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Application of distance sampling for assessing abundance and habitat relationships of a rare Sonoran Desert cactus

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Abstract Accurate abundance estimates of plant populations are fundamental to numerous ecological questions and for conservation. Estimating population parameters for rare or cryptic plant species, however, can be challenging and thus developing and testing new methods is useful. We assessed the efficacy of distance sampling for estimating abundance and habitat associations of the endangered Pima pineapple cactus (*Coryphantha scheeri* var. *robustispina*), a rare plant in the Sonoran Desert of southwestern North America that has traditionally been surveyed with census-based methods. Distance sampling (DS) involves measuring distances between focal objects and samples of lines or points, and modeling detection functions that adjust estimates for variation in detection probability (P). Although often used in animal systems, DS remains largely untested for plants. We encountered 105 live individuals along 36.9 km of transects in 11 study plots placed across much of the geographic range of the species, and estimated an average density of 1.47 individuals/ha (CV = 0.139). Compared to values from intensive censuses, density estimates from DS were underestimated by only 2.3% on average and highly correlated on the untransformed ($r = 0.84$) and logarithmic ($r = 0.93$) scales. Estimates of P averaged 0.49 and declined as soils became increasingly dominated by larger soil substrates, and somewhat with increasing vegetation volume and decreasing cactus height. Local densities increased with increasing slope and soil substrate size and decreased with increasing vegetation volume ($P \leq 0.024$). Combined with careful survey design, DS offers an efficient method for estimating population parameters for uncommon and cryptic plants.

Keywords Abundance estimation · Detection probability · Distance sampling · Habitat · Pima pineapple cactus · Population size · *Coryphantha scheeri* var. *robustispina*

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Introduction

Estimating the abundance and habitat associations of plant populations is fundamental to a broad range of ecological questions and for guiding conservation and management. For uncommon and cryptic plants, however, accurate estimates of population parameters can be costly to obtain, and thus developing new more efficient methods is useful. Although many species of plants are readily detectable in the field, probability of detecting individuals that are present and available for sampling is rarely perfect and can vary with species' traits and environmental and survey conditions (Chen et al. 2009, 2013; Garrard et al. 2013; Junaedi et al. 2018). Understanding factors that influence the detection process can help guide survey and sampling designs, and explicitly modeling these factors can improve the accuracy of inferences (Buckland et al. 2001; Chen et al. 2009; Dénes et al. 2015). Plant species that occur as scattered individuals have often been surveyed with plot-less or point-based techniques that are sometimes referred to as distance methods (Cottam 1947; Cottam and Curtis 1956; Mueller-Dombois and Ellenberg 1974; Elzinga et al. 1998). For these species, such techniques are thought to be faster and more flexible than plot-based methods, but can be challenging to implement in field settings when individuals are rare or cryptic (Elzinga et al. 1998; Ducey 2018).

Distance sampling (DS) is a survey technique similar to—but distinct from—traditional distance methods in plant ecology. This approach involves measuring distances to focal objects from sets of lines or points, and modeling a detection function that quantifies the decline in detection probability with increasing distance from observers, and adjusts abundance estimates for variation in detection probability (Buckland et al. 2001; Thomas et al. 2010). In addition to observed distances, other covariates of detection probability such as individual (e.g., plant size), spatial, and temporal factors can be incorporated into detection function. Hence, DS offers excellent flexibility and can be tailored to specific traits of focal populations and their environment (Marques et al. 2007). Application of DS has proven highly effective for estimating abundance and habitat relationships of wildlife, and been used across a broad range of geographic regions and taxa (Thomas et al. 2002, 2010; Anderson et al. 2001; Rosenstock et al. 2002; Hounsome et al. 2005; Flesch et al. 2016). Although commonly applied to wildlife, DS remains largely untested for plants. To date, DS has been applied to few plant systems (e.g., Buckland et al. 2007; Crase et al. 2010; Kissa and Sheil 2012; Schorr 2013), and its efficacy has not been tested based on parametric values of plant abundance or used to evaluate plant–habitat relationships.

We assessed the efficacy of DS for estimating abundance of a rare plant in an arid environment. As a case study, we considered the Pima pineapple cactus (*Coryphantha scheeri* var. *robustispina* Britton and Rose, Cactaceae; hereafter "PPC"), an endangered species in the Sonoran Desert of southwestern North America. Like many species of concern, the PPC is often surveyed for compliance with federal law and to address conservation and recovery objectives. The recommended survey method for this species, however, calls for a complete census of all individuals in a given focal area, which is time intensive and costly (Roller 1996a; USFWS 2007, 2018). In this and other similar contexts, survey methods based on sampling theory should be capable of accurately estimating population size, distribution, and other parameters with greater efficiency across larger areas.

We compared estimates of population size and densities of the PPC derived from DS to values from intensive recent censuses, and assessed the magnitude of estimation bias and factors that explain bias. Moreover, we evaluated factors that influence detectability during DS and the resulting implications for survey design. Finally, we assessed plant–habitat relationships by modeling variation in local densities and various environmental factors such as vegetation structure and soil substrate size.

Materials and methods

Study system

The PPC is distributed narrowly in the eastern Sonoran Desert of south-central Arizona and adjacent Sonora, Mexico (Baker and Butterworth 2013). In Arizona, it occurs near the ecotone of Sonoran desert-scrub and semi-desert grasslands in the Altar and Santa Cruz valleys (Fig. 1; USFWS 2018). Individuals are small (≤ 46 cm in height), hemispherical succulents with singular or clumped stems covered by 2–3-cm long

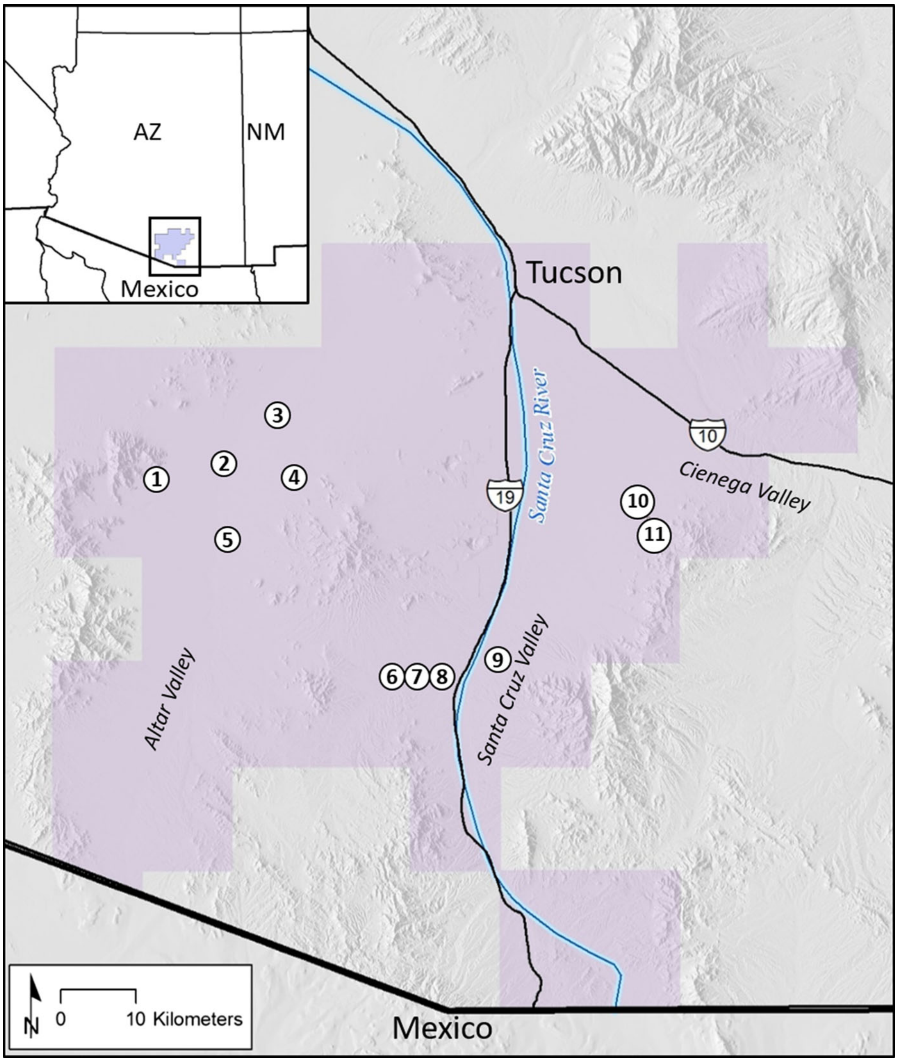

Fig. 1 Plot locations and approximate geographic range (purple) of the Pima pineapple cactus in southern Arizona. Plots are (1) Mendoza, (2) Anvil, (3) Guy Street, (4) Stagecoach, (5) Palo Alto, (6–8) Sopori 1–3, (9) Canoa, and (10–11) Sycamore 1–2

rounded projections (USFWS 2018). Sonoran desertscrub is dominated by small leguminous trees such as velvet mesquite (*Prosopis velutina*) and paloverde (*Parkinsonia* sp.), shrubs such as creosote (*Larrea tridentata*) and bursage (*Ambrosia* sp.), and various cacti, grasses, and forbs (Turner and Brown 1982). Semi-desert grassland is dominated by open woodlands of velvet mesquite and various grasses and subshrubs such as burroweed (*Isocoma tenuisecta*) and snakeweed (*Gutierrezia sarothrae*; Brown and Makings 2014).

In response to threats from urban development, invasion of non-native grasses, wildfire, climate change, and other stressors, the PPC was listed as endangered in 1993 (USFWS 2007; Thomas et al. 2017). The recommended survey protocol for this species attempts to census all individuals in a given focal area (Roller 1996a). While this approach is useful for compliance with U.S. federal law, it is inefficient for other objectives and may be based on unrealistic assumptions of perfect detection probability. Such issues are especially relevant because individuals are small, widely spaced, and sometimes concealed by dense vegetation, which augments the chances some individuals are undetected during surveys. To guide conservation and recovery, efficient survey techniques for estimating abundance across large areas are needed together with data on habitat associations.

Design

We implemented DS at sites across the northern range of the PPC (Fig. 1), along broad natural gradients in densities, and assessed estimation bias by comparing abundance estimates from DS with values from intensive censuses. We selected study plots where either (1) repeated censuses and monitoring had enumerated PPC abundances within ≈1 year, or (2) the presence of PPC was known but abundances were unknown and thus needed to be measured prior to DS. For criteria one, we selected five plots in the Altar Valley and two plots in the Santa Cruz Valley where long-term monitoring began in the late 1990s and 2004, respectively (Fig. 1; see Appendix A, Supplementary Materials, for details). For criteria two, we selected four additional plots where observers different from those that implemented DS completed intensive censuses in the same year. To census plots, multiple observers walked parallel lines 4–6 m apart and exhaustively searched for cacti until plots were completely covered (Roller 1996a). Within long-term study plots (criteria one), all known cacti were monitored and plots surveyed at 1–4-year intervals with new individuals added to results. Thus, assuming accuracy of past censuses and population closure, populations within plots were completely enumerated within ≈1 year of DS.

We systematically placed parallel lines 50 m apart across plots and began DS from a random point on plot boundaries. To guide survey design, we used estimates from preliminary PPC surveys along 37 km of lines in similar environments (Powell 2015, unpubl. data), which found an effective strip half-width (distance from the line at which the number of focal objects missed within that distance equals the number detected beyond that distance but within the truncation distance; Buckland et al. 2015) of 8–13 m and maximum detection distance of 25 m. To assess environmental conditions along lines, we measured various environmental factors, which are described below, around points placed every 100 m (Fig. 2).

Surveys and measurements

For stationary objects, DS has two assumptions to ensure accurate estimation: (1) perfect detection of focal objects on survey lines (or at points), and (2) accurate measurements of distances between lines and objects. Moreover, lines should be placed independently of focal objects so objects are uniformly distributed with respect to distances from lines (Buckland et al. 2015).

During DS, teams of two observers slowly walked lines. One observer focused on and immediately around lines, while another observer walked short serpentine paths within ≈0–6 m of lines scanning lines and surrounding areas (Fig. 2). Observers inspected vegetation clumps near lines to ensure cacti on lines were detected and looked behind them for cacti to check for individuals obstructed from oncoming directions. Because PPC sometimes occur in small groups 10–30 m apart, before leaving lines to measure detected cacti, observers scanned areas for additional individuals. All surveys were during daylight hours when the sun was well above the horizon and in winter and early spring when cover of green grasses and forbs was low.

We recorded the following data for each PPC: (1) perpendicular distance from transect line to center of cactus, (2) height of cactus (cm) from ground to top of tallest spine, (3) width (cm) of cactus, (4) number of pups or stems, (5) status of cactus (live or dead), and (6) location based on GPS coordinates. We used measuring tapes to estimate distances to the nearest dm within 0–8 m of lines, or laser rangefinders to the nearest m beyond 8 m, and used tapes to measure cacti dimensions to the nearest 0.5 cm.

To assess the influence of potential covariates of detection probability and quantify local environmental conditions, we estimated environmental features within 10-m-radius plots centered on points placed every 100 m along lines (Fig. 2). We estimated (1) vegetation volume from 0–1 m above ground, (2) percent grass cover, (3) mean understory height of vegetation, and (4) size class of dominant soil substrate. Volume and cover were visually estimated to the nearest 10% for values between 20 and 80% and nearest 5% otherwise. When measuring volume, we considered vegetation rooted within plots and assumed 100% volume around plant canopies. For grass cover, we considered annual and perennial grasses rooted within plots but excluded small prostrate species (e.g., *Schismus* sp.). For understory height, we visually estimated the mean height of understory plants rooted within plots, which included grasses, forbs, and subshrubs but excluded succulents. For soil substrate size, we considered three size classes: 1 for fine sand with

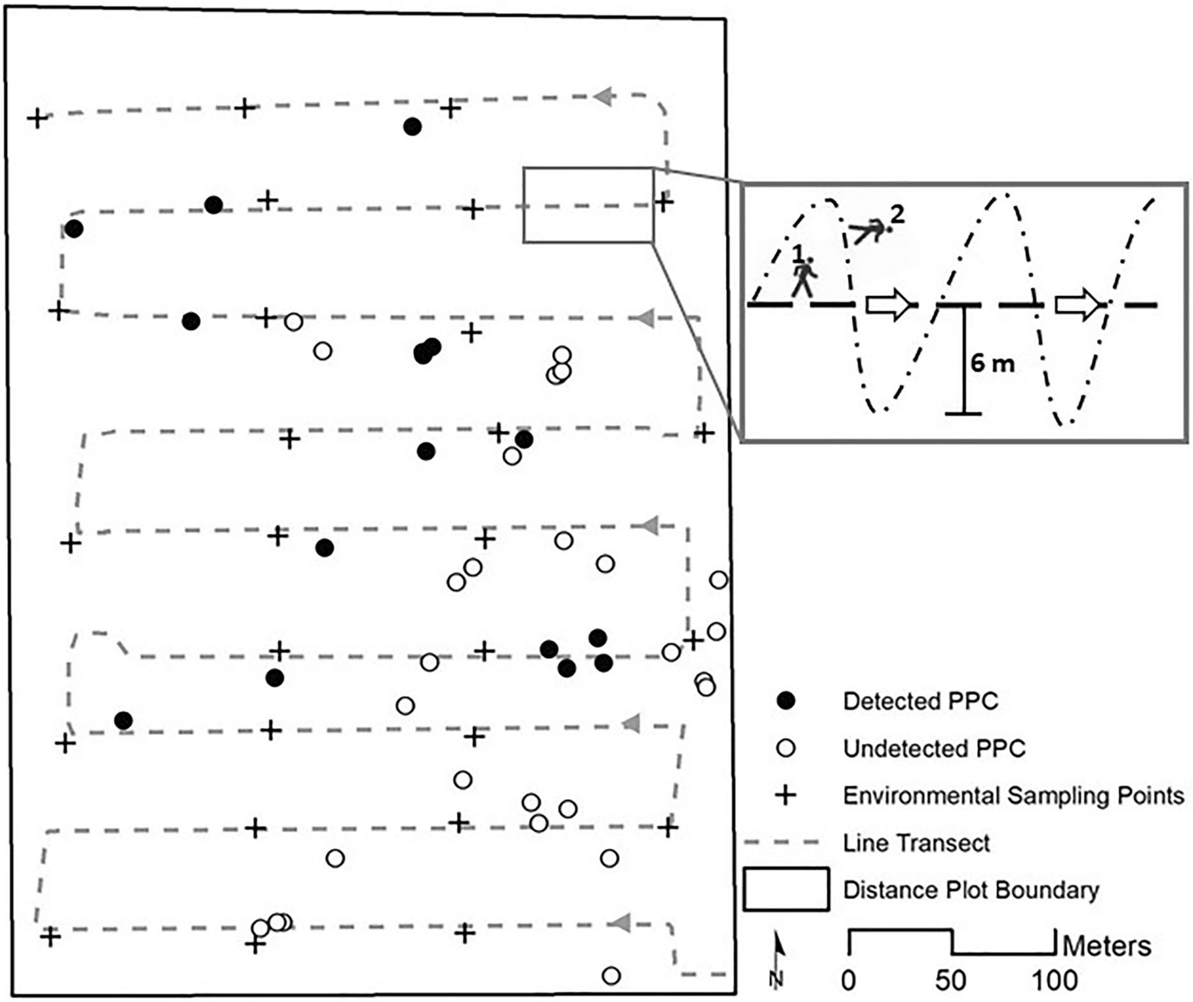

Fig. 2 Arrangement of transect lines (—) and environmental sampling points (+) used to distance sample Pima pineapple cactus (PPC) in southern Arizona, 2016–17. Inset shows sampling strategy by each of two surveyors along lines, with one surveyor focused on center lines, while a second surveyor walked a sinuous path within 6 m of lines

few larger particles, 2 for coarser gravel with particles up to about 1 cm diameter, and 3 for rocky substrate with particles > 2 cm diameter. For each plot we noted dominant vegetation community as Sonoran desert-scrub or semi-desert grassland. Subsequently, we used the slope and interpolate shape tools in ArcGIS 10.5.1 (ESRI 2017) to estimate elevation (m) and slope (%) at each point based on a 3-m resolution digital elevation model.

Analyses

To estimate abundance and density, we treated lines as replicates and stratified by plot to facilitate estimates at both scales, and then weighted by plot areas to estimate overall population size across all plots. Before analyses, we selected bin sizes of 2.5 m after assessing histograms of distance data, and right truncated 5% of observations. Binning can improve model fit by effectively smoothing data, whereas truncation constrains the tails of distributions, which often include little information but require complex adjustment terms to model that are rarely biologically justified (Buckland et al. 2001; Thomas et al. 2010).

We used two strategies to estimate density, population size, and detection probability of live individuals. First, we used conventional distance sampling to fit a detection function to all data. Second, we used multiple-covariates distance sampling to fit detection functions that included each covariate individually and various additive combinations of covariates. As covariates, we considered vegetation volume, grass cover, understory height, soil substrate size, and slope averaged among points along each line. To minimize influence of extreme values, we log transformed slope. To select the best approximating model, we ranked models by Akaike information criteria corrected for small sample sizes (AIC_c), evaluated shapes of detection functions, precision of estimates, and goodness-of-fit among competitive models, and selected the best overall model from which we made inferences (Thomas et al. 2010). We considered uniform, half-normal (HN), and hazard-rate (HR) detection functions for models without covariates, and HN and HR functions for models with covariates. When fitting HN and HR functions, we considered models with ≤ 2 cosine, simple polynomial, and hermite adjustment terms. We used program Distance version 6.2 for all calculations (Thomas et al. 2010). Although we sampled without replacement and detected a relatively large proportion of the focal population, finite population correction factors were not applied but may be appropriate here despite limited influence on estimates of precision (see Buckland et al. 2001, p. 87).

To assess the efficacy of DS, we computed bias as the percent difference between values from censuses and estimates from DS within each plot and for the overall population. To quantify the strength of linear association between census values and estimates, we computed Pearson correlation coefficients on both the raw and log-transformed scales. To assess factors that explained bias at the scale of plots, we used linear regression with bias as a response variable, and considered mean vegetation volume, grass cover, understory height, soil substrate size, log slope, elevation, PPC height, and plot area as potential explanatory variables. Finally to compare effort needed to complete DS versus censuses, we calculated the total effort spent DS on a per ha basis and compared to estimates for censuses based on data from Roller (1996a), which indicates a minimum of 2.3 person hours are required per ha.

To assess environmental factors that explained spatial variation in local densities among lines, we fit linear-mixed effect models. To develop models, we fit log density as a response variable and considered the following potential explanatory factors: mean vegetation volume, grass cover (log transformed), soil substrate size, log slope, vegetation community, and quadratic terms for all continuous factors. Understory height was not considered because it was correlated with vegetation volume, nor was elevation considered because it was correlated with substrate size ($r \geq 0.65$). Because the number of potential explanatory factors was high and data to develop candidate models a priori was limited, we used stepwise procedures with mixed variable selection and the stepAIC function from the MASS library in R (Venables and Ripley 2002; R Core Team 2016) to guide model selection. We fit a random intercept for plot to adjust for correlations among observations from lines within the same plots, and fit models with the nlme library in R (Pinheiro et al. 2012; R Core Team 2016). Data from short lines (< 200 m) needed to cover irregularly shaped plots were censored because they contained too few (0–2) environmental sampling points to adequately describe local conditions.

Results

Effort and detections

We recorded 105 live and 15 dead PPC during DS along 36.9 km of transects ($n = 81$ lines, mean ± SE = 455 ± 17.9 m in length) across the 11 plots. Distances between lines and cacti averaged 7.3 ± 0.6 m (range 0–31 m) with 75% of observations within 10.3 m, and 2.5 m binning and 5% truncation effectively smoothed data (Fig. 3). Although more plots were in desert-scrub, total plot area was similar in both vegetation communities (Table S1).

Detection probability

We fit 14 candidate models of detection functions (Tables 1 and S2). Model selection provided strong evidence that factors in addition to distance influenced detection probability (P), as indicated by little support for a model without covariates ($\Delta AIC_c = 4.55$). The top-ranked model included the covariate substrate size, with P declining as soils became increasing dominated by large particles ($\beta \pm SE = -0.44 \pm 0.19$). At 10 m from lines, for example, P declined from 0.58 in areas with small- to moderate-sized substrates to 0.35 in areas with moderate- to large-sized substrates

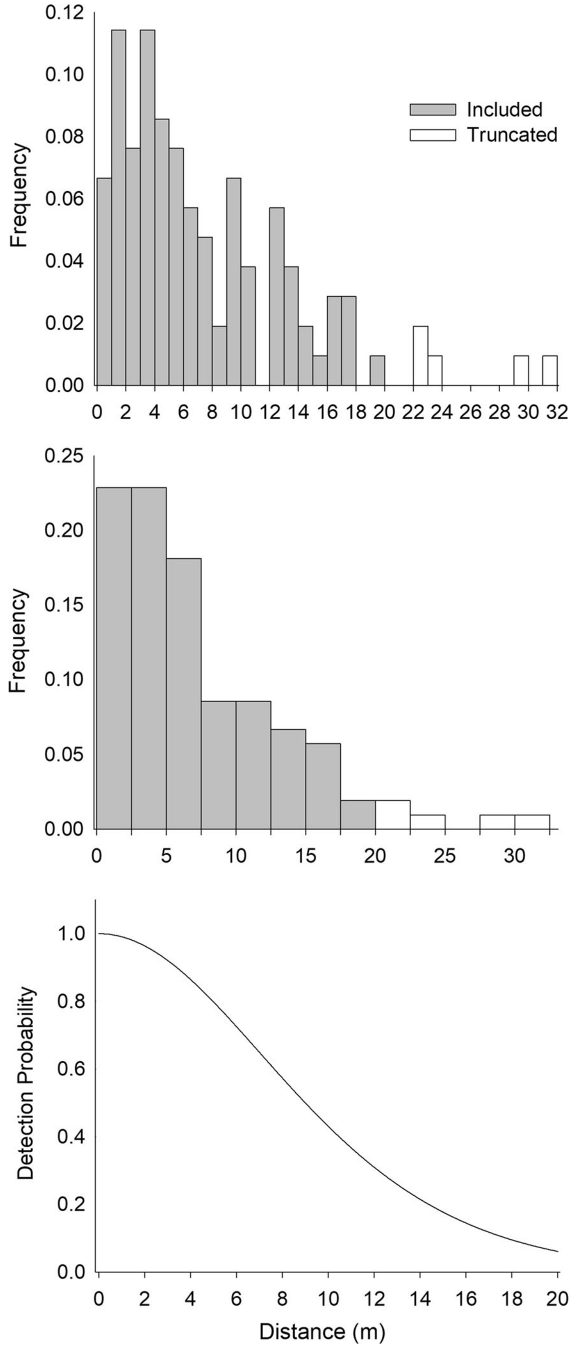

Fig. 3 Detection distances to 105 Pima pineapple cacti observed during distance sampling in southern Arizona, 2016–2017, and resulting detection function model. Frequency histograms of observations in 1- (top) and 2.5-m bins used for modeling (middle) are shown. Detections at distances > 20 m shown as open bars were truncated before model fitting. Bottom figure of top-ranked detection function model is the average function conditioned on the covariates

(Fig. 4). Although understory vegetation volume (− 0.012 ± 0.0066), grass cover (− 0.008 ± 0.004), and cactus height (0.045 ± 0.026) influenced *P* in the expected directions when fit independently (Fig. 4), there was little evidence these factors improved models once substrate size was considered (Table 1). Understory vegetation height (− 0.0056 ± 0.0071) and slope (− 0.091 ± 0.19) had no influence on *P*. Half-normal key functions with cosine adjustment terms provided the best fit.

Estimates of *P* from the top-ranked model averaged 0.49 (95% CI 0.42–0.56) with an effective strip half-width of 9.7 m (95% CI 8.4–11.3; CV = 0.076). At 2 m from lines, *P* averaged 0.96 and declined to 0.92, 0.80, 0.43, and 0.06 at 3, 5, 10, and 20 m from lines, respectively (Fig. 3).

Abundance and bias estimation

Across the entire population of plots, we estimated a density of 1.47 live individuals/ha, and abundance of 294 individuals overall. Precision of estimates was fairly high (CV = 0.139; Table 2). At the plot scale, estimates of density (0.17–5.95 individuals/ha) and abundance (3–125 individuals) ranged widely, with much lower precision (Table 2). Estimates of population size suggest we detected approximately 34% of all individuals during DS.

Across all plots, DS provided relatively unbiased estimates of both density and abundance, with estimation bias averaging only − 2.3% overall. At the scale of individual plots, however, estimates of bias were higher (Table 2). Density estimates from DS were also highly correlated with census values on both the untransformed ($r = 0.84$, $P = 0.002$), and especially, logarithmic scales ($r = 0.93$, $P < 0.001$; Fig. 5). Bias decreased (e.g., changed from over to underestimation) as substrate size ($\beta \pm \text{SE} = -66.6 \pm 27.7$, $P = 0.040$) and understory vegetation volume (− 3.3 ± 1.5, $P = 0.050$) increased. On average, DS took 0.60 ± 0.06 person hours per ha to implement across plots (range 0.35–1.05) with effort increasing linearly with plot-specific PPC densities ($\beta \pm \text{SE} = 0.094 \pm 0.022$, $P = 0.0019$). Thus, we estimate censuses would take a minimum of 4.2 ± 0.4 times more effort to complete on average across the range of PPC densities we considered.

Table 1 Detection function models fit to estimate abundance of Pima pineapple cactus in southern Arizona, 2016–2017

Covariates	*K*	ΔAIC_c	*D*
Substrate size	2	0.00	1.465
Substrate size + grass cover	3	0.12	1.484
Cactus height + substrate size + grass cover	4	1.44	1.493
Cactus height + substrate size	3	1.52	1.472
Substrate size + vegetation volume 0–1 m	3	1.86	1.467
Cactus height + grass cover	3	2.06	1.466
Vegetation volume 0–1 m	2	2.98	1.440
Grass cover	2	3.17	1.439
Cactus height	2	3.21	1.434
Cactus height + grass cover + veg. volume 0–1 m	4	3.85	1.470
None {CDS model}	1	4.55	1.406
Grass cover + vegetation volume 0–1 m	3	4.87	1.443
Understory height	2	5.88	1.412
Slope (log)	2	6.41	1.408

All models are half-normal key functions with cosine adjustments; *K* is the number of parameters and *D* is estimated density (live individuals/ha)

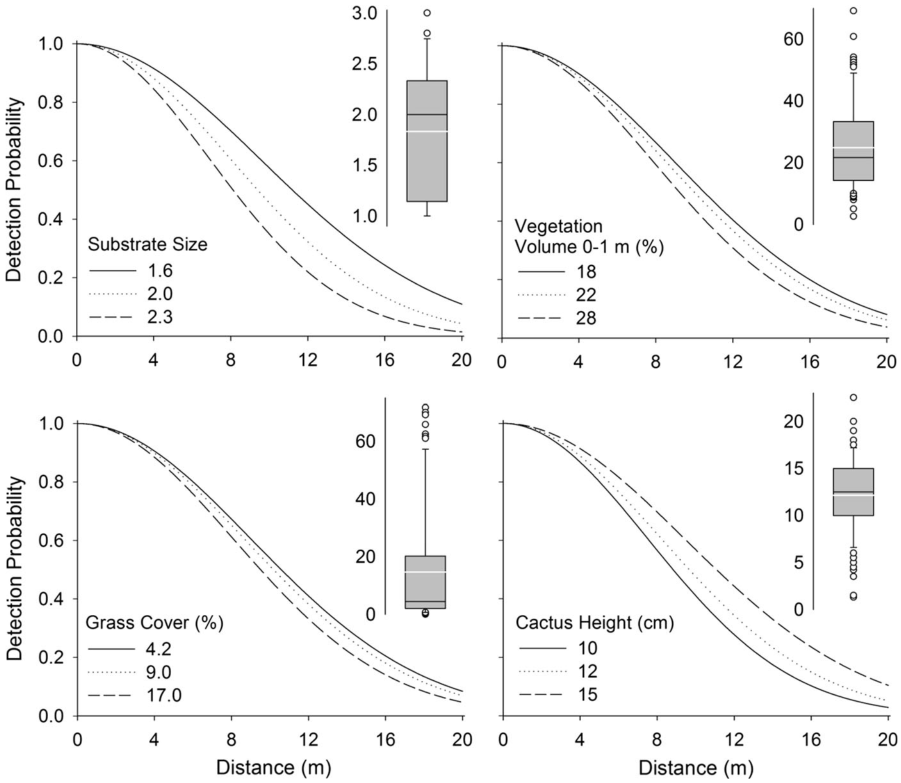

Fig. 4 Influence of four covariates on detection probability of the Pima pineapple cactus based on distance sampling along lines in southern Arizona, 2016–2017. Estimates are from multiple-covariates distance sampling with half-normal key functions and cosine adjustments. Estimates are shown at covariate levels equaled to the lower, middle, and upper quartiles. Inset box plots show distributions of each covariate

Plant–habitat relationships

We considered a total sample of 76 lines averaging 476 m (SE = 16) in length with densities ranging from 0 to 10.5 plants/ha (mean ± SE = 1.5 ± 0.2). Local densities increased with increasing soil substrate size and slope, and decreased with increasing understory vegetation volume (Table 3). There was also some

Table 2 Comparison of estimates of density (D) and abundance (N) of the Pima pineapple cactus based on distance sampling at plot-specific and population scales in southern Arizona, 2016–2017

Site	Plot area (ha)	Census values		Distance sampling estimates						Bias (%)	
		Density (no./ha)	Abundance	Density (no./ha)	Abundance	CV	No. observed	Effort (m)	No. of lines	Density	Abundance
Anvil	18.3	0.055	1	0.146	3	1.004	1	3525	7	167.4	200.0
Canoa	23.4	2.35	55	1.07	25	0.301	10	4825	8	– 54.6	– 54.5
Guy Street	23.8	0.168	4	0.179	4	0.733	2	5745	11	6.9	0.0
Mendoza	24.2	1.86	45	1.30	32	0.287	13	5133	10	– 29.8	– 28.9
Palo Alto	24.6	3.18	78	5.08	125	0.231	38	3902	10	60.0	60.3
Sopori-1	7.4	1.62	12	2.18	16	0.292	4	947	3	34.7	33.3
Sopori-2	8.0	3.86	31	1.56	12	0.452	6	1985	6	– 59.6	– 61.3
Sopori-3	4.0	5.53	22	5.95	24	0.302	10	866	4	7.6	9.1
Stagecoach	31.6	0.222	7	0.363	11	0.469	3	4252	8	64.1	57.1
Sycamore-1	16.7	1.86	31	1.72	29	0.342	9	2696	9	– 7.3	– 6.5
Sycamore-2	18.4	0.817	15	0.686	13	0.505	4	3003	7	– 16.0	– 13.3
All sites	200.4	1.50	301	1.47	294	0.139	100	36,878	83	– 2.3	– 2.3

Census values are from data in Appendix A (Supplementary Materials). Bias denotes % differences between census values and estimates from distance sampling. Population-scale estimates are weighted by plot area

evidence local densities were greater in semi-desert grasslands than in desert-scrub, with densities averaging 38.3 ± 17.2% greater in grasslands after controlling for other factors. Local densities did not vary with grass cover ($P = 0.59$) after considering factors in the best approximating model.

Discussion

We validated a rarely used method for estimating the abundance and density of plant populations. Our study, focused on the endangered Pima pineapple cactus (PPC) in the Sonoran Desert, indicates that distance sampling (DS) can efficiently provide accurate estimates of abundance, and insights into factors that explain local variation in densities and detection probability. Combined with results from a small number of past applications of DS in plant systems, our results indicate that DS is an efficient tool in this and other similar systems, and useful for guiding management and survey design. Distance sampling has been used successfully to assess abundance and detection probability (P) in animal systems, often at much larger spatial scales than that considered here (Thomas et al. 2002, 2010; Buckland et al. 2015; Roberts et al. 2016). To our knowledge, however, this study represents just its eighth application in a plant system (Marsden and Pilgrim 2003; Buckland et al. 2007; Crase et al. 2010; Jensen and Meilby 2012; Kissa and Sheil 2012; Schorr 2013; Phama et al. 2014; Junaedi et al. 2018), and is the first to compare estimates from DS with what we assumed were parametric values of abundances from intensive censuses.

Bias of abundance estimates from DS was very low across the sampled population, averaging just 2.3% underestimation. Importantly, magnitude of bias seemed consistent across the entire range of abundances we considered, except perhaps at lower extremes, suggesting DS performs well across broad spatial variation in abundance. Such results conform generally to studies in animal populations (e.g., Focardi et al. 2005) where DS has accurately captured major declines in densities despite lower precision at low densities, but to our knowledge, no comparable examples exist for plant populations. At very low densities, small differences in estimates and parametric values can have marked effects on bias. In these and other cases, stratification and fitting stratum as a factor-type covariate should enhance precision by explicitly modeling spatial differences in abundance (Buckland et al. 2015).

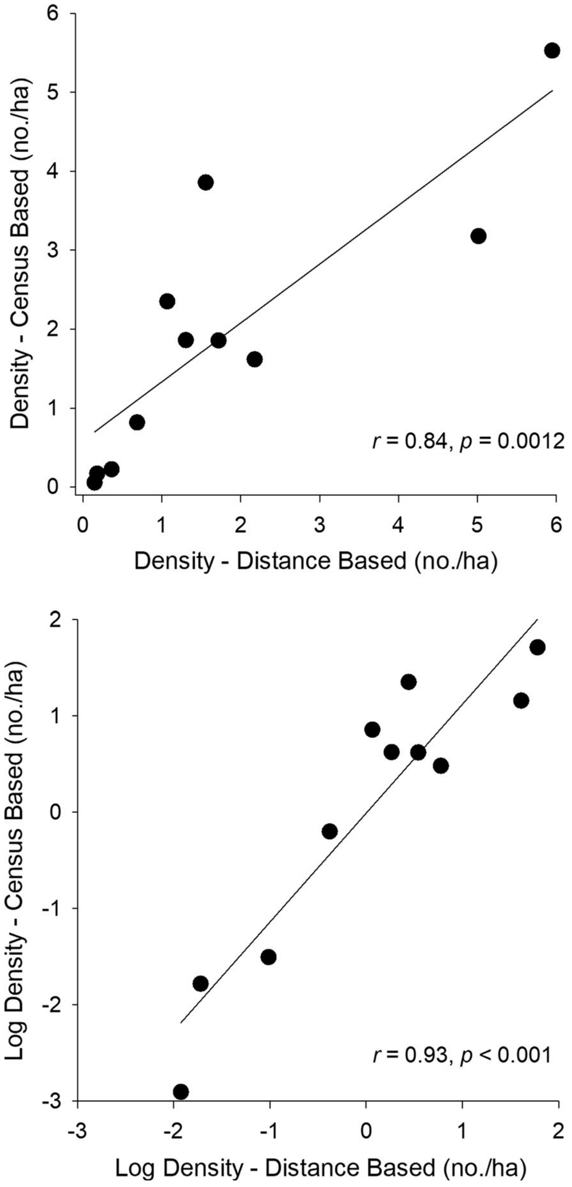

Fig. 5 Linear associations between estimated raw (no./ha; top) and log (bottom) densities of the Pima pineapple cactus in southern Arizona, 2016–2017 based on values from census and estimates from distance sampling. Pearson correlation coefficients (*r*) are noted

Precision of estimates from DS was also fairly high at population scales (CV = 0.139) even despite modest sample sizes of 105 individuals along 81 lines. For DS along lines, a recommended minimum of 60–80 focal objects (or clusters) are recommended for unbiased estimation (Buckland et al. 2001). These results and the broad range of natural variation in PPC densities we considered (0.1–5.5 individuals/ha) suggest DS can yield precise abundance estimates in a range of contexts. Interestingly, our estimate of PPC density (1.47 individuals/ha) was higher than range-wide estimates of ≈ 1 individual/ha (Baker 2013; McDonald 2005) likely because we worked in areas where PPC was known to occur.

Important assumptions of DS along lines include perfect detection of focal objects on transect lines, accurate distance measurements, and designs that ensure lines are positioned independently of focal objects. If individual plants are closely clustered, distributions may not be sufficiently uniform with respect to lines, especially in small plots (Buckland et al 2007). In our study, frequency histograms of detection distances declined monotonically with increasing distance from lines, especially after data were smoothed by binning. Such patterns suggest PPC distribution is sufficiently uniform to eliminate issues imposed by clustering (Buckland et al. 2007, 2015), even though plants sometimes occurred in small groups of individuals 5–20 m apart. In other systems, more extreme clustering may require crossed designs or more complex approaches (see Buckland et al. 2007), or cluster-based estimation where numbers of individuals in clusters is used as detection covariate (Thomas et al. 2010).

With regard to assumptions of perfect detectability of focal objects on transect lines, there was some evidence small plants obstructed by dense vegetation and rocky substrates contributed to underestimation. Nonetheless, the relative openness of arid environments and unique silhouette of PPC should adequately mitigate these issues, especially when combined with recommendations described below. In plant systems such as ours where individual plants are small, often cryptic, scattered over large areas, and thus easily overlooked, DS should be an efficient method for estimating spatiotemporal variation in abundance.

Several factors likely contributed to observed estimation bias. First, while we assumed numbers from past censuses represented parametric values of population sizes, actual abundances were not known exactly. Because plots were censused within ≈ 1 year of DS, the closure assumption (e.g., no recruitment or mortality) was likely violated. Data from seven plots that were intensively monitored over time indicate abundance declined by an average rate of 7.3% per year between 2002 and 2017 (Appendix A,

Table 3 Factors that explained variation in local densities (log no./ha) of Pima pineapple cactus along 76 lines in southern Arizona, 2016–2017

Factor	Estimate	SE	$\|t\|$	P
Intercept	− 0.90	0.33	2.73	0.008
Vegetation volume 0–1 m (%)	− 0.021	0.006	3.19	0.002
Slope (log %)	0.69	0.21	3.34	0.001
Substrate size (rank)	0.40	0.17	2.31	0.024
Semi-desert grassland	0.38	0.17	2.22	0.053

Parameter estimates and standard errors (SE) are from a linear-mixed effects model with plot fit as a random intercept (σ^2 = 0.021 intercept; 0.268 residual)

Supplementary Materials). Thus, mortalities occurring after recent censuses, but before DS, could explain some observed bias. Individuals undetected during censuses were occasionally found during subsequent monitoring, because even by spacing observers 4–6 m apart during census efforts (Roller 1996a), estimates of *P* obtained here suggest 4–8% of individuals are likely to be missed. Finally, although probably a very minor source of bias in our study, ensuring distances are measured precisely and perpendicularly to lines will reduce bias (Marshall et al. 2008).

Detectability-corrected estimates of densities from DS are often used to understand wildlife–habitat relationships (Blank 2013; Miller et al. 2013; Flesch et al. 2016; Roberts et al. 2016), but have not been applied to plants. Past accounts of habitat relationships of PPC often matched our inferences but sometimes varied. Similar to our results for densities, McPherson (2002) found positive associations between PPC occurrence and larger soil substrates (gravel vs. sand), whereas Kidder (2015) suggested sandy soils were associated with larger cacti. The main pollinator of the PPC is a solitary bee (*Diadasia rinconis*) that nests in well-drained areas of bare ground and forages over large areas (Ordway 1987; McDonald 2005; USFWS 2018). Thus, despite local associations with rockier substrates, this species may require a diversity of soils at larger scales. We found that PPC densities declined with increasing grass cover matching observed associations with open areas (Kidder 2015), but contrasting one study that showed associations between occurrence and moderate levels of herbaceous and woody vegetation cover (McPherson 2002). Moreover, we found local densities increased with slope, which may be partially due to the fact that areas with higher slopes also often have larger soil substrates. These patterns contrast lack of observed associations between occurrence and specific landforms or slope positions (McPherson 2002), and may not be biologically important given limited variation in slope across plots we considered. Importantly, differences in the scales of measurement and focal parameters among studies may explain differences in observed habitat associations. Regardless, our results illustrate the application of DS for assessing plant–habitat relationships.

Understanding factors that influence *P* is useful for guiding survey design because optimal survey techniques have a high and consistent probability of detecting the target species and low sampling error (Thompson et al. 1998; Williams et al. 2002). Although few studies assess factors that influence detectability of plants, traits such as color, flowering time, leaf size, height, and observer ability can influence the detection process (Chen et al. 2013; Garrard et al. 2013; Junaedi et al. 2018). We found that detectability during DS was explained by variation in soil substrate size, with lower detectability on rockier soils. Rocky substrates likely make cacti more difficult to see by distorting their unique silhouette. There was also some evidence detectability declined with decreasing plant height and increasing understory vegetation volume and grass cover, patterns we suspect are biologically significant and would have been stronger with greater sample sizes. These patterns and the efficacy of DS in situations where significant proportions of focal populations are undetected support the application of DS for estimating abundance of rare or cryptic plants.

Recommendations

Despite promising results, various design considerations and small modifications to the protocol used here could further improve applications of DS in plant systems. Though our results suggest that only approximately 33% of cacti within plots were detected, one of the strengths of DS is that it allows robust estimates of density and population size even when a majority of focal objects are not detected during surveys (Anderson et al. 2001; Buckland et al. 2001). Precision of estimates from DS, however, is influenced by the absolute number of observations and thus sampling strategies that yield large sample sizes are optimal. In systems where focal plants may be obstructed by either live or dead vegetation, however, more effort on and immediately around lines should improve accuracy. Such effort can be fostered by reducing walking speeds and searching clumps of low vegetation along lines. In our system, surveys on steep slopes and dense vegetation along drainages were often difficult when lines were parallel to elevation contours. Although positioning lines perpendicular to contours will ameliorate these issues (Schorr 2013), to foster unbiased estimates, investigators should ensure lines are placed parallel to any existing density gradients of focal objects, which can be assessed during pilot efforts (Buckland et al. 2015). Finally, timing surveys when focal plants are most detectable (e.g., flowering, in leaf), associated vegetation is dormant or least obstructive, and measuring factors thought to influence the detection process should further improve efforts.

Although we focused on small plots to help foster comparisons with known values of abundance, DS is most powerful when applied at much larger spatial scales (e.g., Flesch et al. 2016; Roberts et al. 2016), where it can produce reliable estimates provided key assumptions are met and a sufficient number of focal objects are detected. Thus, future studies of plant abundance and detection probability based on DS can be framed much more extensively than the largely intensive focus used here. While our results provide strong support for the application of DS, additional field work and simulations across a range of contexts and efforts with populations where abundances are known will be useful for guiding future efforts.

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Author contributions BFP largely conceived of the study that was designed by ADF, IWM, and BFP. Data were gathered by ADF, IWM, S. Mann, M. Garcia, and R. Villa. ADF completed the analyses with assistance from IWM and JMG. The first draft of the manuscript was written by ADF with all authors commenting on and contributing to subsequent drafts. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest No potential conflict of interest was reported by the authors.

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Supplementary Material

Appendix A: Methods and data sources used to compute known estimates of abundances of the Pima pineapple cactus, and to estimate population trends across time.

Census results and methods—We used data from repeated censuses and long-term monitoring to identify individual cacti and to calculate population sizes of the Pima pineapple cactus within five plots in the Altar Valley and two plots in the Santa Cruz Valley. This process was aided by detailed databases and spatial coordinates of all live and dead cacti within plots across time. In addition to long-term monitoring data, we also included any new cacti not documented by past efforts but that we detected incidentally or during distance sampling in estimates of known population sizes.

In the Altar Valley, we considered five of six total plots that had been intensively censused and monitored since 2000 (Anvil, Guy, Mendoza, Palo Alto, and Stagecoach; Schmalzel 2000; Routson 2003; Baker 2013; Molano-Flores and Coons 2018). At the time of our distance sampling (DS) study, the most recent censuses for these five plots were from 2012 (Baker 2013). However, in 2017, Molano-Flores and Coons (2018) repeated censuses and monitoring of all five plots and provided updated estimates. We assumed that all live plants observed by Molano-Flores and Coons (2018) in fall 2017 were also alive during our DS study in 2016, which is justified given they did not document any seedlings during their efforts. Due to the slow-growing nature of this plant, we can infer that all observed cacti were >1 year old at the time of 2017 censuses, and likely substantially older. Cacti that we located during DS that had not been observed by Baker (2013) or by Molano-Flores and Coons (2018) were added to estimates of plot-specific abundances (Table 1). We also located five live Pima pineapple cacti on two plots that Molano-Flores and Coons (2018) subsequently observed as being dead in 2017, but included these individuals in our 2016 estimates of plot abundance. The Pima pineapple cactus is cryptic and easily overlooked, particularly when small. Thus we acknowledge some plots likely harbored live individuals present during our 2016 DS study, which were not detected during census efforts and thus are not accounted for. Nonetheless, given intensive repeated censuses and monitoring across time and our own efforts DS, plot-specific estimates of abundances we used represent the best known estimates of population sizes across the range of the taxon.

At two plots in the Santa Cruz Valley, we estimated numbers of live Pima pineapple cacti at the time of our DS study on both the Sycamore Canyon 1 and Sycamore Canyon 2 plots using monitoring data gathered by WestLand Resources, Inc. (2004, 2017). These plots were monitored annually between 2002 and 2008 (with the exception of 2003) and every four years after 2008. Both plots included cacti that had been transplanted from nearby developments, and cacti that have grown naturally on plots. For the purposes of estimating the total number of cacti within each plot that was present at the time of our DS study, we considered both natural and transplanted individuals. We completed DS surveys on these plots in February of 2016. Abundances reported by WestLand Resources, Inc. (2017) covered surveys that took place in September and December of 2016, as well as during January of 2017. We assume that all live PPC reported during these surveys were also alive and present during our DS surveys in 2016. We also included in our estimates of known population size, three individual cacti on each of the two plots that we detected during our DS study, that WestLand Resources, Inc. (2017) had not detected. WestLand Resources, Inc. (2017) reported two individuals on the Sycamore Canyon 1 plot that were dead during their surveys during the latter part of 2016, while during our DS survey in the early part of 2016 both cacti were live. We included these two cacti in estimates of abundance.

At plots in the Santa Cruz Valley where we conducted censuses for the first time (Canoa and Sopori 1-3), estimates of known densities included all individuals discovered during censuses as well as any new cacti observed incidentally or during distance sampling. In all cases all surveyors had experience identifying the Pima pineapple cactus and practiced survey methods away from study plots prior to initiating surveys.

Abundance trends—To gain insights into sources of potential bias between our estimates from distance sampling and known values from censuses, we estimated abundance trends of the Pima pineapple cactus within the seven long-term monitoring plots. We used data from Baker (2013), WestLand Resources (2014 and 2017), and Molano-Flores and Coons (2018) to assess population trends within study plots that had been monitored across time. For Pima pineapple cacti on the Sycamore Canyon 1 and Sycamore Canyon 2 plots monitored by WestLand Resources, Inc., we did not include cacti that had been transplanted onto plots from nearby areas when estimating trends. Rather we only used cacti that were growing on plots and had never been moved to estimate abundance trends. To estimate trends, we fit the following linear mixed-effects model:

$$y_{it} = (\beta_0 + b_{0i}) + \beta_1 x_{it} + \varepsilon_{it}, \quad \varepsilon_{it} \sim \mathrm{N}(0, \sigma^2)$$

where y_{it} is a vector of observed log +1 transformed counts of the number of cacti in each plot in each year, β_0 is an intercept for the population, b_{0i} is a vector of random intercepts for each transect, β_1 is a trend parameter for a fixed time effect, x_{it} indicates the year of each observation for the i^{th} plot centered at 0, and ε_{it} is an error term that has a normal distribution with a mean of zero and variance σ^2 that measures observation variance. In this model all variance is assumed to be observation error. To model temporal autocorrelation, we used a first-order autoregressive structure and fit models with the nlme library in R. Data used to fit trend models are in Table 2.

Between 2002 and 2017, abundance declined by an estimated average of 7.3 ± 2.2% (± SE) per year ($p = 0.0012$) indicating strong evidence of a decline. Across time and assuming exponential population growth this equals a 67.9% decline in the overall population of cacti within plots. This is a major decline that has broad conservation implications for this endangered subspecies. Because plots were not selected at random these inferences pertain only to the plots themselves and not to the broader population of cacti across the range of the taxon.

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Table 1. Abundance data of the Pima pineapple cactus from five plots in the Altar Valley of Arizona and 2 plots in the Santa Cruz Valley of Arizona used to estimate population trends across time. Data are from long-term monitoring and repeated censuses within plot boundaries

Year	Site	No.	ln No.
2003	Anvil Tank	17	2.8903718
2005	Anvil Tank	13	2.6390573
2006	Anvil Tank	14	2.7080502
2007	Anvil Tank	23	3.1780538
2008	Anvil Tank	22	3.1354942
2009	Anvil Tank	26	3.2958369
2010	Anvil Tank	6	1.9459101
2011	Anvil Tank	6	1.9459101
2012	Anvil Tank	5	1.7917595
2017	Anvil Tank	0	0.00
2003	Guy Street	37	3.6375862
2005	Guy Street	36	3.6109179
2006	Guy Street	38	3.6635616
2007	Guy Street	43	3.7841896
2008	Guy Street	40	3.7135721
2009	Guy Street	43	3.7841896
2010	Guy Street	44	3.8066625
2011	Guy Street	8	2.1972246
2012	Guy Street	6	1.9459101
2017	Guy Street	4	1.6094379
2003	Mendoza	82	4.4188406
2005	Mendoza	57	4.060443
2006	Mendoza	63	4.1588831
2007	Mendoza	63	4.1588831
2008	Mendoza	66	4.2046926
2009	Mendoza	65	4.1896547
2010	Mendoza	76	4.3438054
2011	Mendoza	65	4.1896547
2012	Mendoza	71	4.2766661
2017	Mendoza	40	3.7135721
2003	Palo Alto	81	4.4067192
2005	Palo Alto	72	4.2904594
2006	Palo Alto	92	4.5325995
2007	Palo Alto	92	4.5325995
2008	Palo Alto	97	4.5849675
2009	Palo Alto	94	4.5538769
2010	Palo Alto	99	4.6051702
2011	Palo Alto	86	4.4659081

2012	Palo Alto	80	4.3944492
2017	Palo Alto	70	4.2626799
2003	Stagecoach	14	2.7080502
2005	Stagecoach	11	2.4849066
2006	Stagecoach	12	2.5649494
2007	Stagecoach	12	2.5649494
2008	Stagecoach	14	2.7080502
2009	Stagecoach	11	2.4849066
2010	Stagecoach	11	2.4849066
2011	Stagecoach	9	2.3025851
2012	Stagecoach	7	2.0794415
2017	Stagecoach	7	2.0794415
2002	Sycamore 1	12	2.5649494
2004	Sycamore 1	12	2.5649494
2005	Sycamore 1	14	2.7080502
2006	Sycamore 1	14	2.7080502
2007	Sycamore 1	14	2.7080502
2008	Sycamore 1	12	2.5649494
2012	Sycamore 1	12	2.5649494
2016	Sycamore 1	12	2.5649494
2002	Sycamore 2	19	2.9957323
2004	Sycamore 2	20	3.0445224
2005	Sycamore 2	33	3.5263605
2006	Sycamore 2	30	3.4339872
2007	Sycamore 2	29	3.4011974
2008	Sycamore 2	27	3.3322045
2012	Sycamore 2	20	3.0445224
2016	Sycamore 2	20	3.0445224

Table S1: Comparison of geographic, topographic, and vegetation factors at 11 plots where we implemented distance sampling for the Pima pineapple cactus in southern Arizona, 2016-17. Means and standard errors (SE; or range) are based on sample sizes (*n*) noted for each plots, which are based on measurements at points (elevation, slope), within 10 m of points (vegetation factors), or at the site scale (region, dominant vegetation community). Units for substrate size are: 1-fine sand with few larger particles, 2-coarser gravel with particles up to about 1 cm diameter, 3–rocky substrate with particles >2 cm diameter.

				Elevation (m)		Slope (%)		Substrate Size		Grass Cover (%)		Vegetation Volume 0-1 m (%)		Understory Height (cm)	
Site	Valley	Community	*n*	Mean	Range	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Anvil	Altar	Grassland	42	829	8	1.5	0.1	1.0	0.00	13.7	2.5	13.5	2.2	14.1	1.6
Canoa	Santa Cruz	Grassland	56	934	15	3.7	0.2	2.1	0.11	64.3	4.0	53.2	2.2	63.5	2.5
Guy Street	Altar	Desert-scrub	70	802	7	1.8	0.1	1.1	0.03	1.1	0.3	14.2	1.2	10.3	0.8
Mendoza	Altar	Grassland	66	978	18	5.4	0.3	1.9	0.08	38.1	2.3	25.5	1.9	28.6	1.2
Palo Alto	Altar	Grassland	48	890	20	8.0	1.1	1.7	0.11	10.4	1.6	22.4	2.4	27.9	2.1
Sopori-1	Santa Cruz	Desert-scrub	14	991	9	6.1	0.7	2.2	0.15	3.8	1.0	25.0	5.1	14.4	1.5
Sopori-2	Santa Cruz	Desert-scrub	30	992	11	7.9	1.3	2.2	0.16	3.2	0.9	24.2	2.8	16.6	1.7
Sopori-3	Santa Cruz	Desert-scrub	14	985	11	6.6	0.9	2.0	0.00	2.0	1.0	15.5	2.7	11.5	1.5
Stagecoach	Altar	Desert-scrub	58	1,027	21	3.2	0.1	1.1	0.05	3.9	0.5	14.3	1.1	13.9	1.1
Sycamore-1	Santa Cruz	Desert-scrub	36	1,083	14	3.2	0.1	2.7	0.09	3.0	1.0	31.9	3.0	29.3	3.9
Sycamore-2	Santa Cruz	Desert-scrub	42	1,003	15	2.8	0.1	2.7	0.11	3.1	1.0	34.7	3.1	16.1	2.3

Table S2: Candidate models of detection functions used to estimate density and abundance of the Pima pineapple cactus with distance sampling at 11 sites in southern Arizona, 2016-17. *K* denotes the number of model parameters, *D* is estimated density (no. of live individuals/ha), CV is the coefficient of variation, *N* is total abundance or population size, LCL and UCL are lower and upper 95% confidence intervals, ESW is effective strip half-width, and *P* is average detection probability. Estimates are based on a sample of 105 cacti with 5% of observations truncated. All models are half normal key functions with cosine adjustments.

	Model Selection		Density				Abundance			Detection	
Covariates	*K*	ΔAICc	*D*	*D* CV	*D* LCL	*D* UCL	*N*	*N* LCL	*N* UCL	ESW	*P*
Substrate Size	2	0.00	1.465	0.139	1.109	1.937	294	222	388	9.71	0.485
Substrate Size + Grass Cover	3	0.12	1.484	0.140	1.120	1.965	297	224	394	9.59	0.479
Cactus Height + Substrate Size + Grass Cover	4	1.44	1.493	0.140	1.126	1.979	299	226	397	9.53	0.476
Cactus Height + Substrate Size	3	1.52	1.472	0.139	1.113	1.948	295	223	390	9.66	0.483
Substrate Size + Vegetation Volume 0-1 m	3	1.86	1.467	0.139	1.109	1.941	294	222	389	9.69	0.485
Cactus Height + Grass Cover	3	2.06	1.466	0.139	1.108	1.941	294	222	389	9.70	0.485
Vegetation Volume 0-1 m	2	2.98	1.440	0.138	1.091	1.901	289	219	381	9.88	0.494
Grass Cover	2	3.17	1.439	0.138	1.090	1.899	288	218	381	9.89	0.494
Cactus Height	2	3.21	1.434	0.138	1.087	1.893	287	218	379	9.92	0.496
Cactus Height + Grass Cover + Veg. Volume 0-1 m	4	3.85	1.470	0.140	1.109	1.947	294	222	390	9.68	0.484
None {CDS model}	1	4.55	1.406	0.141	1.059	1.866	282	212	374	10.12	0.506
Grass Cover + Vegetation Volume 0-1 m	3	4.87	1.443	0.138	1.092	1.907	289	219	382	9.85	0.493
Understory Height	2	5.88	1.412	0.137	1.072	1.860	283	215	373	10.07	0.504
Slope (log)	2	6.41	1.408	0.136	1.069	1.853	282	214	371	10.11	0.505