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ORIGINAL PAPER

Declines in a ground-dwelling arthropod community during an invasion by Sahara mustard (*Brassica tournefortii*) in aeolian sand habitats

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Abstract Sahara Mustard (*Brassica tournefortii*; hereafter mustard), an exotic plant species, has invaded habitats throughout the arid southwestern United States. Mustard has reached high densities across aeolian sand habitats of southwestern deserts, including five distinct sand habitats in the eastern Coachella Valley, California. We examined trends in ground-dwelling arthropod community structure concurrent with mustard invasion in 90 plots within those habitats from 2003 to 2011 (n = 773 plot·years). We expected arthropod communities to respond negatively to mustard invasion because previous work documented significant negative impacts of mustard on diversity and biomass of native plants, the primary resource base for many of the arthropods. Arthropod abundance and species richness declined during the study period while mustard cover increased, and arthropod metrics were negatively related to mustard cover across all plots. When controlling for non-target environmental correlates (e.g. perennial frequency and precipitation) and for potential factors that we suspected of mediating mustard effects (e.g. native cover and sand compaction), negative relationships with mustard remained statistically supported. Nevertheless, arthropod richness's relationship decreased slightly in strength and significance suggesting that mechanistic pathways may be both direct (via habitat structure) and indirect (via native cover suppression and sand compaction). However, mechanistic pathways for mustard effects, particularly on arthropod abundance, remain unclear. Most arthropod taxa, including most detritivores, decreased through time and were negatively related to mustard cover. In contrast, many predators were positively related to mustard. In total, our study provides substantial evidence for a negative effect of Sahara mustard on the structure of a ground-dwelling arthropod community.

Keywords Community structure · Arid environments · Invasive species impacts · Bottom-up effects · Aeolian sand dunes

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Introduction

Invasive exotic plants have wide ranging effects on community structure, ecosystem properties, and ecosystem services (Levine et al. 2003; Pejchar and Mooney 2009; Vilà et al. 2011). Extensive literature describes what makes an exotic plant species invasive (Vilà and Weiner 2004; van Kleunen et al. 2010a, b), how they invade (Von Der Lippe and Kowarik 2007; Pyšek et al. 2011), and the consequences of invasion for native communities (Powell et al. 2011; Vilà et al. 2011). Studies have mainly focused on direct negative effects of invasion on native plant species through competition and the alteration of abiotic processes (White et al. 2006), as well as consequences of plant community alterations for ecosystem properties such as total biomass, size of nutrient pools, and disturbance regimes (Ehrenfeld 2010).

In contrast, bottom-up and indirect effects of invasive plants on higher trophic levels are poorly studied. Impacts on consumers are documented but tend to be less consistent and lower in magnitude than direct impacts on native plants (Vilà et al. 2011), and effects on consumers can be weak to non-existent (Osunkoya et al. 2011) or specific to certain functional groups (Herrera and Dudley 2003; de Groot et al. 2007; Fork 2010). Furthermore, studies that simultaneously investigate impacts of plant invasions on multiple trophic levels are scarce (Valtonen et al. 2006; de Groot et al. 2007; Gerber et al. 2008). Further study is needed to understand invasive plant impacts on consumers (Levine et al. 2003; Vilà et al. 2011).

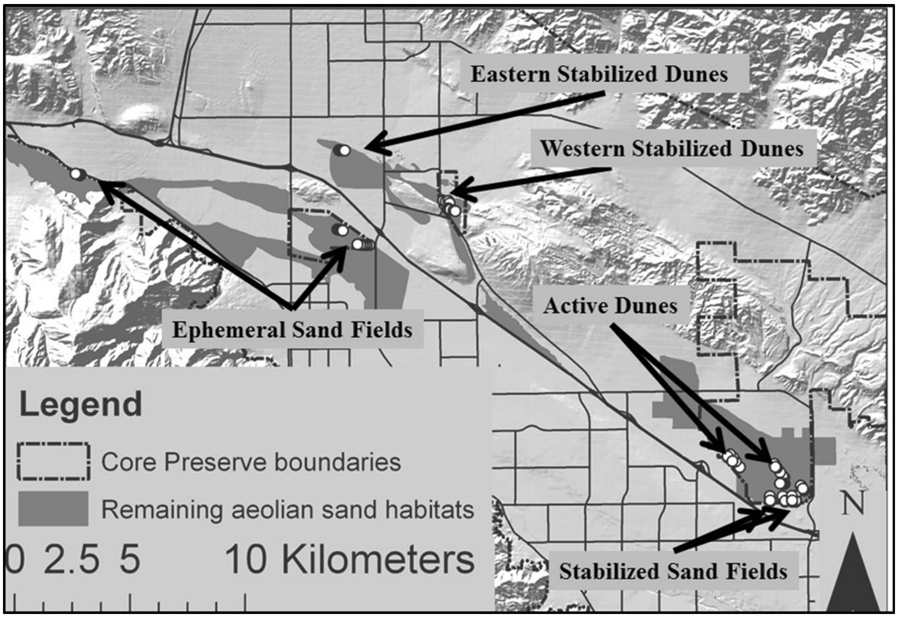
Many deserts of the southwestern U.S. and northwestern Mexico have been invaded by exotic plant species despite challenges imposed on survival by hot, arid conditions, resulting in severe impacts to these systems (Mooney et al. 1986; Rejmanek and Randall 1994; Van Devender et al. 1997). Invasive plants often form large, monotypic stands in these deserts, negatively influencing both species diversity and landscape processes such as sand movement (Thomson 2005; Hart et al. 2012) and fire cycles (Brooks et al. 2004). Sahara mustard (*Brassica tournefortii*) is widespread in the Mojave and lower Sonoran deserts (Sanders and Minnich 2000) and has occurred in Coachella Valley, California for approximately 80 years. Sahara mustard (hereafter mustard) is an annual plant that germinates and fruits earlier in the year than native annual species. Mustard stands are therefore particularly dense in wet years with early precipitation. Previous mustard outbreaks peaked during El Niño-associated wet periods in the late 1970s to early 1980s (Sanders and Minnich 2000), in 1994–1995 (Barrows, *unpubl.*), and in 2005 (Barrows et al. 2009). Mustard has dominated certain sand habitats within the Coachella Valley's dune landscape each year since 2005 independent of extreme wet periods (Barrows et al. 2009).

Barrows et al. (2009) documented strong negative impacts of Sahara mustard on native annual plant biomass and diversity in the Coachella Valley, but impacts on native fauna were less consistent. The Coachella Valley fringe-toed lizard (*Uma inornata*) exhibited negative responses to Sahara mustard, but arthropod responses were generally weak, although limited evidence for taxon- and context-specific responses were reported. However, Barrows et al.'s (2009) analysis of arthropods was taxonomically, spatially, and temporally, limited. In particular, they only studied mustard impacts within two of five aeolian sand communities described in this system (see Barrows and Allen 2007a).

In addition to affecting trophic structure, invasions can affect ecosystem function in ways that alter the physical structure of the environment with consequences for population densities and species diversity (Schwartz et al. 2000; Loeuille et al. 2002). Many arthropod species are endemic to aeolian sand systems of North American deserts, and changes to food availability and environmental structure within these systems could contribute to species extinctions (Andrews et al. 1979; Barrows 2000). In particular, studies have documented responses by arthropods to changing food availability (de Groot et al. 2007) and environmental structure (Pearson 2009) caused by invasive plants. Arthropods typically account for a large proportion of species membership and biomass of multiple trophic levels and functional guilds (Price et al. 2011). Furthermore, they typically have short generation times and are small in size, making ground-dwelling arthropods ideal focal organisms for monitoring annual variation in ecosystem health (Longcore 2003).

Our overall objective was to examine the effects of the mustard invasion in the Coachella Valley on ground-dwelling arthropods. We examined trends in two measures of arthropod community structure, abundance and richness, for a 9-year period

Fig. 1 Map of the study site



(2003–2011). During this period, mustard transitioned from being uncommon to being nearly the only annual plant species that flowers and goes to seed every year. First, we analyzed temporal trends in arthropod community structure and mustard cover, and the relationship between these trends across the landscape. Second, we further explored arthropod-mustard relationships, using multivariate models that controlled for potentially confounding environmental drivers of community structure, as well as potential mechanistic factors mediating mustard effects. Lastly, we examined mustard relationships with individual arthropod taxa to assess variation in mustard impacts among functional groups and trophic levels.

Materials and methods

Data were collected within Coachella Valley aeolian sand habitats (33°47′N, 116°20′W), in southeastern California (Fig. 1) during 2003–2011. These included approximately 1,700 ha of historically contiguous, but now fragmented sand dunes and sand fields distributed across a strong east–west gradient in both wind disturbance intensity and rainfall. Rainfall was also extremely variable among years; minimum rainfall (3–7 mm/year) occurred in 2002 and 2007, and maximum rainfall (210–326 mm year^{-1}) occurred in 2005. Intra-annual daily temperatures also varied, ranging from a low of ~0 °C in winter to highs of ~45 °C in summer. All precipitation data reported here are based on a July-to-June rain year and were recorded at 3 rain gauges distributed across the valley floor.

Coachella Valley's desert ecosystem consists of five different aeolian sand habitats: (1) *active sand dunes*, characterized by low shrub density, high levels of sand movement, and high topographic relief; (2) *stabilized dunes*, with high topographic relief but low sand movement due to stabilization by honey mesquite, *Prosopis glandulosa*; (3) *eastern stabilized sand fields*, with relatively high shrub density, low topographic relief, and compacted sand with low-to-moderate sand movement; (4) *western stabilized sand fields*, similar to *eastern stabilized sand fields* but more mesic and differing in both plant and animal species composition; and (5) *ephemeral sand fields* consisting of high perennial shrub density, hummock topography, and intense wind disturbance. For in-depth descriptions of vegetation and landscape attributes on these communities, see Barrows and Allen (2007a). All aeolian sand habitats were located in the western half of the Coachella Valley. *Active dunes* and *eastern stabilized sand fields* were located near the valley center, *ephemeral sand fields*, and *stabilized dunes* habitats were located further west, and *western* *stabilized sand fields* were located in the western end of the valley (Fig. 1). The five habitats varied in the extent to which they were invaded. *Ephemeral sand fields* had little mustard cover throughout the study period. In contrast, *active dunes, eastern stabilized sand fields,* and *stabilized dunes* experienced substantial increases in mustard cover, particularly following the 2007 drought. Additionally, mustard cover increased dramatically in *active dunes* and *eastern stabilized sand fields* in 2005, an extremely wet year. Mustard cover peaked twice in *western stabilized sand fields* during the study period, but both peaks were followed by declines.

Data collection

Various aspects of the physical environment and biological communities were sampled yearly at a series of plots from 2003 to 2011. Ninety 0.1 ha (100 m × 10 m) plots were sampled in total, of which 68 were sampled in 2003, 75 in 2004, and all 90 in 2005–2011, resulting in 773 plot·years sampled. Plots were separated by $\geq$50 m, a distance greater than the diameter of many ground-dwelling arthropod home ranges, to minimize spatial dependence. We note, however, that home ranges of ground-dwelling arthropod taxa are highly variable and some small degree of spatial overlap could be present.

We measured sand compaction, a fundamental component of habitat structure and driver of plant community structure in aeolian sand habitats of the Coachella Valley (Barrows 1997; Barrows and Allen 2007a), every year and at each plot. We used a pocket penetrometer with an adapter foot for loose soils (Ben Meadows Company, Janesville, WI, USA) to measure sand compaction (kg/cm^2) at 25 points distributed evenly along plot midlines. Precipitation was measured with two rain gauges in relatively xeric *active dunes* and *eastern stabilized sand field* habitats, and one in a *western stabilized sand field* habitat (the most mesic habitat). Study plots were assigned precipitation values recorded by rain gauges nearest to them.

We measured annual plant cover using a one m^2 sampling frame placed at 12 locations along the midline of each plot. Four sampling locations were on alternating sides of the center line at each end of the plot (8 of 12 locations) and two locations were on each side of the plot center point (4 of 12 locations). We measured percent cover rather than abundance to account for size differences among individual plants. The percent cover of each plant species was visually estimated at each location. Mean cover estimates were then calculated for either individual species (mustard) or species groups (native and other exotic annual plants) for each plot in each year. The number of perennial shrubs was also recorded at each plot for each year.

Arthropods were sampled using dry, un-baited plastic pitfall traps 11 cm wide at the mouth, 14 cm deep, 1.0 L in volume, and fitted tightly with a funnel that inhibited the ability of arthropods to escape once captured. A 20 cm × 20 cm × 0.5 cm board was placed over each trap and elevated 1–2 cm with three wooden blocks. Three pitfall traps were deployed at each plot, one at each end and the third at the plot center, during each sampling occasion. Traps were typically set before sunset and checked in early morning. Contents were examined within 24 hours of trap deployment and arthropods were released alive. Specimens identified to the genus or species level were used in our analyses. Consequently, some arthropod groups, such as mites, were left out. However, individuals in these groups were impossible to count accurately because of their very small size and large numbers (in the 1,000's). From these data, we summarized the relative abundance and species richness across all species at each plot during each year.

In a preliminary arthropod inventory conducted prior to 2003, arthropods were sampled with pitfall traps once a month for 10–12 months per year. Arthropod composition varied little within seasons, and abundance and species richness peaked in April–June. We therefore focused our sampling effort towards these months and restrict our inferences to species active during spring.

Data analysis

We analyzed temporal trends in Sahara mustard cover and arthropod community structure using linear mixed equations

$$Y'_{ij} = \beta_0 + \beta_1 T + \varepsilon_i + \varepsilon_{ij}, \tag{1}$$

For these models, Y'_{ij} represents a standardized measure of either relative arthropod abundance, relative arthropod richness, or mustard cover for the *i*th plot ($i = 1, \ldots, 90$) during the *j*th year ($j = 1, \ldots,$

9). T represents the year (2003–2011). We included a plot-level random effect and thus accounted for two sources of error: among-plot error (ε_i) and within-plot error (ε_{ij}). This error structure was suited to the nested structure of our data generated by repeated measurements of each plot. Within-year variance in Y_{ij} varied substantially among years. We standardized Y_{ij} values by dividing them by the sample standard deviation in the ith year, focusing models on temporal trends by removing potentially confounding effects of inter-annual variation in variances. Models were fitted using the *lmer()* function in *R* (R Core Team 2012). *p*-Values were calculated based off of the estimation and inference assumptions in linear mixed models explained by Fitzmaurice et al. (2004). Response variables were checked for overdispersion following Zuur et al. (2007). The standardized data did not exhibit overdispersion.

We then analyzed the direct relationship between mustard cover trends and arthropod metrics (abundance and richness) using a general linear mixed model of the form:

$$\log(Y_{ij}) = \beta_0 + \beta_1 Mustard\_Cover + \varepsilon_i + \varepsilon_{ij}, \qquad (2)$$

where Y_{ij} represents either arthropod abundance or species richness, ε_i represents residual inter-plot variation, and ε_{ij} represents residual within-plot inter-annual variation (*glmer()* function in *R*; R Core Team 2012). We again checked for over dispersion in our response variables (Zuur et al. 2007). We found that arthropod abundance was exhibiting a small degree of overdispersion. We, therefore, corrected our standard errors and *p*-values to account for overdispersion following methods described by Zuur et al. (2007) by using the following equation:

$$P' = 2 * pnorm\left(\frac{Z - score}{\sqrt{\rho}}\right), \qquad (3)$$

where P' is the new *p*-value that accounts for overdispersion, *pnorm()* is a function in R (R Core Team 2012) that computes the probability that a normally distributed random number will be less than that number, and Z-score is the original z-score before overdispersion correction. The overdispersion parameter, ρ, is calculated using *the qcc.overdispersion.test()* function in R (R Core Team 2012). New standard errors are calculated by multiplying the original standard error by $\sqrt{\rho}$ (Zuur et al. 2007).

We further analyzed relationships between mustard and arthropod community metrics using generalized linear models with additional covariates representing other potential environmental drivers of community structure. These included precipitation, perennial shrub frequency, native annual cover, and sand compaction, which we expected to have negative, positive, positive, and negative relationships, respectively, with arthropod community metrics (for importance of these environmental features as drivers, *see* Barrows and Allen 2007a; Barrows et al. 2009). Both native annual cover and sand compaction are potential environmental drivers known to be influenced by mustard cover (*see* Barrows et al. 2009), and could be possible mechanistic pathways for mustard's indirect influence on the ground-dwelling arthropod community. We fit our data using a generalized linear mixed model of the form:

$$\begin{aligned} log(Y_{ij}) = {} & \beta_0 + \beta_1 Mustard\_Cover_{ij} \\ & + \beta_2 Perennial\_Frequency_{ij} \\ & + \beta_3 Precipitation_{ij} + \beta_4 Native\_Annual\_Cover_{ij} \\ & + \beta_5 Sand\_Compaction_{ij} + \boldsymbol{\varepsilon_i} + \boldsymbol{\varepsilon_{ij}}, \end{aligned} \qquad (4)$$

where Y_{ij} represents either arthropod abundance or species richness, ε_i represents residual inter-plot variation, and ε_{ij} represents residual within-plot inter-annual variation (*glmer()* function in *R*; R Core Team 2012). We adjusted standard errors and *p*-values for arthropod abundance results similar to Eq. 2 using Eq. 3.

Strong correlations among explanatory variables can obscure interpretation of regression parameters. We tested for such correlations by examining variance inflation factors, where a variance inflation factor greater than five indicates unacceptable levels of co-linearity between the covariates (Mendenhall and Sincich 2003). Variance inflation factors never exceeded two in our models, so we maintained all environmental variables in our analyses. In addition, there were no obvious patterns that emerged among the residuals.

We explored changes in arthropod community structure in more detail by analyzing temporal and spatial variability in arthropod rarity and occurrences. Arthropod taxa were assigned to a "rarity" subset based on the number of years observed (e.g. all nine years, eight years, etc.). We then compared the rarity subsets based on the number of years observed to both time and average mustard cover using Pearson's Correlation Coefficients (*rcorr()* function, Team 2012). In addition, we calculated the number of plots occupied in each year for each species to better understand spatial changes in the arthropod community.

Finally, we examined temporal trends and relationships with mustard for individual arthropod taxa. We used univariate Poisson regression models to relate species-specific abundances with either time or mustard cover. We grouped arthropod taxa according to ecological functional guilds (detritivore, herbivore, omnivore, nectivore, or predator) and examined which guilds exhibited abundance relationships consistent with overall community patterns. Additionally, we analyzed the relationships to understand whether negative mustard relationships were associated with negative temporal trends in abundance. We grouped arthropod taxa according to the direction of their temporal abundance trends and mustard relationships (positive versus negative) and excluded species that did not exhibit a significant ($p < 0.05$) relationship with either of these. We tested for independence in group membership using a Fisher's exact test (*fisher.test()* function, R Core Team 2012).

Results

During the study period, we observed a positive temporal trend in mustard that was associated with negative trends in both arthropod richness and abundance. Mustard cover increased significantly ($\beta_1 = 0.079 \pm 0.023$, $p < 0.001$; trend estimates from Eq. 1) during the study period from mean values of 0.58 % (2003) to 9.35 % (2011) across all plots (Fig. 2). Furthermore, the proportion of total annual plant cover that consisted of mustard cover increased through time (Fig. 3). Concurrent with this increase in mustard, arthropod abundance declined ($\beta_1 = -0.082 \pm 0.014$, $p < 0.001$) from a mean of 44.18 (2003) to 12.39 (2011; Fig. 2). Similarly, arthropod richness declined ($\beta_1 = -0.12 \pm 0.014$, $p < 0.001$) from a mean of 8.514 (2003) to 4.54 (2011; Fig. 2). When compared directly, both arthropod abundance

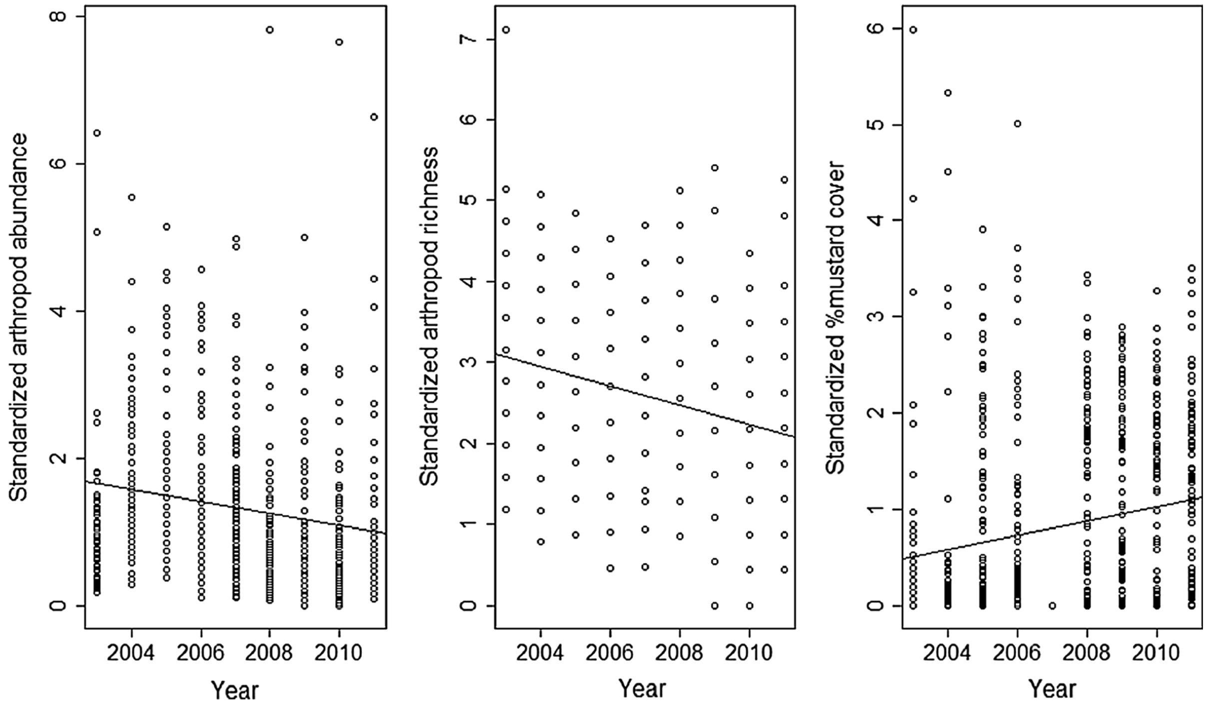


Fig. 2 Temporal trends in percent mustard cover, arthropod abundance, and arthropod richness throughout the study. *Dots* represent standardized values (raw values divided by within-year sample standard deviations) for each observation. *Solid lines* depict temporal trends estimated by regression models

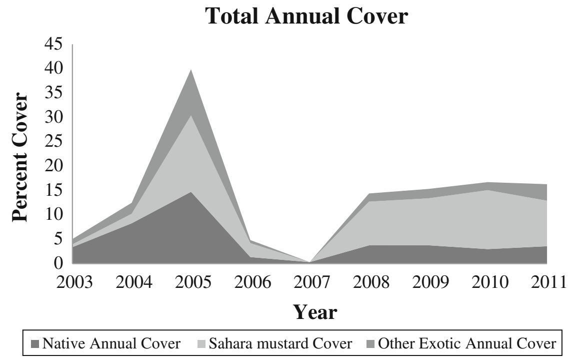


Fig. 3 Contributions of constituent annual vegetation categories to total yearly mean annual plant cover. Exotic annual cover includes all annual exotic species other than mustard

and richness are negatively related to mustard cover ($\beta_1 = -0.049 \pm 0.005$, $p' \leq 0.001$; $\beta_1 = -0.12 \pm 0.043$, $p = 0.004$, respectively).

After controlling for possible confounding effects of environmental drivers other than mustard (3), negative arthropod relationships with mustard continued to be apparent for both arthropod abundance ($\beta_1 = -0.049 \pm 0.0051$, $p' = 0.0013$) and arthropod richness ($\beta_1 = -0.03 \pm 0.002$, $p = 0.067$). The possible mechanistic pathways, native annual cover and sand compaction, have significant positive relationships with arthropod richness (Eq. 3 $\beta_1 = 0.006 \pm 0.002$, $p = 0.003$ and Eq. 3 $\beta_1 = 0.072 \pm 0.022$, $p = 0.001$, respectively), but these do not appear to influence arthropod abundance (Table 1).

The different arthropod rarity categories showed strong differences in their negative correlations with time (Fig. 4) as rarer taxa were more likely to be negatively correlated than common taxa. Mustard correlations with species rarity are not significant; however, we still see that the rare species have a negative relationship with average mustard cover. The average number of plots occupied by each species in each year decreased from 4.8 ± 0.89 in 2003 to 3.40 ± 0.77 in 2011. This decreasing trend had a significant negative relationship with time ($r = -0.68$, one-tailed $p = 0.022$). When the average number of plots occupied per species is plotted together with mustard cover (Fig. 5), we see occupancy drop in peak years of Sahara mustard and peak in years of low mustard cover, with the strongest relationship appearing after 2007. The correlation between plots occupied and mustard cover was marginally significant ($r = -0.48$, one-tailed $p = 0.098$).

Table 1 Regression parameters ($\beta \pm$ SE) from the multivariate model with mustard cover and other potential environmental drivers of arthropod community structure as predictor variables (3)

Equation 3	Arthropod abundance[a]	Arthropod richness
Mustard cover	−0.016 ± 0.005*	−0.003 ± 0.002†
Perennial frequency	0.004 ± 0.002	−0.001 ± 0.001
Precipitation	−0.001 ± 0.001	−0.001 ± 0.000***
Native annual cover	−0.01 ± 0.007	0.006 ± 0.002**
Sand compaction	0.063 ± 0.081	0.072 ± 0.022**

*** $\alpha \leq 0.001$; ** $\alpha \leq 0.01$; * $\alpha \leq 0.05$; † $\alpha \leq 0.10$

[a] Results are adjusted for overdispersion

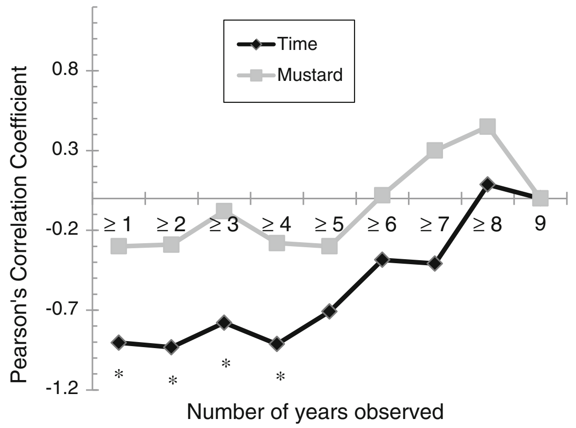


Fig. 4 Rarity influences trends in species richness. Pearson's correlation coefficients *r* for relationships between richness and time are compared across subsets of the data defined by rarity. "Number of years observed" refers to the number of years a species needed to be observed in order to be included in the data subset. For example, a species in the "≥7" category could have been observed in 7, 8, or all 9 of the sampling years. For the "9" category, only species that were seen every year were included in the analyses. *Asterisks* denote correlations that were significant

Of the 122 arthropod taxa observed, 99 exhibited negative temporal trends (35 were significant), 23 exhibited positive trends (9 were significant), 93 exhibited negative relationships with mustard cover (20 were significant), and 29 were related positively to mustard cover (11 were significant; Table 2). Arthropod species exhibiting significant negative trends and

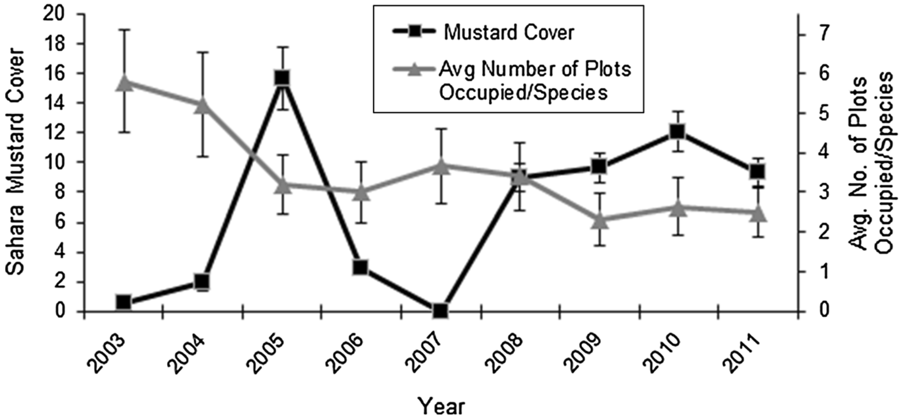


Fig. 5 Mean Sahara mustard cover plotted against the average number of plots a species occupied through time. *Error bars* represent standard error

mustard relationships consisted mainly of detritivores with inclusion of some granivores and nectivores but not predators (Table 2). Eight species exhibited positive temporal trends and mustard relationships. These consisted mainly of predators, largely spiders and beetles (Table 2). In total, 56 species exhibited either a significant temporal trend or relationship with mustard. For this set of species, positive temporal trends tended to be associated with positive mustard relationships and negative trends with negative mustard relationships more frequently than expected by chance (Table 3; $p = 0.014$; observed deviated from expected by ~3.9 species).

Discussion

We found substantial evidence for a negative effect of Sahara mustard on the structure of a ground-dwelling arthropod community. During the study period, declines in both arthropod species richness and total abundance paralleled an overall increase in mustard cover. Arthropod species that declined in abundance tended to be those that experienced significant negative relationships with mustard more often than expected by chance. Finally, negative arthropod-mustard relationships were apparent even when controlling for other potential environmental drivers of community structure, suggesting some direct effect of mustard on arthropods.

A negative relationship between arthropod metrics and mustard was apparent even after controlling for the effects of native annual plants. We anticipated a negative relationship between mustard and ground-dwelling arthropods because of the strong negative mustard impacts on native annual plants (Barrows et al. 2009), and the importance of native annual plants as a resource base for arthropods. Native annual cover was positively related to arthropod species richness as expected. Yet, contrary to our expectations, native annual cover tended to be negatively related to arthropod abundance, albeit not strongly enough for the relationship to be statistically supported. Even though both native annual cover and mustard cover increase simultaneously, albeit in different proportions, the relationship between arthropod richness and mustard cover is opposite in direction to that of richness and native annual cover. This further supports the hypothesis that mustard is one of the factors contributing to the decline of the arthropod community as its negative relationship remains strong even after including factors that might mask its negative impacts. Nevertheless, when other environmental covariates were added to the analyses, mustard cover's influence on arthropod richness decreased in strength and in significance. This suggests these environmental covariates may contribute to the mechanisms that are influencing arthropod richness. Mustard effects on arthropod abundance may be more of a direct influence, while the influence of mustard on arthropod richness may be a combination of both indirect and direct mechanisms. Thus, from the data presented here, we have not been able to easily attribute negative impacts of mustard and associated declines in arthropod abundance to mustard impacts on native plants.

Table 2 Relationships between arthropod taxa and time and mustard as determined by generalized linear models

Species	Guild	Common guild	Temporal trend	Mustard relationship
Messor pergandei	Granivore	Ant	−0.051 ± 0.02	−0.112 ± 0.013***
Myrmecocystus kennedyi	Nectivore	Ant	−0.131 ± 0.015***	−0.016 ± 0.004***
Myrmecocystus tenuinodis	Nectivore	Ant	−0.094 ± 0.025***	−0.103 ± 0.014***
Pogonomymex magnacanthus	Granivore	Ant	−0.406 ± 0.018***	−0.037 ± 0.005***
Crematogaster opuntiae	Detritivores	Ant	−0.007 ± 0.083	−0.862 ± 0.398*
Dorymyrex spp.	Omnivore	Ant	−0.009 ± 0.026	−0.131 ± 0.02***
Forelius pruinosus	Omnivore	Ant	−0.039 ± 0.042*	−0.387 ± 0.091***
Pheidole barbata	Detritivore	Ant	−0.003 ± 0.024	−0.173 ± 0.024***
Pheidole psammophila	Detritivore	Ant	−0.005 ± 0.162*	−0.283 ± 0.218
Solenopsis xyloni	Detritivore	Ant	−0.01 ± 0.075	−0.101 ± 0.04*
Solenopsis aurea	Detritivore	Ant	−0.006 ± 0.193*	−0.063 ± 0.054
Niptus venticulus	Detritivore	Beetle	−0.009 ± 0.023	−0.02 ± 0.007**
Cymatodera punctata	Detritivore	Beetle	−0.002 ± 0.436*	−0.094 ± 0.129
Sibinia spp.	Herbivore	Beetle	−0.003 ± 0.39*	−0.305 ± 0.336
Trigonoscuta imbricata	Detritivore	Beetle	−0.005 ± 0.078*	−0.035 ± 0.025
Corticaria spp.	Detritivore	Beetle	−0.004 ± 0.243**	−0.528 ± 0.497
Catops spp.	Detritivore	Beetle	−0.002 ± 3,500*	−0.148 ± 0.236
Trichocrus spp.	Detritivore	Beetle	−0.002 ± 0.293*	−0.116 ± 0.132
Cysteodemus armatus	Herbivore	Beetle	−0.007 ± 2,100*	−2.167 ± 1.645
Eupompha spp.	Detritivore	Beetle	−0.002 ± 0.293*	−0.014 ± 0.052
Asidina confluens	Detritivore	Beetle	−0.005 ± 0.144	−0.063 ± 0.049**
Batulius setosus	Detritivore	Beetle	−0.092 ± 0.024***	−0.015 ± 0.006*
Chilometopon abnorme	Detritivore	Beetle	−0.008 ± 0.055	−0.011 ± 0.014*
Chilometopon brachystomum	Detritivore	Beetle	−0.017 ± 0.045*	−0.085 ± 0.022***
Chilometopon pallidum	Detritivore	Beetle	−0.027 ± 0.161***	−0.5 ± 0.203*
Edrotes barrowsi	Detritivore	Beetle	−0.001 ± 0.035	−0.057 ± 0.014***
Edrotes ventricosus	Detritivore	Beetle	−0.341 ± 0.014***	−0.036 ± 0.004***
Eupsophulus castaneus	Detritivore	Beetle	−0.004 ± 0.115	−0.142 ± 0.085*
Notibius puberulus	Detritivore	Beetle	−0.075 ± 0.02***	−0.001 ± 0.004
Telabis aliena	Detritivore	Beetle	−0.015 ± 0.098***	−0.119 ± 0.049*
Loxosceles spp.	Predator	Spider	−0.003 ± 0.455**	−0.123 ± 0.14
Smeringurus mesaensis	Predator	Other Arachnid	−0.011 ± 0.241***	−0.108 ± 0.062
Vaejovis spp.	Predator	Other Arachnid	−0.012 ± 0.07***	−0.003 ± 0.015
Tetragonoderus pallidus	Predator	Beetle	0.0545 ± 0.03***	0.037 ± 0.004***
Araeoschizus hardyi	Detritivore	Beetle	0.005 ± 0.018	0.017 ± 0.003***
Eleodes armata	Herbivore	Beetle	0.011 ± 0.074**	0.008 ± 0.013
Embaphion depressum	Detritivore	Beetle	0.003 ± 0.163*	0.045 ± 0.016**
Tarsonops spp.	Predator	Spider	0.036 ± 0.033***	0.018 ± 0.006***
Syspira spp.	Predator	Spider	0.009 ± 0.050	0.021 ± 0.008**
Psilochorus spp.	Predator	Spider	0.089 ± 0.016***	0.019 ± 0.016
Steatoda triangulosa	Predator	Spider	0.005 ± 0.197**	0.015 ± 0.003***
Mecynotarsus delicatulus	Detritivore	Beetle	0.014 ± 0.089	−0.064 ± 0.03*
Asbolus laevis	Detritivore	Beetle	0.023 ± 0.009	−0.02 ± 0.003***
Callilepis spp.	Predator	Spider	0.001 ± 0.076	−0.086 ± 0.039*
Dermacentor spp.	Predator	Other Arachnid	0.17 ± 0.036**	−0.059 ± 0.009***

Table 2 continued

Species	Guild	Common guild	Temporal trend	Mustard relationship
Pogonomyrmex califonricus	Granivore	Ant	−0.483 ± 0.005*	0.01 ± 0.001***
Calosoma spp.	Predator	Beetle	−0.009 ± 0.111**	0.058 ± 0.009***
Calosoma pravicollis	Predator	Beetle	−0.02 ± 0.075***	0.03 ± 0.009**
Ophryastes desertus	Herbivore	Beetle	−0.008 ± 0.06*	0.006 ± 0.012
Asbolus verrucosa	Detritivore	Beetle	−0.025 ± 0.031*	0.002 ± 0.007
Cheriodes celifornica	Detritivore	Beetle	−0.021 ± 0.072***	0.033 ± 0.008***
Cryptoglossa muricata	Detritivore	Beetle	−0.124 ± 0.062*	0.014 ± 0.011
Oonops spp.	Predator	Spider	−0.009 ± 0.121**	0.001 ± 0.024
Scopoides spp.	Predator	Spider	−0.006 ± 0.141**	0.002 ± 0.005
Steatoda fulva	Predator	Spider	−0.062 ± 0.025***	0.039 ± 0.017*
Averivaga spp.	Predator	Other Arachnid	−0.017 ± 0.042**	0.004 ± 0.009

The arthropod taxa are grouped by the direction the estimated slopes have with time and mustard cover

*** $\alpha \leq 0.001$; ** $\alpha \leq 0.01$; * $\alpha \leq 0.05$

Table 3 Summary of the direction of regression parameters for arthropod taxa with time and mustard cover

Arthropod taxa and mustard		
Relationship	Positive	Negative
Arthropod taxa and time		
Positive	8 (4.1)	4 (7.9)
Negative	11 (14.9)	33 (29.1)

Only arthropod taxa with significant parameters at the $\alpha \leq 0.05$ are included. Expected cell frequencies are reported in parentheses. A test of independence (Fisher's exact test) fund cell frequencies to deviate significantly from expected frequencies ($p = 0.014$)

Native plants may still mediate mustard impacts on arthropods in ways not observable from regression analysis. For example, arthropods may exhibit a lagged response to declines in native annual plants, which could explain why broad mustard impacts on arthropods were only apparent after long-term study (*contra* Barrows et al. 2009). Alternatively, other factors may mediate negative impacts of mustard on arthropods or contribute to arthropod declines. Arthropods were also related with precipitation and sand compaction after controlling for relationships with mustard and native annual plants, so the role of these drivers in mediating arthropod declines and negative relationships with mustard would be of further interest.

Aside from direct competitive effects on native plant diversity, mustard also influences native plant communities, and consequently food resources for arthropods, by altering the physical structure of the landscape. The excessive biomass created by Sahara mustard can stabilize the sand surface (Hart et al. 2012) and alter habitat structure. Arid landscapes in southwestern North America experience reduced sand transport rates when highly vegetated (Lancaster and Baas 1998; Reinhardt et al. 2010; Munson et al. 2011), and vegetation growth, driven by increased precipitation, appears to explain transitions between active and stabilized states of arid aeolian landscapes. In coastal dunes, stabilization by invasive plants (particularly *Ammophila* grasses) has long been recognized as a core threat to biodiversity and ecosystem function (Wiedemann and Pickart 1996; Hacker et al. 2012; Hart et al. 2012). Interestingly, ground-dwelling arthropods in this study were positively related with sand compaction after controlling for effects of mustard and precipitation. Non-invaded annual plant communities are richer and provide more standing biomass in stabilized sand habitats (i.e., *eastern stabilized sand fields*, *stabilized dunes*, and *western stabilized sand fields*), which may benefit arthropods. If arthropods benefit from stabilization via this pathway, mustard invasion should counter-act the benefits of sand stabilization. The overall negative mustard relationship with arthropods found here would be consistent with this hypothesized relationship between sand compaction and ground-dwelling arthropod diversity.

We also see that we are losing rare species through time. However, the trend of the total number of species observed is not significantly related with average mustard. Mustard is highly variable between plots, and when we average mustard cover, we may lose the ability to predict trends since rare species may be only disappearing on heavily invaded plots. Additionally, we see species becoming rarer (occupying less plots) within the landscape, and this trend loosely follows mustard cover through time. Mustard cover may reduce habitability of plots as well as reduce access from neighboring plots by colonizers. Reduced native annual cover and above ground structural changes may operate in concert to inhibit dune arthropod populations and limit diversity. Both trophic and habitat structural impacts of plant invasions on particular insect communities have been observed, resulting in reduced detritivore foraging rates (Srivastava 2006) and changes in predator hunting efficiency (Denno et al. 2002; Finke and Denno 2002; Pearson 2009).

When examined individually, the majority of arthropod taxa decreased through time and had a negative relationship to mustard cover. Many of the arthropods in the Coachella Valley aeolian desert ecosystem are detritivores and seed predators (Ayal et al. 2005; Barrows 2012).The species that were negatively related to both time and mustard cover were largely detritivores whereas predators tended to be positively related to mustard. Dead mustard may not readily disarticulate into fine particles of detritus and may instead maintain its standing structure for long periods. Thus, the size and structure of mustard detritus may be creating an ideal hunting space for some generalist predators. However, most of the arthropod taxa that were positively related with mustard cover were still decreasing with time. A recent study by Engelkes et al. (2012) found that invasive plant species harbored greater arthropod predator pressure on arthropod herbivores than native plants. This effect may help explain why we are observing a positive relationship between mustard and predators and a negative relationship with detritivores and herbivores. The increased aboveground biomass arising from mustard invasion may also physically impede arthropod movement (Crist and Wiens 1994; Shelef and Groner 2011) or change habitat selection cues.

Diverse native plant assemblages may provide a mix of essential nutrients or other resources not available in monotypic mustard stands, causing a decline in species richness. Dead mustard may not readily disarticulate into fine particles of detritus and may instead maintain its standing structure for long periods, leaving less food for detritivores. Additionally, chemical defenses may make mustard unpalatable to many native arthropods that have not encountered such defenses during their evolutionary histories. Our observations suggested low abundance of native phytophagous insects on mustard at our study sites (C. Barrows personal observation). In contrast, two non-native species, a Homopteran (an aphid) and a Hemipteran (*Bagrada hilaris*) were commonly observed on mustard and at heavily invaded plots. *Bagrada hilaris* is indigenous to the same region of North Africa and the southern Mediterranean where Sahara mustard originated, and therefore may be especially adapted for taking advantage of food resources provided by mustard. A pilot experiment with a saprophagous tenebrionid beetle failed to find differences in beetle survival or maintenance of mass when fed native versus mustard detritus (Simon et al., unpublished data), but additional studies are required to fully address this issue.

We did not account for spatial or temporal variation in detectability, which can influence measurements of diversity and abundance (Kéry et al. 2009; Kéry and Royle 2010). Reduced movement of arthropods could diminish detectability by reducing the chances of arthropods encountering traps, which in return may inflate apparent negative effects on arthropod diversity and abundance. Nevertheless, if mustard does impede arthropod movement, negative impacts on arthropod fitness are likely to occur along with any effects mustard might have on detectability via pitfall traps. However, pitfall traps were never covered by or even touched any vegetation as that would potentially offer an arthropod a “ladder” to climb out of the pitfall. The pitfall traps were always set to have open ground on all sides (360° access), but were set near vegetation so an arthropod could easily move from the cover of the vegetation to the pitfall trap. Estimation of arthropod detectability and examination of the factors that influence arthropod mobility would further inform interpretation of the results from this study.

Our results suggest some potential directions for a future study of mechanisms underlying mustard impacts on arthropods. Specifically, researchers should consider impacts via changes in trophic structure and physical aspects of the environment. Understanding system-wide impacts of invasive species on native biodiversity is critical for informing land management decisions and directing limited funding to maximize conservation objectives (Barrows and Allen 2007b). Mustard cover appears to influence both community structure and the amount of spatial coverage by arthropod taxa. Our data suggest that the invasion of mustard negatively impacts the arthropod community across multiple aeolian sand habitats within the Coachella Valley, and a better understanding of the mechanisms responsible may help mitigate mustard impacts.

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