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ORIGINAL PAPER

Effects of a nonnative, invasive lovegrass on *Agave palmeri* distribution, abundance, and insect pollinator communities

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Abstract Nonnative Lehmann lovegrass (*Eragrostis lehmanniana*) has invaded large areas of the Southwestern United States, and its impact on native plants is not fully understood. Palmer's agave (*Agave palmeri*), an important resource for many pollinators, is a key native plant potentially threatened by *E. lehmanniana*. Understanding potential impacts of *E. lehmanniana* on *A. palmeri* is critical for anticipating the future of the desert community where they coexist and for addressing management concerns about associated threatened and endangered species. Our study provides strong indications that *E. lehmanniana* negatively impacts *A. palmeri* in several ways. Areas of high *E. lehmanniana* abundance were associated with significantly lower densities and greater relative frequencies of small *A. palmeri*, suggesting that *E. lehmanniana* may exclude *A. palmeri*. There were no significant differences in species richness, abundance, or community composition when comparing flower associates associated with *A. palmeri* in areas of high and low *E. lehmanniana* abundance. However, we did find significantly lower connectedness within the pollination network associated with *A. palmeri* in areas with high *E. lehmanniana* abundance. Although *E. lehmanniana* forms thick stands that would presumably increase fire frequency, there was no significant association between *E. lehmanniana* and fire frequency. Interestingly, medium to high densities of *A. palmeri* were associated with areas of greater fire frequency. The complex ramifications of *E. lehmanniana* invasion for the long-lived *A. palmeri* and interlinked desert community warrant continued study, as these

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species are likely to continue to be found in close association due to their similar soil preferences.

Keywords *Agave palmeri* · *Eragrostis lehmanniana* · Fire history · Indicator species · Pollinator community · Network analysis

Introduction

Invasive grasses present considerable challenges for land managers in desert ecosystems by competing with native species and generating fuel loads that can increase fire frequency and intensity (Whisenant 1990; Brooks and Pyke 2001; Brooks et al. 2004). Such non-native plants can aggressively spread into new habitat, monopolizing essential resources such as nutrients (Stohlgren et al. 1999), water (Holmes and Rice 1996), and light (Dyer and Rice 1999; MacDougall and Turkington 2005), often negatively impacting the persistence of native species and disrupting native plant communities (Morse et al. 1995). One such invasive grass, Lehmann lovegrass (*Eragrostis lehmanniana*), has become a major plant species on about 140,000 ha, primarily located in southeastern Arizona (Halvorson and Guertin 2003). The species has been shown to negatively impact native xeric grassland communities in the region and elsewhere (Litt and Steidl 2010; Brooks and Pyke 2001). In this study we assessed potential impacts of *E. lehmanniana* on *Agave palmeri*, a prominent native plant of the Sonoran grasslands of south-central Arizona.

Eragrostis lehmanniana is a nonnative perennial grass that was introduced in southern Arizona in 1932 to control soil erosion and provide forage for cattle, and has since spread throughout the southwestern United States (Crider 1945; Gori and Enquist 2003; Bock et al. 2007). The biomass of *E. lehmanniana* is typically two to four times greater (based on visual estimates and harvest weights) than the biomass produced by native grass vegetation (Anable et al. 1992). In its native Africa, the frequency and intensity of natural fires is greater in areas where *E. lehmanniana* is present and the species has been shown to benefit competitively from frequent fires (Kupfer and Miller 2005), though a similar positive feedback dynamic has not been found in North American populations (Geiger 2006). Attempts to control *E. lehmanniana* with prescribed fire have been unsuccessful, often resulting in regrowth during subsequent seasons (Rogers 2004). Currently, *E. lehmanniana* grows at elevations of 200–1830 m (Flora of North America Editorial Committee 2007). However, under changing climate conditions, its future distribution is predicted to spread to areas higher in elevation and much farther north than its present range (Schussman et al. 2006). Under these climate change scenarios, *E. lehmanniana* has the potential to spread over an additional 7,000,000 ha (Huang and Geiger 2008). Therefore, the potential for *E. lehmanniana* to dominate and influence ecosystems will likely increase.

Agaves (*Agave* spp.) are primarily found in Meso-America and are important ecological resources in many arid ecosystems, providing food (nectar, fruit, and leaves) for wildlife (Gentry 2003; USFWS 1999), while also maintaining significant economic value to humans (Good-Avila et al. 2006). In Arizona, *A. palmeri* is a state protected species that grows in sandy to gravelly places on limestone in oak woodlands and grassy plains at elevations between 900 and 2000 m (Flora of North America Editorial Committee 2002). The species lives for up to 25 years and has only one reproductive event, after which it rapidly senesces and expires. The reproductive stalk can reach heights greater than 3 m, producing a large number of blooms. The umbels of the *A. palmeri* flower are both diurnally and nocturnally available, making this species an important nectar and pollen resource for a large variety of pollinators (Slauson 2000), with the dominant taxa of pollinators including bats, bees, birds, and hawkmoths (Good-Avila et al. 2006; National Park Service 2007).

Though the full extent of the impacts of *E. lehmanniana* on *A. palmeri* is unknown, it is believed that *E. lehmanniana* strongly competes with agave seedlings (USFWS 1999). Additionally, if *E. lehmanniana* invasion results in increased fire frequency, *A. palmeri* abundance may be reduced (Geiger 2006; Gucker 2006), because while older agave plants seem to be fire tolerant, seedlings are susceptible to fire-related mortality (Robinett 1994). Fire may also cause reductions in the size of the *Agave* flowering stalks and in the number of blooms, or complete loss of the stalk, either reducing or completely eliminating plant reproductive potential (Howell 1996; USFWS 1999). Because agave stalks often remain available following fire when other food resources are limited, wild herbivores may favor them (USFWS 1999), reducing overall flowering stalk abundance, thus further reducing the reproductive potential of agave populations. In addition to direct impacts on germination, growth, and abundance, it is conceivable that *E. lehmanniana* could indirectly impact *A. palmeri* by reducing the abundance or diversity of pollinators available to agave and other flowers in the interconnected local plant–pollinator network (Litt and Steidl 2010; Olesen et al. 2006). The relatively higher biomass and dry-season persistence of *E. lehmanniana* could negatively impact pollinators by crowding-out native plants and reducing the availability of nectar sources and nesting sites (e.g. woody stems and bare ground used by bees). Finally, fire and the posited post-fire rise in herbivory on agave stalks could further impact pollinators by reducing the availability of nectar and pollen.

In this study we examined the impacts of *E. lehmanniana* on a key ecological component of northern Sonoran grasslands, including possible linkages with fire and soil type on the distribution and abundance of both *E. lehmanniana* and *A. palmeri*, and further examined the effect of *E. lehmanniana* abundance on *A. palmeri* flower associates (the insect pollinator community, including both direct and indirect pollinators and potential pollinators). We implemented a "network science" approach for describing and analyzing the structure of pollination linkages among *Agave* and other plants in the grassland community, with the objective of detecting any differences in those ecological relationships that might be associated with low and high *E. lehmanniana* abundance. Visualization and analysis of pollination networks can provide key insights into ecological relationships that foster species biodiversity, community stability, and the persistence of rare species (Aizen et al. 2009; Carvalheiro et al. 2008; Jordano et al. 2006; Fontaine et al. 2006; Memmott et al. 2004).

Methods

Study locale

We conducted our study on Fort Huachuca, an Army installation located in Cochise County of southeastern Arizona (Fig. 1). Nearly 3000 ha of *Agave* have been documented (Danzer and Roberts 2003) on the 33,000 ha installation. Fort Huachuca has well characterized vegetative communities, supports a number of rare plants and pollinators (USFWS 1999), and has a high diversity of pollinators (USFWS 1999). Our study area (21,200 ha; N 31.50776513, W 110.29905505) did not include the northeast section of the base, as *A. palmeri* was not present and fire history data was not available. We used prior

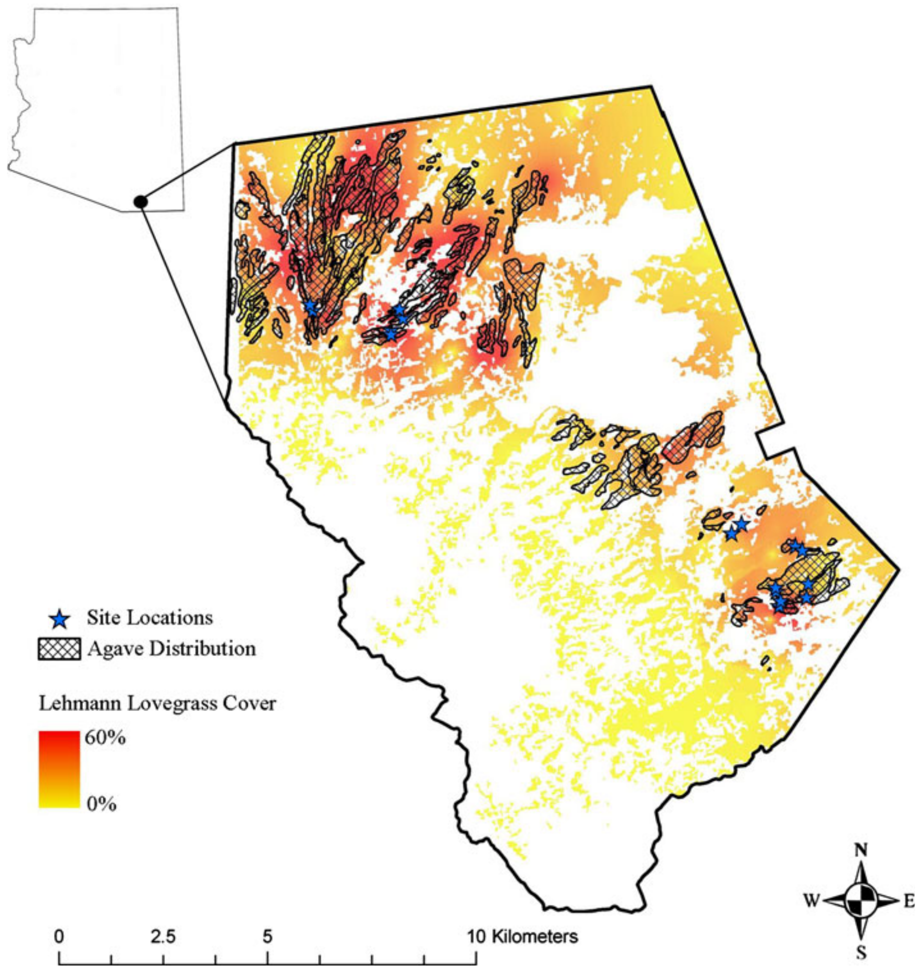

Fig. 1 Map of study area and sample site locations (*stars*) on Fort Huachuca, Arizona, including *Agave palmeri* distribution (cross-hatched polygons) and *Eragrostis lehmanniana* percent cover (*shaded*). *E. lehmanniana* distribution was determined by interpolation of percent cover found on ground plots, which was masked to the extent of grasslands as determined by the Southwest Regional Gap Analysis Program (SWReGAP; Lowry et al. 2007)

data (Schlichting 2006) to select areas characterized by high (≥35%) and low (≤15%) *E. lehmanniana* abundance (measured as percent cover of non-arboreal cover), and low, medium, and high densities of *A. palmeri*. Agave densities were determined by Danzer and Roberts (2003) through the use of high resolution (<0.3 m) aerial photographs, where agave density (mean number of agave plants ± 80% CI) was characterized as high (280 ± 41 ha^{-1}), medium (113 ± 12 ha^{-1}), and low (48 ± 9 ha^{-1}). Our study sites (0.25 ha each) were paired for high and low *E. lehmanniana* abundance over relatively homogenous terrain (elevation ranged from about 1450–1550 m) to minimize environmental variance. Average distance between site pairs was 204.3 m (range: 93.4–345.2 m). Percent cover of *E. lehmanniana* was estimated visually over the entire plot area using the National Vegetation Classification System technique. Mean (±SE) *E. lehmanniana* percent cover for our two classes of study sites (high = 52.83 ± 7.50%, low = 5.67 ± 1.87%) was determined to be significantly different ($F_{1,11} = 37.24$, $P = 0.0001$) using PROC GLM (SAS Institute 2005). Surveys and sampling were conducted during the summer of 2008.

Distribution of *Eragrostis lehmanniana* and *Agave palmeri* in relation to fire and soil

We obtained geographic information systems (GIS) data, including Environmental Systems Research Institute, Inc. (ESRI) shapefiles of fire history from 1975 to 2006, soil-type data from the Soil Survey Geographic (SSURGO; Soil Survey Staff), and data on *A. palmeri* distribution and density from prior installation surveys (Schlichting 2006). High resolution (1 m) 2007 color infrared imagery (USDA National Agriculture Imagery Program) was classified to cover types using a supervised classification to differentiate areas of tree canopy from grasslands. With this imagery, we were able to detect the presence of larger shrubs and trees (crown diameter >1 m) and quantify canopy cover of shrubs and other woody vegetation.

Spatial analyses were performed by overlaying ESRI shapefiles and rasters to determine overlap of fire, soil-type, *E. lehmanniana* abundance, and *A. palmeri* density. To increase sampling efficiency and allow for the extraction of a continuous dataset for statistical analyses, we generated 1000 random points each for the high, medium, and low density *A. palmeri* datasets (Beyer 2004). We analyzed trends in the distribution and density of *A. palmeri* relative to the distribution and abundance of *E. lehmanniana* by using an inverse distance weighting interpolation from point data (all percent cover of *E. lehmanniana*) collected in 2004 and 2006 (Schlichting 2006), and 2008. The output of this interpolation was a spatial dataset of percent cover of *E. lehmanniana* across Fort Huachuca. We also assessed the relationship of *E. lehmanniana* cover and fire occurrence, to further investigate the possible indirect effects of *E. lehmanniana* on *A. palmeri* survival and feeding guilds. The digital fire dataset was lacking temporal quality (e.g. some years were combined, missing, or duplicated in the dataset), and, thus, we were not able to accurately quantify fire frequency or time since fire. We also could not reliably discern ignition sources (e.g. natural or prescribed fires) from the dataset; therefore we focused on the role of fire distribution. This was accomplished by creating 1000 random points in the area of *A. palmeri* distribution (high, medium, and low density) and masking the *E. lehmanniana* dataset to each fire occurring from 1975 to 2006. At each random point within each fire year, we obtained percent cover of *E. lehmanniana* and compared this to cover not burned during that year. An analysis of variance (ANOVA; SPSS 16.0, 2007) was used to compare *A. palmeri* density with both fire occurrence and percent coverage of *E. lehmanniana* ($\alpha = 0.05$).

Interpolated percent cover of *E. lehmanniana* was masked to the extent of grasslands as determined by the Southwest Regional Gap Analysis Program (SWReGAP; Lowry et al. 2007) and the distribution of *A. palmeri* was excluded. We generated 1000 random points that overlaid the potential *E. lehmanniana* distribution (e.g., grasslands and non-agave) and extracted *E. lehmanniana* percent cover on these points. Percent cover of *E. lehmanniana* was also determined by generating 1000 random points within the distribution of *A. palmeri* and comparing to percent cover of *E. lehmanniana* in non-agave areas with an ANOVA. To determine which soil-types *E. lehmanniana* prefers, we generated 1000 random points and extracted soil-type from a SSURGO soils dataset and used an ANOVA to determine whether mean percent cover of *E. lehmanniana* differed significantly between soil-types.

Agave palmeri surveys

In addition to the distribution and density data for agave that we obtained from Schlichting (2006), we quantified the relative abundance and size class of *A. palmeri* at each of 10 sites characterized by high (N = 5) and low (N = 5) *E. lehmanniana* abundance in the grassland vegetation community. We quantified the total number of live and dead *A. palmeri* per site, and calculated size class by measuring the average diameter of each living *A. palmeri* using a standard measuring tape. Diameter was calculated by averaging two perpendicular measurements across the top of the plant. Comparisons of the number of live and dead *A. palmeri* between sites with high and low *E. lehmanniana* abundance were conducted with an ANOVA using PROC GLM (SAS Institute 2005). We then performed a Kolmogorov–Smirnov test to compare size class differences between high and low *E. lehmanniana* abundance sites using PROC NPAR1WAY (SAS Institute 2005).

Insect sampling and network analyses

We conducted complementary efforts to assess pollinator visitation to *A. palmeri* and to explore *A. palmeri*-centric pollinator networks in areas of both low and high *E. lehmanniana* abundance. First, we completed a directed assessment of insects visiting *A. palmeri* flowers. For this study, we sampled insects from *A. palmeri* during their peak flowering season (July and August). Once per month, we collected insects on blooms from 7 to 10 individual *A. palmeri* per site, at each of 12 sites characterized by high (N = 6) and low (N = 6) *E. lehmanniana* abundance. All blooming agave occurring inside the plot boundaries were sampled, as well as nearby agave outside the plot boundaries, in order to maximize the number of agave sampled overall and to more closely match the number of individual agaves sampled/site. Individual agaves were systematically sampled for two consecutive minutes with battery powered handheld vacuums modified for insect collection. In order to reach flowering stalks that ranged in height from 3 to 6 m, we modified vacuums to have 60 cm nozzle extensions and collectors stood on orchard ladders. Insects were identified to the lowest possible taxonomic level. Efforts were made to record pollination by hummingbirds on agave during 15 min observation periods prior to vacuum sampling, but due to very few recorded interactions and difficulties with species identification, we did not include hummingbird data in our analyses. Likewise, we did not include data on nocturnal pollinators.

We assessed *A. palmeri* pollinator community differences between high and low *E. lehmanniana* abundance sites by comparing mean species richness and species abundance with a one-way ANOVA (PROC ANOVA; SAS Institute 2005). We conducted a species indicator analysis with a Monte Carlo test of significance using PCORD 5.10 (McCune and Mefford 2006) to determine whether specific insect taxa responded to high or low *E. lehmanniana* abundance. We used a multi-response permutation procedure (MRPP) using Primer 6 (Clarke and Gorley 2006) as a quantitative measure to explain pollinator community differences between high and low *E. lehmanniana* abundance sites. A non-metric multidimensional scaling (NMS) scatter plot (Clarke 1993) was used as a descriptive method to examine similarities of pollinator communities based on Bray-Curtis distance (Beals 1984; McCune and Beals 1993).

In another effort, we examined plant–pollinator networks in 16 plots (100 $\times$ 25 m) characterized by high (N = 8) and low (N = 8) *E. lehmanniana* abundance. Plots were surveyed monthly for pollinator–plant interactions from April to September, with the exception of June (due to dry conditions and a lack of flowering plants). Each plot was divided into five sampling lanes, four of which were randomly selected for sampling by a randomly assigned field technician. Sampling was conducted using the same battery powered handheld vacuums modified for insect collection as used with the agave-centric pollinator sampling. All insects found on flowers (any species) along each of the four selected transects over a 20 min period were collected and stored in individual tubes (using a separate tube for each plant species), with collection on individual plants limited to two consecutive minutes. Plots were sampled once per month, with the order of sampling both among and within plot pairs randomly assigned during each sampling trip. Plants on each plot were identified to species and the collected insects were identified to the lowest possible taxonomic level. As before, hummingbird and nocturnal pollinator activity on plots was not obtained.

All flower associates (both direct and indirect pollinators/potential pollinators), and the plant species on which they were collected, were used to create rectangular weighted adjacency matrices and corresponding bipartite (2-mode) networks: one set for low *E. lehmanniana* abundance (combined data from all low *E. lehmanniana* abundance sites and all months) and another set for high *E. lehmanniana* abundance (combined data from all high *E. lehmanniana* abundance sites and all months). In the bipartite network, each plant and pollinator corresponds to a node, and the number of pollinators captured on a plant provide a weighting for the edges (=links) between plant and pollinator nodes. In order to visualize and analyze the structure of plant–plant interactions (=shared pollinators), the weighted adjacency matrices were dichotomized and collapsed to create new, square weighted adjacency matrices and corresponding unipartite (1-mode) networks. In the new weighted adjacency matrices, the constituent plants comprise both column and row categories and the matrix cells correspond to the number of pollinator species shared by pairs of different plant species. In the unipartite network, each species of plant corresponds to a node, and the number of pollinator species shared by two plant species corresponds to a weighted edge between nodes. In order to focus our analyses on *A. palmeri*, reduced matrices corresponding to the unipartite "ego networks" of agave (all plants linked directly to *A. palmeri* through shared pollinators) were extracted from the broader data sets. Because many of the available analyses can only be used to analyze unweighted (binary) networks, the weighted agave ego network matrices were dichotomized to create unweighted adjacency matrices and corresponding unweighted unipartite networks. Other common network measures, such as diameter or closeness centrality, would have been meaningless or redundant with other statistics for the agave ego network, and were thus not included. The significance of differences in standard network measures, described earlier, for unipartite networks from areas with high and low *E. lehmanniana* abundance were determined following bootstrap procedures described by Snijders and Borgatti (1999). All matrix processing and network analyses were executed using UCINET 6.0 (Borgatti et al. 1999). Network parameters of interest (reviewed in Börner et al. 2007) included those related to topology, such as the number of nodes or size of the network (N), number of edges or links (E), density of the network $\left(D = \frac{2E}{N(N-1)}\right)$, and several measures of network connectedness, including mean number of edges per node ($\bar{k}$) or mean degree centrality ($\overline{C_D}$), mean betweenness centrality ($\overline{C_B}$; the proportion of shortest network paths between other nodes that incorporate a node), mean eigenvector centrality ($\overline{C_E}$; a measure of the degree to which a node is a component of overall connectedness in the network), and mean Bonacich power ($\overline{C_\beta}$; when the attenuation factor, β, is positive, power is a positive function of being connected to well-connected nodes). Network creation and visualization was executed with Netdraw 2.085 (Borgatti 2002), with random positioning of nodes and strength of weighted edges (number of shared pollinators) represented by scaled line thicknesses (stronger edge = thicker line).

Results

Agave palmeri and *Eragrostis lehmanniana* distributions

Agave palmeri occupied 8.7% (1837 ha) of the study area (21,200 ha; Fig. 1), with an estimated 249 ha being designated as high density (280 ± 41 plants/ha), 993 ha designated as medium density (113 ± 12 plants/ha), and 595 ha designated as low density (48 ± 9 plants/ha). There were no areas where *A. palmeri* was present without *E. lehmanniana*. Mean *E. lehmanniana* cover in the study area was 7.3 ± 0.3%; while throughout the distribution of *A. palmeri* mean *E. lehmanniana* cover was 25.7%. Areas of low density *A. palmeri* were significantly associated with areas of high *E. lehmanniana* abundance ($F = 42.50$, $P < 0.0001$; Fig. 2). The size of *A. palmeri* plants ranged from 0.03 to 2.64 m diameter, with a significantly higher relative frequency (5.23:1; $KSa = 1.9578$, $P = 0.0009$) of smaller agave plants (≤0.4 m radius) in areas with high *E. lehmanniana* abundance.

Different levels of *A. palmeri* density were associated with different soil-types, with 76% of the high density *A. palmeri* populations being located on the Terrarossa–Blacktail–Pyeatt Complex, which only comprises 8% of soil within the study area. Both the medium and low density *A. palmeri* populations were found more equally distributed among three of the eight soil-types found in the study area (Table 1 in Supplementary material). *E. lehmanniana* abundance was also associated with certain soil-types (Table 1 in Supplementary material), and although it was much more uniformly distributed among soil-types than agave, it was also most abundant on the Terrarossa–Blacktail–Pyeatt Complex (19%). Percent cover of *E. lehmanniana* was significantly higher ($F = 398.33$, $P < 0.001$) within the distribution of *A. palmeri* than outside this distribution (Fig. 2).

There were no significant associations between burn history (natural and prescribed) and *E. lehmanniana* distribution and abundance. For *A. palmeri*, however, areas of high and medium density were significantly associated with more frequent burning ($F = 3.26$, $P < 0.05$; Fig. S1 in Supplementary material).

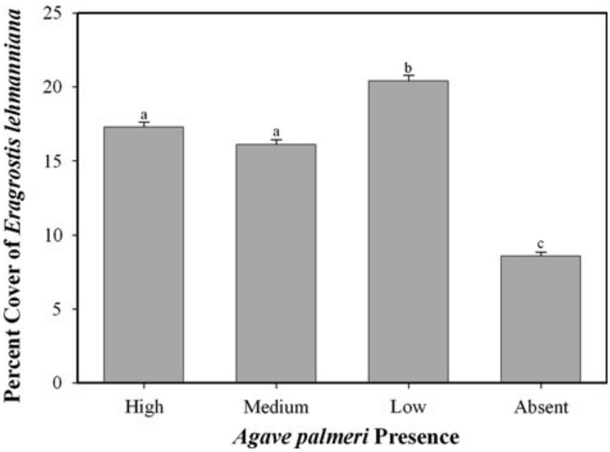

Fig. 2 Results of ANOVA on mean percent cover of *Eragrostis lehmanniana* as compared to high density (280 ± 41 ha^{-1}), medium density (113 ± 12 ha^{-1}), and low density (48 ± 9 ha^{-1}) *Agave palmeri* ($F = 42.50$, $P < 0.0001$), as well as *A. palmeri* absence ($F = 398.33$, $P < 0.001$). Percent cover of *E. lehmanniana* was extracted at 1000 random points both within and outside the distribution of *A. palmeri*. Error bars represent standard error of mean

Pollinator community analysis

There was no significant difference in pollinator species richness ($F_{1,23} = 0.14$, $P = 0.7076$) or species abundance ($F_{1,23} = 0.50$, $P = 0.4868$) between sites with high ($N = 11$) and low ($N = 13$) *E. lehmanniana* abundance. Nor were there any significant differences in pollinator community composition between high and low *E. lehmanniana* abundance sites ($R = -0.015$, $P = 0.726$). Of the 70 taxa identified (Appendix A in Supplementary material), only one species was an indicator of either high or low *E. lehmanniana* abundance. With a mean observed indicator value of 20.8 ± 3.67, *Agapostemon angelicus*, a sweat bee, was found to be an indicator species associated with *A. palmeri* in high *E. lehmanniana* abundance areas ($P = 0.0472$).

Pollinator network analyses

In each *Agave*-centric network (low vs. high *E. lehmanniana* abundance), *A. palmeri* was directly linked (shared ≥1 pollinator species) with 11 other plants (Fig. 3). In addition to *A. palmeri*, the two networks had only three plant species in common, namely *Acacia angustissima*, *Calliandra eriophylla*, and *Prosopis velutina*. The low *E. lehmanniana* abundance *Agave*-centric network included 30 different insect pollinators, while the high *E. lehmanniana* abundance network contained 14 different insect pollinators, where "pollinators" refers to all flower associates (all insects captured on flowers, including indirect pollinators, such as predators and herbivores). Nine species of pollinators (*Apis melifera*, *Dialictus microlepoides*, *Hemiargus isola*, *Microclepi* spp., *Bruchophagus* spp., *Myrmecosystus* spp., *Crematogaster* spp., *Lydella radicus*, and *Trupanea* spp.) were found in both classes of *Agave*-centric networks. In both of the larger pollination networks that incorporated all interactions among all plants (not just those linked to *Agave*) the plants of the *Agave*-centric networks were prominent, comprising 40% of all plant species. However, there were notable differences between the *Agave*-centric networks in the low and high *E. lehmanniana* abundance plots, including a relatively higher degree of pollinator sharing among plants in the low plots ($E = 92$ vs. 72; $D = 63.64$ vs. 43.64%). Significant differences (one-tailed *t*-tests, 10,000 bootstraps) between the unweighted unipartite networks (low vs. high, respectively) included mean node degree centrality ($\overline{C_D} = 7.667$ vs. 5.833, $P = 0.041$) and mean node power ($\overline{C_\beta} = 1160.109$ vs. 662.263, $P > 0.001$). In regards to the weighted unipartite networks, the same trends hold true with $\overline{C_D}$ (14.500 vs. 8.500, $P = 0.010$), $\overline{C_B}$ (22.792 vs. 2.583, $p = 0.034$), and mean cluster coefficient ($\bar{c} = 1.821$ vs. 1.213, $P = 0.002$). There were no significant differences in betweenness centrality ($\overline{C_B} = 1.667$ vs. 2.583, $P = 0.653$) or eigenvector centrality ($\overline{C_E} = 0.280$ vs. 0.276, $P = 0.910$) for the unweighted networks, nor in eigenvector centrality for the weighted networks ($\overline{C_E} = 0.268$ vs. 0.246, $P = 0.697$). *A. palmeri* also appears to play a more central role in the network from low *E. lehmanniana* plots, as indicated by a higher 2-step reach (the percentage of other nodes within 2-links of agave; 93.10 vs. 86.21%).

Discussion

While "comparisons of native- and nonnative-dominated communities are inextricably confounded by soils" (Geiger 2006), there were several key patterns that emerged from this study: (1) *A. palmeri* and *E. lehmanniana* prefer the same soil types, though lovegrass

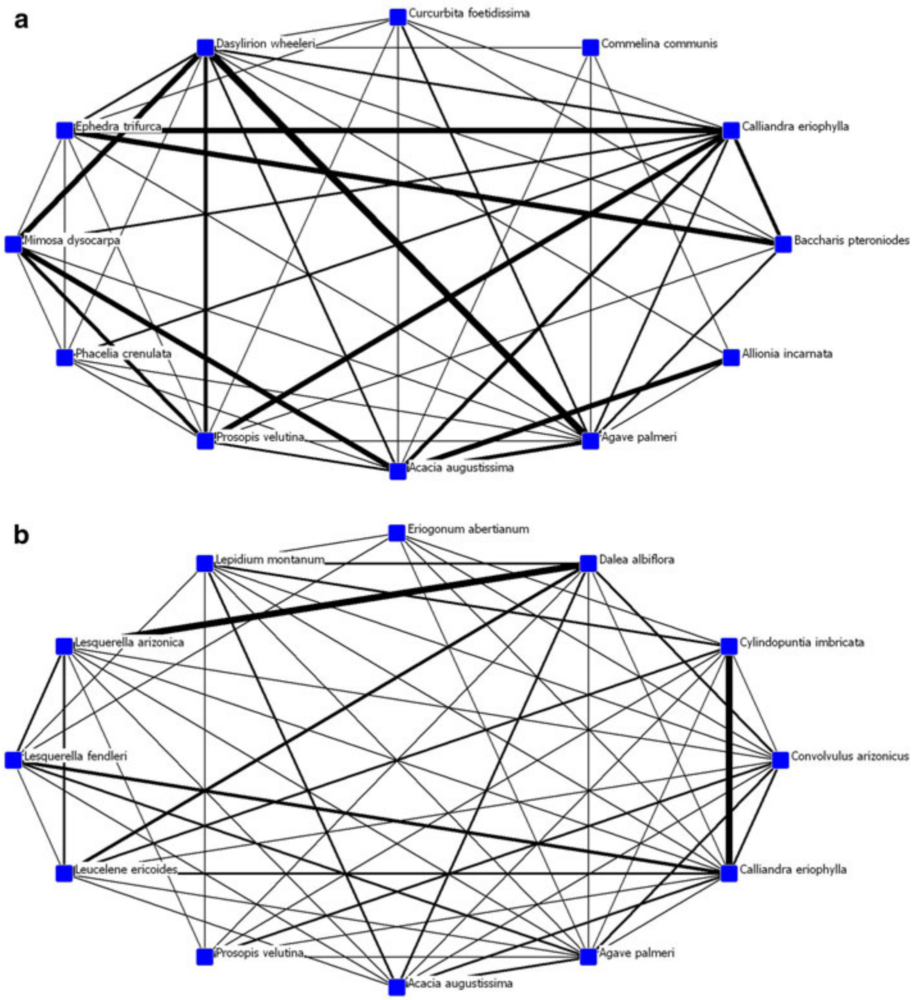

Fig. 3 Unipartite networks of plants linked through shared pollinator species from **a** low *E. lehmanniana* abundance plots and **b** high *E. lehmanniana* abundance plots. Link thickness increases with the number of pollinator species shared by plants

grew in a broader range of soils, (2) there appears to be a threshold response by *A. palmeri* to *E. lehmanniana* abundance, where *A. palmeri* density was two- to six-fold lower and small size class rossettes were relatively more common in the highest areas of *E. lehmanniana* abundance, (3) there was no apparent increase in the frequency of fire relative to *E. lehmanniana* abundance, but *A. palmeri* densities were higher in areas that experienced more frequent fires, (4) there were no differences between high and low *E. lehmanniana* abundance sites in regard to the average *A. palmeri* pollinator species richness, and (5) despite a lack of differences in pollinator abundance or richness between site classes, the *Agave*-centric pollination network suggested a reduction in interactions among plants in areas of high *E. lehmanniana* abundance.

Eragrostis lehmanniana was preferentially found on the same three soil-types where *A. palmeri* most commonly occurred, and percent cover of *E. lehmanniana* was significantly higher within *A. palmeri* areas. While both species preferred and were found on well-drained, coarse textured soils (e.g. Terrarossa and Whitehouse Complexes), *E. lehmanniana* grew on a wider range of soil-types (Cox et al. 1988; Cumming 1989). For example, *E. lehmanniana* was found in relatively high abundance (>10% cover) on the Ubik soil type, while *A. palmeri* was rarely found on this soil-type, likely due to the increased water holding potential of Ubik soils (Cumming 1989). Cox et al. (1988) also showed long term persistence of *E. lemanniana* on coarse textured soils.

We identified a few apparent negative associations between *E. lehmanniana* and *A. palmeri*. First, relative to areas of high or medium density *A. palmeri*, high *E. lehmanniana* abundance was significantly associated with low *A. palmeri* density. Second, there was a higher ratio of small to large *A. palmeri* plants in areas of high *E. lehmanniana* abundance, indicating that *E. lehmanniana* might competitively exclude, or retard growth in, *A. palmeri*. Within a population, agave plant size is indicative of time to reproductive maturity. Throughout the Southwest, areas with a higher ratio of small to large agave plants are a management concern because stands of small plants are considered to be important future nectar-feeding centers for the endangered lesser long-nosed bat (*Leptonycteris curasoae yerbabuenae*) and the threatened Mexican long-tongued bat (*Choeronycteris mexicana*), and should thus be protected (Schlichting 2006). Although the small/young agave plants are important, higher density stands of agave also need to be protected, as the total amount of nectar produced is of conservation concern.

Areas burned with high *E. lehmanniana* abundance had not burned more frequently than areas of low *E. lehmanniana* abundance. These results follow the observation of Geiger (2006) that the proportion of *E. lehmanniana* on burned versus unburned areas does not increase (Geiger 2006), unlike patterns found in Africa (Cox et al. 1988). However, relative to low density *A. palmeri*, areas of high density *A. palmeri* did coincide with areas that had burned more frequently. While this may indicate a positive relationship between fire and *A. palmeri*, fire is known to reduce seedling survival (Geiger 2006), and in a related species, *A. lechuguilla*, burning was associated with reduced plant abundance (Ahlstrand 1982). Burns that resulted in greater than 50% destruction of green leaves typically killed *A. lechuguilla* and less damaged plants exhibited reduced growth rates (Ahlstrand 1982). This result also follows the observation of Geiger (2006) that survival of agave varies with soil-type.

There were no significant differences in *A. palmeri* flower associate species richness, species abundance, or community composition between sites with high and low *E. lehmanniana* abundance, suggesting that *E. lehmanniana* does not have a negative influence on the *A. palmeri* pollinator guild. *A. palmeri* flowering stalks often tower over the maximum height of *E. lehmanniana*, thus allowing pollinators to access agave blooms with ease. However, high *E. lehmanniana* abundance is concomitant with low densities of *A. palmeri*, which suggests that pollinator activity should also follow this pattern. One potential explanation for this somewhat counterinutitive pattern is that in areas of high *E. lehmanniana* abundance, the invasive lovegrass could be outcompeting other native flora, thus increasing the amount of pollinator activity on the limited numbers of *A. palmeri*. One pollinator appeared to be a significant indicator of *A. palmeri* in areas of high *E. lehmanniana* abundance. This species, *Agapostemon angelicus*, is a native, pollen-feeding sweat bee. The sweat bees are considered generalist species, pollinating a wide variety of flower species. *A. angelicus* could be utilizing *A. palmeri* as a major pollen source, or the association may be due to *E. lehmanniana* providing cover or nesting material for the bee, though the second scenario is unlikely considering that *Agapostemon* spp. nest in ground burrows (Michener 2000). In general, bees are the most common pollinators in these latitudes, a trend also observed in this study. Our collection of *A. palmeri* flower associates included 30 species of Hymenoptera (bees), 21 species of Diptera (flies), 11 species of Coleoptera (beetles), 4 species of Lepidoptera (butterflies), 2 species of Hemiptera (aphids, leafhoppers and cicadas), and 2 species of Araneae (spiders). The most dominant bee genera in our study (*Lasioglossum*, *Halictus*, and *Diadasia*) are ground nesters that are often specific to south facing, sparsely vegetated slopes of either sandy or clay soil (Cane et al. 2006; Westrich 1996), indicating that increased ground cover in the form of *E. lehmanniana* may be detrimental to the survival of common native bee species (Potts and Willmer 2003; Potts et al. 2005).

Network descriptions of the interconnectedness and co-reliance among plants that share pollinators provide potentially important insights into the combined community's robustness and resilience to changes in composition (e.g. loss of species; Aizen et al. 2009; Fontaine et al. 2006; Memmott et al. 2004). Network approaches also provide important insights into the role of a particular species, plant or pollinator, in supporting community structure, as well as that species' susceptibility to extinction within the community (Carvalheiro et al. 2008). In the desert grassland community we studied, it appears that *A. palmeri* and its ego network (the plants to which it is directly linked through shared pollinators) are major components of the overall pollinator network and likely lend a large degree of stability to the pollination dynamics of the community. It also appears that *A. palmeri* and the plants in its ego network are well established and supported by multiple pollinator linkages, but are significantly more strongly interconnected within low *E. lehmanniana* abundance areas. One possible explanation for observations leading to the apparent greater connectedness within low *E. lehmanniana* areas may be a rarefaction bias in the sampling due to the higher density of *A. palmeri* in low *E. lehmanniana* abundance areas and, consequently, greater likelihood of detecting additional pollinator species. And, as noted, percent cover of *A. palmeri* was significantly higher within areas of low *E. lehmanniana* abundance sites ($F = 4.88$, $P = 0.0444$). Another potential explanation for the observed pattern is that increasing *E. lehmanniana* abundance may increasingly depress plant and pollinator diversity and abundance, which would reduce network connectedness. Geiger (2006) noted that both biomass and species richness of native plants declined with increasing *E. lehmanniana* abundance. However, in the sampling component of our study for the direct assessment of *A. palmeri* insect pollinators, where numbers of agave sampled in low and high *E. lehmanniana* abundance habitat were equivalent, significant differences in pollinator diversity did not exist.

One interesting finding was that the three plant species common to both the low and high *E. lehmanniana* abundance plots, aside from *A. palmeri*, were all legumes (Fabaceae). Legumes, as a family, are common in the Sonoran Desert—e.g. 8% of all plant species in the Tucson Mountains (Dimmitt 2000), 6% of all plant species in Ironwood Forest National Monument (Dimmitt et al. 2003), and 15% of all plant species in our study plots—and all three common species (*Acacia angustissima*, *Prosopis velutina*, and *Calliandra eriophylla*) are abundant woody-stemmed perennials with many flowers. The flowers of these plants, furthermore, are conspicuous and available to a general assortment of pollinators. It is likely, therefore, that legumes are substantial components of plant–pollinator communities, and pollination networks, throughout the Sonoran Desert and other arid regions. Also of note, *P. velutina* is considered an invasive species in Sonoran Desert grasslands because, though native, it has been spreading or increasing dramatically in abundance (shrub encroachment) as a result of fire suppression, livestock grazing, and, perhaps, climate change (*reviewed in* Van Auken 2000). In this agave-centric study, *A. palmeri* appears to be well-connected within the plant–pollinator network, and reduced abundance in any single species, even *P. velutina*, would seem unlikely to severely threaten *A. palmeri*.

The results of this study are a component of a much larger study of the impacts of *E. lehmanniana* on plant–pollinator communities in the Sonoran Desert and will be leveraged against ongoing work on pollinator systems by Fort Huachuca, the state of Arizona, and the US Army Engineer Research and Development Center. Further analyses of the greater pollinator network, of the network topology over space and time, and of the topology under different climatic scenarios will add considerably to our understanding of this system.

Conclusions

We have found several indications that the invasive nonnative grass *E. lehmanniana* may negatively impact a key native plant, *A. palmeri,* which is an important resource for many pollinators in the desert communities of the Southwestern United States. Our study is the first to document negative impacts. *E. lehmanniana* may exclude *A. palmeri*, as areas of high *E. lehmanniana* abundance (>35% cover) were associated with significantly lower densities of *A. palmeri*, greater numbers of small/young *A. palmeri* plants, and lower pollinator network connectedness. Although *E. lehmanniana* abundance had no significant effect on fire frequency, medium and high density *A. palmeri* areas were associated with increased fire frequency. While a positive relationship was observed between agave density and fire, there exists the possibility of negative impacts on overall nectar production if the timing of fire prevents agave plants from blooming or destroys agave seedlings. Because *E. lehmanniana* and *A. palmeri* are likely to continue to be found in close association based on similar soil preferences, further study and monitoring of the invasion and impacts of *E. lehmanniana* on these desert communities and their associated threatened and endangered species would benefit future management decisions.

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