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Effects of invasives on the distribution
of keystone desert plants on military lands

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Effects of a Nonnative, Invasive Lovegrass on *Agave palmeri* Distribution, Abundance, and Insect Pollinator Communities

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PURPOSE: This technical note is a product of the Department of Defense Legacy Resource Management Program work unit titled "Effects of invasives on the distribution of keystone desert plants on military lands." The objective of the work unit is to provide a better understanding of the impacts of invasive species on key components of ecosystems and pollinator communities. The study documented herein emphasized the integration of invasive nonnative plant invasion with other ecological processes through assessments of the spatial effects and fire dynamics of Lehmann lovegrass (*Eragrostis lehmanniana*) on the distribution and abundance of Palmer's agave (*Agave palmeri*), investigations of changes in *A. palmeri* pollinator community composition and diversity in the presence of high *E. lehmanniana* abundance, and implementation of a focused network analysis of *A. palmeri* and the plants with which it directly interacts with through shared pollinators. The purpose of this technical note is to provide information (such as key insights into important ecological relationships that foster species persistence, biodiversity, and community stability) that can be leveraged against ongoing work on pollinator systems by Fort Huachuca, the state of Arizona, and the U.S. Army Engineer Research and Development Center, to address management concerns for desert plant communities and their associated threatened and endangered species.

INTRODUCTION: Invasive plants are considerable challenges for land managers in desert ecosystems, especially invasive grasses, which both benefit from and promote recurrences of fire, often reducing the persistence of native species and converting native plant communities to annual grasslands (Brooks and Pyke 2001). Invasive plants are capable of aggressively spreading into new habitat and monopolizing essential resources such as nutrients, water, and light, consequently out-competing native species. Impacts of invasive species on natural environments have contributed to the decline of 42 percent of federally threatened and endangered species nationwide (U.S. Environmental Protection Agency (USEPA) 2001), and following direct loss of habitat, invasive species are the next greatest threat to the survival of native species. Potential negative impacts of invasive species include the disruption of ecosystem structure and function via the alteration of community composition, the reduction of available resources, and diminished reproductive efficiency.

The genus *Agave* is an important native taxa to assess the effects of invasive grasses because agaves are keystone species (one whose impact on its ecosystem is disproportionately large

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relative to its abundance) of semiarid and arid regions of the southwest with considerable eco-logical and economic value (Good-Avila et al. 2006). The Palmer's agave (*Agave palmeri*) is state protected in Arizona and is currently threatened by the invasive African plant, Lehmann lovegrass (*Eragrostis lehmanniana*), as grasses strongly compete with agave seedlings (U.S. Fish and Wildlife Service (USFWS) 1999). *A. palmeri* grows in sandy to gravelly places on limestone in oak woodlands and grassy plains at elevations between 900-2,000 m in Arizona, New Mexico, and Mexico (Flora of North America Editorial Committee 2002). Agave plays a key role in the life history of the federally endangered lesser long-nosed bat (*Leptonycteris curasoae*) and state listed Mexican long-tongued bat (*Choeronycteris mexicana*). It is an important nectar and pollen resource for a large variety of pollinators, including bees, hummingbirds, orioles, butterflies, and wasps (National Park Service (NPS) 2007). However, little is known regarding the effect of agave on insect pollinators.

E. lehmanniana was introduced in southern Arizona in 1932 to control soil erosion and provide forage for cattle and has since spread throughout the southwest (Crider 1945; Gori and Enquist 2003; Bock et al. 2007). It is now considered a major plant species on about 140,000 hectares (ha), primarily located in southeastern Arizona (Halvorson and Guertin 2003), and has the potential to spread to over 7,000,000 ha under predicted climate change scenarios (Huang and Geiger 2008). The biomass of *E. lehmanniana* is typically two to four times greater than the biomass produced by native grass vegetation (Anable et al. 1992); thus, it can indirectly impact pollinators by crowding out native plants and reducing the availability of nectar sources and nesting sites (e.g. woody stems and bare earth used by bees). Currently, *E. lehmanniana* grows at elevations from 200-1,830 m (Flora of North America Editorial Committee 2007). The potential for *E. lehmanniana* to dominate and influence ecosystems is likely increasing because under changing climate conditions, its future distribution is predicted to be much greater than its cur-rent distribution (Schussman et al. 2006), with colonization spreading to areas higher in elevation and much farther north than its present range.

Additionally, the lovegrass can indirectly affect plant interactions by altering fire dynamics throughout the ecosystem. Prescribed fires to remove *E. lehmanniana* populations have been unsuccessful in maintaining control, often resulting in regrowth during subsequent seasons (Rogers 2004). Furthermore, the lovegrass has been shown to increase the frequency and inten-sity of natural fires (Kupfer and Miller 2005), which could alter *A. palmeri* germination, growth, abundance, and resource availability and foraging behavior of pollinators (Geiger 2006; Gucker 2006). Agave stalks are edible to wild herbivores such as deer, javelina, rodents, and rabbits (USFWS 1999). Because agave stalks often remain available following fire when other food resources are limited, herbivores may favor them, negatively impacting the availability of flow-ering stalks for pollinators, such as the nectar-feeding bats (USFWS 1999). In addition to the direct mortality of agave, fire may alter the availability of blooms, as agaves physiologically commit to bolt by early spring. If an agave survives a burn, bolting continues although the stalk is then smaller and has fewer flowers (Howell 1996; USFWS 1999), and if an agave stalk burns directly, the reproductive effort and the availability of nectar for that plant is completely lost (USFWS 1999). Both of these situations result in reduced availability of nectar for pollinators.

This study assesses the impacts of invasive species on key components of ecosystems and polli-nator communities. To integrate aspects of invasive nonnative plant invasion with other ecologi-cal processes, the spatial effects of fire, soil type, and *E. lehmanniana* on the distribution and

density of *A. palmeri* are assessed, and changes in agave pollinator community composition and diversity in the presence of high *E. lehmanniana* abundance are investigated. A network approach was implemented (Jordano et al. 2006; Olesen et al. 2006) to describe and analyze how agave interacts through shared pollinators with other plants, and to detect any differences in the structures of these agave "ego networks" associated with low and high *E. lehmanniana* abundance. Network visualization and analysis of pollination communities can provide key insights into important ecological relationships that foster species persistence, biodiversity, and community stability (Aizen et al. 2009; Carvalheiro et al. 2008; Fontaine et al. 2006; Memmott et al. 2004). The agave ego network was restricted to only those plants directly connected to *A. palmeri*, making other common network measures, such as diameter or closeness centrality, meaningless or redundant with other statistics. Information gained from this study will be leveraged against ongoing work on pollinator systems by Fort Huachuca, the state of Arizona, and the U.S. Army Engineer Research and Development Center, to address management concerns for desert plant communities and associated threatened and endangered species.

METHODS:

Study Locale. The study was conducted on Fort Huachuca, located in Cochise County of southeastern Arizona (Figure 1). Nearly 3,000 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, and has a high diversity of pollinators. The overall study area (21,200 ha) did not include the northeast section of the base, as agave was not present and fire history data were not available. Study sites were selected using prior data[1,2] to locate areas characterized by high ($\geq$ 35 percent) and low ($\leq$ 15 percent) abundance *E. lehmanniana*, and low, medium, and high densities of *A. palmeri*. These study sites were chosen in paired locations for high and low abundance *E. lehmanniana* over relatively homogenous terrain (elevation ranged from about 1450-1550 m) to minimize environmental variance. Mean *E. lehmanniana* percentage was determined between two classes of study sites (high = 52.83 percent $\pm$ 18.37 percent, low = 5.67 percent $\pm$ 4.59 percent) 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. Geographic information systems (GIS) data were obtained, including shapefiles of fire history from 1975-2006, soil types (Soil Survey Geographic (SSURGO)), and agave distribution and density (provided by D. Schlichting). High-resolution (1-m) 2007 color infrared imagery (USDA National Agriculture Imagery Program) was obtained for determining canopy cover of overstory tree species (e.g. *Prosopis* spp.). High-resolution imagery was classified using a supervised classification to differentiate areas of tree canopy from grasslands. With this imagery, the authors were able to remotely detect the presence of larger shrubs and trees (crown diameter > 1 m), and quantify canopy cover.

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[2] Personal communication. 2009. D. Schlicting, Range Training Lands Assessment Coordinator, Colorado State University Center for Environmental Management of Military Lands, Ft. Huachuca, AZ.
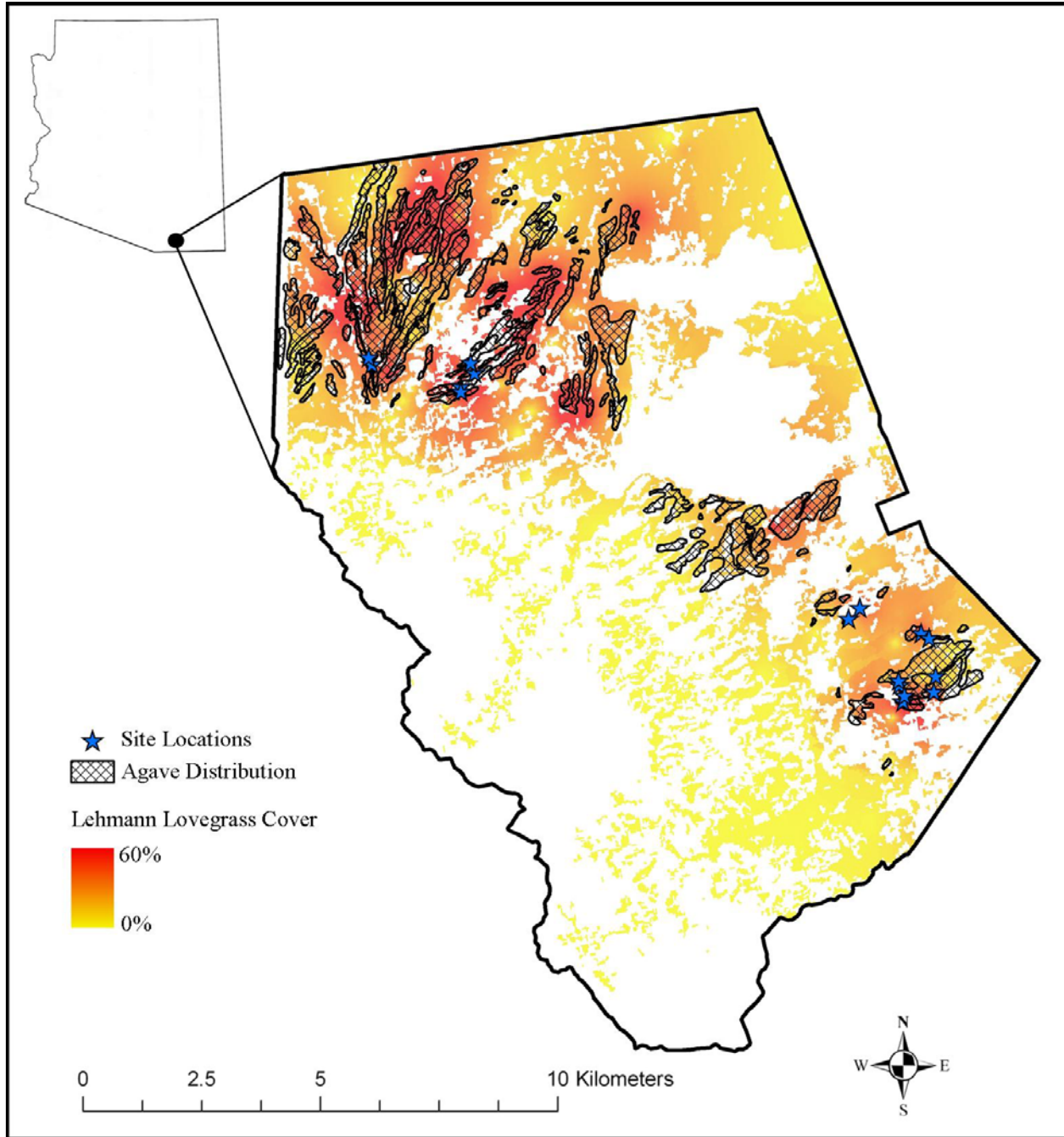
Figure 1. Map of study area and sample site locations (stars) on Fort Huachuca, Arizona, including *Agave palmeri* distribution (cross-hatched) and *Eragrostis lehmanniana* percent cover (shaded). *E. lehmanniana* was masked to the extent of grasslands as determined by the Southwest Regional Gap Analysis Program (SWReGAP) (Lowry et al. 2007).

Spatial analyses were performed by overlaying shapefiles and rasters to determine the interactions of spatial distributions of fire, soil-type, *E. lehmanniana*, and *A. palmeri*. To increase sampling efficiency, 1,000 random points were generated for the high, medium, and low density *A. palmeri* datasets (Beyer 2004). Trends in the distribution and density of *A. palmeri* were analyzed relative to the distribution and density of *E. lehmanniana* by using an inverse distance

weighting interpolation from point data (all percent cover of *E. lehmanniana*) collected in 2004 and 2006[1] and 2008 which occurred on the study area. The output of this interpolation was a spatial dataset of percent cover of *E. lehmanniana*. The relationship of *E. lehmanniana* density to fire occurrence was also assessed, to further investigate the effects of *E. lehmanniana* on *A. palmeri* through potential impacts to *A. palmeri* survival, and thus *A. palmeri* pollinator guilds. This was accomplished by creating 1,000 random points in the area of *A. palmeri* distribution (high, medium, and low) and masking the *E. lehmanniana* dataset to each fire occurring from 1975-2006. At each random point within each fire year, the percent cover of *E. lehmanniana* was compared to cover not burned during that year. An analysis of variance (ANOVA) was used to compare *A. palmeri* density with both fire occurrence and percent coverage of *E. lehmanniana*, and all significant values were accepted at the 0.05 probability level using SPSS 16.0 (SPSS, Inc. 2007).

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. Then 1000 random points were generated 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 1,000 random points within the distribution of *A. palmeri* and compared to percent *E. lehmanniana* in non-agave areas with an ANOVA. To determine which soil types are preferred by *E. lehmanniana*, 1,000 random points were generated and soil type was extracted from a SSURGO soils dataset, and percent cover was extracted from the interpolated *E. lehmanniana* dataset. An ANOVA was used to determine whether percent cover of *E. lehmanniana* differed significantly between soil types.

***Agave palmeri* Surveys.** The relative abundance and size class of *A. palmeri* were quantified at each of 10 sites characterized by high (N = 5) and low (N = 5) *E. lehmanniana* abundance in the grassland vegetation community. The total number of live and dead *A. palmeri* were quantified per site, and size class was calculated 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 analysis of variance using PROC GLM (SAS Institute 2005). A Kolmogorov-Smirnov test was performed to compare size class differences between high and low *E. lehmanniana* abundance sites using PROC NPAR1WAY (SAS Institute 2005).

Pollinator Sampling. Two related pollinator studies were conducted. The first was a directed assessment of insect pollinators visiting *A. palmeri* flowers. For this study, pollinators from *A. palmeri* were sampled during the peak agave flowering season (July and August). Once per month, pollinators were collected on blooms from 7-10 individual *A. palmeri* per site, at each of 12 sites characterized by high (N = 6) and low (N = 6) *E. lehmanniana* abundance. Individual agaves were systematically sampled for 2 consecutive minutes with battery-powered handheld vacuums modified for insect collection while perched on orchard ladders to reach flowering stalks that range in height from 3-6 m. Insects were identified to the lowest possible taxonomic

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level. Efforts were made to observe pollination by hummingbirds on agave, but due to very few interactions and difficulties with species identification, hummingbird data were not included in the analyses. Likewise, data on nocturnal pollinators were not included.

A. palmeri pollinator community differences between high and low *E. lehmanniana* abundance sites were assessed by comparing mean species richness and species abundance among sites with a one-way analysis of variance using PROC ANOVA (SAS Institute 2005). Species indicator analysis was conducted with a Monte Carlo test of significance to determine whether specific pollinator taxa responded to high or low *E. lehmanniana* abundance. A multi-response permutation procedure (MRPP) was used to determine pollinator community composition differences between high and low *E. lehmanniana* abundance sites.

The second pollinator study examined plant-pollinator networks from a complementary ongoing study of all pollinators associated with grasslands on Fort Huachuca to assess networks for *A. palmeri* insect pollinators. For this study, 16 plots (100 m × 25 m) characterized by high (N = 8) and low (N = 8) *E. lehmanniana* abundance were surveyed for pollinator-plant interactions monthly from April through September, with the exception of June. 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 handheld vacuums used for the agave-centric pollinator sampling and focused on capturing all insects found on flowers (any species) along each of the four selected transects over a 20-minute period, with collection on individual plants limited to 2 consecutive minutes. Plots were sampled once per month, with the order of sampling both among and within plot pairs randomly assigned. Plants on each plot were identified to species and collected insects were identified to the lowest possible taxonomic level. As explained earlier, hummingbirds and nocturnal pollinator activity on plots was not recorded.

All flower-feeding Hymenoptera and Lepidoptera, and the plant species on which they were collected, were used to create rectangular weighted adjacency matrices and corresponding bipartite (or 2-mode) networks: one set for native (combined data from all low *E. lehmanniana* abundance sites and all months) and another set for invaded (combined data from all high *E. lehmanniana* abundance sites and all months). In these matrices, plant species comprise the row categories and insect pollinators the column categories, with the number of individuals of an insect species captured on a plant represented in the corresponding matrix cell. For the bipartite network, each plant and pollinator corresponds to a node, and the number of pollinators captured on a plant provides a weighting for the edges (= links) between plant and pollinator nodes. 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 (or 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. For 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 analyses on *A. palmeri*, reduced matrices corresponding to the unipartite (1-mode) "ego networks" of agave (all plants linked directly to *A. palmeri* through shared pollinators) were extracted from the broader data sets.[1] Because many of the available analyses can only be used

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[1] Treatment of the full pollination network data will be presented in a separate publication.

to analyze unweighted (binary) networks, the weighted agave ego network matrices were dichotomized to create unweighted adjacency matrices and corresponding unweighted unipartite networks. 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), and network creation and visualization were executed with Pajek 1.02 (Batagelj and Mrvar 1998). Network parameters of interest (reviewed in Börner et al. 2007) included those related to topology, such as: number of nodes or size of the network (N), number of edges or links (E), density of the network $\left(D = \dfrac{2E}{N(N-1)} \right)$ and several measures of network connectedness, including mean number of edges per node $\left(\bar{k} \right)$ or mean *degree centrality* $\left(\overline{C_D} \right)$, mean *betweenness centrality* $\left(\overline{C_B} \right)$; 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 were 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.** *A. palmeri* was present in 1837 ha across the study area (21,200 ha; Figure 1), with an estimated 249 ha being designated as high density, 993 ha designated as medium density, and 595 ha designated as low density. The overall agave distribution grew with a mean of 25.7 percent *E. lehmanniana* cover, while mean *E. lehmanniana* cover in the study area was 7.3 percent ± 0.3 percent. Although the presence of high *E. lehmanniana* abundance did not significantly alter the number of live ($F_{1,9} = 0.71$, $P = 0.4231$) or dead ($F_{1,9} = 2.38$, $P = 0.1615$) *A. palmeri* among the sample sites, areas of low density agave had significantly higher percent coverage of *E. lehmanniana* than either medium- or high-density areas of agave across the study area ($F = 42.50$, $P < 0.0001$; Figure 2). Additionally, a significantly higher ratio of smaller agave plants (≤ 0.4 m radius) to larger agave plants (> 0.4 m radius) was found in sites corresponding to high *E. lehmanniana* abundance ($KSa = 1.9578$, $P = 0.0009$). Overall, *A. palmeri* plants ranged in size from 0.03–2.64 m in diameter.

There were several fundamental differences among levels of agave density. Percent canopy cover of overstory trees was highest (1.9 percent) in high-density agave areas and lowest (1.0 percent) in low-density agave areas. Agave density also varied by the relative abundance of soil type. High density agave was largely (76.0 percent) found on the Terrarossa-Blacktail-Pyeatt Complex, while low-density agave was found equally on the Terrarossa Complex and White House Complex (Table 1). Soil type also influenced percent cover of *E. lehmanniana* on Fort Huachuca. Aside from the Ubik Complex, the three most common soil types where agave was found (Terrarossa-Blacktail-Pyeatt Complex, Terrarossa Complex, and White House Complex) had the most *E. lehmanniana* cover of any soil type (13-19 percent; Table 1). Percent cover of

E. lehmanniana was significantly higher ($F = 398.33$, $P < 0.001$) within the distribution of agave than in non-agave areas (Figure 3).
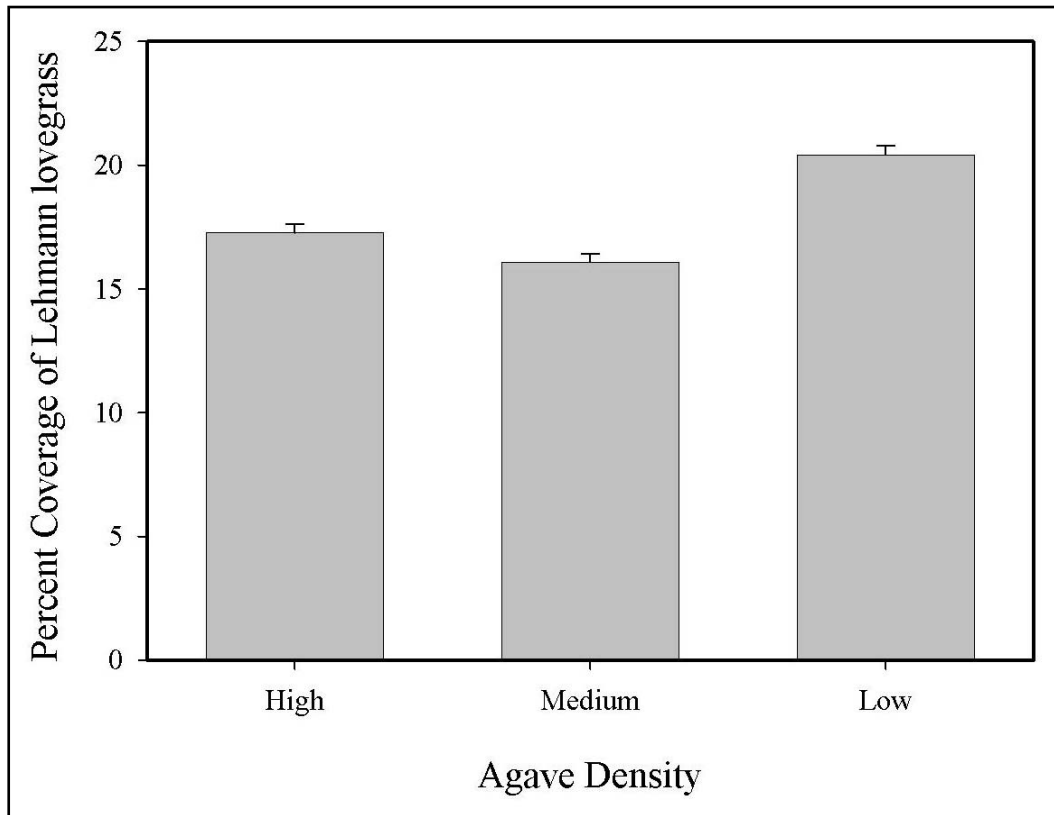

Figure 2.   Low-density *Agave palmeri* corresponds to significantly higher percent coverage of *Eragrostis lehmanniana* than either medium- or high-density agave ($F = 42.50$, $P < 0.0001$).

Table 1. Influence of soil type on *Agave palmeri* distribution and *Eragrostis lehmanniana* abundance.[1]

Soil Type	Mean ± SD *Eragrostis lehmanniana* Percent Cover	Percent Soil Abundance of *Agave palmeri* Distribution			Amount of Landscape Comprised of by Soil Type
		High Density	Medium Density	Low Density	
White House Complex	10.9 ± 0.7	4.3	21.2	30.3	14.7
Terrarossa Complex	11.8 ± 0.6	11.7	21.6	30.6	12.6
Budlamp-Woodcutter Complex	3.2 ± 0.4	0.00	5.4	0.6	12.1
Far-Hogris Asscociation	1.8 ± 0.3	0.00	0.00	0.00	11.5
Gardencan-Lanque Complex	10.0 ± 0.7	1.8	3.6	6.5	10.2
Terrarossa-Blacktail-Pyeatt Complex	19.1 ± 0.9	76.1	37.4	24.7	8.00
Ubik Complex	14.7 ± 2.7	0.00	0.1	0.3	1.4
Carbine Very Gravelly Loam	7.8 ± 1.3	5.2	9.8	4.5	1.3

[1] High densities of agave were preferentially found on Terrorossa-Blacktail-Pyeatt Complex, as was *E. lehmanniana*. Percent cover of *E. lehmanniana* was higher in soil types preferred by agave, but was also abundant on other soil types (e.g., Ubik Complex).
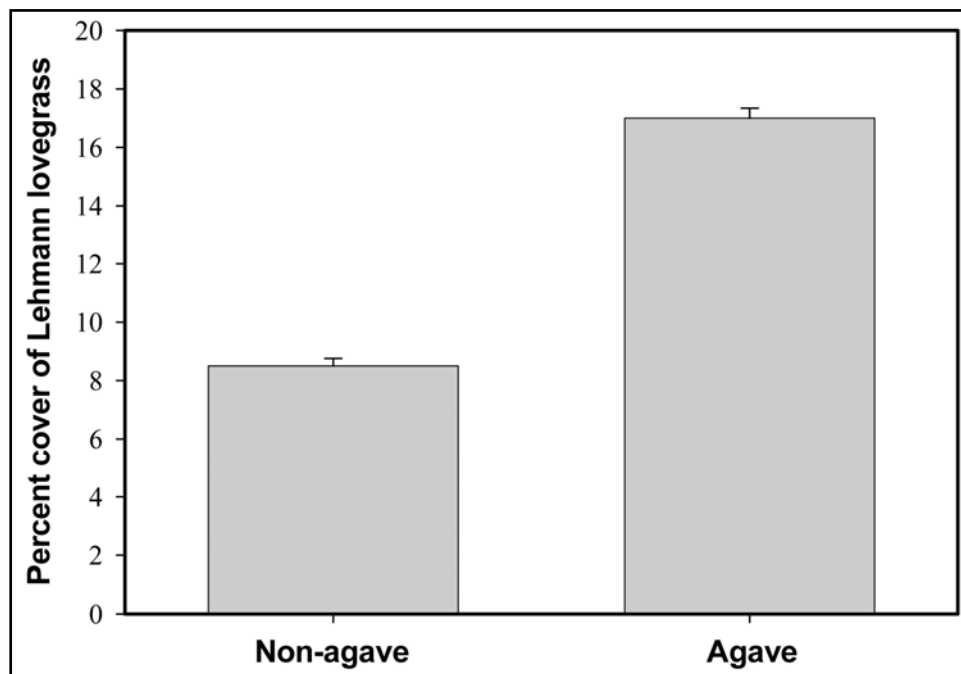
Figure 3. *Eragrostis lehmanniana* exhibits significantly higher percent cover in areas where *Agave palmeri* occurs compared to areas with no agave ($F = 398.33$, $P < 0.001$).

Interactions of natural and prescribed burn history with *E. lehmanniana* distribution and density showed no discernible pattern. Areas with high *E. lehmanniana* abundance did not burn more frequently than areas of low *E. lehmanniana* abundance. For *A. palmeri*, however, areas of high and medium density were significantly associated with more frequent burning ($F = 3.26$, $P < 0.05$; Figure 4).

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 and low *E. lehmanniana* abundance (Table 2). Pollinator community composition analysis revealed no significant differences between high and low *E. lehmanniana* abundance sites ($r = -0.015$, $P = 0.726$). Of the 70 taxa identified (Appendix A), 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* was found to be an indicator species of *A. palmeri* located in high *E. lehmanniana* abundance sites ($P = 0.0472$).
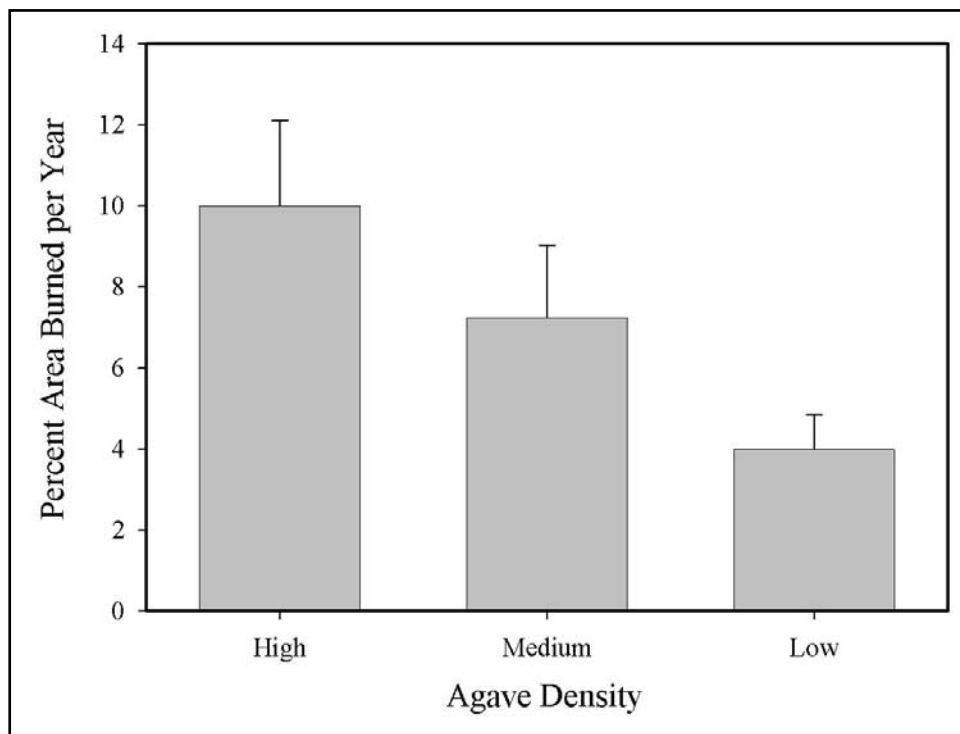
Figure 4. *Agave palmeri* density significantly decreases with increasing percentage of area burned per year ($F = 3.26$, $P < 0.05$).

Table 2. Pollinator species richness and species abundance for eight high (>35 percent) and eight low (<15 percent) *Eragrostiis lehmanniana* abundance sites.					
		Species Richness		Species Abundance	
Eragrostis lehmanniana Abundance	n	Mean	SE	Mean	SE
High	8	11.45	1.52	53.27	7.84
Low	8	12.23	1.37	67.54	17.28

Pollinator Network Analyses. In each agave ego network (native vs. invaded), agave was directly linked (shared ≥ 1 pollinators) with 11 other plants (Figure 5). In addition to *A. palmeri*, however, the two networks only have three plant species in common, including *Acacia augustissima*, *Calliandra eriophylla*, and *Prosopis velutina*. The native network included 30 different insect pollinators, while the invaded network contained 14 different insect pollinators. 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 within the agave ego networks in both native and invaded plots. In both of the larger community networks, the agave ego network played an important role, comprising 40 percent of the plant species. However, there were notable differences between the native and invaded agave ego networks, including a higher degree of pollinator sharing among plants in the native network relative to the invaded network ($E = 92$ vs. 72; $D = 63.64$ percent vs. 43.64 percent). Significant differences (one-tailed t-tests, 10,000 bootstraps) between the *unweighted* unipartite networks (native vs. invaded, *p-value*) included mean node degree

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centrality $\left(\overline{C_D} = 7.667 \text{ vs. } 5.833, p = 0.041\right)$ and mean node power $\left(\overline{C_\beta} = 1160.109 \text{ vs. } 662.263, p > 0.001\right)$. 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 $\left(\overline{c} = 1.821 \text{ vs. } 1.213, p = 0.002\right)$. There were no significant differences in betweenness centrality $\left(\overline{C_B} = 1.667 \text{ vs. } 2.583, p = 0.653\right)$ or eigenvector centrality $\left(\overline{C_E} = 0.280 \text{ vs. } 0.276, p = 0.910\right)$ for the *unweighted* networks, nor in eigenvector centrality for the *weighted* networks $\left(\overline{C_E} = 0.268 \text{ vs. } 0.246, p = 0.697\right)$. Agave also appears to play a more central role in the native ego network as indicated by a higher two-step reach (the percentage of other nodes within two-links of agave; 93.10 percent versus 86.21 percent).

DISCUSSION: High abundance of *E. lehmanniana* significantly altered the distribution of *A. palmeri* size classes, resulting in a higher ratio of small to large plants. Areas with a higher ratio of small to large agave plants are a management concern on Fort Huachuca because stands of small plants are considered to be important future nectar-feeding centers, and should thus be protected.[1] However, areas of low-density agave had significantly higher percent coverage of *E. lehmanniana* than either medium- or high-density areas of agave, indicating that high *E. lehmanniana* abundance tends to exclude *A. palmeri*. Although the small/young agave plants are important, the more dense stands of agave also need to be protected, as total amount of nectar produced is the main conservation concern for the endangered lesser long-nosed bat.

Although Kupfer and Miller (2005) found that the presence of *E. lehmanniana* increases both the frequency and intensity of natural fires, Geiger (2006) determined that the proportion of *E. lehmanniana* does not increase following burns. Similarly, it was determined that areas with high *E. lehmanniana* abundance did not burn more frequently than areas of low *E. lehmanniana* abundance. However, fires did occur significantly more in areas of high-density agave than in areas of low-density agave. Because fire has the potential to reduce or eliminate agave bloom production by damaging or destroying plants, this could have a negative effect on overall nectar availability. Agave density also varied by soil type, with high-density agave being associated with the Terrarossa-Blacktail-Pyeatt Complex, also following an observation of Geiger (2006) that survival of agave varies with soil type. Because *E. 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 agave areas, the two species will likely be in close association for the foreseeable future. This suggests that areas of agave may be more prone to invasion by *E. lehmanniana* than areas without agave.

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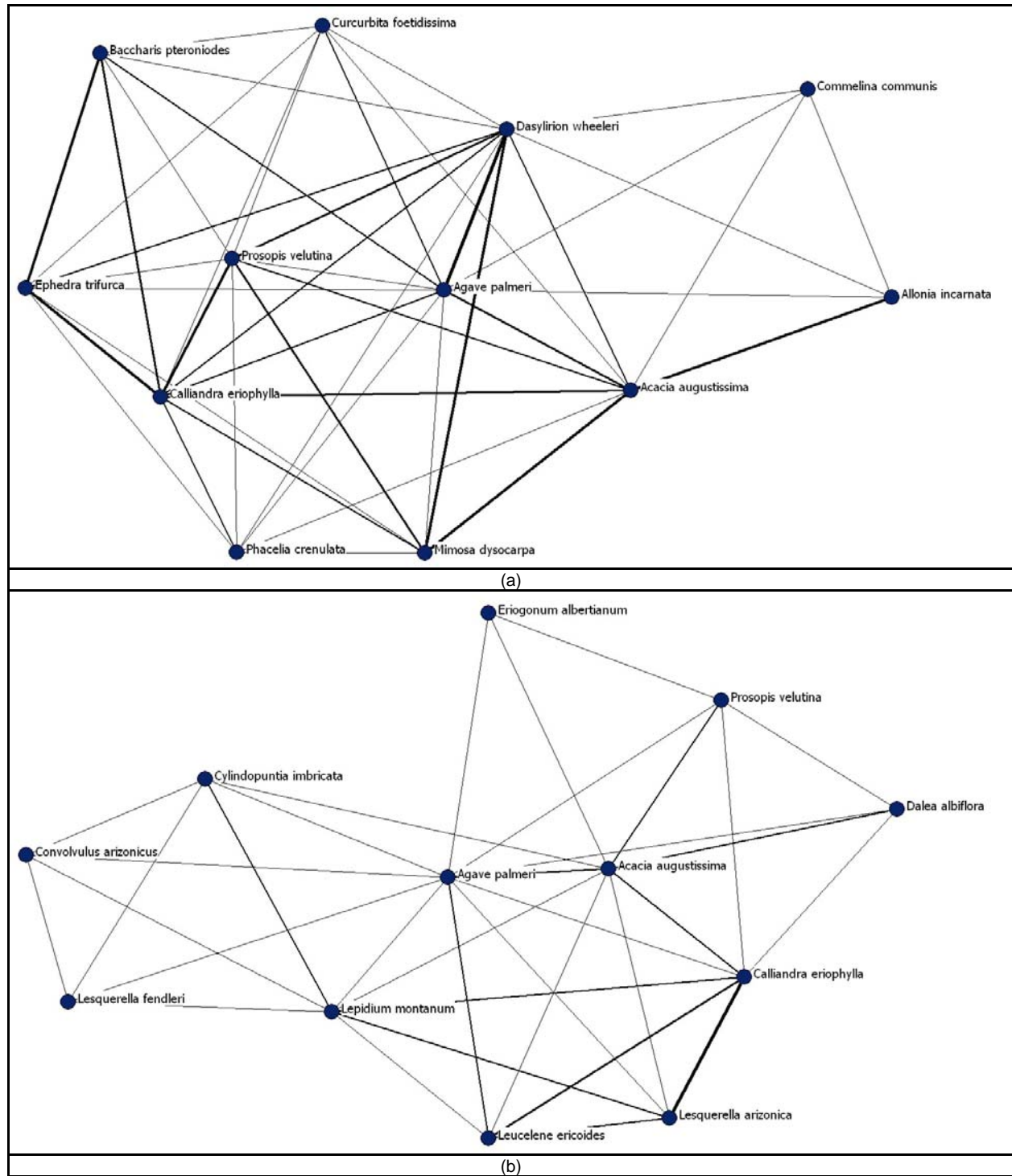
Figure 5.   Unipartite networks of plants linked through shared pollinator species from a) native grass dominated plots, and b) invaded plots dominated by the nonnative grass *Eragrostis lehmanianna*. Line thickness reflects edge weighting (number of pollinator species shared).

There was no significant difference in *A. palmeri* pollinator 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 agave pollinator guild. Agave flowering stalks often tower over the maximum height of *E. lehmanniana*, thus allowing pollinators to access agave blooms with ease. High *E. lehmanniana* abundance is concomitant with low densities of *A. palmeri*, which suggests that pollinator activity should also follow this pattern. However, sites with high *E. lehmanniana* abundance could be outcompeting other native flora, thus increasing the amount of pollinator activity on the limited numbers of *A. palmeri* in high *E. lehmanniana* abundance sites. *Agapostemon angelicus*, a native, pollen-feeding sweat bee, was the only pollinator observed to be an indicator species of *A. palmeri* in high *E. lehmanniana* abundance sites. The sweat bees are considered generalist species, pollinating a wide variety of flower species. Though *A. angelicus* could be utilizing *A. palmeri* as a major pollen source, the association may be due to *E. lehmanniana* providing cover or nesting material for *A. A. angelicus;* however, that may be unlikely considering that *Agapostemon spp.* nest in ground burrows (Michener 2000). In general, bees are the most common pollinator, a trend also observed in this study. *A. palmeri* pollinators collected in this study included 30 species of Hymenoptera (bees), 21 species of Diptera (flies), 9 species of Coleoptera (beetles), 4 species of Lepidoptera (butterflies), and 2 species of Hemiptera (aphids, leafhoppers, and cicadas). Two species of Coleoptera and two species of Araneae (spiders) that were herbivores or predators were also collected.

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, such as 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 case of agave in the Sonoran desert grassland community that was studied, it appears that *A. palmeri* and its one-step ego network (the plants to which it is directly linked through shared pollinators) are major components of the overall community pollinator network and likely lend a large degree of stability to the community pollination dynamics. It also appears that *A. palmeri* and the plants in its ego network are well established and supported by multiple pollinator linkages, but appear to be significantly more linked within the native network. One possible reason for the apparent greater connectedness of the native agave ego network may be a rarefaction bias in the sampling results arising from the higher density of agave in native habitat and concomitant higher probability of detecting more pollinator species. Percent cover of agave was significantly higher within native sites ($F = 4.88$, $P = 0.0444$). In the sampling component of this study for the directed assessment of *A. palmeri* insect pollinators, where numbers of agave sampled in native and invaded habitat were equivalent, significant differences in pollinator diversity did not exist. An additional factor could be different portions of plants in the low and high *E. lehmanniana* abundance sites that are pollinator generalists, or pollinators that are flower generalists.

CONCLUSIONS: The nonnative grass *E. lehmanniana* has negatively impacted the native plant *A. palmeri,* which is an important resource for many pollinators in the desert communities of the Southwestern United States. *E. lehmanniana* may exclude *A. palmeri*, as areas of high *E. lehmanniana* abundance 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, which can decrease overall nectar production through direct or indirect means. Due to similar soil preferences, *E. lehmanniana* and *A. palmeri* are likely to continue be found in close association; therefore, continued 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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> Lindsay, D. L., P. Bailey, R. F. Lance, M. J. Clifford, R. Delph, and N. S. Cobb. 2010. *Effects of a nonnative, invasive lovegrass on* Agave palmeri *distribution, abundance, and insect pollinator communities*. ERDC/EL TN-10-1. Vicksburg, MS: U.S. Army Engineer Research and Development Center.

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Appendix A. *Agave palmeri* pollinator species list grouped by feeding guild.

Guild	Order	Family	Genus and Species
pollen-feeder	Hymenoptera	Andrenidae	*Perdita albovittata*
pollen-feeder	Hymenoptera	Andrenidae	*Perdita spp.*
pollen-feeder	Hymenoptera	Anthophoridae	*Diadasia rinconis*
pollen-feeder	Hymenoptera	Apidae	*Apis melifera*
pollen-feeder	Hymenoptera	Apidae	*Bombus sonorus*
pollen-feeder	Hymenoptera	Apidae	*Xylocopa californica*
pollen-feeder	Hymenoptera	Colletidae	*Colletis spp.*
pollen-feeder	Hymenoptera	Colletidae	*Ptiloglossa arizonensis*
pollen-feeder	Hymenoptera	Halictidae	*Agapostemon angelicus*
pollen-feeder	Hymenoptera	Halictidae	*Dialictus comulus*
pollen-feeder	Hymenoptera	Halictidae	*Dialictus microlepoides*
pollen-feeder	Hymenoptera	Halictidae	*Dialictus pruinosiformis*
pollen-feeder	Hymenoptera	Halictidae	*Dialictus spp. 1*
pollen-feeder	Hymenoptera	Halictidae	*Dialictus spp. 2*
pollen-feeder	Hymenoptera	Halictidae	*Halictus tripartitus*
pollen-feeder	Hymenoptera	Halictidae	*Sphecodes stygius*
pollen-feeder	Hymenoptera	Megachilidae	*Lithurgus apicalis*
pollen-feeder	Hymenoptera	Halictidae	unknown
nectar-feeder	Lepidoptera	Lycanidae	*Timolus azia*
nectar-feeder	Lepidoptera	Lycanidae	*Leptotes marina*
nectar-feeder	Lepidoptera	Sphingidae	*Hyles lineata*
nectar-feeder	Lepidoptera	Zygaenidae	*Ctenucha venosa*
nectar/herbivore	Diptera	Sepsidae	unknown
nectar/herbivore	Diptera	Otitidae	unknown 1
nectar/herbivore	Diptera	Otitidae	unknown 2
nectar/herbivore	Diptera	Lonchaeidae	*Lonchaea spp.*
nectar/herbivore	Diptera	Sciaridae	unknown
nectar/herbivore	Diptera	Chloropidae	unknown
nectar/herbivore	Diptera	Chloropidae	*Thaumatomyia spp.*
nectar/herbivore	Diptera	Phoridae	unknown
nectar/herbivore	Diptera	Anthomyiidae	unknown 1
nectar/herbivore	Diptera	Anthomyiidae	unknown 2
nectar/herbivore	Diptera	Anthomyiidae	unknown 3
nectar/herbivore	Diptera	Sarcophagidae	*Sarcophaga spp.*
nectar/herbivore	Diptera	Sarcophagidae	unknown
nectar/herbivore	Diptera	Caliphoridae	*Phaenicia spp.*
nectar/herbivore	Coleoptera	Cleridae	*Enoclerus abdominalis*
nectar/herbivore	Coleoptera	Scarabaeidae	*Cotinus texana arizonica*
nectar/herbivore	Coleoptera	Scarabaeidae	*Euphoria testacea*
nectar/herbivore	Coleoptera	Lycidae	*Lycus sanguineus*
nectar/herbivore	Coleoptera	Bruchidae	unknown 1
nectar/herbivore	Coleoptera	Bruchidae	unknown 2
nectar/herbivore	Coleoptera	Curculionidae	*Apion spp.*
nectar/herbivore	Coleoptera	Curculionidae	*Peltophorus polymitus*
nectar/herbivore	Coleoptera	Mordellidae	unknown

Guild	Order	Family	Genus and Species
nectar/herbivore	Hemiptera	Coreidae	*Acanthocephala thomasi*
nectar/predator	Hymenoptera	Scolitidae	unknown
nectar/predator	Hymenoptera	Vespidae	*Polistes castanelcolor*
nectar/predator	Hymenoptera	Vespidae	*Polistes fuscatus*
nectar/predator	Hymenoptera	Vespidae	*Eumenes bollii*
nectar/predator	Hymenoptera	Tiphiidae	*Tiphia spp.*
nectar/predator	Hymenoptera	Bethyliidae	unknown
nectar/predator	Hymenoptera	Braconidae	*Bruchophagus spp.* 1
nectar/predator	Hymenoptera	Braconidae	*Bruchophagus spp.* 2
nectar/predator	Hymenoptera	Braconidae	unknown 1
nectar/predator	Hymenoptera	Braconidae	unknown 2
nectar/predator	Hymenoptera	Braconidae	unknown 3
nectar/predator	Hymenoptera	Eulophidae	unknown
nectar/predator	Diptera	Tachinidae	*Juriniopsis adusta*
nectar/predator	Diptera	Tachinidae	*Lydella radicus*
nectar/predator	Diptera	Tachinidae	unknown 1
nectar/predator	Diptera	Tachinidae	unknown 2
nectar/predator	Diptera	Syrphidae	*Eristalis tenax*
nectar/predator	Diptera	Syrphidae	*Neocnemodon sp.*
nectar/predator	Diptera	Conopidae	*Conops sp.*
nectar/predator	Hemiptera	Anthocoridae	*Orius insidiosus*
herbivore	Coleoptera	Chrysomelidae	*Zygospila continua*
predator	Coleoptera	Carabidae	unknown
predator	Araneae	Thomisidae	*Misumena vatia*
predator	Araneae	Salticidae	unknown