks test was employed, which is nonparametric analogue of a paired *t*-test (Zar 1974). This allowed us to determine treatment effects and minimize idiographic plot differences. In all cases  $P \leq 0.05$  was used as a threshold for statistical significance.

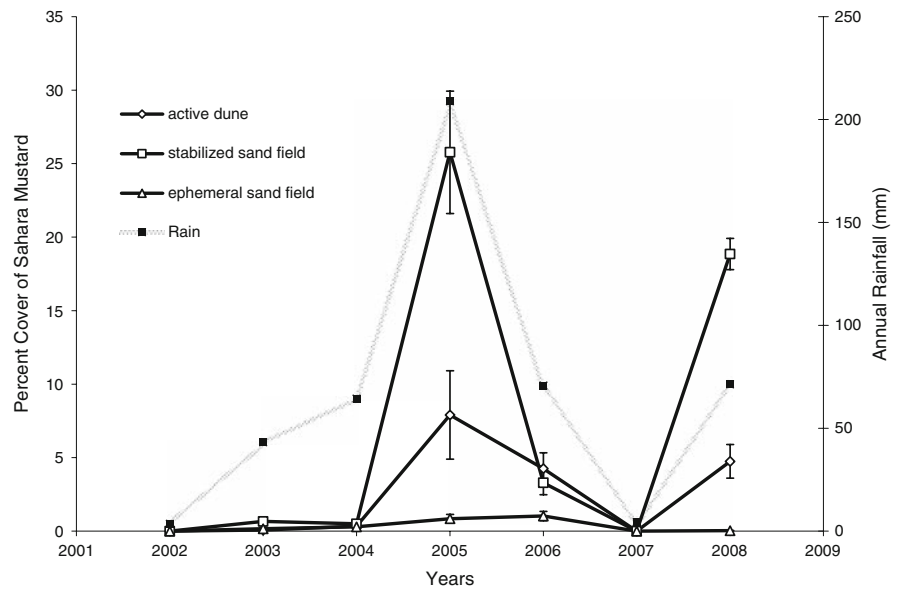
## Results

### Patterns across the aeolian sand landscape

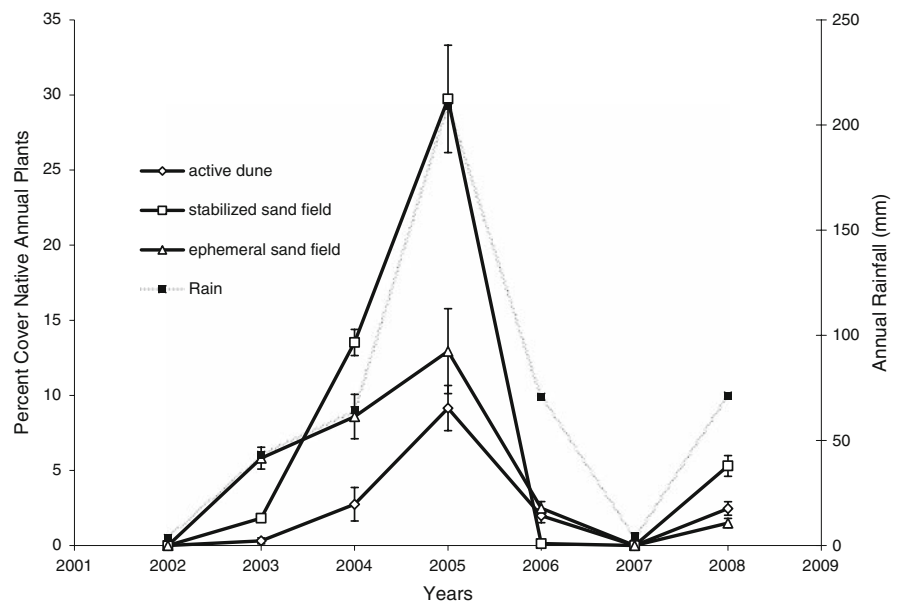
Mustard responses varied temporally and spatially with both rainfall and community type (Fig. 2). No annual plants, including Sahara mustard, occurred on any of our plots in 2002 or 2007 due to drought conditions; spatial and temporal variation in the percent cover of native annual plants were similar to that of the mustard (Fig. 3). Between 2004 and 2005 we measured increases in mustard cover in both stabilized sand field (Mann–Whitney *U* test,  $P < 0.0001$ ), and active dune (Mann–Whitney *U* test,  $P < 0.0001$ ) communities. As the active dunes and stabilized sand fields occurred within the same rainfall regime. The different levels of increase were community-specific rather than due to differences in available water.

Native annual plants responded to annual variation in precipitation as well. In 2003 and 2004 the overall percent cover of native annual plants exceeded that for Sahara mustard (Wilcoxon Signed Rank test,  $P < 0.0001$  for both years) (Fig. 4). Even in 2005 the cover of native annuals exceeded that of mustard (Wilcoxon Signed Rank test,  $P < 0.032$ ). Once again in 2007 there was insufficient rain to germinate plants. However, in 2006 and 2008 there was a shift

**Fig. 2** Temporal and spatial patterns of Sahara mustard percent cover, compared to rainfall, across the aeolian sand communities of the Coachella Valley during March–April 2002–2008. Error bars indicate one standard error



**Fig. 3** Temporal and spatial patterns of percent cover of native annual plants, compared to rainfall, across the aeolian sand communities of the Coachella Valley during April 2002–2008. Error bars indicate one standard error



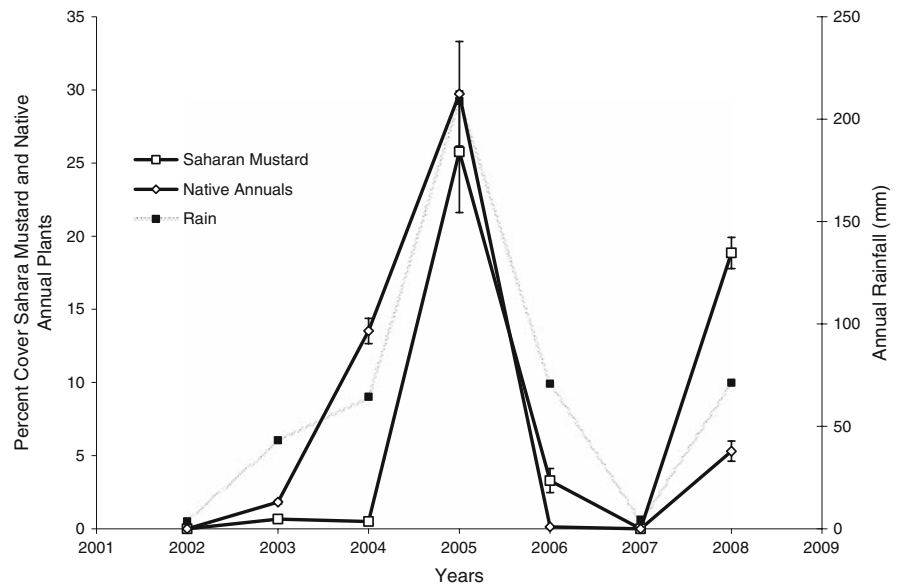
when Sahara mustard cover exceeded native cover (Wilcoxon Signed Rank test,  $P < 0.001$ , both years).

#### Mustard removal experiments

Differences in native annual plant species richness, density and percent cover between weeded and control (non-weeded) plots are shown in Table 1. There was no detectable impact on species richness. In both 2005 and

2008, annual plant species occurring on both weeded and control plots with densities  $\geq 0.1/m^2$  included *Abronia villosa*, *Camissonia claviformis*, *Cryptantha* spp. *Geraea canescens*, *Eremalche exilis*, *Oenothera deltoides*, and *Palafoxia arida*. The strongest effect was on the percent cover of native annuals, with nearly double the native annual plant cover on weeded plots in 2005. Functionally, reduced cover resulted in fewer stems and fewer flowers. *Oenothera deltoides*,

**Fig. 4** Temporal patterns of Sahara mustard and native annual plant percent cover on stabilized sand fields with respect to variation in annual precipitation during April 2002–2008. Annual plant species included here are listed in Table 1. Error bars indicate one standard error



**Table 1** Impacts of Sahara mustard on native annual plant species

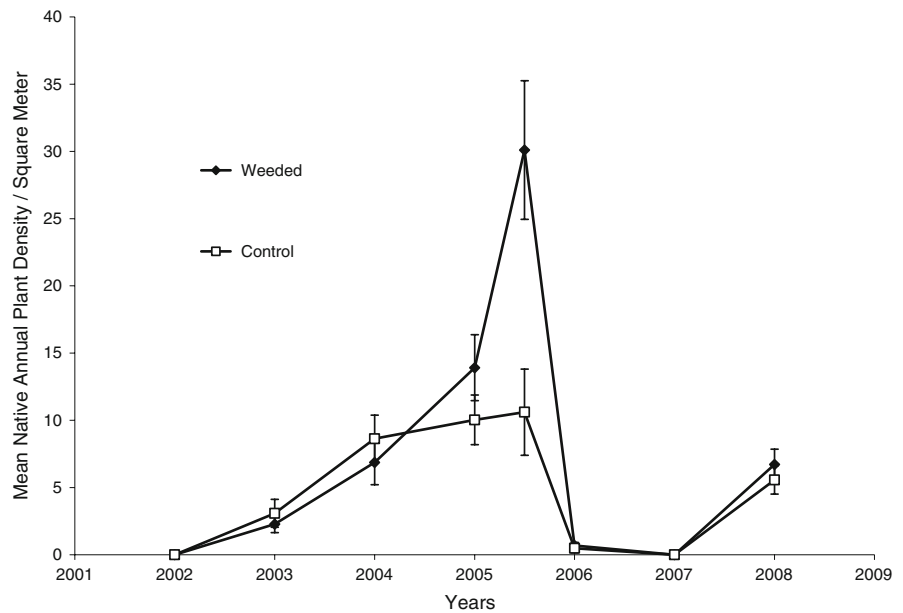
	Weeded	Control
Species richness		
Mean	9.4	8.4
Standard Error	0.476	0.412
Wilcoxon Signed Ranks test	$P = 0.136$	
Density		
Mean	14.063	10.030
Standard Error	2.430	1.847
Wilcoxon Signed Ranks test	$P = 0.036$	
Percent cover		
Mean	41.232	23.343
Standard Error	5.952	3.743
Wilcoxon Signed Ranks test	$P = 0.036$	

(dune primrose), on weeded plots averaged more than 50 flowers per plant whereas those on control plots averaged less than ten flowers (Wilcoxon Signed Ranks test,  $P = 0.005$ ). No additional mustard weeding occurred in 2008; however each of the experimental plots were re-surveyed to determine if there were lasting impacts to the weeding experiments of 2005. In 2008 dune primrose was the only native annual to occur in lower densities on plots weeded in 2005 compared to the non-weeded control plots (Wilcoxon Signed Ranks test,  $P = 0.007$ ).

Active sand dunes are an important habitat for a federal and California State designated endangered annual plant species, the Coachella Valley milkvetch. Although the density and cover of mustard was lower and patchier on active sand dunes, some dense mustard patches did occur there. Two and a half months after the milkvetch were “released” from the dense mustard canopy by weeding they averaged more than 40 seed pods per plant ( $n = 52$ , range 0–270, 13% had no pods) whereas those that remained beneath the mustard canopy averaged less than five pods ( $n = 29$ , range 0–20, 41% of the plants had no seed pods). These differences between weeded and control plots were significant (Mann–Whitney  $U$  test,  $P < 0.0001$ ).

Comparisons of the cumulative density of native annual plants on weeded and control plots are shown in Fig. 4. After the near record precipitation in the 2005 rain year, another 54.5 mm of rain fell on the plots in October 2005. This event catalyzed a second wave of annual plant germination in the fall of 2005 (Table 2). The difference in native annual plant density between the weeded and control plots in the November of 2005 was significant (Wilcoxon Signed Ranks test,  $P = 0.001$ ) (Fig. 5). In addition to native annual plant germination, the mustard germinated as well. Mean Sahara mustard densities on the previously weeded plots was 124.5 plants/m<sup>2</sup> (range 47–284) whereas on the control plots the mean density was 289.2 plants/m<sup>2</sup> (range 46–920) (Table 2). Only 11.5 mm of rain fell

**Fig. 5** Temporal comparison of the density of native annual plants on 15 paired plots where all Sahara mustard was removed (weeded) versus un-weeded (control). Weeding occurred in January 2005 prior to the germination of most native annual plants. Plant density was recorded as a mean count/m<sup>2</sup> for all native species combined during April 2003–2008, and additionally during November of 2005. Error bars indicate one standard error



through the following winter and spring; all annual plants within the stabilized sand field community, including the mustard, withered and died prior to setting seed. The only exception was on the active dunes where plants were able to flower and set seed. There was insufficient additional rain to stimulate any annual plant germination through 2007. In 2008 there were no statistical differences in mustard density between weeded and non-weeded plots (Wilcoxon Signed Ranks test,  $P = 0.116$ ), although there was a significant increase of native annual plants on the weeded plots (Wilcoxon Signed Ranks test,  $P = 0.036$ ).

To evaluate longer-term impacts to native plants we collected soil samples from the weeded and control plots in the fall of 2006 to analyze seed bank composition. Relatively few plants germinated from our soil samples, either due to small samples and/or high spatial variance or due to a depletion of the seed bank with no seed set following the October 2005 rain event. The mean number of native annuals germinating from three samples/plot for the weeded sites was 1.364, or roughly 34 plants/m<sup>2</sup>; for the control plots just 0.364 plants germinated (9 plants/m<sup>2</sup>) (Mann–Whitney  $U$  test,  $P = 0.268$ ). The mean number of Sahara mustard plants germinating from three samples/plot for the weeded plots was 1.636 (41 plants/m<sup>2</sup>); for the control plots it was 5.273 (132 plants/m<sup>2</sup>) (Mann–Whitney  $U$  test,  $P = 0.333$ ). Although these mean values

indicate a potential treatment effect, the sampling effort appeared to be insufficient to statistically detect one.

Harvester ant (*Pogonomyrmex californicus*, *P. magnacanthus*, and *Messor pergandieri*) mean abundance appeared unaffected by the presence or absence of mustard in the stabilized sand fields (Wilcoxon Signed Rank test,  $P = 0.124$ ). Similarly on the active dunes there were no significant differences for harvester ants between weeded and control plots in either during or immediately following the dense mustard conditions in 2005 or 2006 (Mann–Whitney  $U$  test,  $P = 0.719$ , 0.216). Total beetles, which comprised the pooled abundance of approximately 40 species, were more abundant on the stabilized sand field weeded treatments in 2005 (Wilcoxon Signed Rank test,  $P = 0.018$ ), but showed no differences between weeded and control plots on active dunes in either 2005 or 2006 (Mann–Whitney  $U$  test,  $P = 0.942$ , 0.215).

Five species of vertebrates, two reptiles and three mammals, were analyzed to determine their response to the weeding treatments (Table 3). Flat-tailed horned lizards (*Phrynosoma mcallii*), round-tailed ground squirrels (*Spermophilus tereticaudus chlorus*), and Merriam's kangaroo rats (*Dipodomys merriami*) demonstrated no response to the mustard removal. Only Coachella Valley fringe-toed lizards had a positive response to mustard removal in 2005. There were no



**Table 2** Differences in germination rates of annual plants measured after a large rainfall event in October 2005

	Weeded	<i>P</i>	Control
Native annual species richness			
Mean density	7.857		5.929
Wilcoxon Signed Ranks test		0.002	
<i>Abronia villosa</i>			
Mean density	3.143		2.185
Wilcoxon Signed Ranks test		0.152	
<i>Oenothera deltooides</i>			
Mean density	3.476		0.649
Wilcoxon Signed Ranks test		0.002	
<i>Geraea canescens</i>			
Mean density	7.214		1.333
Wilcoxon Signed Ranks test		0.013	
<i>Palafoxia arida</i>			
Mean density	7.929		2.952
Wilcoxon Signed Ranks test		0.001	
<i>Camissonia claviformis</i>			
Mean density	2.536		1.048
Wilcoxon Signed Ranks test		0.101	
<i>Baileya pauciradiata</i>			
Mean density	0.226		0.042
Wilcoxon Signed Ranks test		0.012	
<i>Cryptantha</i> sp.			
Mean density	5.571		2.393
Wilcoxon Signed Ranks test		0.001	
<i>Brassica tournefortii</i>			
Mean density	124.488		289.190
Wilcoxon Signed Ranks test		0.002	
<i>Schismus barbatus</i>			
Mean density	28.524		15.060
Wilcoxon Signed Ranks test		0.006	

Density values represent means (plants/m<sup>2</sup>) from 15 plots for both weeded and control treatments. There were 13 degrees of freedom for each of the *t*-tests conducted; values presented here are *P*-values resulting from those tests

differences between these paired plots in any of the years prior to or following 2005 (Fig. 6). Additional plots were established in the active dunes to determine if the lizard responded similarly in that community. Unlike the stabilized sand fields, mustard plants that germinated after the October 2005 rains continued to grow and produced flowers and seed. Here we weeded those plots designated for treatment in both 2005 and 2006 (unlike the stabilized sand fields where there was

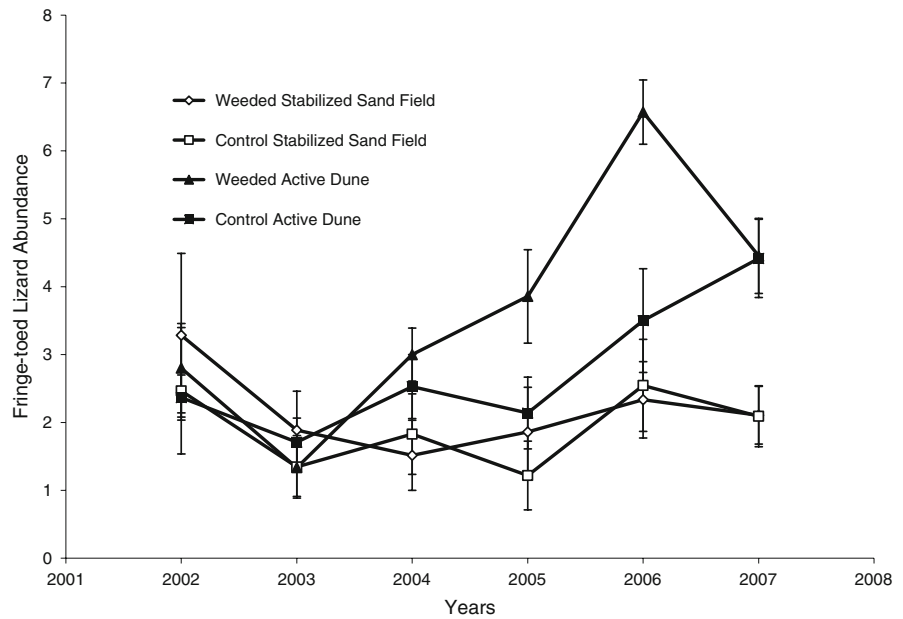
**Table 3** Impacts of Sahara mustard on indigenous vertebrate species

	Weeded	Control
Coachella Valley fringe-toed lizard		
Mean	2.505	1.629
Standard Error	0.787	0.641
Wilcoxon Signed Rank test	<i>P</i> = 0.027	
Percent change 2004–2005	37%	–17%
Flat-tailed horned lizard		
Mean	0.138	0.111
Standard Error	0.057	0.046
Wilcoxon Signed Rank test	<i>P</i> = 0.717	
Percent change 2004–2005	–49%	–55%
Round-tailed ground squirrel		
Mean	0.915	1.004
Standard Error	0.158	0.171
Wilcoxon Signed Rank test	<i>P</i> = 0.433	
Percent change 2004–2005	44%	59%
Desert kangaroo rat		
Mean	6.213	5.287
Standard Error	0.324	0.383
Wilcoxon Signed Rank test	<i>P</i> = 0.209	
Percent change 2004–2005	46%	33%
Merriam's kangaroo rat		
Mean	3.287	3.695
Standard Error	0.433	0.368
Wilcoxon Signed Rank test	<i>P</i> = 0.211	
Percent change 2004–2005	78%	81%

nothing left to weed). The differences in fringe-toed lizard abundance between weeded and control plots increased from a mean of 1.97 in 2005 (Mann–Whitney *U* test, *P* = 0.022) to a mean of 3.36 in 2006 (Mann–Whitney *U* test, *P* = 0.015), (Fig. 6).

Comparing sand compaction from 2004 to 2005 on aeolian sand habitats throughout the Coachella Valley, sand compaction increased on 89% of our plots. On our weeded and control plots in 2005 the difference in sand compaction was slight (weeded mean = 0.202 kg/cm<sup>2</sup>; control mean = 0.228kg/cm<sup>2</sup>), but compaction was consistently less on weeded plots as compared to adjacent control plots (Wilcoxon Signed Ranks test, *P* = 0.012). Compared to 2004, there was a mean decrease in sand compaction of 0.017 kg/cm<sup>2</sup> on the weeded treatments, whereas there was a mean increase of 0.032 kg/cm<sup>2</sup> on the

**Fig. 6** Patterns of Coachella Valley fringe-toed lizard abundance on paired plots where Sahara mustard was removed (weeded) and left in situ (control) on both active dune and stabilized sand field community types. Lizard abundance was recorded as the mean detections/0.1 ha during May–July 2002–2007. Error bars indicate one standard error



control plots. However, that difference may have been the result of the activity associated with physically removing the mustard plants on the experimental plots. Within the stabilized sand field community on the 20 plots where there was no mustard removal, there was no correlation between percent mustard cover and a percent change in sand compaction from 2004 to 2005 (Pearson's pairwise correlation,  $r = 0.134$ ).

## Discussion

Our analyses were conducted at two scales: across the remaining aeolian sand landscape of the Coachella Valley, and more intensively within the eastern valley where mustard densities far exceeded those in the windier and wetter western valley. This allowed us to describe broad spatial and temporal patterns as well as specific species response to experimental mustard removal. Sahara mustard's occurrence and effects were uneven across the aeolian sand communities and native species that comprise them. The mustard's impact on arthropods and vertebrates was generally benign except with regard to the endemic fringe-toed lizard, a species listed as threatened (Federally) and endangered (State of California) and a focus for local conservation efforts. This species is consistently more abundant in aeolian sand communities with higher sand dynamics such as

the active dunes (Barrows and Allen 2007) where the mustard densities were lower, yet measurable negative impacts were still evident.

Differences between fringe-toed lizard abundance on weeded versus control plots on both active dunes and stabilized sand fields lasted only as long as the mustard did. After 2005 on the stabilized sand fields, and 2005 and 2006 on the active dunes, any measurable negative impact from the mustard had disappeared. From the perspective of fringe-toed lizards the aeolian sand communities appear to be resilient to this perturbation. Temporal fluctuations in fringe-toed lizard populations are closely tied to annual precipitation, especially in active dunes (Barrows 2006). The decline in lizard numbers was therefore not surprising after low rainfall in 2006 and essentially no rain in 2007. However, the lizard population on the active dune control plots increased through 2007. Harvester ant and beetle populations, both important lizard foods (Barrows 2006), also increased on the active dune control plots relative to the weeded plots in 2007 (Barrows, unpubl. data). Whether these latent resource increases were related to the mustard density the prior year is tantalizing but untested.

Persistence of Sahara mustard on active dunes in 2006 was a result of the greater ability of deep aeolian sand to hold water (Seely 1991; Lei 2004; Rosenthal et al. 2005). The high rainfall of the winter of 2005 coupled with a short but intense rainfall period in the

fall of 2005 provided ample water storage in the dunes. Annual plants germinating after the fall 2005 rains were able to utilize that stored water and complete their flowering and seed set cycles in the spring of 2006. The stabilized sand field sands are shallow and are interspersed with clay lenses both which limit water storage capacity. Plants germinating there after the fall 2005 rains withered and died before flowering and setting seeds.

Sahara mustard's effects on native annual plants were negative for all species we measured. In 2005 on the stabilized sand fields the mustard formed a thick, inter-meshed canopy between 0.3 m and 1.0 m from the ground. Native annuals under the mustard canopy were often taller, and were etiolated, at the expense of producing branches, flowers and fruits. For those species measured, the result was an 80–90% reduction in flower and seed production for native annuals growing beneath the mustard canopy compared to those released from mustard competition. The following year's composition of germinating annual plants shifted from being native to Sahara mustard dominated. Subsequent seed bank analyses trended in the same direction, but were not statistically significant, possibly due to high spatial variance in seed distributions and insufficient sample size.

It is important to remember that this was not the first invasion of Sahara mustard in the Coachella Valley. Sahara mustard has occurred there for nearly 80 years, with years of “explosive” abundance in 1977–1983, 1994–1995 and again in 2005 (Sanders and Minnich 2000; Barrows, unpubl. data). Each of these periods of mustard dominance corresponded to periods of precipitation that were at least double annual means. While we were not able to quantify the pre 1927 mustard invasion conditions, there likely were impacts to the abundance and relative frequency of the native flora and fauna. Nevertheless, the native species were able to re-establish numerical dominance during moderate rainfall years following each “explosion” by the mustard. A key to understanding these patterns may lie in the variability of precipitation in the lower Sonoran Desert. Pake and Venable (1995) were able to model coexistence in Sonoran Desert annual plants, including a non-native invasive grass, *Schismus barbatus*, by including the variation in precipitation and the plants' differential responses to that variation.

The high degree of variation in desert rainfall provided conditions for intermittent “explosions” of

Sahara mustard as well as the continued coexistence of native annuals and follows the theoretical framework proposed by Davis et al. (2000). Our data showed that native desert annuals' cover exceeded that for Sahara mustard during the low to moderate rainfall years of 2003 and 2004, despite a similar mustard explosion in 1994–1995. Based on their work with Sahara mustard in greenhouse studies, J. Holt and R. Marushia (unpubl data) concluded that rather than having any particular ability to withstand heat or drought, its success in an arid ecosystem may be due to its rapid phenology during wet years. Our data are consistent with that conclusion. Fall and early winter rains may favor Sahara mustard's abundance whereas the onset of rains in later winter and early spring may give a competitive edge to the native flora. Larger rainfall accumulations occurred in February and March in both 2003 and 2004 whereas in 2005 and 2008 the greater rainfall events were in November and December. The ability of native desert annuals to tolerate moderate droughts, and complete their life cycles during those conditions may prevent an erosion of biodiversity.

Within the adaptive strategies for plants presented by Grime (2001), native sand dune plants are most closely aligned with his “stress tolerant” category. The stresses that dune plants tolerate include wind erosion, sand abrasion, drought and low nutrients (Pickart et al. 1998). As long as those processes and characteristics are present, this community may be resistant to invasions from weeds, or ruderal species (*sensu* Grime 2001). This prediction is supported by our empirical data. Sahara mustard became dominant within the aeolian sand communities only when and where stresses from drought and wind erosion were reduced. Our results are consistent with community ecology theory as well; there were higher levels of “niche opportunity” (low resistance to invasibility) (Shea and Chesson 2002) and by far the highest Sahara mustard densities in the stabilized sand field community where wind erosion was reduced due to higher shrub densities and lower sand movement. The community with the highest levels of wind erosion and abrasion, the ephemeral sand fields, had the lowest niche opportunities (highest resistance to invasibility) and the lowest occurrence of Sahara mustard. The intensity and interaction between wind abrasion and available soil moisture appears to dictate where and when Sahara mustard can dominate aeolian sand communities;

rainfall dictates mustard density on a temporal scale, and wind and sand abrasion determines its density on a spatial scale.

A long-term threat to the biodiversity of the aeolian sand communities of the Coachella Valley would be manifested variability in annual rainfall was reduced, especially if late fall and winter rains were higher and more consistent. Some climate change models (i.e. McCabe et al. 2004) indicate the potential for increased wet patterns for the southwestern US. Increased rain with fewer intervening droughts would result in higher mustard density, and so put the dunes on a trajectory to reduced plant diversity and increased stabilization (Lancaster 1995; Lancaster and Baas 1998). Such a scenario could alter the aeolian processes that maintain the dynamic character of these communities and perhaps cross a resilience threshold cascading these communities toward further and permanent stabilization. However, Hayhoe et al. (2004), the IPCC (2007) and Seager et al. (2007) all suggest that the southwestern US. will likely experience reduced precipitation, a prediction consistent with observed weather patterns of the past decade. The changing dynamic of drought and wet weather fluctuations will impact the intensities and location of future Sahara mustard invasions by changing the stresses, and niche opportunities that currently restrict or facilitate its occurrence. While a drier weather pattern would inhibit Sahara mustard, impacts to native desert biodiversity would depend on the severity of the predicted drought patterns.

Applied research should provide decision support for managers (Buckley 2008) and our results, by putting the threats posed by Sahara mustard into a temporal and spatial context, inform land managers how they could allocate their limited resources for controlling this exotic species. The modest mustard control we conducted during the course of our research produced short-term measurable benefits to species and processes. Three years later there were few lasting indications of the previous mustard removal. However dune primrose, a species positively associated with active dunes and higher levels of sand and wind abrasion, continued to have higher densities on the previously weeded plots. The dune primrose response indicates a shift in ecosystem processes toward reduced sand movement and abrasion on the non-weeded plots, consistent with predictions based on Lancaster and Baas' (1998) results. In the region encompassed by our study, species associated with high aeolian sand

movement, such as the Coachella Valley fringe-toed lizard and milkvetch, had the greatest potential to be negatively effected by Sahara mustard invasions. Those species occur in their greatest densities on the active dunes and ephemeral sand fields (Barrows and Allen 2007), communities that appear to be resistant to mustard invasions. Managers should be vigilant for increased mustard dominance on these communities, but if current patterns continue control of mustard there may not be warranted.

Beyond endangered species management, our experimental mustard removal plots had an additional visual benefit to area visitors who were able to see a desert wildflower display "released" from the monochrome canopy of the mustard. Native wildflower densities are highest in the more stabilized habitats where the Sahara mustard can dominate. If land managers value maintaining those wildflower displays, or value maintaining the lower densities of aeolian sand movement-sensitive species also found there, then control of the mustard on those communities during wetter years may be an appropriate management direction. If mustard control is pursued, another consideration is that less than complete mustard control may have little impact on future mustard abundance during wet years. Trader et al. (2006) found that Sahara mustard thinning, without complete removal, increased the volume of seeds produced by those mustard plants that remained and could result in a greater contribution to seed banks than with no control at all. Managers need to put these findings into the context of their local rainfall regimes, soil types and wind characteristics.

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