



Exotic *Prosopis juliflora* suppresses understory diversity and promotes agricultural weeds more than a native congener

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Abstract Exotic invasive plant species alter ecosystems and locally extirpate native plant species, and by doing so alter community structure. Changes in community structure may be particularly important if invaders promote species with certain traits. For example, the positive effects of most invaders on soil fertility may promote species with weedy traits, whether native or not. We examined the effects of two co-occurring *Prosopis* congeners, the native *P. cineraria* and the exotic invader *P. juliflora*, on species

identified as “agricultural weeds” and species that were not agricultural weeds in the United Arab Emirates. When compared to plots in the open, *P. cineraria* canopies were associated with lower richness and density of non-weeds while having no impact on agricultural weed species. In contrast, there was lower richness and densities of non-weeds under canopies of *P. juliflora*, but higher densities of agricultural weeds than in the open surrounding the canopies. These patterns associated with *Prosopis* congeners and understory plant community composition might be due to the much higher litter deposition, if litter is inhibitory, and shallow root biomass under *P. juliflora*, or the different soil properties that corresponded with the two *Prosopis* canopies. In general, soils contained more nitrogen under *P.*

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juliflora than *P. cineraria*, and both understories were more fertile than soil in the open. Our results suggest that evolutionary history may play a role in how exotic invasive species may select for some traits over others in plant communities, with an exotic invader potentially creating reservoirs of agricultural weeds.

Keywords Agricultural weeds · Arid lands · Facilitation

Introduction

Exotic invasive species commonly outcompete and replace native species (MacDougall and Turkington 2004; Besaw et al. 2011; Vilá et al. 2011; Lekberg et al. 2018) and may drive shifts in the structure of remaining native communities. One such possible shift might be an increase in the relative abundance of species with “weedy” traits regardless of nativity, including weeds common in agricultural lands. Agricultural weed species often exhibit strikingly different traits than non-agricultural weed species, including greater vegetative spread and seedling vigor, higher growth rates, and higher probabilities of having an annual life history (Kuester et al. 2014). Such *r*-selected traits of species with weedy habits (see Radosevich et al. 2007) might be favored by the ecosystem changes wrought by invasive species, such as increased soil fertility (including soil nitrogen and phosphorus concentrations; Ehrenfeld 2003; Blackshaw and Brandt 2008; Liao et al. 2008; McLeod et al. 2016; Kaur et al. 2012). If agricultural weeds are disproportionately facilitated by exotic invaders, the latter might provide reservoirs or sanctuaries for agricultural weeds from which they can colonize agricultural ecosystems.

Native plant species can facilitate growth and establishment of exotic invasive plant species (Callaway et al. 1991; Lenz and Facelli 2003; Cavieres et al. 2008; Iponga et al. 2009; Griffith 2010; Llambi et al. 2018) and exotic species also often promote other exotics (Cushman et al. 2011; Wundrow et al. 2012; Flory and Bauer 2013; Stinca et al. 2015). The latter is dubbed “invasional meltdown” (Simberloff and Von Holle 1999; Braga et al. 2017). However, these studies generally focus on the effects of foundational non-native species on other non-native species. We know

of no studies that explore how exotic invasive species might affect agricultural weeds, regardless of their biogeographic origin. However, since exotic invasive species both improve soil fertility and create intense competitive conditions, this could promote the relative abundance of agricultural weed species, which can be particularly strong competitors (Baker 1965; Zimdahl 2007). The aim of this paper is to study the relative impact of exotic invasive species on agricultural weeds versus non-agricultural weeds.

Of the approximately 45 species in the genus *Prosopis*, many have been introduced to new biogeographic ranges, and four species—*P. glandulosa*, *P. velutina*, *P. juliflora* and *P. pallida*—have become widely invasive (Burkart 1976; Pasiecznik et al. 2001). In some cases morphologically similar native and exotic *Prosopis* species co-occur, providing opportunities to compare their relationships with other species. For example, in India, Kaur et al. (2012) found that the canopies of *P. cineraria*, native to Western Asia and the Indian subcontinent, were associated with much higher plant species diversity than the exotic *P. juliflora*. Both *P. juliflora* and *P. cineraria* can also have strong impacts on soil chemistry which may drive their influence on understory plant species (El-Keblawy and Al-Rawai 2007; Kaur et al. 2012).

Here, we explore the canopy-understory relationships of these two congeners, but focus on their relationships with understory species that are considered agricultural weeds; henceforth “ag-weeds”, in the UAE compared to species that are not agricultural weeds; henceforth “non-weeds”. We classified these species using a flora which recorded the species we call ag-weeds as common on farms or other disturbed areas (Karim and Fawzi 2007; see Methods). We focused on the following questions: (1) Is non-weed diversity higher under canopies of the native *P. cineraria* and lower under canopies of the exotic *P. juliflora*?, (2) Does the exotic *P. juliflora* increase ag-weeds more than the native *P. cineraria*, thus potentially creating reservoirs of these species?, and (3) Does soil under canopies of the exotic *P. juliflora* have higher soil fertility than the native *P. cineraria*? To answer these questions, we compared the richness and density of non-weeds and ag-weeds beneath *P. cineraria* and *P. juliflora* canopies, and measured soil properties, litter depth, and fine tree root mass beneath canopies of both species.

Methods

Study area

Our study site was a roughly 2×3 km area in the Ras Al Khaimah Emirate on the eastern coast of the UAE at 25.662480 latitude, 55.972372 longitude. Total annual precipitation, averaged over 21 years, is 106.9 mm with roughly 70 mm falling in February and March. These months are the peak of the growing season and are among the coolest with average mean temperatures of roughly 18–22 °C. Soils in the upper 15 cm ranged from sand to loamy sand (A. El-Keblawy, *unpublished data*). The only trees present were *Prosopis juliflora* and *P. cineraria*, and these were scattered across the site and interspersed with open areas with no canopy cover.

Sampling took place on two separate occasions. To understand the spatial associations of *P. juliflora* and *P. cineraria* with the richness and diversity of weed and non-weed understory species, we sampled the understory and adjacent open ground of thirty trees in May 2017 (15 trees of each *Prosopis* species). We also investigated how understory plant richness and diversity varied depending on the location of sampling within a canopy for each species (under the canopy or at its edge). At the same study site and on the same date, we evaluated soil properties and soil composition beneath five randomly selected trees of each *Prosopis* species. Finally, we compared litter depth and fine tree root mass under the two *Prosopis* congeners in a separate set of quadrats on February 2019 for five haphazardly selected individuals of each *Prosopis* species.

Spatial associations with understory species

Prosopis juliflora and *P. cineraria* were well inter-mixed at the site. *Prosopis cineraria* is a native tree, but *P. juliflora* has appeared in the last 40–50 years (also see Issa and Dohai 2008). We ran two line-transects from east to west at the site and sampled understories and adjacent open ground of 15 individuals of each *Prosopis* species along these transects, choosing trees at the site with canopy diameters between 9 and 11 m. Tree trunks were typically 10–15 m from each other, with a minimum distance of 4 m between canopies. Understories and open areas at the site are periodically grazed by goats and sheep, but

the site was not grazed in the rainy season prior to our sampling.

For each of the 30 individual trees (fifteen for each *Prosopis* species), we located four quadrats, each 1 m², on an east–west transect. One quadrat was placed at the midpoint between the trunk of the tree and the canopy edge on the west side of the trunk, and another at the midpoint on the east side (under). Similarly, we located one quadrat at the west edge of the canopy with the center of the plot at the dripline, and another at the east edge (edge). For each individual tree, we also located one quadrat in open ground, without any canopy overhead, in a random direction four meters from the canopy edge. Thus, for a 10-diameter canopy, the quadrat under the canopy was 2.5 m from the trunk, the quadrat at the edge was 5 m from the trunk, and the outside quadrat was 9.5 m from the trunk. This sampling scheme resulted in 30 quadrats in the open, 60 fully under each *Prosopis* species, and 60 at the canopy edge of each *Prosopis* species (Online Resource Fig. 1).

For each quadrat, we recorded the number of individual plants for each understory species. All species were categorized as ag-weeds or non-weeds as described above. Species we call agricultural weeds were recorded when present on farms and agriculturally disturbed and ruderal sites. In addition, during co-author El-Keblawy's compilation of the Sharjah Seed Bank & Herbarium, these species were confirmed as either common in agricultural habitats or not. To be sure, this classification is less binary than exotic vs. native, and should be considered with some caution. We used these data to determine understory species richness and plant density. To our knowledge, all species other than *P. juliflora* were native to the study region (Karim and Fawzi 2007).

Soil sampling and analyses

To evaluate differences in soil fertility, the ability of soil to supply the essential nutrients needed for plant growth, we randomly selected ten of the trees used above (5 of each *Prosopis* species) for soil sampling. We haphazardly collected three cores of soil each 10 cm in depth (~ 100 g) from beneath each tree's canopy (under) roughly 2.5 m from the tree trunk and 4 m away from the tree canopy in the open. All soil samples were air-dried, ground, homogenized (within a location for a single tree), and passed through a

2-mm sieve to remove large particles. Soil organic matter (OM) content, soil texture (percentage of sand, silt, and clay), electrical conductivity (EC), pH, K, Na, Ca, Mg, N, and P were estimated. The OM content was estimated using loss of mass by combustion at 430 °C on the < 2-mm soil fraction. Soil water extracts (1:2.5 of soil:water) were prepared to determine EC and pH using conductivity and pH meters, respectively. Total nitrogen was extracted using 2 M KCl and determined by the micro-Kjeldahl method (Bremner and Mulvaney 1982). Phosphate-P was estimated using Olsen's solution (0.5 M sodium bicarbonate) as an extracting agent. Na, Ca and Mg were estimated using flame photometry (see Black 1965).

We also compared litter depth and fine tree roots under the two *Prosopis* congeners in a separate set of quadrats. Five individuals of each *Prosopis* species were randomly chosen, and four 20 × 20 cm (0.04 m²) quadrats were placed under each tree. Two were located directly under canopies (1.5 m away from the trunk) along an east–west transect, and two at the dripline (edge) of tree canopies along the same transect. In each quadrat, litter depth was measured from the surface to the soil. In these same locations, fine tree roots were collected using cores that were 30 cm diameter and 30 cm in depth. Roots were sieved from the soil, washed, and dried at 90 °C until constant weight.

Statistical analyses

All analyses were performed in R version 3.5.1 (R Core Team 2018). To evaluate the influence of *P. cineraria* and *P. juliflora* on understory ag-weeds and non-weeds, we explored patterns in understory species richness and density (Q1 and Q2). To reduce imbalances in our data, we averaged plant richness and density under tree canopies for the two quadrats located beneath each tree canopy (under) and for the two quadrats located at the edge of each canopy. We used the presence of each understory species per tree as an index of species richness and the number of individual plants of each understory species as an index of plant density. Differences in species richness and plant density were evaluated with generalized linear mixed models (two separate GLMMs), due to skewness in our data, with understory plant type (non-weed or ag-weed), plant location (under or at the edge of *P. cineraria* or *P. juliflora* canopies or in the open),

and their interaction treated as fixed factors. Study tree was treated as a random variable and over-dispersion was accounted for with the gamma distribution using the MASS (Venables and Ripley 2002) and lme4 (Bates et al. 2015) packages in R.

To understand how soil chemistry varied beneath tree canopies for each species and in the open (Q3), we evaluated the effect of soil sampling location (under *P. cineraria* or *P. juliflora* canopies or in the open) as a fixed effect with the soil properties (pH, EC, Ca, Mg, Na, K, N, P, OM, % Clay, % Silt, % Sand) modeled as a response variables and tree replicate included as a random factor in a GLMM, accounting for over-dispersion by applying the gamma family and log-link function. We conducted principal components analysis (PCA) to illustrate relationships among the twelve soil properties from soils sampled under *P. cineraria* or *P. juliflora* or the open using the R package factoextra (Kassambara and Mundt 2017).

Finally, litter thickness and fine tree root biomass were averaged for each *Prosopis* canopy between the two quadrats located beneath the tree canopy and the two quadrats located at the edge of each canopy (Q3). Litter thickness was modeled as a response variable with sampling location (under and at the edge of *P. cineraria* and *P. juliflora* canopies) modeled as a fixed effect and study tree included as a random factor in a GLMM. Since we found no fine *P. cineraria* roots in our soil cores, we used a one-sample Wilcoxon signed rank test to determine if the median amount of fine tree roots under *P. juliflora* was greater than zero while accounting for data skewness with the R package ggpubR (Kassambara 2019).

For all GLMMs, we examined residuals with normality tests and homogeneity of variance with Levene's test, which in all cases were reasonable. X^2 - and p -values were estimated with the analysis of variance (Anova) function in the car package (Fox and Weisberg 2011) and *post hoc* contrasts were conducted with the emmeans package when appropriate which corrects for multiple pairwise comparisons using a Tukey's HSD test (Lenth 2018).

Results

We sampled 29 understory species, 23 of which were non-weeds in the UAE, and six were ag-weeds or *P. juliflora* seedlings (Online Resource Table 1). Open

microhabitats had the highest non-weed species richness, with the understories of both *P. cineraria* and *P. juliflora* demonstrating a 21% and 87% decrease in the richness of non-weed species under canopies and 16% and 42% decrease in the richness of non-weed species at the edge of canopies, respectively (Table 1; Fig. 1). The richness of ag-weed species did not differ among plots in the open, under or at the edge of *P. cineraria* or *P. juliflora* understories. When combined, plots located in the open contained the entire species pool that we sampled. Similarly, all species other than the ag-weed *Portulaca oleracea* and non-weed *Salsola imbricata* were found beneath *P. cineraria* canopies. In contrast, *Prosopis juliflora* understories harbored all ag-weed species other than the ag-weed *Amaranthus graecizans* but only four non-weed species—*Aizoon canariense*, *Plantago ovata*, *Suaeda aegyptiaca*, and *Zygophyllum simplex*.

Understory ag-weed and non-weed densities varied among canopy microhabitats and *Prosopis* species. Ag-weed species density in plots at the edge of *P. juliflora* canopies was roughly two times higher than in open plots, or in plots at the edge of or under *P. cineraria* canopies (Table 1; Fig. 1). Ag-weed density was 1.8 and 13 times higher than non-weed density in *P. juliflora* plots at the edge and under the canopy, respectively. There were no differences in the density of ag-weed species among open, under *P. cineraria*, or edge-*P. cineraria* plots and non-weeds were more abundant than ag-weeds at the edge of *P. cineraria* canopies. It is important to note, that although we included *P. juliflora* seedlings in the ag-weed category, *P. juliflora* seedlings were actually 30% denser under *P. cineraria* canopies than *P. juliflora* canopies and therefore did not skew our results.

Both *Prosopis* species were associated with different soil chemistry than in open soils; further, soil

chemistry beneath the two *Prosopis* was different (Fig. 2; Online Resource Tables 2 and 3; Online Resource Fig. 2). The first principal component (PC1) separated soil properties under *P. cineraria* and *P. juliflora* canopies from plots in the open (Fig. 2; Online Resource Table 2). PC1 corresponded with 80% of the variance among these plots, and indicated that each microsite was associated with a different suite of characteristics. The second PCA axis (PC2; 11.06% of the variation) primarily reflected differences in soil properties between *P. cineraria* and the other two locations (*P. juliflora* and in the open) (Fig. 2; Online Resource Table 2). Soil under *P. juliflora* was lower in pH and higher in % Clay, % Silt, EC, total N, Mg, and Na, and showed no difference in % Sand, Ca, K, P or OM, in comparison to *P. cineraria* ($P < 0.05$ from Tukey HSD; Online Resource Fig. 2; Online Resource Table 3). The most striking differences between the tree species were an approximate 50% increase in total soil N, an almost three-fold increase in EC, and a doubling in Na and Mg in soil under *P. juliflora* in comparison to *P. cineraria*.

Litter depth was six to nine times greater at the edge and under *P. juliflora* canopies compared to *P. cineraria* (Table 2, Fig. 3). Soil under *P. juliflora* canopies contained more fine tree roots than soil under *P. cineraria* canopies ($P = 0.0227$ from Wilcoxon test). Within *P. juliflora* canopies, the mass of fine tree roots in the upper 30 cm of soil (from 30 cm diameter soil cores) was 57 times greater under the canopy than at the edge.

Discussion

Competition with agricultural weeds is the primary cause of yield losses in agricultural systems (Rao

Table 1 Results from two GLMMs used to compare the effect of sampling location (open or under or edge of *P. cineraria* or *P. juliflora* canopies) and understory plant type (ag-weed or non-weed) on understory plant richness and understory plant density

	Understory plant richness			Understory plant density		
	df	χ^2	<i>p</i> -value	df	χ^2	<i>p</i> -value
Location	4 (124.2)	106.2	< 0.0001	4 (124.1)	41.81	< 0.0001
Plant type	1 (124.3)	93.40	< 0.0001	1 (124.3)	11.94	0.0005
Location × Plant type	4 (124.2)	142.4	< 0.0001	4 (124.1)	138.6	< 0.0001

Significant results are in bold $p < 0.05$

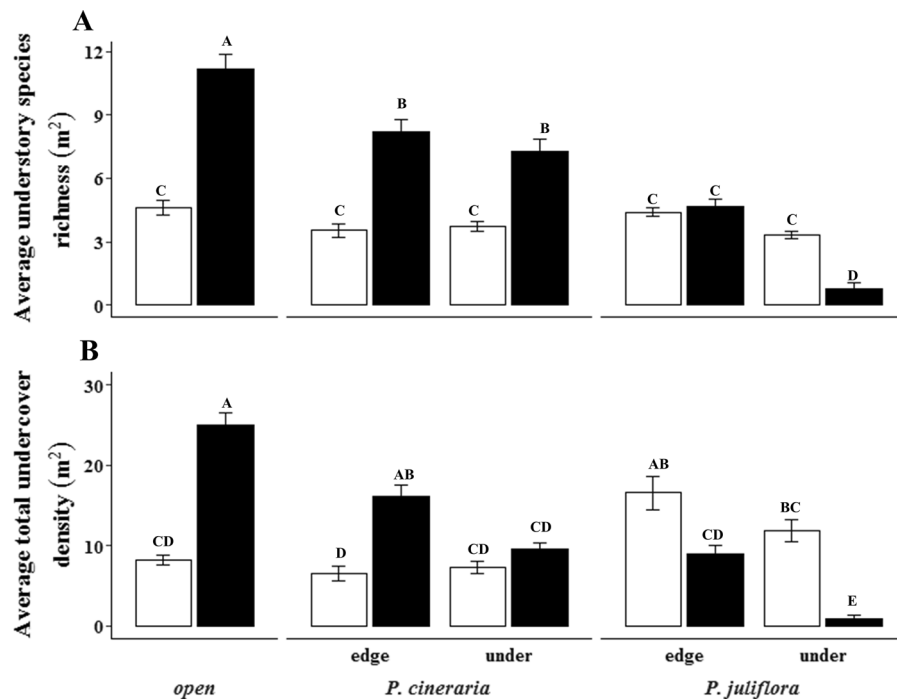


Fig. 1 Average total species richness (a) or plant density (b) $\pm$ 1 s.e. of ag-weed (open bars) and non-weed plant species (filled bars) at canopy edges and under canopies of *P. cineraria* or *P. juliflora*, and in the open. Bars that share a letter are not significantly different

2000; Oerke 2006; Kraehmer and Baur 2013), yet we know of no examples of research evaluating the relative impact of exotic invasive species on ag-weeds versus non-weeds. In this context, our most important finding was that the exotic invasive *P. juliflora* suppressed non-weed species and increased density of ag-weed species potentially creating local repositories of ag-weeds and a liability to nearby agriculture. Non-weed species richness and density were also lower under canopies of the native *P. cineraria*, but these effects were weaker than those of *P. juliflora*. Richness and density of non-weeds were greater at the margins of *P. cineraria* canopies, but not directly underneath. This drove a shift from plant communities composed mostly of non-weeds in the open and at the edge of *P. cineraria* canopies to understory plant communities with particularly high densities of ag-weeds under *P. juliflora*, a pattern that is consistent with “biotic homogenization” (Olden and Poff 2003) if it occurs at larger scales. Thus, our congeneric comparison indicated that biogeographic nativity of key species, *Prosopis* trees, played a large role in the relative impact on ag-weed species, which is analogous to invasional meltdown, but instead focuses on

species with generally weedy traits rather than biogeographical origin (Simberloff and Von Holle 1999).

Prosopis juliflora is native to the New World, but the understory species in this study are not, meaning that *P. juliflora* was just as “novel” (e.g., Callaway and Aschehoug 2000) to the ag-weed species as to the non-weed species. Yet, ag-weed and non-weed species differed in their associations with the two *Prosopis* congeners. It is unlikely that just “eco-evolutionary experience” based on biogeography and phylogenetic novelty (Saul et al. 2013) explained the differences between ag-weed and non-weed forbs and grasses in our study, but rather than various growth-related traits that ag-weed species often share matched them better to the abiotic and biotic environment under *P. juliflora* trees (Kuester et al. 2014; Pearson et al. 2018).

The general patterns of *P. juliflora* and *P. cineraria* on overall diversity shown here in Ras Al Khaimah Emirate of the UAE are consistent with those in other parts of its range. *Prosopis cineraria* generally has weak negative to weak positive effects on understory diversity in its native ranges, whereas *P. juliflora*-understory patterns indicate more consistent and

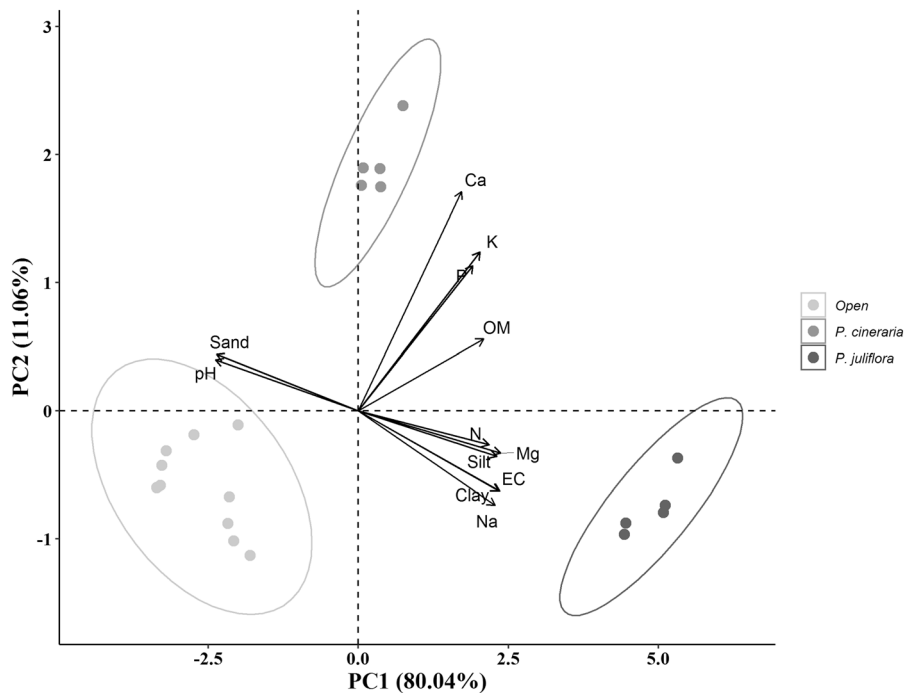


Fig. 2 Principal components analysis (PCA) of twelve soil properties measured under *P. cineraria* or *P. juliflora* canopies or in the open. Each point is a homogenized soil sample extracted from a single sampling location (under a *Prosopis*

canopy or in the open) and sampling locations are bordered by 95% CI ellipses. PC1 = 80.04% of the variance; PC2: 11.06% of the variance

Table 2 Results from a GLMM used to compare the effect of sampling location (under or at the edge of *Prosopis* canopies) and *Prosopis* species on litter thickness

	df	χ^2	<i>p</i> -value
Location	1 (18)	253.7	< 0.0001
<i>Prosopis</i> species	1 (17)	23.05	< 0.0001
Location $\times$ <i>Prosopis</i> species	1 (16)	0.764	0.3819

Significant results are in bold $p < 0.05$

strong suppression of the diversity and richness of subcanopy species (Aggarwal et al. 1976; Kaur et al. 2012; El-Keblawy and Abdelfatah 2014). None of these studies considered native and exotic understory species, or ag-weeds versus non-weeds, separately. Interestingly, *P. juliflora* is associated with *higher* understory species richness in its native Venezuela (Larrea-Alcázar and Soriano 2008; Kaur et al. 2012), the very opposite of the pattern that is widely observed in the species' non-native ranges around the world (Kaur et al. 2012; El-Keblawy and Abdelfatah 2014).

The different patterns of community composition and structure we describe might be affected by apparent changes in soil conditions. Other *Prosopis* species are correlated with higher soil fertility in their native ranges with resulting higher concentrations of OM, N, P and K beneath their canopies facilitating other species (Tiedemann and Klemmedson 1973, 1977, 1986; Virginia and Jarrell 1983; Archer et al. 1988; Franco-Pizaña et al. 1995, 1996; Carillo-Garcia et al. 2000; Rossi and Villagra 2003). In its native range of northwestern India, *P. cineraria* can facilitate native species (Aggarwal et al. 1976) and farmers keep *P. cineraria* in their fields to increase crop production (Aggarwal et al. 1993). Our findings are consistent with this body of research in that soil fertility was higher beneath both *Prosopis* species than in the open. However, soil fertility also differed between the co-occurring *Prosopis* species with higher clay, silt, N, Mg, and Na occurring in soil beneath *P. juliflora* canopies than *P. cineraria* canopies, conditions that non-weed species did not appear to thrive in.

The biogeographic, or nativity-based, pattern we found using these two *Prosopis* congeners is

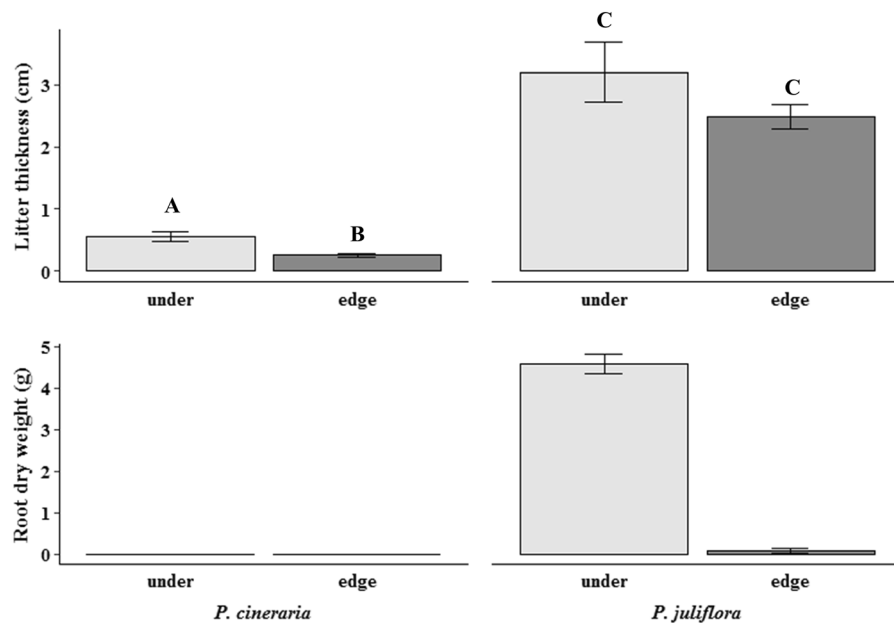


Fig. 3 Mean litter thickness at the edge or under *P. cineraria* and *P. juliflora* canopies (upper; $\pm$ 1 s.e). Bars that share a letter are not significantly different (Tukey HSD). Mass of fine tree roots at the edge or under *P. cineraria* and *P. juliflora* canopies

(lower). We found no fine *P. cineraria* roots in our soil cores so used a one-sample Wilcoxon signed rank test to determine if the median amount of fine tree roots under *P. juliflora* was greater than zero

conceptually consistent with a large number of studies that compare patterns for a single species in its native and non-native ranges (Callaway et al. 2012; Shah et al. 2014; Ledger et al. 2015; Pal et al. 2015; Becerra et al. 2018; Brewer et al. 2018; Davis et al. 2019). Our results are also conceptually similar to other studies that compare native to non-native congeners (Graebner et al. 2012; He et al. 2012; Meisner et al. 2012; Montesinos and Callaway 2018).

We do not know the mechanisms by which *P. juliflora* exerted stronger negative effects on non-weedy understory species than *P. cineraria*, but observations in the field and the literature suggest several non-mutually exclusive possibilities. First, *P. juliflora* individuals appear to grow faster than those of the native congener, based on litter production and observations throughout the UAE. Higher growth rates may elicit stronger competitive impacts on some species in the understory through competition for light or water, or particular nutrients. Also, there were far more fine woody roots in the upper soil profile under *P. juliflora* than under *P. cineraria*. These roots may have suppressed understory species in general or disproportionately suppressed non-weed species.

It is not clear why non-weed species would be competitively suppressed more than ag-weed species. Our measurements indicated much higher soil fertility under *P. juliflora* than *P. cineraria*. High soil fertility is likely to promote species with weedy traits (Besaw et al. 2011). There is also evidence for greater allelopathic effects of *P. juliflora* litter than *P. cineraria* litter, but again it is not clear why this would affect non-weed species more than ag-weed species. *Prosopis juliflora* leaf litter and litter leachate contains higher concentrations of total phenolics and L-tryptophan than litter from *P. cineraria* and is known to inhibit plant germination and growth while *P. cineraria* litter and litter leachates are associated with neutral to positive effects on plant germination and growth (Al-Humaid and Warrage 1998; Kaur et al. 2012; El-Keblawy and Abdelfatah 2014; Kaur et al. 2014). These effects, and the difference between the effects of *P. cineraria* and *P. juliflora*, may be due to higher concentrations of active biochemicals produced by the latter.

In sum, our results are consistent with a growing body of evidence suggesting that the origin of a species can, in some cases, determine how it interacts with other species. Not only was the invasive *P.*

juliflora associated with far lower non-weed species diversity than the native *P. cineraria*, in its native range *P. juliflora* is associated with disproportionately high understory diversity—i.e., it appears to have a strong facilitative effect (Kaur et al. 2012). This indicates an evolutionary context to plant community organization and understanding how an evolutionary context affects invader impacts may help to prioritize invasive species management (Blackburn et al. 2014). In this particular case, an exotic invasive tree species more strongly facilitated ag-weeds, potentially creating local reservoirs of these species from which they can colonize agricultural systems. Our results also indicated that the biogeographical origin of a species can have important effects on the organization of native communities, but the origin of our *Prosopis* species cannot explain why native non-weeds responded differently than native ag-weeds. An interesting avenue of future research would be to experimentally remove *P. juliflora* trees and rehabilitate their underlying soil to better support non-weed species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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