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Research Article

Demographic Analysis of the Endangered Plant *Pectis imberbis* Highlights Tradeoffs Between Deer Browse and Interspecific Competition

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ABSTRACT

Pectis imberbis is an endangered plant found in the Madrean Archipelago ecoregion of southern Arizona. Numerous, potentially interacting stressors, such as drought, shifting fire regimes, invasive species, and grazing by domesticated and wild ungulates, affect this species and region. We used Integral Projection Models (IPMs) to describe dynamics of the largest documented *P. imberbis* population. While collecting census data, we quantified impacts of species interacting with *P. imberbis*, including pollinators, Coues deer (*Odocoileus virginianus couesi*), and co-occurring vegetation, and evaluated their impact on *P. imberbis* population vital rates. Despite a large overall size ($N = 794$), the growth rate for this population was below replacement level ($\lambda = 0.9519$). Browse by Coues deer negatively impacted demographic vital rates. Woody species and perennial grasses afforded protection against browse, especially for small individuals, but in the absence of browse, coincidence with heterospecific vegetation decreased growth, survival, and reproduction of *P. imberbis*. We observed 12 taxa of invertebrates interacting with *P. imberbis* flowers, including native bees, flies, and wasps. Seed production by bagged flowers indicated that flowers are self-compatible. In summary, we detected a unique interplay between deer, which negatively impacted *P. imberbis* populations via browse, and vegetation, which reduced incidence of browse, while simultaneously depressing *P. imberbis* vital rates when no browse occurred. Findings suggest that shifts in community dynamics, such as introduction of invasive grasses or fluctuations in deer populations, could impact *P. imberbis* population trajectories. Management actions, including exclusion of herbivores and removal of invasive grasses, should be considered to aid species recovery.

Index terms: Arizona; Asteraceae; Coues deer; Madrean Archipelago; *Pectis imberbis* A. Gray; population ecology

INTRODUCTION

Contemporary extinction rates of North American vascular plants are an estimated 500 times or more compared to background extinction rates (Humphreys et al. 2019, 2020; Knapp et al. 2020), with upwards of 40% of extant plants believed to be at risk of extinction (Nic Lughadha et al. 2020). Environmental change factors driving plant population decline may include altered fire regimes, novel grazing systems, invasion of nonnative species, and climate change (Barnosky et al. 2011; Balch et al. 2013; Eldridge et al. 2016). Compounding the direct effects of these threats, disruption of critical interspecific interactions such as pollination can negatively impact plant fitness (Bond 1994; Kremen and Ricketts 2000). Alarming rates of extinction in combination with potential for nonlinear viability responses to environmental change suggest an urgent need to investigate multiple, potentially interacting stressors on plant population dynamics in order to prevent further decline of threatened or endangered plants.

Pectis imberbis A. Gray (Asteraceae) is an herbaceous perennial endemic to southern Arizona and was recently listed under the Endangered Species Act (ESA; USFWS 2021). Known populations ($N < 15$) consist of ca. 10–794 individuals and occur at elevations ranging from 1100 to 1700 m in a variety of habitats, including oak woodlands, desert grasslands, oak savannas, and disturbed areas in Arizona (road cuts, arroyos; USFWS 2012). In the past, populations were also identified in Mexico (Keil 1978; USFWS 2012); however, recent searches revealed no individuals at known locations of Mexican populations (D.J. Keil, pers. comm., 1982; Falk and Warren 1994; Sanchez-Escalante 2018). Resurveys of known *P. imberbis* sites suggest significant decline in abundance over the last two decades and have documented the extirpation of 9 populations and 1 subpopulation. Initial decline of *P. imberbis* is believed to have resulted from overgrazing by domesticated livestock, although other potential threats include competition with nonnative species, increased drought severity and frequency, mining, road construction, and recreational activities (Phillips et al. 1982). In addition to these extrinsic stressors, rarity itself may reinforce population decline by reducing per capita reproduction (i.e., Allee effect) and decreasing offspring viability when inbreeding results in the expression of deleterious alleles (Courchamp et al. 1999, 2006). Rarity drives Allee effects by reducing visibility of rare plants to pollinators relative to more abundant species and decreasing the likelihood of successful pollination from generalist pollinators, as pollen loads are attenuated from heterospecific visitation (Courchamp et al. 1999, 2006; Hackney and McGraw 2001). Moreover, when plant–pollinator mutualisms are tightly coupled, loss of one species may reduce fitness of the codependent species, further hastening decline (Dunn et al. 2009). To our knowledge, no study has described the reproductive ecology or population dynamics of this species.

Units of the National Park System are tasked with protecting biological diversity, and host high levels of diversity across numerous taxa (Burns et al. 2003; Naughton-Treves et al. 2005; Lawrence et al. 2011). Persistence of *P. imberbis* will depend on the management decisions and restoration actions of the Coronado National Memorial in southern Arizona, which contains an estimated 90% of all known individuals of this species. Studies of *P. imberbis* are urgently needed to provide information critical to develop an effective recovery plan for this species, while simultaneously highlighting factors and interaction pathways that may threaten this and other species within the ecosystem. Here, we present the first demographic and reproductive analysis of *P. imberbis*, describing population dynamics, breeding system, and pollinator visitation. Using this information, we then asked (1) what factors, including deer browse, competition, and pollination, explain patterns in growth, survival, and reproduction of *P. imberbis*; and (2) how do these relationships inform conservation of this species?

MATERIALS AND METHODS

Site Description

Pectis imberbis individuals occurred on a south-facing slope in the Coronado National Memorial in southeastern Arizona near the Mexican border within the Madrean Archipelago ecoregion (*the specific location is withheld due to species rarity*). This region is characterized by high topographic relief that results in the formation of "sky islands," where vegetation found at higher elevations is noncontiguous, isolated from similar vegetative communities by lowland regions. From sky island peaks, montane coniferous forests grade into oak-dominated systems, with montane areas surrounded by shortgrass prairie, and subtropical shrublands and deserts. *Pectis imberbis* individuals occurred at an oak-dominated site on a south-facing slope at an elevation of 1637 m, characterized by an open canopy with sparse clusters of Emory (*Quercus emoryi*) and Arizona white (*Quercus arizonica*) oak. Other common species at the site include beargrass (*Nolina macrocarpa*), sotol (*Dasylirion wheeleri*), mountain yucca (*Yucca schottii*), Palmer's agave (*Agave palmeri*), evergreen sumac (*Rhus virens*), Arizona bluecurls (*Trichostema arizonicum*), and native bunch grasses (*Sporobolus cryptandrus*, *Elymus elymoides*, *Bouteloua curtipendula*, *Bothriochola barbinodis*), with nonnative bunch grasses occurring at the population periphery (*Eragrostis curvula*, *Eragrostis lehmanniana*).

Demographic Census

Marking and Relocating Individuals: All *P. imberbis* plants in the population were tagged with individual identification numbers and mapped to assist relocation (Figure 1). Height, the continuous state variable that best predicted reproduction, was measured for all plants in 2019 and 2020 (Supplemental Appendix S1). Relative growth rate (RGR) was calculated using the following equation (McGraw and Garbutt 1990):

$$RGR = \frac{lnH_2 - lnH_1}{t_2 - t_1}$$

where H indicates plant height and t indicates time (i.e., one year). We scored any plant not observed in 2020, but formerly extant, as "dead," even though this likely overestimated mortality, since it may have included dormant individuals. In order to estimate the magnitude of this source of error, we tracked the fate of plant stems, flagged as living plants by an independent field crew in 2018 and missing in 2019, through census year 2020. Of the 28 such plants followed, only 2 reemerged in 2020, yielding a 7.1% chance of reemergence if not observed during a growing season.

In addition to height and survival, we derived seed production from floral head tallies. Direct seed counts to quantify fecundity were not possible, since flowers were numerous and floral parts within and among plants developed at different times throughout the season. To estimate flower production from floral head counts, we counted flowers on 110 floral heads, and calculated average number of flowers produced per flower head (averages; $N_{\text{total}} = 10.3$, $N_{\text{ray}} = 4.6$, $N_{\text{disc}} = 5.7$), which varied between 7 and 15 total flowers, and multiplied the average value by the floral head count to estimate total potential seed production, since each ray and disk flower produces a one-seeded fruit. Seeds from ray and disc flowers did not differ significantly in probability of germination, and thus are likely to set seed at similar rates (Supplemental Appendix S2).

While censusing individuals, we collected additional information on factors potentially influencing *P. imberbis* population dynamics. Browse by Coues deer (*Odocoileus virginianus couesi* (Coues and Yarrow 1875)) was recorded when the stem and associated foliage were visibly torn from the primary stem structure (McGraw and Furedi 2005). Browse intensity was assessed by visually estimating the proportion of the plant removed by deer, with 33% or less of the plant removed assigned as a low level of browse, 34–66% removed as a moderate level, and 67% or more removed as high browse intensity. Additionally, we noted when heterospecific branches or other plant structures overtopped *P. imberbis* individuals (referred to herein as "canopy cover"), as these structures appeared to deter browse. Since canopy cover was almost exclusively provided by woody perennials, the presence of canopy cover was coded as a simple binary (0/1) and functional groups of canopy species not recorded. We also documented the dominant ground cover in a 2.5 cm radius around individual *P. imberbis* stems (referred to herein as "ground cover"). Ground cover at times overtopped the individual, and that feature was captured with the canopy cover assessment described above. Ground cover was classified by functional group, which included perennial grass and woody perennials, including shrubs, trees, and agaves. No annual species and only two perennial forbs were observed in proximity to *P. imberbis* individuals. Litter was broadly categorized as vegetation no longer rooted in the ground, and included both herbaceous and woody litter of varying sizes.

Seed Cage Experiment: In order to describe seed dynamics and germination in the focal population, we placed 5 seed cages at 5 randomly located microsites across the *P. imberbis* population, located uphill from major clusters of plants to prevent additional seed dispersal into cages (seed cages arranged

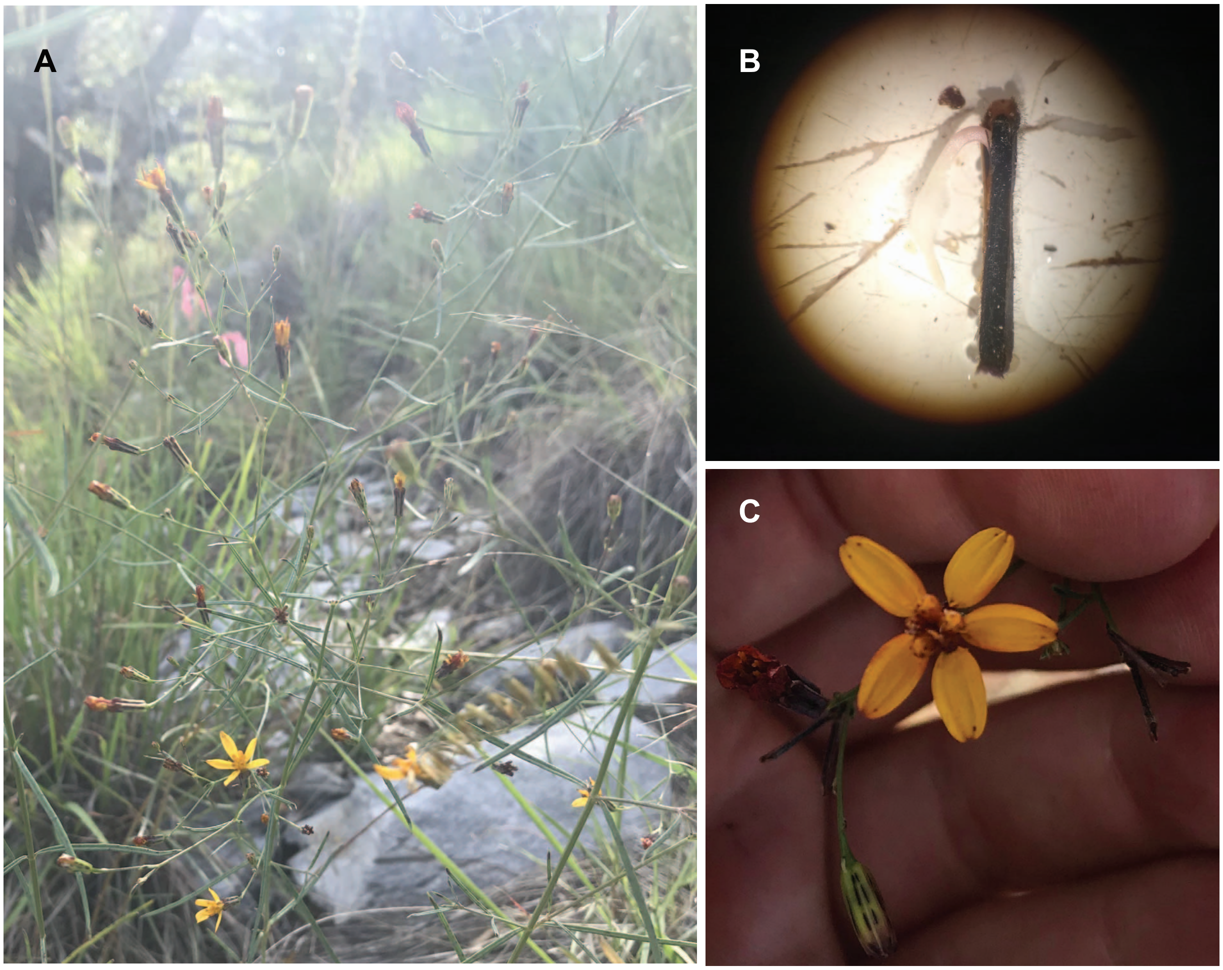

Figure 1.—(A) A *P. imberbis* individual in flower at the study population in CNM, (B) a *P. imberbis* seed germinating, and (C) a close-up of a *P. imberbis* inflorescence, including floral buds, flowers, and seeds.

in a 30 × 40 cm circular plot, each set of 5 seed cages separated by at least 5 m). Seed cages consisted of a 3.8 inch diameter and 2 inch in height collar created from a biodegradable cup. These collars were placed in the ground with a 1 inch collar protruding from the soil surface, in order to hold seeds in place. Twenty *P. imberbis* seeds were placed on the soil surface within collars, simulating natural dispersal (total $N = 500$). To avoid drawing attention to the site, we did not add a protective covering overtop the seed cages. Thus, failure to germinate indicates a combination of both nonviable seeds and seed predation. While not ideal for discerning causes of seed loss, uncovered seed cages may be more representative of microclimatic conditions in this hot and arid environment, which would be strongly affected by any form of covering. Germination from seed cages, which was low, mirrored estimated germination rates across the population. No signs of rodent activity (chewed cups or discarded seed husks) were observed near the cages. Germination was tallied the following year (2020).

Demographic Model: Integral Projection Models (IPMs) described population dynamics based on a continuous state variable according to the following equation:

$$n_{t+1}(z') = \int_{L}^{U} K(z', z) n_t(z) dz$$

where $n_{t+1}(z')$ indicates the size distribution of individuals at time t + 1, the kernel, $K(z', z)$, describes how the size distribution changes over this time interval, $n_t(z)$ is the size distribution at time t, and the upper and lower limits of the integral indicate lower and upper size limits (Ellner and Rees 2006; Merow et al. 2014; Rees et al. 2014). The kernel, K, can be partitioned into survival/growth (P) and fecundity components (F). In this case, overall plant height was found to be the best predictor of demographic vital rates (Supplemental Appendix S1), and thus is the state variable for this model, with the lower limit of the integral calculated as the minimum size of an individual and upper limit calculated as the maximum size plus one standard deviation to account for potential growth beyond conditions observed. Combining the P and F sub-kernels yields the following model:

$$n_{t+1}(z') = \int_{L}^{U} [P(z', z) + F(z', z)] n_t(z) dz$$

where $P(z', z)$ indicates the size-based probability of an individual surviving to the next census and the probability distribution for its size the following year contingent on survival. The fecundity sub-kernel, $F(z', z)$, describes per capita offspring production and the size distribution of new recruits. The fecundity sub-kernel can be further decomposed into the following equation:

$$F(z', z) = p_{\text{flower}}(z) f_{\text{seeds}}(z) p_{\text{establish}} f_{\text{recruitsize}}(z)$$

where p_{flower} is the probability of an individual plant producing flowers as a function of size (z), f_{seeds} is the number of seeds produced as a function of maternal plant size conditional on floral development, $p_{\text{establish}}$ is the probability of establishment derived by dividing the number of observed germinants by the number of seeds produced at time t, and $f_{\text{recruitsize}}$ the size distribution of germinants.

We used numerical integration under the midpoint rule to discretize the kernel, $K(z', z)$, to a 100 × 100 cell matrix (Ellner and Rees 2006; Merow et al. 2014; Rees et al. 2014). We analyzed matrix dimensions to ensure that outputs were insensitive to grid size. Once constructed, we calculated the dominant eigenvalue, λ, of the matrix along with 95% confidence intervals using Tukey's Jackknife (Rodgers 1999). In order to examine the contribution of transition elements to λ, we calculated sensitivities, the absolute contribution of elements to λ, and elasticities, the relative contribution of model elements.

Demographic Analyses: For all analyses of demographic response to deer browse and competition with co-occurring vegetation, we used generalized linear models (GLMs) with the error specified according to the response variable (R Core Team 2020). Specifically, we tested for effects of browse and competition on demographic response variables, treating "browse" and "competition" (ground cover or canopy cover) as main effects, and including height as a covariate for analyses of survival and reproduction, since both metrics vary as a function of size. For continuous response variables (growth), we specified a Gaussian distribution, for count data (floral production) a Poisson distribution, and for binomial data (survival) a binomial distribution. Similarly, we examined the role of co-occurring vegetation on likelihood of a plant being browsed using GLMs modeled with a binomial error distribution, coding browse as a binary variable, with "1" indicating browse and "0" indicating no browse. We tested our census methodology in year 1 (2019) and implemented the final census protocols in year 2 (2020). For this reason, as in the instance of floral head counts, we collected information on browse and cover for a subset of plants in 2019, and for the full population in 2020. When possible, we analyzed the 2020 dataset to test for patterns between vital rates and browse/co-occurring vegetation, as it represented a complete sampling of the population. For some metrics that depend on two years of data (e.g., growth, survival), we used browse/co-occurring vegetation in 2019 as the predictor variable of growth from 2019–2020, acknowledging that these analyses represent only ca. 70% of the plants measured in 2019. Since this was a natural experiment, sample sizes varied among factor levels. In cases of higher model complexity, we reduced level numbers to prevent unequal sample sizes. For instance, when testing for a three-way interaction between browse, ground cover, and height on *P. imberbis* growth, deer browse was generalized into two levels, "no browse" and "browse." For three-way interactions investigating the interplay of browse and co-occurring vegetation, nonsignificant variables were removed and analyses re-run with simplified models. For dependent variables characterized by a Gaussian distribution (i.e., growth), residuals were tested for normality using a Shapiro-Wilk test and for heteroscedasticity using a Levene test. For dependent variables characterized by Poisson and binomial distributions, deviation from the specified error distribution was tested with a χ^2 goodness-of-fit test. Response variables were transformed as necessary.

Pollinator Community Assessment

Systematic Flower Visitation Observations: To determine the suite of flower visitors for *P. imberbis* at the study site, we performed systematic flower visitation observations using established protocols that permit calculation of visitation frequency and visitation importance by taxon (Renne et al. 2000; Aslan et al. 2019). Observations were conducted in 10 min time-blocks from a distance of 1–2 m from focal flowering plants. The first minute of each block was devoted to scan sampling, wherein an observer recorded all insects interacting with the focal plants in any way, as well as the total number of open flowers on the focal plants. For the remaining 9 min of the time-block, the observer performed focal individual observations (after Manson 1997). Via this method, the observer selects the most visible insect visitor and records the number of flowers it interacts with as well as the nature of that interaction (e.g., flower probing for nectar or pollen, nectar robbing, florivory) for as long as the visitor remains visible or until 60 sec have elapsed. The observer then selects another visitor to observe. If possible, the observer selects a new visitor taxon for each subsequent observation; if this is not possible, the observer selects another individual of a taxon that has previously been observed. At the end of the 10 min period, the observer moved to another patch of flowering plants and began a new time-block. Observations were performed in non-rainy weather in 2019 and 2020, during August, September, and October, and between the hours of 0700 and 1700.

Although broad functional groups can be distinguished by sight, identification of flower-visiting insects to genus or species level usually requires a microscope. When possible, we therefore collected voucher specimens of each visitor taxon. Vouchers were collected after focal individual observations were performed. We pinned specimens using standard entomological procedures and examined them under a microscope (Olympus brand, model 341546) using a dichotomous key for identification. Since the majority of visitation was performed by a limited diversity of large bees and flies (see Results), we were able to confirm identification to genus level (for bees) and family level (for flies) (Borror and White 1970; Michener et al. 1994; Tripplehorn and Johnson 2005) and, thereafter, did not collect further specimens of known taxa.

Pollen Transport Assessment: All collected individuals exhibited confirmed flower visitation that contacted flower reproductive structures (pollen-presenting anthers or reflexed stigmas) and are therefore potential pollinators. For those taxa with voucher specimens, we additionally determined whether vouchers were carrying pollen visible under the microscope. We

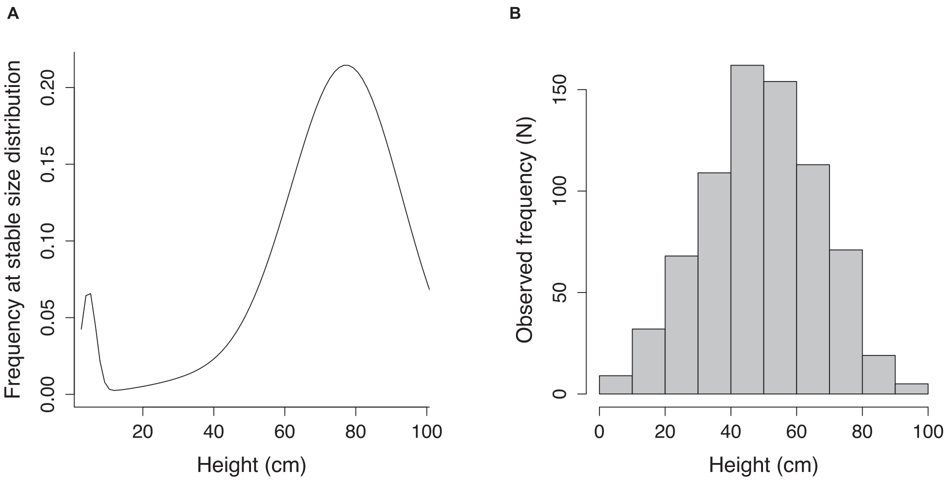

Figure 2.—(A) Stable size distribution estimated by the IPM for the 2019–2020 transition and (B) observed size distribution.

used a dissecting needle to brush that pollen onto a cube of fuchsin gel, which stains pollen grains a dark pink color. We used a handheld lighter to melt the gel onto a microscope slide with a coverslip. We examined each prepared microscope slide under a Reichert Microstar IV microscope (Reichert Technologies, Depew, New York, USA) at 200× magnification to determine the morphotype of the stained pollen grains (after Kearns and Inouye 1993) and visually compare them with a voucher slide of stained *P. imberbis* pollen grains. In our Results section we distinguish those visitor taxa that both contacted flower reproductive structures and for which we confirmed transport of *P. imberbis*-morphotype pollen; such taxa are likely pollinators.

Flower Visitation Data Analysis: To analyze flower visitation data across the duration of the study, we calculated the average number of individuals of each visitor taxon per open flower per minute, as well as the average number of flowers probed per minute, with flower reproductive structure contact, by each taxon. We then multiplied these values to generate an overall importance value for each visitor taxon (after Renne et al. 2000; Aslan et al. 2019). This analysis enabled us to identify the most important visitors as those that either interact frequently with the plants or visit a large number of flowers when they are present (or both). Because importance values are per-minute and per-flower rates, they are robust to variation in total observation time per session as well as to variation in available flowers over the course of each flowering season, and do not assume that repeated observations of the same taxon are independent (i.e., they do not assume that each observation is a unique individual). To standardize importance values and more easily allow comparison, since the per-minute and per-flower calculations result in very small decimals, we calculated the Relative Importance Value by setting the importance value of the most important visitor equal to 1.0, and recalculated all other importance values as their proportion of that maximum.

Self-Compatibility Trials: Environmental change can filter across environmental communities and reduce pollinator populations, indirectly affecting rare plants (Potts et al. 2010). Pollination disruption is of concern for plant species with high dependence on outcrossing, unable to produce viable seed via self-fertilization (Nayak and Davidar 2010). We performed flower bagging trials to determine whether plants are self-compatible. For each of 10 plants in the study population, we contrasted seed production in three bagged floral heads vs. three open floral heads per individual. Bags were placed over floral heads in bud stage to exclude all pollinators and assess seed production in the absence of visitation by pollinators. We used a simple unpaired *t*-test to compare seed treatments, treating multiple flowers within the same treatment from the same plant as subsamples. Data were analyzed in the statistical environment R 2.14.1 (R Core Team 2020), with significance accepted at $P = 0.05$.

RESULTS

Population Dynamics

In 2019 and 2020, we tallied 754 and 794 live *P. imberbis* individuals, respectively, and estimated an asymptotic population growth rate (λ) of 0.95192 (95% CI = 0.95185–0.95199), slightly below replacement levels ($\lambda < 1$). The stable size distribution was bimodal, with peaks in abundance at small size classes (seedlings) and mid-sized adult plants around 80 cm in height. The stable size distribution did not correspond with the observed size distribution of the population during this time period (Figure 2A, 2B). Sensitivity analyses indicated that survival, more than growth and reproduction-related parameters, most strongly influenced population growth (Figure 3A). Plotting the contribution of individual transition elements to population growth revealed that mid-size adult plants, around 80 cm in height, contributed disproportionately to population growth (Figure 3B). This size corresponded to the maximum size plants attain before they tend to shrink and/or experience increased likelihood of mortality. Plants of this size also maximize reproductive output, which increased as a function of size until plateauing or declining at the largest sizes (>80 cm). Based on observed growth rates, 13.1 years are required for a new seedling to attain this size, and the mean life expectancy of a plant that reaches this size is 14 years. The net reproductive rate (R_0), or the average number of offspring produced by a *P.*

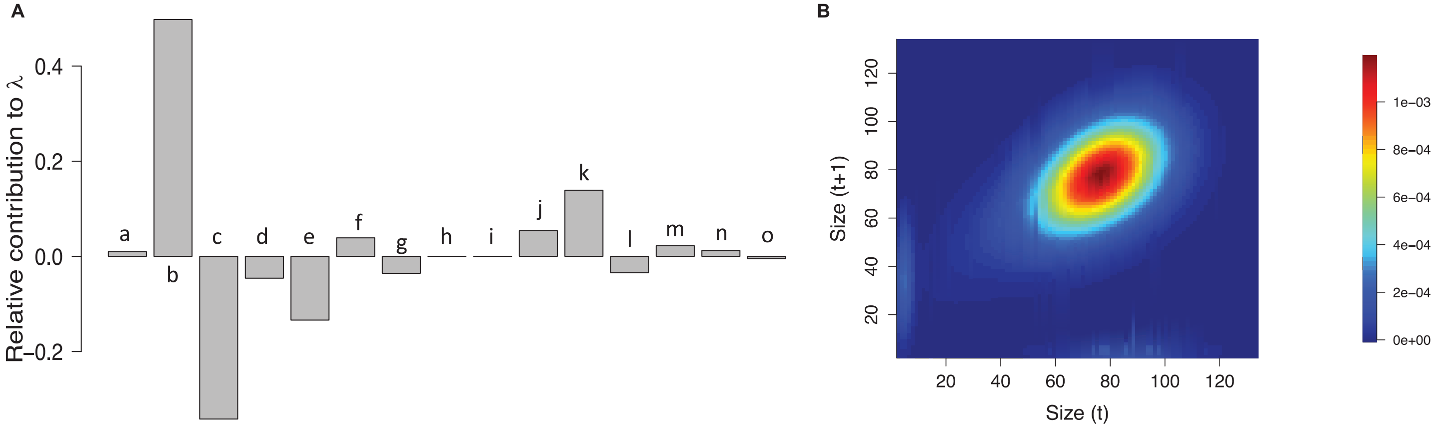

Figure 3.—(A) Elasticity of population growth rate to model components relating survival, growth and reproduction metrics to size, including influence of (a) survival (mean value, herein referred to as "*intercept*"), (b) survival (linear relationship with size, herein referred to as "*linear model*"), (c) survival (polynomial relationship to size, herein referred to as "*polynomial model*"), (d) growth (intercept), (e) growth (linear model), (f) growth (polynomial model), (g) likelihood of producing flowers (intercept), (h) likelihood of flowering (linear model), (i) likelihood of flowering (polynomial model), (j) seed production (intercept), (k) seed production (linear model), (l) seed production (polynomial model), (m) germination rate (constant), (n) seedling size (intercept), and (o) seedling size (variation), on population growth. Elasticity estimates indicate that increasing survival as a function of height has the strongest positive relationship to population growth. (B) Elasticity of population growth to transition probabilities of the IPM matrix. Darker red coloration indicates a strong influence of these parameters on population growth, while dark blue indicates a lack of effect.

imberbis individual over its lifetime, was estimated at 0.28 individuals per maternal plant.

Factors Influencing Population Growth

Browse by Coues Deer: Deer browsed 71.5% and 50.6% of *P. imberbis* individuals in 2019 and 2020, respectively. In all cases, the effect of browse depended on initial size of the individual and varied depending on browse intensity, although the direction and magnitude of browse effects differed by response variable. In the case of growth, high-intensity browsing corresponded to higher growth at smaller initial sizes and lower growth at larger sizes ($F = 7.49$, $P = 0.01$; Figure 4A) while there was a tendency for low browse levels to depress survival more than higher intensity browse levels or no browse at all, particularly for smaller sized individuals ($\chi^2 = 7.22$, $P = 0.07$; Figure 4B). Finally, browse was linked to lower production of flowers per unit height ($F = 7.33$, $P < 0.01$). Depression of floral production by browse was particularly apparent among larger individuals, responsible for the majority of seed production within the population (Figure 4C).

Taller plants were preferentially browsed ($\chi^2 = 5.90$, $P = 0.02$; Figure 5A). Additionally, plants had a greater likelihood of being browsed if they were consumed in the past ($\chi^2 = 7.09$, $P = 0.01$; interaction between height and previous browse nonsignificant; Figure 5B) and if they were not overtopped by other plants ($\chi^2 = 16.63$, $P < 0.01$; Figure 5C). Co-occurrence with other vegetation, measured as cover within 2.5 cm radius of the *P. imberbis*, was also related to browse rates. While woody plants afforded protection, ground cover by herbaceous plant materials was generally linked with increased browse rates, except at smaller size classes ($\chi^2 = 15.98$, $P < 0.01$; Figure 5D).

Role of Co-occurring Vegetation: Of the 794 *P. imberbis* individuals censused in 2020, 43% occurred on bare ground, 32% with perennial grass, 24% with litter, and 1% with woody perennials. The effect of ground cover on *P. imberbis* growth from 2019–2020 depended on whether or not plants were browsed by deer ($F = 5.85$, $P = 0.02$). Among browsed individuals, *P. imberbis* growth rates were greater when occurring with perennial grasses for larger individuals, while the opposite was true as smaller size classes. When plants were not browsed, individuals grew more rapidly when occurring without associated vegetation in all but the smallest size classes (<25 cm in height; Figure 6A). We observed no effect of ground cover on survival; however, canopy cover did influence survival rates ($\chi^2 = 4.82$, $P = 0.03$). In the absence of browse, canopy cover reduced survival rates of larger individuals relative to plants growing without overtopping vegetation. When plants were browsed, canopy cover still depressed survival relative to free-growing plants across all size classes; however, severely negative impacts of canopy cover observed for unbrowsed plants in larger size classes were not detected (Figure 6B). Ground cover reduced floral production, particularly if the co-occurring vegetation was a shrub or tree ($\chi^2 = 10.03$, $P = 0.02$; Figure 6C). Similarly, canopy cover was associated with a reduction in reproduction, with this effect intensified when plants were not browsed, especially among larger individuals ($\chi^2 = 140.30$, $P < 0.01$; Figure 6D).

Flower Visitation and Breeding System: In all, we completed 236 ten-minute observation blocks, for a total of 39.33 hr of flower visitation observations over the course of the study. We observed a total of 12 taxa of insect flower visitors (Figure 7), including bees, flies, and wasps. The most important visitor and also the most frequent visitor was the leafcutter bee, *Megachile* sp. (Figure 7), followed by flies in the family Bombylliidae. Other frequent visitors included longhorned bees (*Melissodes* sp.), paper wasps (*Polistes* sp.), and other wasps (*Steniolia* sp.), but each of these exhibited disproportionately low importance because they interacted with low numbers of flowers when

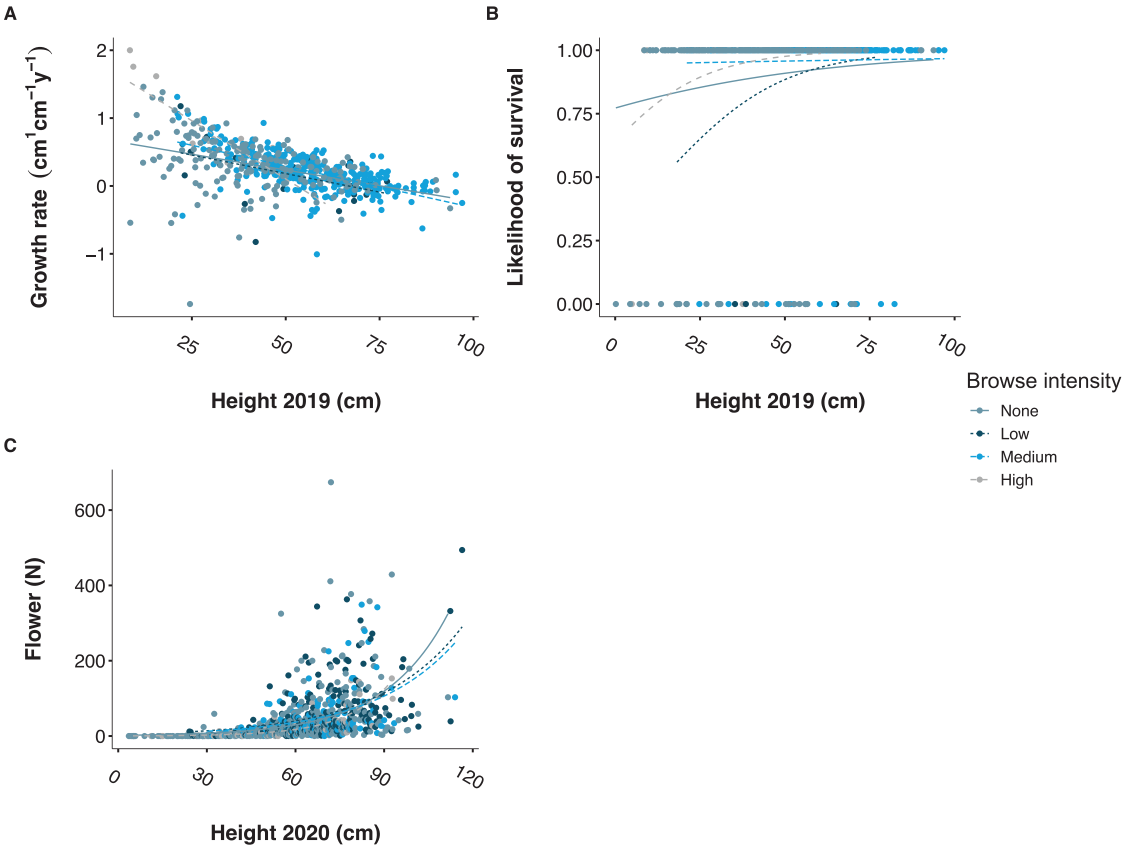

Figure 4.—Response of (A) growth rate, (B) survival, and (C) flower production to deer browse as a function of initial size. Line types correspond to browse intensity, low intensity (<33% of the plant removed by deer), medium intensity (34–66% removed), and high intensity (>67% removed).

present. By contrast, visitors that were rarely observed but emerged with disproportionately high importance because they probed large numbers of flowers included the bees *Ashmeadiella* sp., *Andrena* sp., and *Hylaeus* sp., as well as flies in the family Muscidae. *Pectis imberbis*–morphotype pollen transport, in large quantities, was confirmed under the microscope for all bee species. Much lower pollen loads were transported by flies in the Bombylliidae and Syrphidae. Pollen transport was not confirmed for the remaining visitor taxa (Figure 7).

The bagging experiment indicated that selfing is occurring and plants are able to set fruit without visitors: untreated control floral heads produced 10.5 ± 0.54 SE achenes, and bagged floral heads produced 9.41 ± 1.22 achenes. There was no significant difference between treatments ($t = 83$; $P = 0.42$).

DISCUSSION

We described for the first time the population dynamics, life cycle, and reproductive ecology of *P. imberbis*. Building on this information, we examined the role of interspecific interactions, including herbivory by Coues deer, competition with native plant species, and pollination, in shaping patterns of growth, survival, and reproduction of *P. imberbis*. Herein, we apply the outcomes of these analyses to inform the conservation of *P. imberbis*, and assist recovery of this recently listed endangered plant species.

Population Dynamics

Population growth rate (λ) of this *P. imberbis* population, calculated at 0.9512 for the 2019–2020 transition year, was below replacement level, but did not indicate an immediate risk of extirpation. The observed growth rate may be lower than typical, since both census years occurred within a multiyear drought occurring in southern Arizona (https://www.drought.gov/data-maps-tools/us-drought-monitor). The large size of this population ($N_{2020} = 794$) buffers against loss if depressed population growth indeed resulted from a short-term phenomenon, such as drought. Smaller populations of *P. imberbis*, however, may face extirpation from even brief episodes of population decline, especially if detrimental processes acting on small populations hastens descent into extinction. At small population sizes, genetic drift, or random change in allele frequency driven by demographic stochasticity and chance mating events, erodes genetic diversity and is linked to fitness declines, particularly in directionally changing environments (Ellstrand and Elam 1993; Newman and Pilson 1997; Pertoldi et al. 2007). Moreover, small population size increases the likelihood of experiencing inbreeding depression, a reduction in offspring fitness due to expression of deleterious recessive alleles (Lynch 1991; Ellstrand and Elam 1993; Frankham 1995). Genetic factors, in combination with demographic consequences of rarity, like Allee effects, in which per capita reproduction is reduced at small population sizes due to loss of mating opportunities, positively feeds back to further drive rarity (Courchamp et al. 2006; Melbourne and

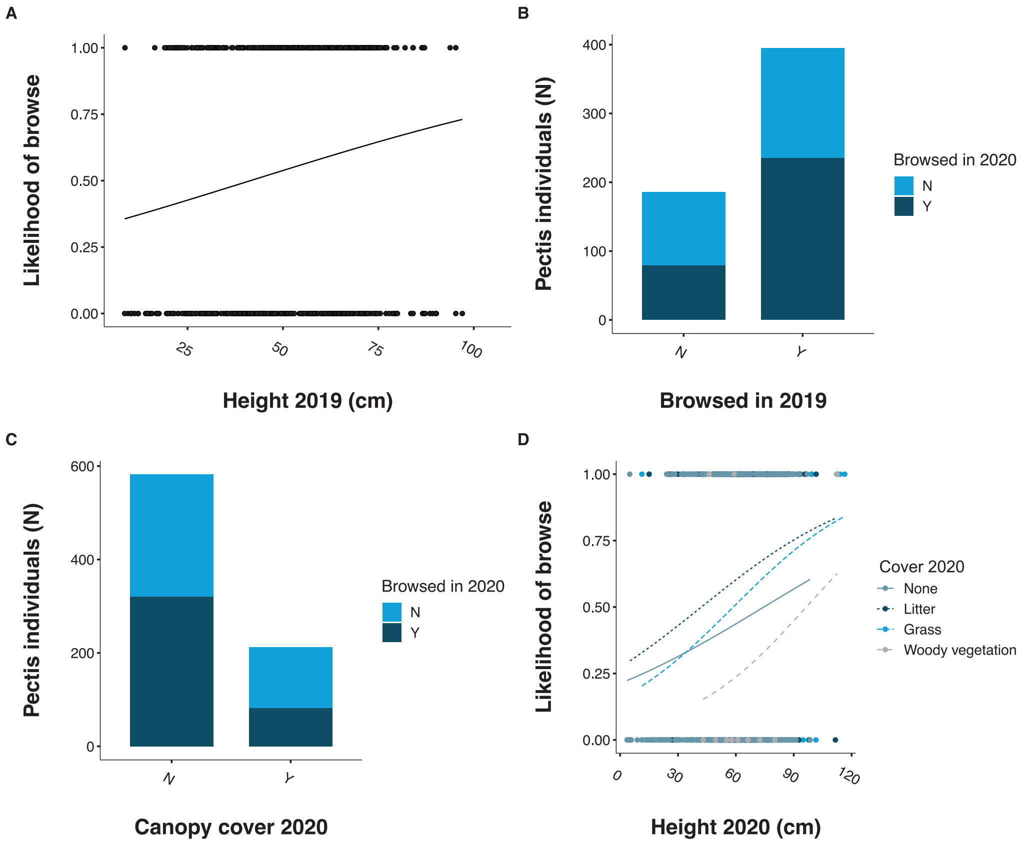

Figure 5.—Predictors of a *P. imberbis* individual being browsed by deer, including (A) height, (B) previous instance of browse, (C) canopy cover, and (D) ground cover.

Hastings 2008; Bakker and Doak 2009). In the case of *P. imberbis*, populations have been documented at 15 sites since the 1960s, with population persistence confirmed at only 6 of these locales currently. Aside from the population described here, all populations are currently composed of less than 60 individuals (mean population size = 25 individuals, range 2–56). Extirpation or decline of these populations would represent a significant loss of genetic diversity for this species, especially if populations are adaptively differentiated across environments. Resurveys of areas where *P. imberbis* was found in the past, and demographic censuses of these populations paired with genetic sampling efforts, are urgently needed in order to accurately assess the conservation status of this species.

Demographic sensitivity analysis indicated that survival, more than growth and reproduction-related parameters, most strongly influenced overall *P. imberbis* population growth. Dependency of growth rates on survival is frequently observed in longer-lived perennial species, for which longevity provides repeated opportunities for reproduction, which are lost if an individual dies prematurely (Silvertown et al. 1996; Pfister 1998; Adier et al. 2014). Relating sensitivity analyses to size classes, we found that mid-size adult plants, around 80 cm in height, contribute disproportionately to population growth. This size both corresponds to a maximal reproductive output and represents a threshold size that plants attain before they tend to shrink and/or experience increased likelihood of mortality. For context, a *P. imberbis* individual reaches 80 cm in height in about 13.1 y, while mean life expectancy narrowly exceeds 14 y. The observed decrease across demographic vital rates, including growth, reproduction, and likelihood of survival, in *P. imberbis* after plants attain a size of ca. 80 cm may suggest an aging effect in this species. Precise mechanisms for aging of perennial plants are not fully understood, but could result from oxidative stress, genetically based limitations on meristematic divisions and/or physiological constraints to water and nutrient acquisition imposed by larger size (Munné-Bosch 2007; Thomas 2013). Focus on protection of established adults (mid-sized to large individuals) is recommended, in order to provide numerous occasions for reproduction over the lifetime of this perennial plant. This strategy allows opportunistic seedling recruitment when climatic conditions are amenable, thus maximizing genetic diversity of offspring and likelihood of adaptive response to changing environmental conditions.

Uncertainty within Demographic Models: We detected a departure of the observed size distribution of plants from the stable distribution, which may indicate nonequilibrium conditions within the population. Unusual environmental conditions, like the drought event during this study, may represent transient dynamics that deviate from equilibrium (Tremblay et al. 2015). Additional years of data collection will improve our understanding of *P. imberbis* population ecology and permit the incorporation of stochasticity into population growth rate projections, thus providing a more comprehensive understanding of the trajectory of these populations (Menges 1992;

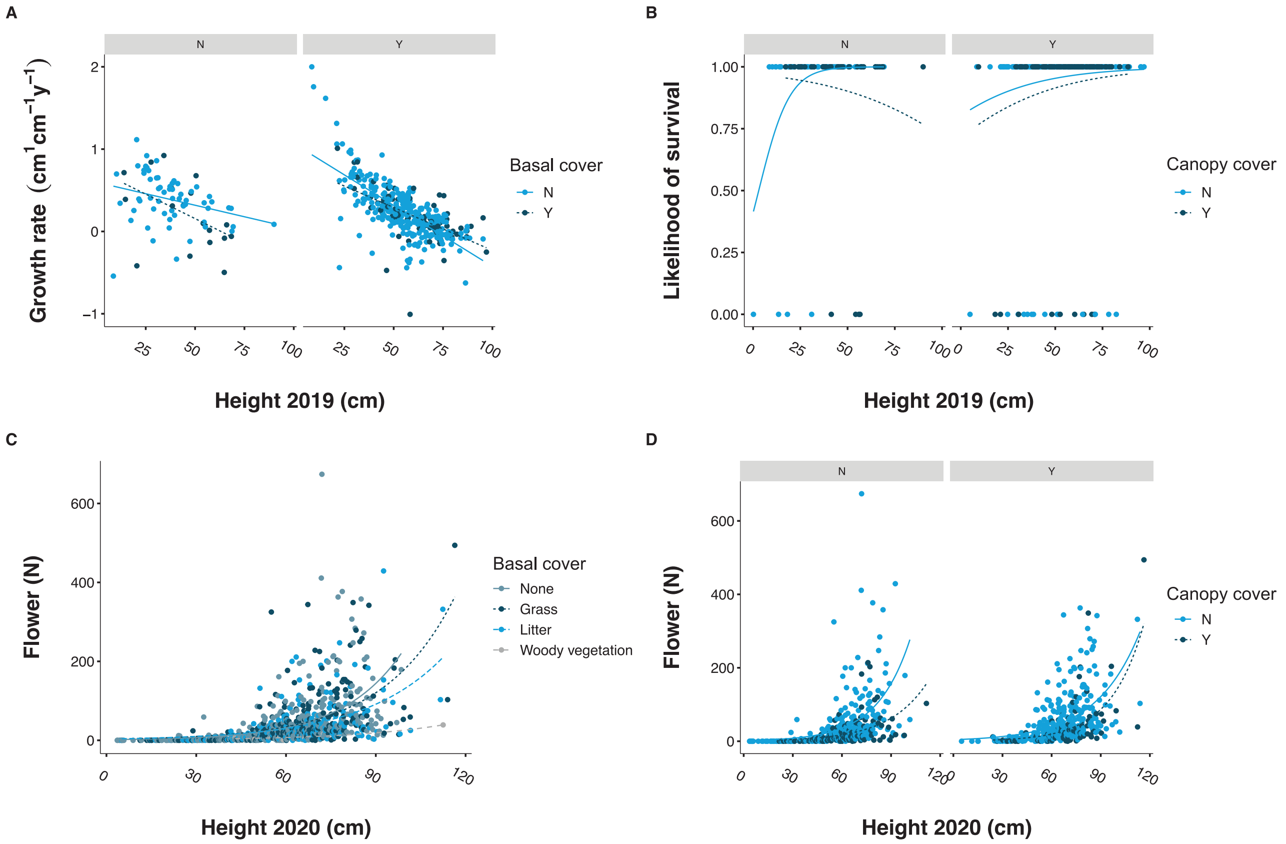

Figure 6.—Relationship between co-occurring vegetation and vital rates, including (A) growth, (B) survival, and (C, D) flower production, all shown as a function of plant height. Significant interactions with deer browse are illustrated in figures A, B, and D, with "N" located within the top, shaded gray area of the panel indicating that plants did not experience browse, and "Y" indicating that plants were browsed. The effect of ground cover on floral production did not depend on browse, and hence is not partitioned by this factor.

Melbourne and Hastings 2008). Estimates of reproduction remain a source of uncertainty. Seed bank dynamics are not yet fully described, and while the demographic model presented here did not depend on input from these cryptic life stages, understanding related constraints on reproduction may provide valuable insights for *P. imberbis* conservation. Based on our cursory observations, plant dormancy is uncommon in this species, with only 2 of 28 plants missing during a growing season reemerging the following year, suggesting that chance of reemergence if not observed during a growing season is low (7.1%). Longer-term studies would permit researchers to better quantify dormancy rates and improve census protocols.

Factors Influencing Population Growth

Deer Browse and Co-occurring Vegetation: Deer browsed 71.5% and 50.6% of the *P. imberbis* population in 2019 and 2020, respectively. The likelihood of browse increased if the plant was taller, had been previously browsed, and was unprotected by overtopping woody vegetation. While bunchgrasses sheltered *P. imberbis* seedlings and juveniles, perennial grasses and vegetative litter were linked with increased browse rates of larger individuals. This pattern could suggest that deer preferentially browse bunchgrasses, inadvertently browsing *P. imberbis* at higher rates when plants emerge from grasses.

Browse corresponded to a reduction in growth and reproduction of larger *P. imberbis* individuals and decreased survival of smaller individuals. Response of vital rates to browse, however, was not always straightforward. For instance, as anticipated, high-intensity browse decreased growth rates of large individuals, while unexpectantly increasing growth rates of smaller-sized individuals. Similarly, low levels of browse reduced reproduction more than medium and high browse severity levels. These unexpected responses were likely a relic of mismeasurement when the plant was browsed early in the season of either the first or second year of the transition and we failed to accurately assess the extent of browse; however, these patterns could also indicate compensatory growth in response to browse, which has been documented for other species (Shelton and Inouye 1995).

Co-occurring vegetation may also affect the response of *P. imberbis* individuals to browse. While woody perennials guarded against browse, in the absence of browse, woody canopy cover was a liability, reducing survival and reproductive rates. Similarly, perennial grasses appeared to prevent browse of juvenile plants, but reduced growth and reproductive rates of larger individuals in the absence of browse. Interestingly, small *P. imberbis* individuals co-occurring with perennial grasses tended to exhibit higher growth rates relative to plants with no ground cover, suggesting that perennial grasses serve as nurse

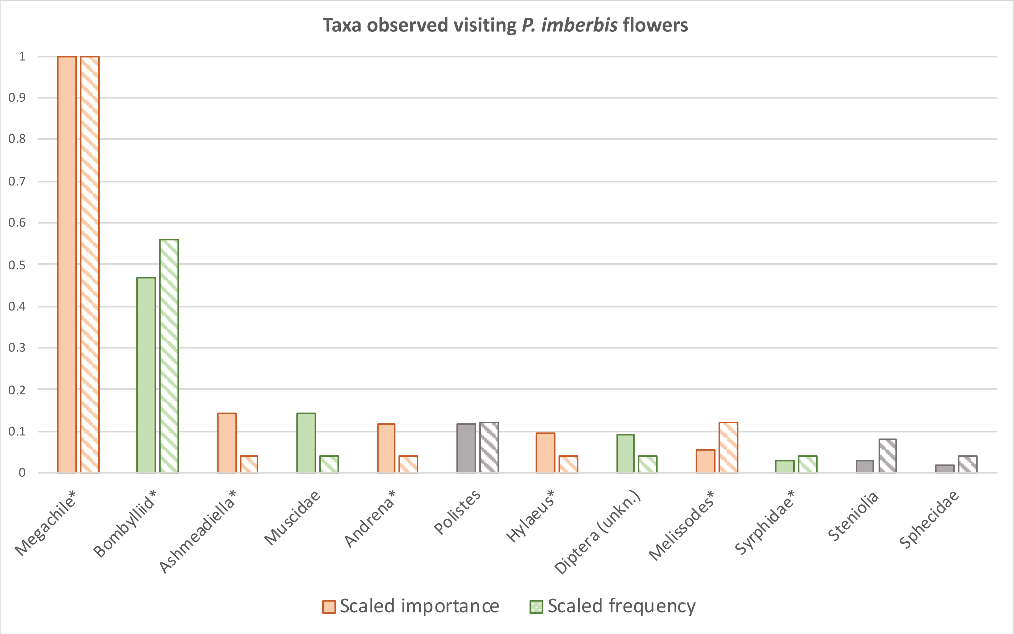

Figure 7.—Scaled importance and frequency values for insect taxa observed visiting flowers of *P. imberbis* during this study. Importance (solid bars) is the product of the frequency of visitation, the average number of visiting individuals per open flower, and the average number of flowers visited per minute by each individual. Frequency (hashed bars) is the proportion of observation blocks in which each visitor taxon appeared. Both values are scaled as proportions of the most important or most frequent visitor (the *Megachile* sp. bee). Bees are identified to genus and indicated by orange bars; flies are identified to family and indicated by green bars; wasps are identified to genus when possible and indicated by gray bars. *Pollen transport confirmed via swabbing of sampled insects and staining with fuchsin gel.

plants to *P. imberbis* seedlings. Alternatively, this pattern could be the result of bunch grasses trapping seeds in favorable microsites, or represent greater allocation to aboveground growth due to competition for light resources. Nonnative perennial lovegrasses are abundant across *P. imberbis*'s range and could potentially reduce seedling recruitment if competitively superior to native grasses, suggesting that targeted removal of nonnative grasses in *P. imberbis* habitat is warranted. Overall, however, browsing appeared pervasive and negatively impacted *P. imberbis* individuals. Unraveling the precise interplay between browse and competition on population demography will require targeted, experimental studies.

Pollinator Community Assessment: Most Asteraceae species produce open, accessible flowers with abundant pollen, making them attractive to a diverse suite of potential visitors (e.g., Fornoff et al. 2017; Cane 2017; Aslan et al. 2019). Our flower visitation observations confirmed that *P. imberbis* demonstrates such generality, interacting with small and large visitors across Hymenoptera and Diptera. This diversity of visitors also of course spans a gradient of traits including important morphological characteristics such as proboscis length and density and texture of pollen-carrying hairs, as well as behavioral characteristics such as flight patterns, pollen harvesting techniques, and daily activity patterns. The most important visitors, in particular, were relatively large: robust *Megachile* bees and bombyliid flies. Both of these taxa transported pollen, with particularly heavy pollen loads detectable on captured *Megachile* specimens. Furthermore, many visitors moved from flower to flower (across all observed flower visitor taxa, the average number of flowers visited per minute was >10), suggesting abundant opportunity for pollen transfer among flowers. Overall, our pollinator community assessment results suggest that at this time *P. imberbis* interacts with a robust and diverse community of pollinators across its full flowering season, indicating likely frequent gene flow among individuals and subpopulations in the study area. Moreover, our breeding trials found no indication that self-incompatibility is a concern for *P. imberbis*.

CONCLUSIONS

Shifts in ecological communities shape population trajectories of individual species and are critical for formulating effective conservation and management efforts. Here, we describe a complex interplay between deer and competing vegetation on *P. imberbis* population dynamics. Altering established competition regimes through the introduction of nonnative plant species or increasing the incidence and/or frequency of browse would most likely result in decline of this rare species. Efforts to reestablish *P. imberbis* should consider erecting deer exclosures around restoration sites. Although we infrequently encountered invasive or nonnative species during our census, invasive bunchgrasses, including Lehmann's lovegrass (*Eragrostis lehmanniana* Nees), occur frequently in *P. imberbis* habitat. Given the negative impact of competition from native species on *P. imberbis* vital rates, removal of invasive and nonnative species prior to restoration is recommended. Invasive removal within extant populations could be beneficial if ground disturbance due to removal is minimized. Future studies should expand the temporal and spatial scale of *P. imberbis* demographic monitoring, to determine how the intensity of browse and competition vary across the landscape, and how these factors interact with other variables like climate to affect *P. imberbis* population viability. The use of prescribed fire to reduce competition should also be explored as a potential management strategy for *P. imberbis*.

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LITERATURE CITED

Adier, P.B., R. Salguero-Gómez, A. Compagnoni, J.S. Hsu, J. Ray-Mukherjee, C. Mbeau-Ache, and M. Franco. 2014. Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences USA 111:740–745.

Aslan, C.E., A.B. Shiels, W. Haines, and C.T. Liang. 2019. Non-native insects dominate daytime pollination in a high-elevation Hawaiian dryland ecosystem. American Journal of Botany 106:313–324.

Bakker, V., and D. Doak. 2009. Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox. Ecological Monographs 79:77–108.

Balch, J.K., B.A. Bradley, C.M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology 19:173–183.

Barnosky, A.D., N. Matzke, S. Tomiya, G.O.U. Wogan, B. Swartz, T.B. Quental, C. Marshall, J.L. McGuire, E.L. Lindsey, K.C. Maguire, et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471:51–57.

Bond, W.J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society of London Series B 344:83–90.

Borror, D.J., and R.E. White. 1970. A Field Guide to Insects: America North of Mexico. Houghton Mifflin Harcourt, New York, NY.

Burns, C.E., K.M. Johnston, and O.J. Schmitz. 2003. Global climate change and mammalian species diversity in U.S. national parks. Proceedings of the National Academy of Sciences 100:11474–11477.

Cane, J.H. 2017. Specialist bees collect Asteraceae pollen by distinctive abdominal drumming (*Osmia*) or tapping (*Melissodes*, *Svastra*). Arthropod–Plant Interactions 11:257–261.

Courchamp, F., E. Angulo, P. Rivalan, R.J. Hall, L. Signoret, L. Bull, and Y. Meinard. 2006. Rarity value and species extinction: The anthropogenic Allee effect. PLoS Biology 4:e415.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 14:405–410.

Dunn, R.R., N.C. Harris, R.K. Colwell, L.P. Koh, and N.S. Sodhi. 2009. The sixth mass coextinction: Are most endangered species parasites and mutualists? Proceedings of the Royal Society B 276:3037–3045.

Eldridge, D.J., A.G.B. Poore, M. Ruiz-Colmenero, M. Letnic, and S. Soliveres. 2016. Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing. Ecological Applications 26:1273–1283.

Ellner, S.P., and M. Rees. 2006. Integral projection models for species with complex demography. American Naturalist 167:410–428.

Ellstrand, N.C., and D.R. Elam. 1993. Population genetic consequences of small population size: Implications for plant conservation. Annual Review of Ecology and Systematics 24:217–242.

Falk, D.A., and P.L. Warren. 1994. Rare plants of the Coronado National Forest: Population studies and monitoring recommendations. The Nature Conservancy, Tucson, AZ.

Fornoff, F., A.-M. Klein, F. Hartig, G. Benadi, C. Venjakob, H.M. Schaefer, and A. Ebeling. 2017. Functional flower traits and their diversity drive pollinator visitation. Oikos 126:1020–1030.

Frankham, R. 1995. Conservation genetics. Annual Review of Genetics 29:305–327.

Hackney, E., and J. McGraw. 2001. Experimental demonstration of an Allee effect in American ginseng. Conservation Biology 15:129–136.

Humphreys, A.M., R. Govaerts, S.Z. Ficinski, E. Nic Lughadha, and M.S. Vorontsova. 2019. Global dataset shows geography and life form predict modern plant extinction and rediscovery. Nature Ecology & Evolution 3:1043–1047.

Humphreys, A.M., M.S. Vorontsova, R. Govaerts, and E. Nic Lughadha. 2020. Reply to: Regional records improve data quality in determining plant extinction rates. Nature Ecology & Evolution 4:515–516.

Kearns, C.A., and D.W. Inouye. 1993. Techniques for Pollination Biologists. University Press of Colorado, Niwot, CO.

Keil, D.J. 1978. Revision of *Pectis* section *Pectidium* (Compositae: Tageteae). Rhodora 80:135–146.

Knapp, W.M., A. Frances, R. Noss, R.F.C. Naczi, A. Weakley, G.D. Gann, B.G. Baldwin, J. Miller, P. McIntyre, B.D. Mishler, et al. 2020. Erratum to: Global dataset shows geography and life form predict modern plant extinction and rediscovery (Nature Ecology & Evolution, 2019, 3:1043–1047). Nature Ecology & Evolution 4:512–514.

Kremen, C., and T. Ricketts. 2000. Global perspectives on pollination disruptions. Conservation Biology 14:1226–1228.

Lawrence, D.J., E.R. Larson, C.A.R. Liermann, M.C. Mims, T.K. Pool, and J.D. Olden. 2011. National parks as protected areas for U.S. freshwater fish diversity. Conservation Letters 4:364–371.

Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression. Evolution 45:622–629.

Manson, J.H. 1997. Does female rank or age affect mate choice in free-ranging rhesus macaques? Folia Primatologica 68:366–369.

McGraw, J.B., and M.A. Furedi. 2005. Deer browsing and population viability of a forest understory plant. Science 307:920–922.

Melbourne, B.A., and A. Hastings. 2008. Extinction risk depends strongly on factors contributing to stochasticity. Nature 454:100–103.

Menges, E.S. 1992. Stochastic modeling of extinction in plant populations. Pp. 253–275 *in* P.L. Fiedler and S.K. Jain, eds., Conservation Biology. Springer, Boston, MA.

Merow, C., J.P. Dahlgren, C.J.E. Metcalf, D.Z. Childs, M.E.K. Evans, E. Jongejans, S. Record, M. Rees, R. Salguero-Gómez, and S.M. McMahon. 2014. Advancing population ecology with integral projection models: A practical guide. Methods in Ecology and Evolution 5:99–110.

Michener, C.D., R.J. McGinley, and B.N. Danforth. 1994. The bee genera of North and Central America (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, DC.

Munné-Bosch, S. 2007. Aging in perennials. Critical Reviews in Plant Sciences 26:123–138.

Naughton-Treves, L., M.B. Holland, and K. Brandon. 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annual Review of Environment and Resources 30:219–252.

Nayak, K.G., and P. Davidar. 2010. Pollinator limitation and the effect of breeding systems on plant reproduction in forest fragments. Acta Oecologica 36:191–196.

Newman, D., and D. Pilson. 1997. Increased probability of extinction due to decreased genetic effective population size: Experimental populations of *Clarkia pulchella*. Evolution 51:354–362.

Nic Lughadha, E., S.P. Bachman, T.C.C. Leão, F. Forest, J.M. Halley, J. Moat, C. Acedo, K.L. Bacon, R.F.A. Brewer, G. Gâteblé, et al. 2020. Extinction risk and threats to plants and fungi. Plants, People, Planet 2:389–408.

Pertoldi, C., R. Bijlsma, and V. Loeschcke. 2007. Conservation genetics in a globally changing environment: Present problems, paradoxes and future challenges. Biodiversity and Conservation 16:4147–4163.

Pfister, C.A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213–218.

Phillips, A.M. III, B.G. Phillips, L.T. Green III, J. Mazzoni, and N. Brian. 1982. Status report: *Pectis imberbis* Gray. US Fish and Wildlife Service, Alburquerque, NM.

Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W.E. Kunin. 2010. Global pollinator declines: Trends, impacts and drivers. Trends in Ecology & Evolution 25:345–353.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rees, M., D.Z. Childs, and S.P. Ellner. 2014. Building integral projection models: A user's guide. Journal of Animal Ecology 83:528–545.

Renne, I.J., S.A. Gauthreaux, and C.A. Gresham. 2000. Seed dispersal of the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) by birds in coastal South Carolina. American Midland Naturalist 144:202–215.

Rodgers, J.L. 1999. The bootstrap, the jackknife, and the randomization test: A sampling taxonomy. Multivariate Behavioral Research 34:441–456.

Sanchez-Escalante, J. 2018. Interim report on surveys for *Cirsium wrightii* and other rare plants in northeastern Sonora and northern Chihuahua, Mexico. Unpublished report to US Fish and Wildlife Service, Tucson, AZ.

Shelton, A.L., and R.S. Inouye. 1995. Effect of browsing by deer on the growth and reproductive success of *Lactuca canadensis* (Asteraceae). American Midland Naturalist 134:332–339.

Silvertown, J., M. Franco, and E. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conservation Biology 10:591–597.

Thomas, H. 2013. Senescence, ageing and death of the whole plant. New Phytologist 197:696–711.

Tremblay, R.L., J. Raventos, and J.D. Ackerman. 2015. When stable-stage equilibrium is unlikely: Integrating transient population dynamics improves asymptotic methods. Annals of Botany 116:381–390.

Tripplehorn, C.A., and N.F. Johnson. 2005. Borror and DeLong's Introduction to the Study of Insects. Thomson Brooks/Cole, Belmont, CA.

[USFWS] US Fish and Wildlife Service. 2012. Endangered and Threatened wildlife and plants; 90-day finding on a petition to list *Graptopetalum bartramii* (Bartram stonecrop) and *Pectis imberbis* (beardless chinch weed) as Endangered or Threatened and designate critical habitat. Federal Register Proposed Rules 77:47352–47356.

[USFWS] US Fish and Wildlife Service. 2021. Endangered and Threatened wildlife and plants; Endangered status for the beardless chinchweed and designation of critical habitat. Federal Register 86:31830–31868.