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Monitoring the Rare Dune Endemic Eureka Valley Dune Grass, *Swallenia alexandrae* (Poaceae)

Eureka Valley dune grass growing on drifting sands at Main Dune, Eureka Valley, California.
USGS / S. SCOLES-SCIULLA

Monitoring the Rare Dune Endemic Eureka Valley Dune Grass, *Swallenia alexandrae* (Poaceae)

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Contents

Figures

Page

Figures (continued)

Page

Tables

Page

Abstract

Swallenia alexandrae is a long-lived perennial grass that occurs solely on active inland sand dunes within Eureka Valley at Death Valley National Park and was recently down-listed from Endangered to Threatened status. To standardize monitoring of population trends through time, National Park Service (NPS) established a 1-ha georeferenced grid system overlaid on the entire range of the species during 2007/08. Annual survey methods have shifted since that time in an effort to strike a balance between optimizing time to survey populations and a design that has appropriate statistical power to detect meaningful population change. Using local weather stations to adjust spatially-modeled weather (Parameter-elevation Regressions on Independent Slopes Model, PRISM) data, we found that greater abundance of *S. alexandrae*, as measured through density classes, was related to warmer than average maximum temperatures the July prior to spring surveys. This result is consistent with *S. alexandrae* and other warm season species whose growth is greatest during summer and fall. In contrast, a combined analysis using stage classes found that cooler and wetter than average winter/spring conditions prior to surveys were related to greater probability of plants in non-reproductive rather than reproductive status. Collectively, these results suggest that *S. alexandrae* population fluctuations reflect non-reproductive growth with negligible recruitment during the past decade, although focused demography studies remain crucial to estimate parameters for population viability. Lastly, we conducted a power analysis to compare different subsampling scenarios to inform future monitoring efforts. Power analysis simulations using quantitative and qualitative abundance measurements for *S. alexandrae* revealed that surveys using density classes were more powerful to detect population changes than those using direct counts. Importantly, a completely random subsampling design (10% of total grid cells annually surveyed during 2017–2019) includes too many unoccupied grid cells to capture meaningful trends in the population. Instead, 200 grid cells randomly selected from occupied grid cells (i.e., those with *S. alexandrae* present during prior whole-population distribution surveys) or weighted-stratified subsampling (drawing from proportionally more grid cells in the 0 and 1 density classes to capture their greater variability among classes) are needed to detect a 20% decrease in the population. In addition, 300–400 grid cells are needed to detect a 20% increase in the population under the same sampling designs. These occupied-only and weighted-stratified subsampling designs equate to slightly more field effort than the completely random subsampling implemented during 2017–2019 but are more powerful to detect population trends.

Introduction

Eureka Valley contains an ecologically distinct dune environment that supports several endemic plant and invertebrate species. Of these endemics, *Swallenia alexandrae* (Eureka Valley dune grass) was recently reclassified from Endangered to Threatened under the Endangered Species Act (USFWS 2018). The range of *S. alexandrae* occurs on active sand dunes at three locations separated by at least 4 km within Eureka Valley–Eureka Dune (also referred to as Main Dune), Marble Canyon Dune and Saline Spur Dune. Historically, recreational activities such as ATV-riding and camping on the dunes were believed to damage many plants and their habitat and contributed directly to the species' initial listing. These activities have been prohibited since 1978 when the species was granted Endangered status. During the late 1990s, the National Park Service (NPS) restricted other recreational activities on the dunes, including sandboarding and horseback riding, to provide additional protection for the endemic species. Visitor day use is greatest at Main Dune due to its proximity to established roads; a few day hikers visit Marble Canyon Dune, while visitation to Saline Spur Dune is limited mainly to people studying the endemic species.

Swallenia alexandrae is a robust hummock-forming perennial that grows rapidly during March through November (Pavlik 1980). The species occurs at all elevations on the sand dunes, including the steepest upper slopes. Adults are considered long-lived based on >90% survival estimated for mature hummocks during a wet period in the mid-1980s (Pavlik and Barbour 1988). High water use efficiency, typical of warm season species that use the C_4 photosynthetic pathway, allows the dune grass to persist on sandy soils by sustaining high rates of photosynthesis and growth during summer, thereby maintaining shoot production within shifting sands (Pavlik 1980). However, decreased rainfall following the mid-1970s may have reduced dune soil moisture below levels favorable for adults of even this water-efficient species. Although no demographic study has followed *S. alexandrae* through a drought period, adult mortality occurred for six of seven common desert perennial species caused by episodic dry periods in southern California in the late 1980s and early 2000s, which can have far-reaching effects on population dynamics of long-lived desert species (Miriti et al. 2007). Seed production of *S. alexandrae* is generally low compared with many desert species, with seed set potentially restricted by limited opportunities for wind pollination among widely dispersed individuals (Pavlik and Barbour 1985), and seedling establishment is uncommon and dependent on heavy late summer rainfall (Pavlik and Barbour 1988). Re-measurement of historical transects at the northwest end of Eureka Dunes in January 2008 indicated that *S. alexandrae* had declined 96% in this area since spring 1976 (Margoles 2008). Records for Marble Canyon Dune are limited to photographs, but re-photography at the site also suggested a decrease in dune grass hummocks since June 1985 (Margoles 2008).

The NPS monitored populations annually for five years as a condition of the U.S. Fish and Wildlife Service down-listing of *S. alexandrae* (USFWS 2018, p. 8592). A robust monitoring strategy is important for capturing changes in distribution, population size, and demography on the three known dune sites at Death Valley National Park. We were asked to review the historical monitoring strategies and evaluate the distribution and population trends using recent (2007–2019) data,

potentially combined with historical (1970s/1980s) data. We evaluated whether the current monitoring approach (revised in 2017) of an annual 10% random subsample of the total number of grid cells has appropriate statistical power to detect critical distribution, population, and demographic changes in *S. alexandrae*. Ultimately, we assessed the adequacy of historical efforts to monitor *S. alexandrae* populations, analyzed population trends to date, and streamlined methods for future monitoring that build upon the efforts during the 12 years of surveys.

Monitoring for *S. alexandrae* has varied considerably over the years. Early efforts used hand-drawn distribution maps (1979 and 1997–1998, as in Slaton 2008). Repeat photography of plants in habitat occurred at localized photo points (some photographed in 1979, others in 1985, and all points re-photographed in 2008; Margoles 2008). Density was measured on localized transects at the north end of Main Dune (some measured in 1979, the others in 1985, with some transects revisited in 2007 and remaining transects in 2008; Bagley 1986; Henry 1976; Slaton 2008). More recently, NPS established quantitative monitoring (summarized in Table 1) that included direct counts of plants and demography on subsamples of grid cells at all three dunes (2007–2011; Del Favero 2009; Slaton 2008), indirect measures of abundance using density categories for the entire population (2011–2015; Kaiser 2015), and most recently, density categories on a random annual 10% subsample of total grid cells across all three dunes (2017–2019; Hoines and Ellis, unpublished).

Table 1. Summary of survey methods for *Swallenia alexandrae* at three dunes in Eureka Valley at Death Valley National Park, California.

Survey Type	Dune	'07	'08	'09	'10	'11	'12	'13	'14	'15	'17	'18	'19
Population Size [A]	Main	#	–	#	#	#, Cat_p	Cat_p	Cat_p	Cat_p	Cat_p	Cat_s	Cat_s	Cat_s
	Marble	–	#	#	#	#, Cat_p	–	Cat_p	Cat_p	Cat_p	Cat_s	Cat_s	Cat_s
	Saline	–	#	#	#	#, Cat_p	–	Cat_p	Cat_p	Cat_p	Cat_s	Cat_s	Cat_s
Distribution [B]	Main	P	–	–	–	P	P	P	P	P	–	–	–
	Marble	–	P	–	–	P	–	P	P	P	–	–	–
	Saline	–	P	–	–	P	–	P	P	P	–	–	–
Demography [C]	Main	S	–	S	S	S	–	–	–	–	S	S	S
	Marble	–	S	S	S	S	–	–	–	–	S	S	S
	Saline	–	S	S	S	S	–	–	–	–	S	S	S

[A] "#" = quantitative counts per grid cell (# plants/ha); "Cat_p" = qualitative count per grid cell across population (abundance categories = 0, 1–10 plants, >10–60 plants, >60 plants); "Cat_s" = qualitative count per grid cell on random 10% subsample of grid cells for each population (abundance categories same as Cat_p).

[B] P = whole-population surveys.

[C] S = population subsample surveys.

Methods

After initial review of available information, we agreed with previous assessments (Slaton 2008; USFWS 2018) that the 1979 and 1985 data are too spatially limited for determining population trends, although they do have value in documenting changes to localized distribution of *S. alexandrae*. Specifically, data do not allow for population-wide inferences to detect annual changes in plant abundance (Slaton 2008). Consequently, we focus on the quantitative data that were collected across the entire population starting in 2007/08 and, with adjustments in methods, were continued almost annually through 2019.

Abundance and Distribution Surveys

The distributional range for *S. alexandrae* is known to occur on the Main, Saline Spur, and Marble Canyon dunes (Figure 1). One additional population was noted in July 1978 on an isolated deposit of sand in the Saline Range from a helicopter by B. Pavlik and M. DeDecker (USFWS 1982), but observers did not estimate the spatial extent and number of individuals at that time, and the site has not been revisited in subsequent years to our knowledge. Our analysis includes all surveyed sites (Main, Saline Spur and Marble Canyon dunes). As summarized by reports and the ArcGIS and Microsoft Access databases provided by NPS, whole-population surveys occurred on fixed 1-ha georeferenced grids superimposed on aerial imagery and assigned a unique alphanumeric code for between-year tracking (Figure 1). The full set of grid cells was initially surveyed for presence/absence of *S. alexandrae* in 2007 (Main Dune, Figure 2A) or 2008 (Marble Canyon Dune, Figure 3A; Saline Spur Dune, Figure 4A). Subsequent surveys were conducted during 2011–2015 (whole-population) and 2017–2019 (sub-sample), with plant abundances on these same 1-ha grid cells recorded by observers in the following density classes: 0 (no plants), 1 (1–10 plants), 2 (11–60 plants), and 3 (>60 plants). During surveys, stems were counted as the same individual if they occurred within 50 cm of one another on a hummock or within 30 cm of each other off a hummock (Slaton 2008). Whole-population surveys were conducted annually during 2011–2015 at the Main (1,680 grid cells, Figure 2A), Marble Canyon (440–617 grid cells, Figure 3A) and Saline Spur (394–517 grid cells, Figure 3A) dunes, except Saline Spur and Marble Canyon dunes were not surveyed in 2012. Less extensive abundance surveys were conducted at each of the three dune sites in 2017–2019 by randomly subsampling 10% of all grid cells with replacement during each year (Figures 2A, 3A, and 4A). Surveys were conducted annually during early spring (mid-March to early May) in combination with surveys of two other rare species on the dunes (*Oenothera californica* ssp. *eurekensis* and *Astragalus lentiginosus* var. *micans*). This survey period is appropriate for capturing active growth and early reproduction of *S. alexandrae* (Pavlik 1980; Scoles-Sciulla and DeFalco, unpublished data).

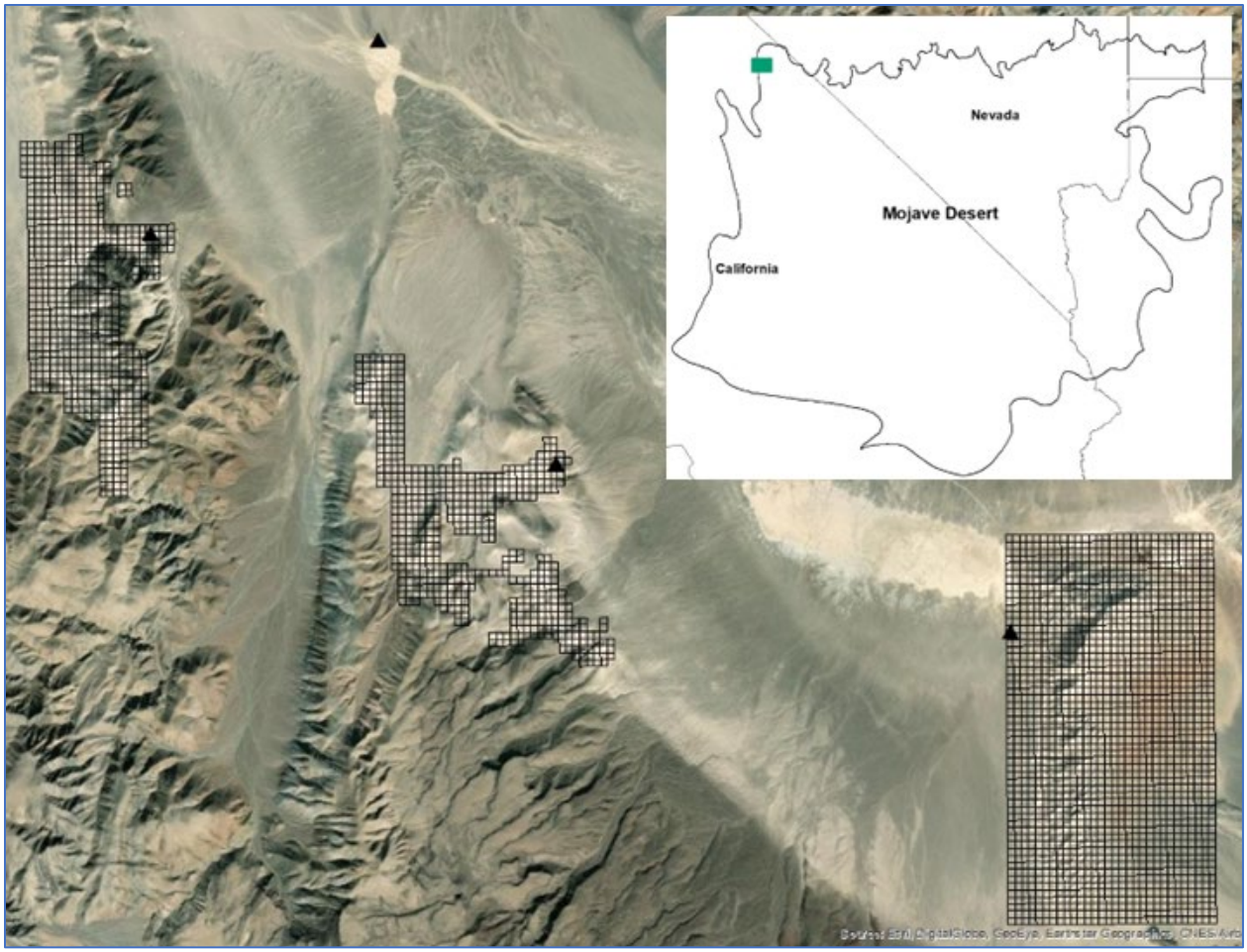

Figure 1. Location of Eureka Valley within the Mojave Desert (inset) and location of 1-hectare (100 m × 100 m) *Swallenia alexandrae* sampling grids within Eureka Valley at the Marble Canyon (left), Saline Spur (middle) and Main (right) dune sites. The National Park Service (NPS) weather station established approximately 6 km north of the Saline Spur Dunes in March 2013 and temporary U.S. Geological Survey (USGS) weather stations maintained at each dune site from December 2012 through February 2016 are indicated by black triangles.

NPS

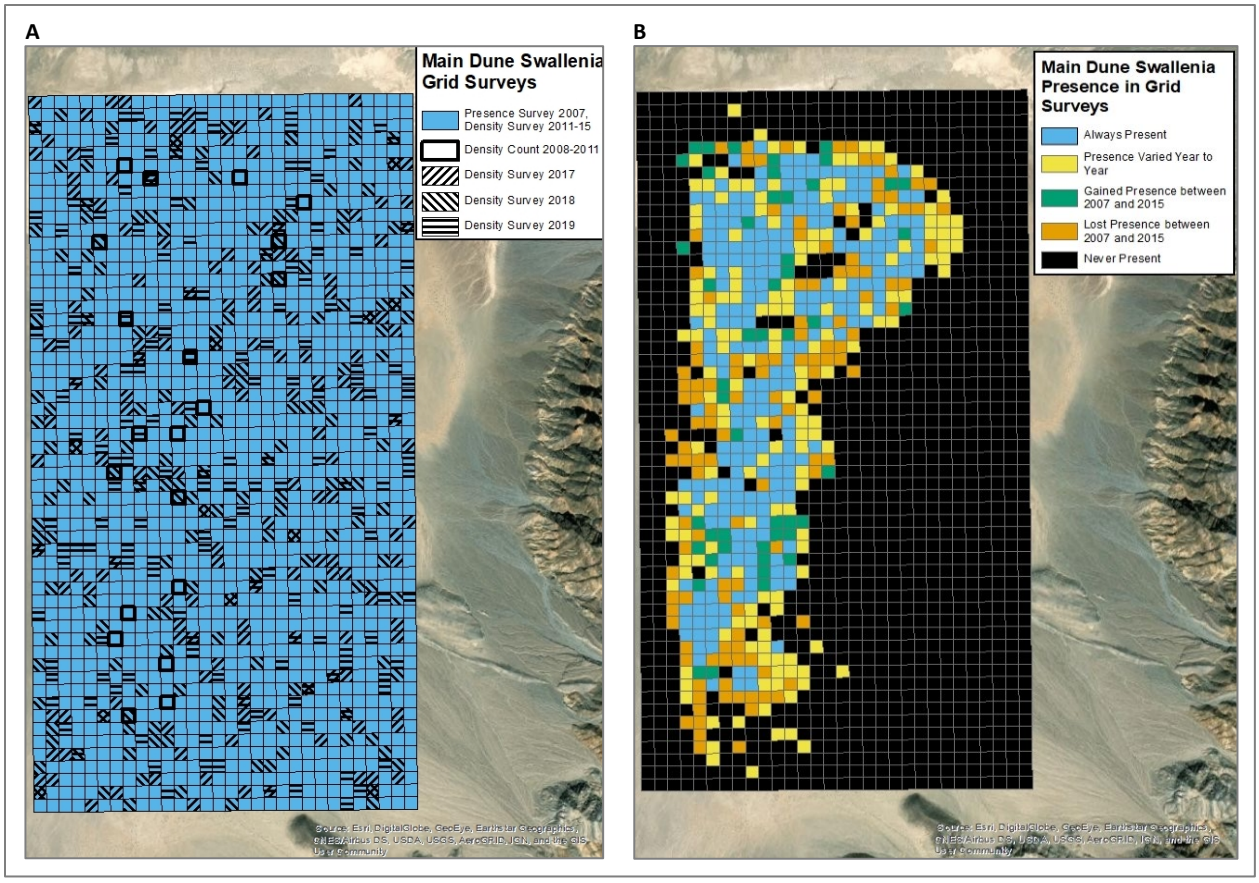

Figure 2. Surveys for *Swallenia alexandrae* at Main Dune: (A) Survey efforts from 2007 to 2019 and (B) Survey results from 2007 to 2015. “Presence survey” = presence/absence recorded within each grid cell; “Density count” = all plants counted and their phenology/reproductive status (see text) recorded within each grid cell; “Density survey” = plant abundance estimated in density classes (see text) within each grid cell. No surveys or counts were conducted at the Main Dune in 2008.

NPS

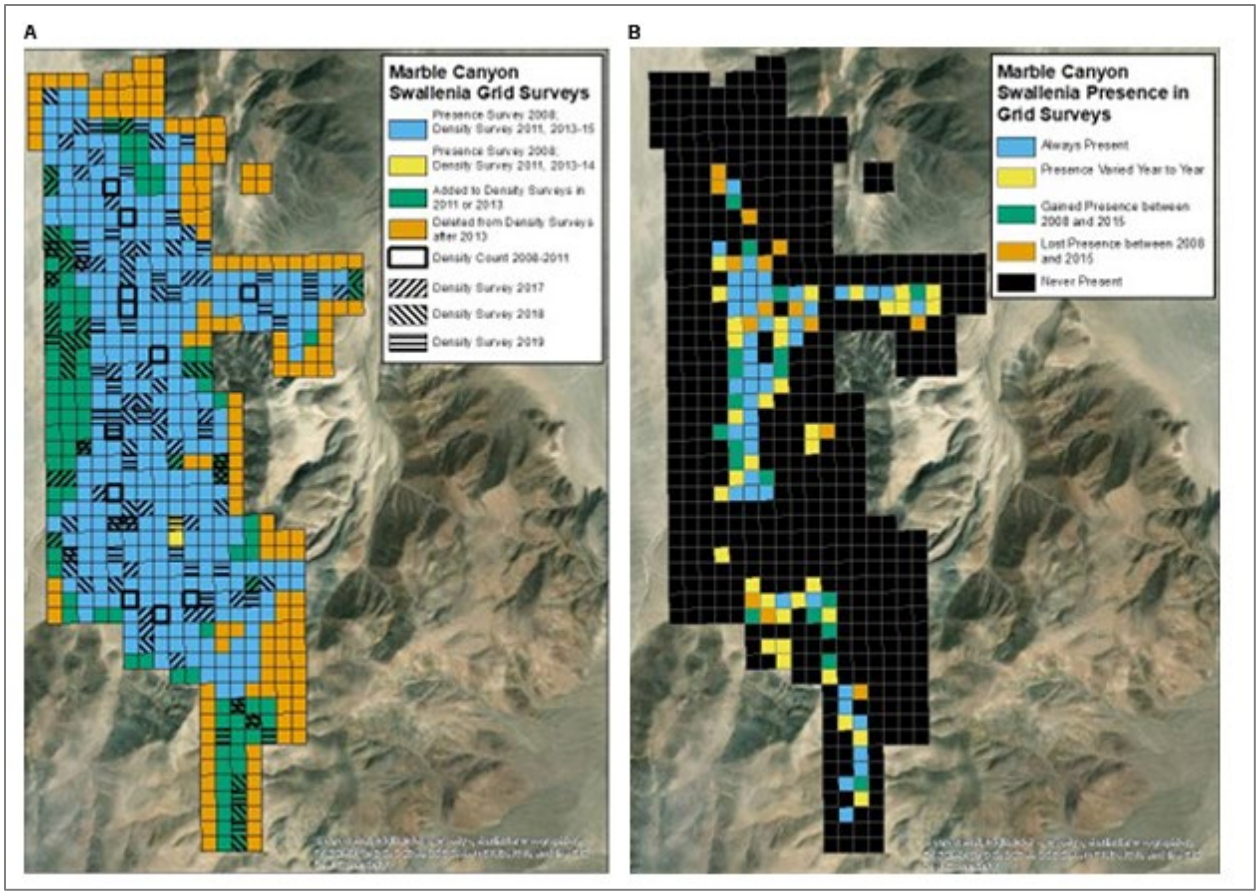

Figure 3. Surveys for *Swallenia alexandrae* at Marble Canyon Dune: (A) Survey efforts from 2008 to 2019 and (B) Survey results from 2008 to 2015. “Presence survey” = presence/absence recorded within each grid cell; “Density count” = all plants counted and their phenology/reproductive status (see text) recorded within each grid cell; “Density survey” = plant abundance estimated in density classes (see text) within each grid cell. No surveys or counts were conducted at Marble Canyon Dune in 2012.
NPS

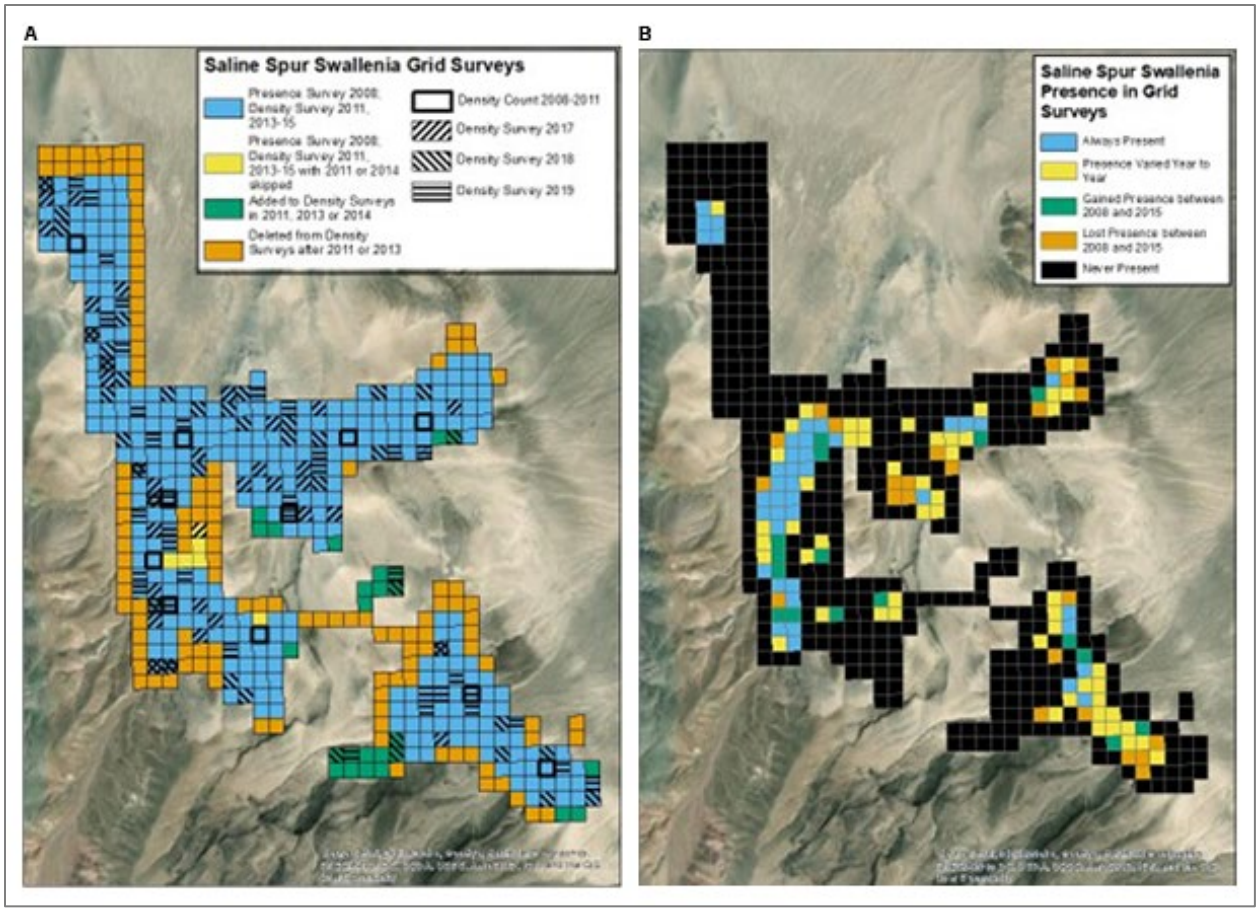

Figure 4. Surveys for *Swallenia alexandrae* at Saline Spur Dune: (A) Survey efforts from 2008 to 2019 and (B) Survey results from 2008 to 2015. "Presence survey" = presence/absence recorded within each grid cell; "Density count" = all plants counted and their phenology/reproductive status (see text) recorded within each grid cell; "Density survey" = plant abundance estimated in density classes (see text) within each grid cell. No surveys or counts were conducted at Saline Spur Dune in 2012.
NPS

Demography

Demographic data consist of two separate survey periods: 1) annual counts of all seedlings, non-reproductive adults, reproductive adults, and senescent adults (Figure 5) on the same subsample of grid cells at Main (n = 20 grid cells, 471–821 plants/year), Marble Canyon (n = 11 grid cells, 82–139 plants/year) and Saline Spur (n = 11 grid cells, 619–1115 plants/year) dunes during 2007/08–2011, and 2) counts of up to 26 plants per grid cell in 2017–2019 categorized as seedling, juvenile and adult at each dune (n = 21–33 grid cells, 140–263 plants/year for Main; n = 4–8 grid cells, 43–65 plants/year for Marble Canyon; and n = 4–11 grid cells, 92–203 plants/year for Saline Spur). The difference between sampling periods is that the 2007/08–2011 surveys recorded *all* plants on the *same* subsample of grid cells each year, and the 2017–2019 surveys recorded a *subset of plants* on a *different* randomly selected subsample of grid cells for each year (Table 1).

Figure 5. Demographic stages of *Swallenia alexandrae*–seedling (left) and reproductive adult (right). Intervening stages, such as juveniles versus non-reproductive adults, are more difficult to differentiate without following individual plants over time, as in the case of Pavlik and Barbour (1985) and Slaton (2008).

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Plant canopies were also measured on the random subset of plants counted during the 2017–2019 sampling period. Although the objectives associated with these measurements were not documented, canopy volume may be used as a predictor of seed production. However, a 4-fold difference in seed production for the same sized plants between two years (Pavlik and Barbour 1988) means that predicting seed production using canopy volume would need to correct for differences in variable seed crops (i.e., due to differences in seasonal temperatures and/or rainfall) and to represent the broader population (e.g., select from plants stratified within and across the three dunes).

Precipitation and Temperature

Based on Parameter-elevation Regressions on Independent Slopes Model (PRISM, https://prism.oregonstate.edu), maximum (July) and minimum (December) temperatures in Eureka Valley from 1970–2020 ranged from 36.7–42.2°C and −5.2–2.2°C, respectively (Figure 6). During the mid-1970s to mid-1980s when studies on *S. alexandrae* began, summer/fall precipitation (April–September) was equal to or higher than the long-term average; since the early 2000s, summer/fall precipitation has been below average but increasing slowly to normal or above-normal levels since 2010 (Figure 6). Above-average winter/spring precipitation (October–March) has occurred approximately every 5 years. Precipitation values at weather stations do not always agree with PRISM modeled data, with large discrepancies in the southwestern U.S. occurring during summer in particular (Buban et al. 2020); this discrepancy indicates that localized rain gauges or weather stations are important for validating the usefulness of spatial models to understand population trends in rare and geographically restricted plants.

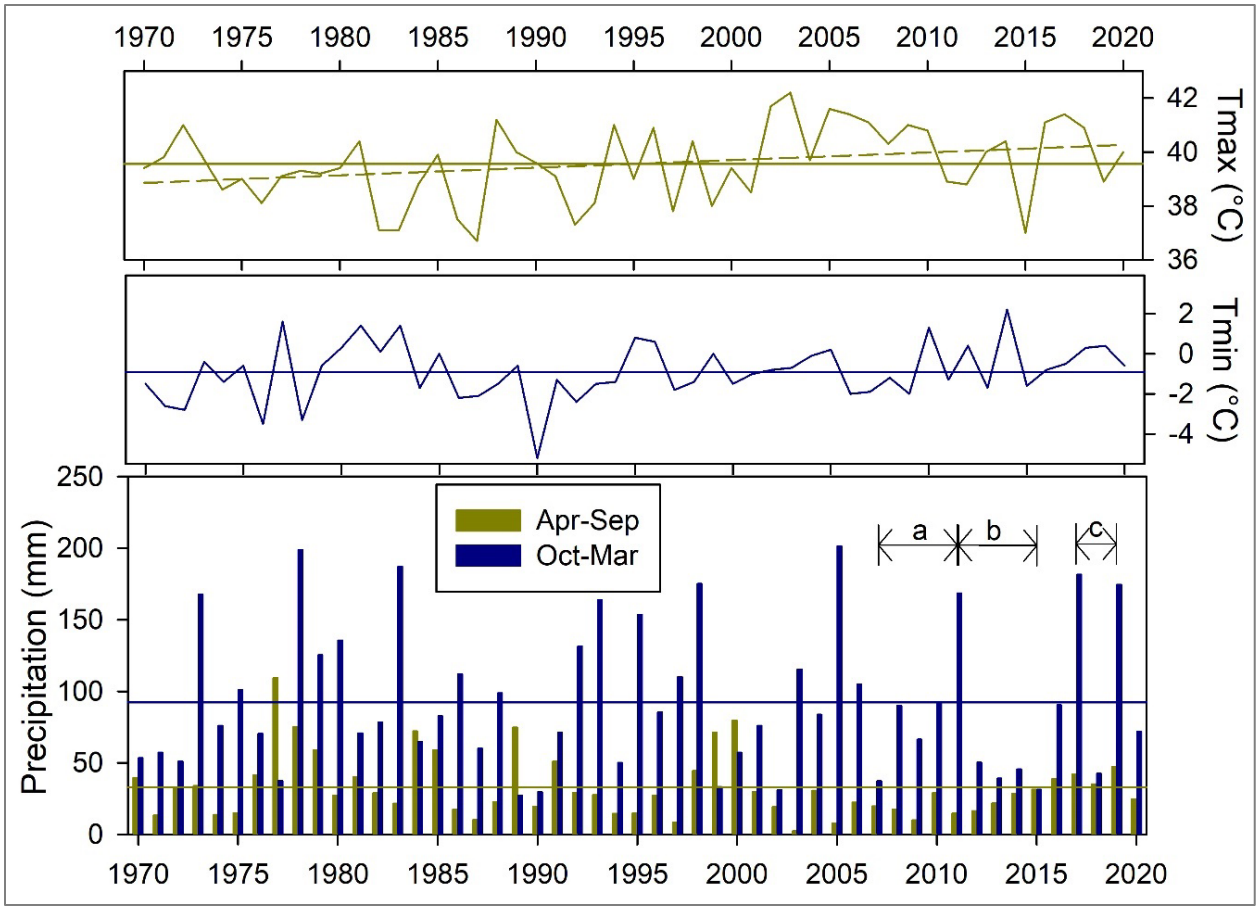

Figure 6. Maximum (July) and minimum (December) temperatures and seasonal precipitation from 1970 to 2020 when *Swallenia alexandrae* studies were conducted in Eureka Valley (PRISM, Oregon State University). X-axis represents the weather for the year corresponding to the spring surveys, not the calendar year, to relate the influence of antecedent weather to distribution, density and demography: for example, "2010" is the *S. alexandrae* survey with the corresponding T_{max} and T_{min} from 2009, April–September 2009 precipitation and October 2009–March 2010 precipitation. Horizontal lines indicate averages across the 50-year period. Dashed line for T_{max} denotes a marginally significant increase in temperature over time ($T_{max} = -16.6764 + 0.0282 \times Year$); no other trends were significant. Ranges refer to surveys in a) 2007/08–2011 by Slaton (2008), b) 2011–2015 by Kaiser (2015), and c) 2017–2019 by Hoines and Ellis (unpublished).

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NPS installed a permanent weather station in Eureka Valley (37.176250°, −117.788494°; elev. 907 m) in late March 2013, which recorded precipitation and hourly temperature during a portion of the survey period (2013–2019, excluding the first 5 months of 2018). U.S. Geological Survey (USGS) installed and maintained temporary weather stations at Main (37.099731°, −117.685841°; elev. 876 m), Marble Canyon (37.151276°, −117.825402°; elev. 992 m), and Saline Spur (37.121492°, −117.759633°; elev. 1023 m) dunes from mid-December 2012 through mid-February 2016 (Figure 1). All stations recorded precipitation and temperature hourly but did not cover the full time-span of *S. alexandrae* surveys. We downloaded PRISM monthly precipitation and average maximum and minimum temperature data for each of the weather station locations during the time period when

S. alexandrae surveys were conducted (https://prism.oregonstate.edu, 2006–2019; downloaded 6 May 2021) and compared values to understand the usefulness of the spatially modeled data.

Analytic Approaches

Population Trends and Influence of Precipitation and Temperature

The relationship between weather and overall population trends is unclear for *S. alexandrae*, although above-average summer rainfall has been correlated with seedling recruitment based on demographic work conducted during a period of above average precipitation (Pavlik and Barbour 1986). Accordingly, we developed a set of possible regression models to evaluate relationships between *S. alexandrae* abundance and seasonal precipitation and temperatures. Trends in *S. alexandrae* abundance were analyzed separately for surveys that consisted of direct counts of plants across the same annual subsample of grid cells (2007/08–2011), plant density classes for all grid cells within each population (2011–2015), or plant density classes on an annual 10% random subsample of grid cells (2017–2019; Table 1). Direct counts were converted to the density classes used in subsequent surveys so that data could be collectively analyzed using proportional odds model, a statistic that tests the odds of a change in density classes between years and across dune sites. Correlations between PRISM and local weather stations were used to adjust seasonal precipitation in the year prior to population surveys for each dune and each year included total precipitation across the hydrological year (March–April), during winter/spring (October–March) and summer/fall (April–September), and minimum and maximum temperatures for December and July, respectively. These weather variables were included as explanatory factors in modeling the odds of annual population change. Multicollinearity was avoided by only including variables in the same model with Pearson correlation coefficients $|r| < 0.7$. The assumption of proportional odds was tested for our models with continuous predictors based on parallel slopes (Agresti 2013) and odds ratios between years were compared using Wald's chi-square. The most plausible model explaining changes in *S. alexandrae* abundance was determined by the lowest Akaike Information Criterion (AIC). The plausibility of other models explaining density is indicated by the difference from the best model (ΔAIC), with a $\Delta AIC < 2$ indicating plausible models, models with $\Delta AIC < 7$ indicating less support, and those with $\Delta AIC > 7$ poorly supported (Burnham and Anderson 2002). Included for comparison in our set of models was an intercept-only model (i.e., the weather variables have no value in explaining density changes) and a year-only model (i.e., some factor other than weather but associated with year is important).

For demography, we similarly analyzed stage classes in a proportional odds model by first testing a set of candidate models for the separate survey periods because different methods were used for counts of stage classes (i.e., all plants within the same subsample of grid cells each year versus a subset of plants from a different random subsample of grid cells each year). Because best models were similar between the two survey periods, we then consolidated stage classes to roughly maintain important transitions (e.g., seedling establishment, non-reproductive to reproductive) and compared years that represent variation in seasonal temperatures and precipitation. This consolidation entailed dropping the senescent stage class from the 2007–2011 surveys (seedlings, non-reproductive adult, reproductive adult only) to approximate the stage classes used in 2017–2019 (seedlings, juveniles, and adults). Seedlings comprised a very small number of plants, so shifts in demography reflected changes in the abundances of non-reproductive and reproductive adults.

Power Analyses and Adequacy of Subsampling

The recovery plan for *S. alexandrae* does not specify quantitative guidelines for detection limits that would trigger management action. Through our informal inquiry with U.S. Fish and Wildlife Service (USFWS) for this species, we recognized that determining population change thresholds for triggering management action is a complex issue (USFWS 2016) and depends on an understanding of population age structure, size, and trajectory of increases and declines among and within plant populations (Mary Crawford, Brian Croft, USFWS, pers. comm., 9 March 2021*).* For a narrow endemic perennial grass like *S. alexandrae*, detection of a 15–30% decline over 5 years is a suggested starting place for evaluating and planning for conservation actions such as translocation, assuming threats are managed (Mary Crawford, pers. comm., 9 March 2021). However, discussion between USFWS and NPS could help with developing conservation decision frameworks or scenario planning (e.g., alternate management strategies, Mary Crawford, pers. comm., 9 March 2021) and/or further establish meaningful criteria for this species (e.g., evaluating adaptive capacity via population size and trends across annual surveys, Thurman et al. 2020). We therefore explored several power analysis scenarios, each involving a 20% change in total plant counts over the entire *S. alexandrae* population. This threshold is also consistent with Slaton's (2008) analysis of grid cell sample size where she used plant numbers and standard deviations from Mark Bagley's plot data to determine the sample size that would be sufficient to detect a 20% change in population size at the Main Dune with an $\alpha = 0.10$.

We simulated populations from the 2007–2015 data and iteratively subsampled grid cells for optimizing surveys to detect meaningful change in *S. alexandrae* populations. We simulated populations using a negative binomial distribution (mu = 9, size = 0.6), which closely fits the prior survey data distribution, and introduced temporal trends by increasing or decreasing plant counts from simulated distributions on annual time steps. Grid cells were randomly selected for adjustment based on multinomial distribution, with probabilities weighted toward grid cells with more plants to adjust for where most plants occur. This procedure allows simulating a percentage reduction or increase in total plants through time. The simulated population was then subsampled with a different number of grid cells (i.e., sample size) each year ranging from 100–2,000 grid cells. Models that we compared included proportional odds linear regression on the density classes, zero-inflated negative binomial generalized linear model on random and stratified samples, and negative binomial generalized linear model on presence/absence sampling. For the proportional odds linear regression, the continuous data were split into the density classes implemented by NPS.

While familiarizing ourselves with the survey efforts across years, we recognized that the subsample of grid cells selected in 2007/08 were all occupied by *S. alexandrae* (100% with plants, presumably designed to track demography), and grid cells subsampled at random during 2017–2019 had markedly fewer occupied grid cells (<30% with plants, presumably designed as a random sample to monitor population trends, Tables 2–4). Because of the preponderance of unoccupied grid cells, subsampling the entire grid system at random over time could affect the power to detect population change, so we evaluated four different subsampling approaches. Each approach is based on subsampling from grid cells during the most recent (2011–2015) surveys: "occupied" cells are those that had any occurrences during the survey period, and "unoccupied" cells never had any

occurrences. The “completely-random subsampling” draws a different random subset of grid cells to survey, which includes both formerly occupied and unoccupied grid cells, as performed by NPS during 2017–2019. In contrast, “occupied-only subsampling” draws a different random subset each year from *only* those grid cells determined to be occupied (i.e., grid cells that were unoccupied by *S. alexandrae* during 2011–2015 whole-population surveys were omitted). Two other subsampling approaches involve drawing a random subset of grid cells and repeating surveys on those *same* cells across years, such as during the 2007–2011 surveys: “balanced-stratified subsampling” draws an equal number of grid cells across density classes while “weighted-stratified subsampling” draws proportionally more grid cells in the 0 and 1 density classes because they are the most variable of all classes.

Table 2. Summary of survey effort for *Swallenia alexandrae* at Main Dune in Eureka Valley.

	Sub-Sample Surveys				Whole-Population Surveys					10% Sub-Sample Surveys		
Survey Effort	**2007/08**	**2009**	**2010**	**2011**	**2011**	**2012**	**2013**	**2014**	**2015**	**2017**	**2018**	**2019**
Total grid cells surveyed	20	20	20	20	1,680	1,680	1,607	1,647	1,667	156	166	168
# Occupied cells (%)	20 (100)	18 (90)	20 (100)	18 (90)	446 (26)	397 (24)	345 (21)	352 (21)	357 (22)	21 (13)	26 (16)	33 (20)
# Unoccupied cells (%)	0 (0)	2 (10)	0 (0)	2 (10)	1,234 (74)	1,283 (76)	1,262 (79)	1,295 (79)	1,310 (78)	135 (87)	140 (84)	135 (80)

Table 3. Summary of survey effort for *Swallenia alexandrae* at Marble Canyon in Eureka Valley.

	Sub-Sample Surveys				Whole-Population Surveys					10% Sub-Sample Surveys		
Survey Effort	**2007/08**	**2009**	**2010**	**2011**	**2011**	**2012**	**2013**	**2014**	**2015**	**2017**	**2018**	**2019**
Total grid cells surveyed	11	11	11	11	440	–	470	469	469	41	44	47
# Occupied cells (%)	11 (100)	11 (100)	11 (100)	10 (91)	79 (18)	–	80 (17)	74 (16)	79 (17)	8 (20)	6 (14)	4 (9)
# Unoccupied cells (%)	0 (0)	0 (0)	0 (0)	1 (9)	361 (72)	–	390 (73)	395 (74)	390 (73)	33 (80)	38 (86)	43 (91)

Table 4. Summary of survey effort for *Swallenia alexandrae* at Saline Spur in Eureka Valley.

	Sub-Sample Surveys				Whole-Population Surveys					10% Sub-Sample Surveys		
Survey Effort	**2007/08**	**2009**	**2010**	**2011**	**2011**	**2012**	**2013**	**2014**	**2015**	**2017**	**2018**	**2019**
Total grid cells surveyed	11	11	11	11	394	–	386	396	400	34	40	41
# Occupied cells (%)	11 (100)	11 (100)	11 (100)	11 (100)	87 (22)	–	86 (22)	69 (17)	94 (24)	10 (29)	4 (10)	11 (27)
# Unoccupied cells (%)	0 (0)	0 (0)	0 (0)	0 (0)	307 (78)	–	300 (78)	314 (83)	306 (76)	24 (71)	36 (90)	30 (73)

Results

Weather Stations and PRISM Spatial Data

Seasonal precipitation modeled by PRISM correlated well with precipitation measured by the NPS weather station installed within Eureka Valley in 2013, although winter-spring precipitation (October–December and January–March) was overpredicted by PRISM (Figure 7). The same pattern emerged when PRISM data were compared with precipitation measured by local USGS stations at each dune site (Figure 8). The main difference between stations is that late summer/early fall precipitation (July–September) recorded at the local dune stations was underpredicted by PRISM in contrast to the comparison between the single NPS station and PRISM. Using the equations from the NPS Eureka Valley station and the USGS stations at each dune, we adjusted precipitation from PRISM during winter/spring (October–March) and summer/fall (April–September) and calculated the difference in seasonal precipitation during 2006–2019 from the 30-year Normals (1981–2010).

July average maximum temperature modeled by PRISM correlated well with maximum temperatures measured by the NPS weather station installed within Eureka Valley ($PRISM\_T_{max} = 0.96560 \times NPS\_T_{max}$; $r^2 = 0.9999$) and by local stations at each dune site ($PRISM\_T_{max} = 0.97886 \times USGS\_T_{max}$; $r^2 = 0.9994$). The correlation was weaker between December average minimum temperature modeled by PRISM and minimum temperatures measured by the NPS weather station ($PRISM\_T_{min} = 1.57138 \times NPS\_T_{min} – 2.91570$; $r^2 = 0.8024$) or USGS stations at each dune site ($PRISM\_T_{min} = 1.32376 \times USGS\_T_{min} – 0.70806$; $r^2 = 0.5265$).

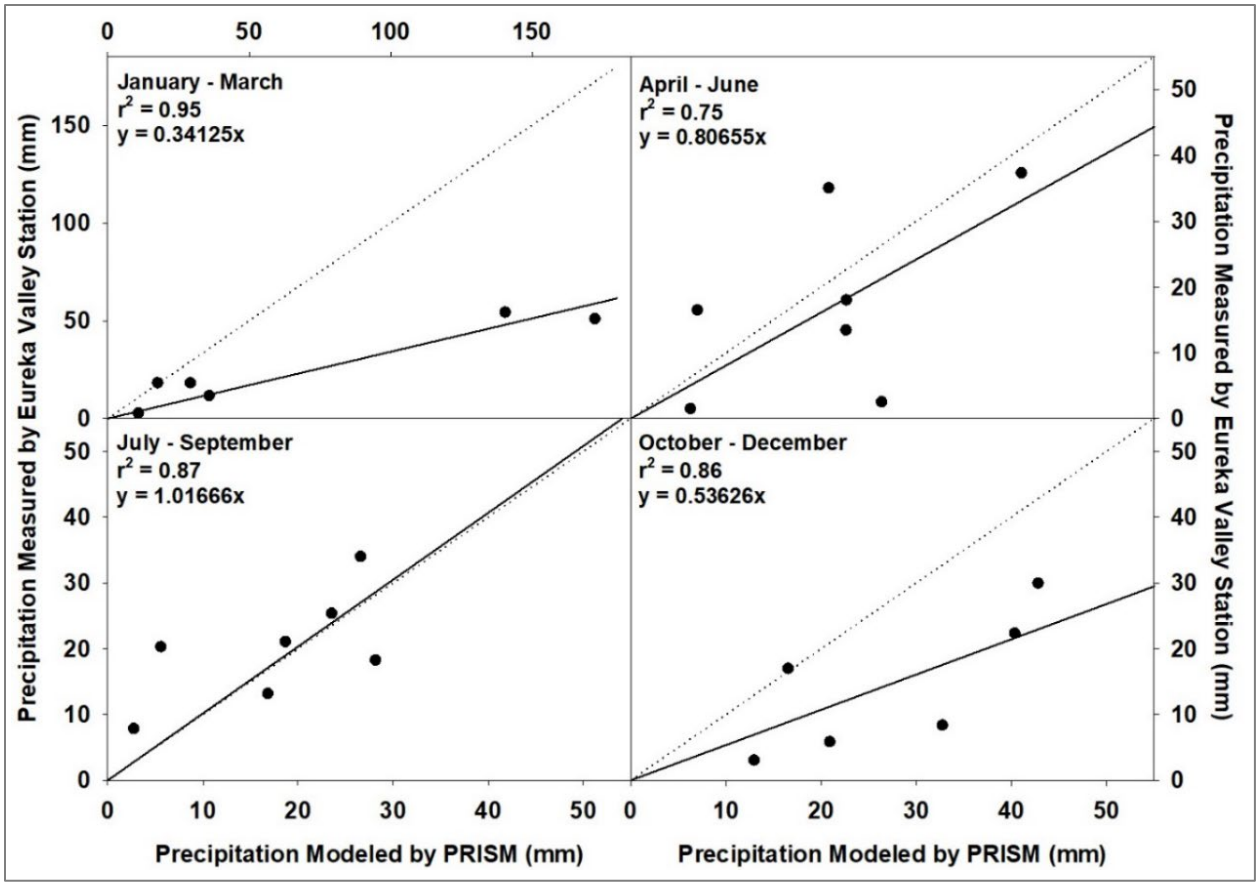

Figure 7. Seasonal precipitation measured in Eureka Valley by a National Park Service (NPS) weather station compared with precipitation modeled by PRISM from 2013 to 2020. The dotted line within each panel represents a 1-to-1 relationship, while the solid line depicts the regression line for the data (equation shown within panel). A slope less than one indicates overprediction and a slope greater than one indicates underprediction of precipitation by the PRISM model. Goodness of fit for the regression line is shown by the r-squared value within the panel. Note that the scale is different for January–March compared with all other seasons. No data is available from the NPS station between 29 December 2017 and 4 May 2018.

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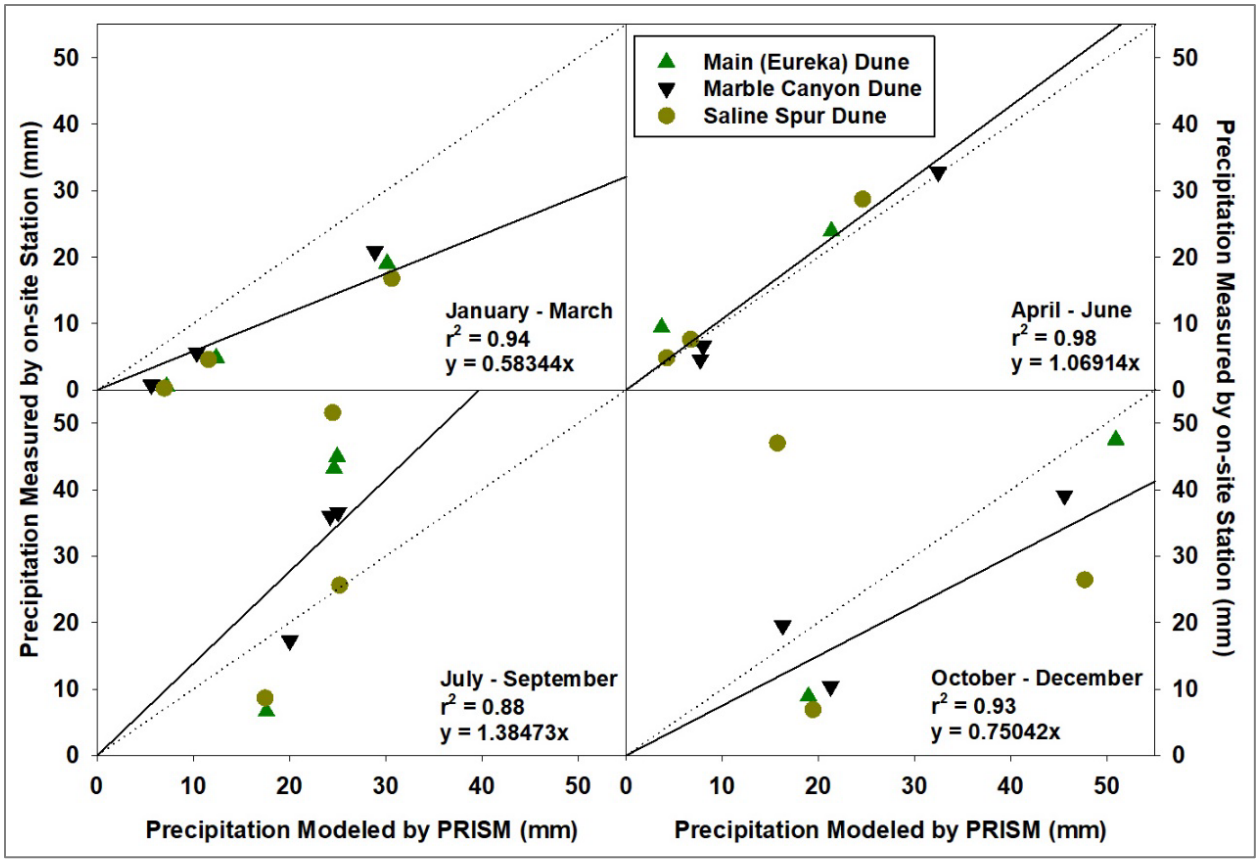

Figure 8. Seasonal precipitation measured at Eureka (Main), Marble Canyon, and Saline Spur dune sites by temporary U.S. Geological Survey (USGS) weather stations compared with precipitation modeled by PRISM from 2013 to 2015. The dotted line within each panel represents a 1-to-1 relationship, while the solid line depicts the regression line for the data (equation shown within panel). A slope less than one indicates overprediction and a slope greater than one indicates underprediction of precipitation by the PRISM model. Goodness of fit for the regression line is shown by the r-squared value within the panel. The October–December regression excludes one outlying point from Saline Spur Dune. No data is available from the Main Dune station between October and December 2013.
USGS / SARA SCOLES-SCUILLA

Distribution and Abundance of *S. alexandrae*, 2007–2019

The spatial distribution of *S. alexandrae* was most recently determined in 2015 when all 1-ha grid cells across all three dunes were surveyed and compared with the same whole-population survey from 2011. Changes in distribution, as determined from net change in the number of occupied grid cells for each dune, were reported in Kaiser (2015), indicating a large loss of occupied area at Main Dune and negligible changes at Marble Canyon and Saline Spur dunes. No whole-population surveys have been completed since 2015, so the status of *S. alexandrae* distribution across the three dunes since then is unknown.

The abundance of *S. alexandrae* measured in density classes varied across years, and seasonal precipitation and temperature correlated with abundance. Declines in densities were detected at Main Dune during the 2007–2011 and 2011–2015 surveys, but not during the recent 2017–2019 surveys

(Table 5). In contrast, densities of *S. alexandrae* at the other dunes increased during the 2011–2015 surveys but did not change during the 2008–2011 and 2017–2019 surveys (Table 5). Considering all dunes and years collectively in our analysis, the best model showed correlation between density classes and the prior-year maximum temperature alone followed by similarly plausible models that had a combination of maximum temperature and prior-year summer/fall precipitation (PRISM-adjusted based on either the local USGS or the NPS stations, $\Delta AIC < 2$; Table 6). The best model indicates that a 1°C increment in the difference between maximum temperature and long-term mean (i.e., warmer than normal) increases the odds of greater *S. alexandrae* densities by a factor of 1.380 (95% CI = 1.309–1.456, Figure 9). Across all models, maximum temperature was the most explanatory variable (sum of $w_i s = 1.0000$) followed by April–September precipitation ($w_i s = 0.4242$ and 0.4107 for PRISM adjusted by USGS and NPS stations, respectively) and July–September precipitation ($w_i s = 0.1477$, based on both USGS and NPS stations). Whereas models that include precipitation were also plausible ($\Delta AIC < 2$), the 95% confidence intervals for their odds ratios overlap 1; thus, the odds of greater densities associated with wetter-than-normal years are not statistically significant (e.g., odds ratio between 0.964 and 1.066 for 10 mm increase in April–September precipitation adjusted by USGS stations).

Table 5. Trends in *Swallenia alexandrae* abundance during different surveys conducted 2007–2019. Wald's chi-square tests for annual decline in density. Odds ratio and 95% CI greater than 1 denotes the odds of a population decline over a one-year increment; less than 1 denotes the odds of a population increase. "–" and "+" denote significant decline and increase, respectively, at $0.01 < \alpha < 0.05$; "– –" and "++" denote significance at $\alpha < 0.01$.

Dune	Years	Wald's Chi-square	p-value	Odds ratio (95% CI)	Trend
Main	2007–2011	4.1993	0.0404	1.448 (1.016–2.063)	–
	2011–2015	18.2967	<0.0001	1.119 (1.063–1.177)	– –
	2017–2019	0.2795	0.5970	0.894 (0.589–1.356)	0
Marble Canyon	2008–2011	0.0182	0.8926	0.963 (0.558–1.663)	0
	2011–2015	30.0928	<0.0001	0.756 (0.685–0.836)	++
	2017–2019	0.5333	0.4652	1.309 (0.635–2.697)	0
Saline Spur	2008–2011	0.0767	0.7819	0.933 (0.571–1.524)	0
	2011–2015	40.3355	<0.0001	0.789 (0.734–0.849)	++
	2017–2019	0.0146	0.9040	1.042 (0.532–2.040)	0

Table 6. Model comparisons explaining the relationship between weather variables, adjusted by local (USGS) or single Eureka Valley (NPS) stations, and the densities or life stages of *Swallenia alexandrae* during 2007–2019 surveys. Only models with some level of support (ΔAIC < 7) and the intercept-only model for comparison are presented. Tmax is maximum temperature (Jul) and Tmin is minimum temperature (Dec) based on PRISM (no adjustment using stations). AprSepUSGS and AprSepNPS (spring-summer precipitation), JulSepUSGS (summer precipitation) and OctMarNPS (winter-spring precipitation) are based on station adjustments of PRISM. Other models tested with little support (ΔAIC ≥ 7) included combinations of year, OctMarUSGS, JulSepNPS, and total annual precipitation (corrected by either station).

Plant Response	Model	AIC	ΔAIC	Wald's Chi-sq	p-value	w_is
Density	T_{max}	10297.716	0.000	139.4393	<0.0001	0.3873
	$AprSep_{USGS} + T_{max}$	10299.431	1.715	139.8070	<0.0001	0.1643
	$AprSep_{NPS} + T_{max}$	10299.496	1.780	139.7324	<0.0001	0.1590
	$JulSep_{USGS} + T_{max}$	10299.685	1.969	139.4922	<0.0001	0.1447
	$AprSep_{NPS} + T_{max}$	10299.685	1.969	139.4922	<0.0001	0.1447
	Intercept only	10437.335	139.619	–	–	–
Stage	$OctMar_{NPS} + T_{min}$	9951.552	0.000	382.1196	<0.0001	1.0000
	Intercept only	10355.070	403.516	–	–	–

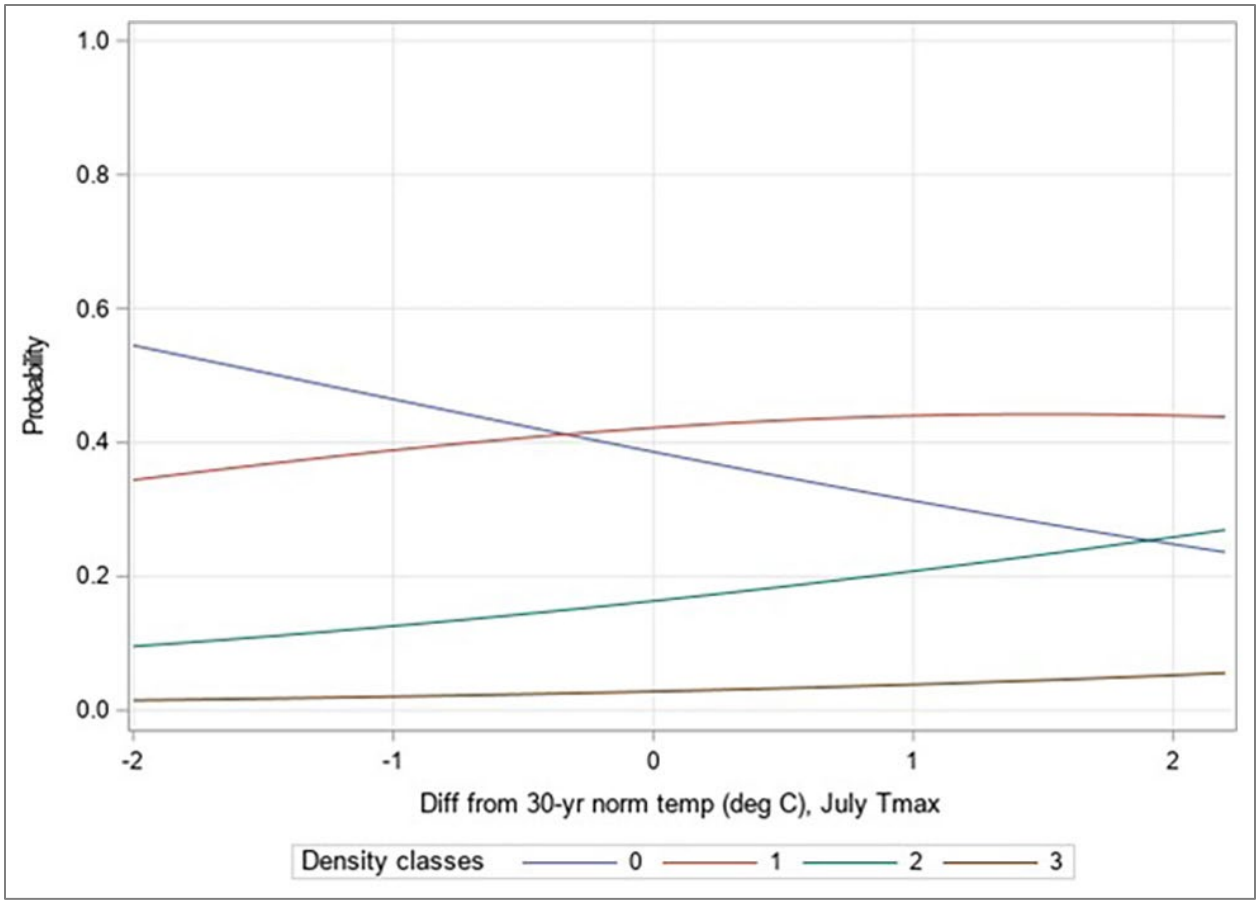

Figure 9. Predicted probabilities for density classes related to the difference in maximum (July) temperature from the long-term average. Analysis includes all dunes across years 2007–2019. Density classes: 0 = 0 plants, 1 = 1–10 plants, 2 = 11–60 plants, and 3 = >60 plants.
USGS / LESLEY DEFALCO

Demography, 2007–2011 and 2017–2019

Seedlings were rare during the sampling periods (10 total seedlings during 2007–2011; 19 total seedlings during 2017–2019); therefore, the analysis of life stages primarily reflects shifts between the proportions of non-reproductive and reproductive plants. Combining the survey periods in the same analysis (but removing the senescent stage plants from the earlier surveys), the best model suggests more non-reproductive plants during years with cooler, wetter conditions prior to the spring survey (Table 4). A 10 mm increment in the difference between winter/spring (October–March) precipitation and the long-term mean (i.e., wetter than normal) increases the odds of non-reproductive plants by 1.417 (Wald's 95% CI = 1.363–1.474), and a 1°C decrement in the difference between minimum (December) temperature and the long-term mean (i.e., colder than normal) increases the odds of non-reproductive plants by a factor of 1.463 (95% CI = 1.361–1.573).

Power Analyses and Adequacy of Subsampling for Future Monitoring

The proportional odds linear regression on density classes proved the most powerful to detect population changes, while generalized linear models or linear models on the continuous simulated

density data were largely ineffective under our scenarios (analyses not presented). Our simulations of subsampling scenarios demonstrate that an annual completely random subsample of ~200 grid cells like that conducted during 2017–2019 (Table 2) is not sufficient to detect a 20% increase or decrease in the *S. alexandrae* population using density classes; detecting a 20% decrease under this scenario would instead involve surveying ~800 grid cells per year, thereby requiring additional personnel resources (Figure 10). The power to detect meaningful population change increased when we simulated occupied-only subsampling and weighted-stratified subsampling (Figure 11 and Figure 12). A decrease of 20% could be detected by subsampling 200 occupied-only or weighted-stratified grid cells, and approximately 300–400 grid cells were needed to detect a 20% increase in plants through these subsampling approaches. Finally, balanced-stratified subsampling required selecting more grid cells to be repeatedly sampled each year: >300 grid cells and >500 grid cells for detecting declining and increasing populations, respectively (Figure 13).

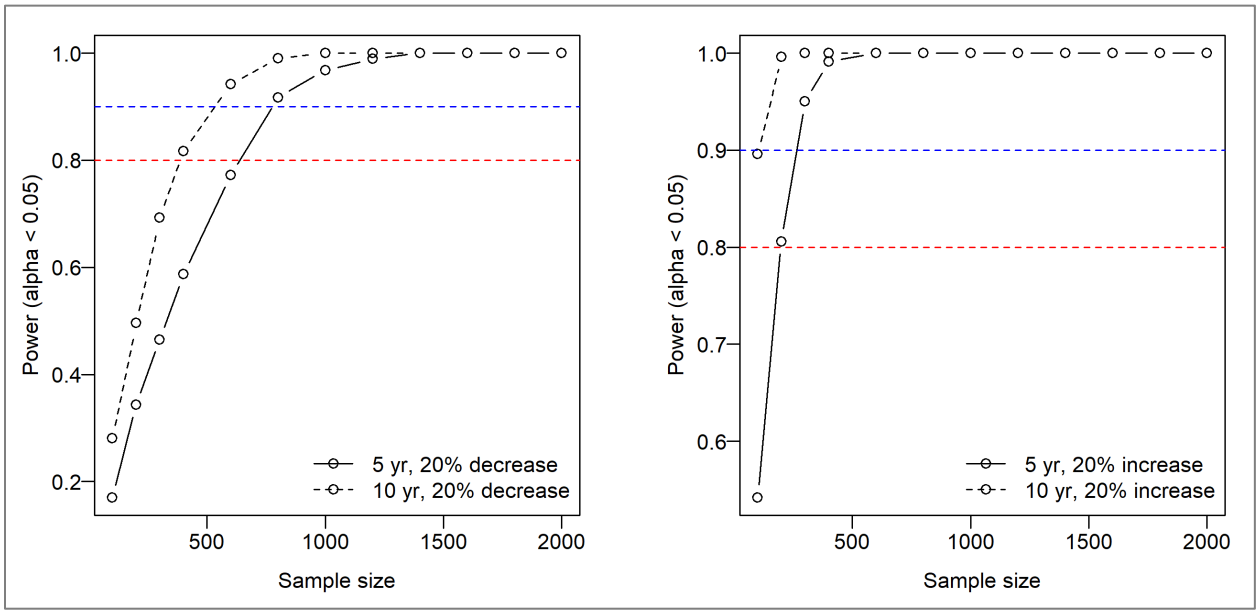

Figure 10. Power analysis for annual completely-random subsampling (i.e., randomly selected grid cells each year that include unoccupied grid cells) illustrating number of grid cells needed (i.e., sample size) to achieve sufficient power to detect 20% decrease (left panel) and 20% increase (right panel) in *Swallenia alexandrae* population over 5- and 10-yr periods. The 80% and 90% probability of correctly detecting a true trend are indicated by the horizonal red and blue dashed lines, respectively. Note different scales on the y-axis.

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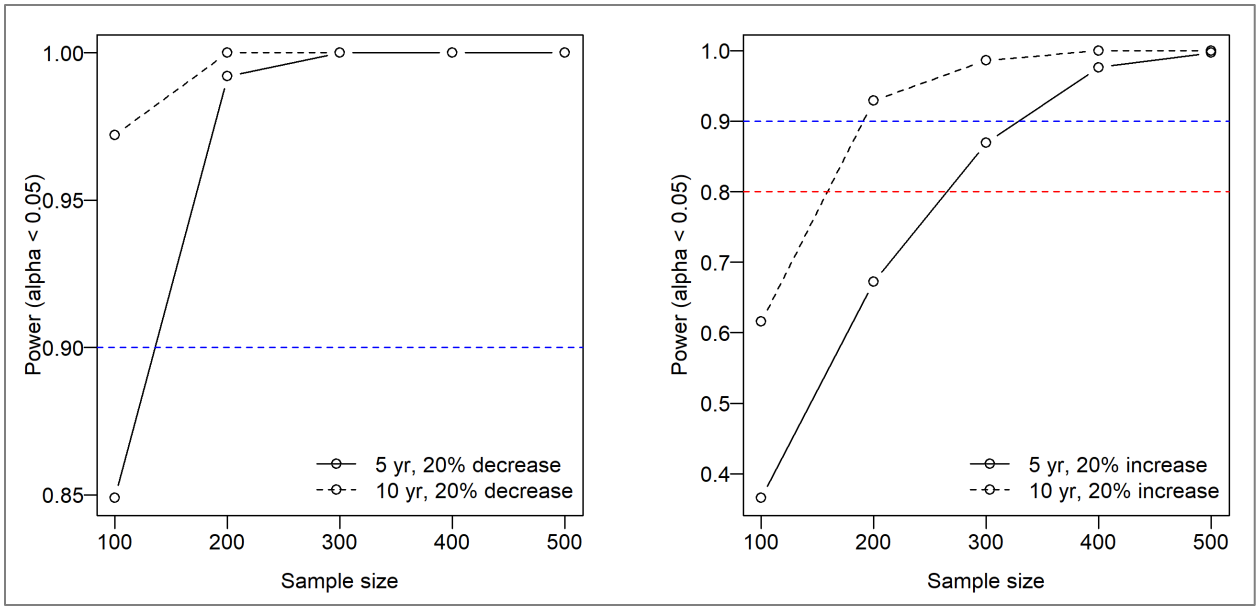

Figure 11. Power analysis for occupied-only subsampling (i.e., randomly selected grid cells each year omitting previously unoccupied grid cells). Graphs illustrate the number of grid cells needed (i.e., sample size) to achieve sufficient power to detect 20% decrease (left panel) and 20% increase (right panel) in *Swallenia alexandrae* populations over 5- and 10-yr periods. The 80% and 90% probability of correctly detecting a true trend are indicated by the horizonal red and blue dashed lines, respectively. Note different scales on the y-axis.

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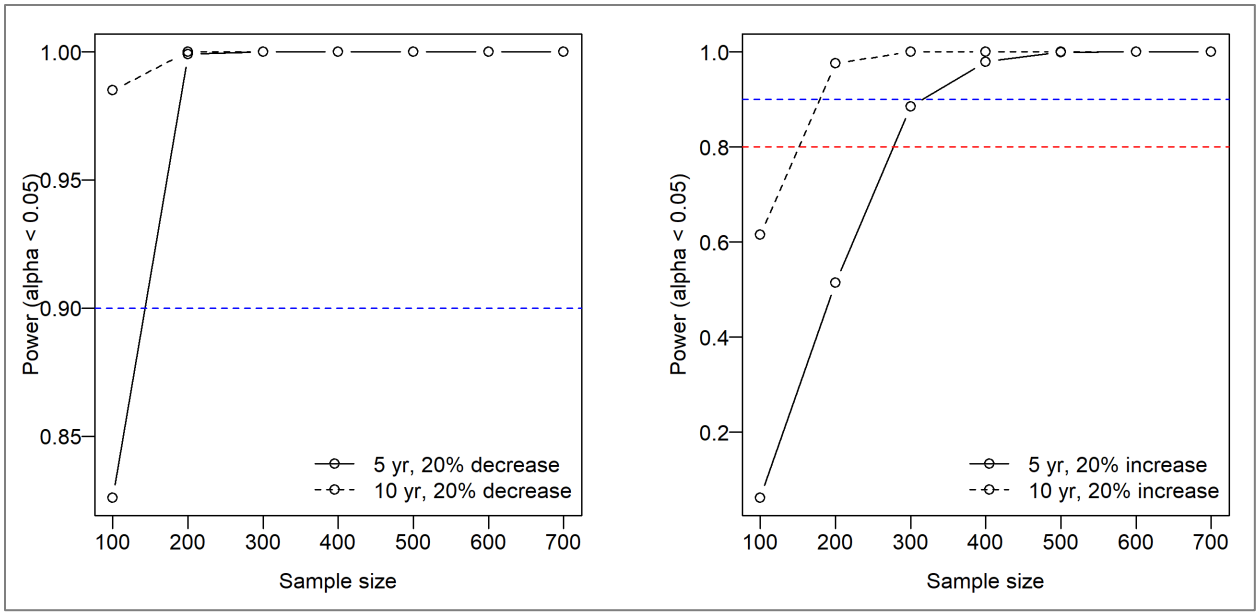

Figure 12. Power analysis for weighted-stratified subsampling (i.e., repeat sampling on same grid cells, but proportionally more grid cells surveyed in 0 and 1 density classes). Graphs illustrate the number of grid cells needed (i.e., sample size) to achieve sufficient power to detect 20% decrease (left panel) and 20% increase (right panel) in *Swallenia alexandrae* populations over 5- and 10-yr periods. The 80% and 90% probability of correctly detecting a true trend are indicated by the horizonal red and blue dashed lines, respectively. Note different scales on the y-axis.

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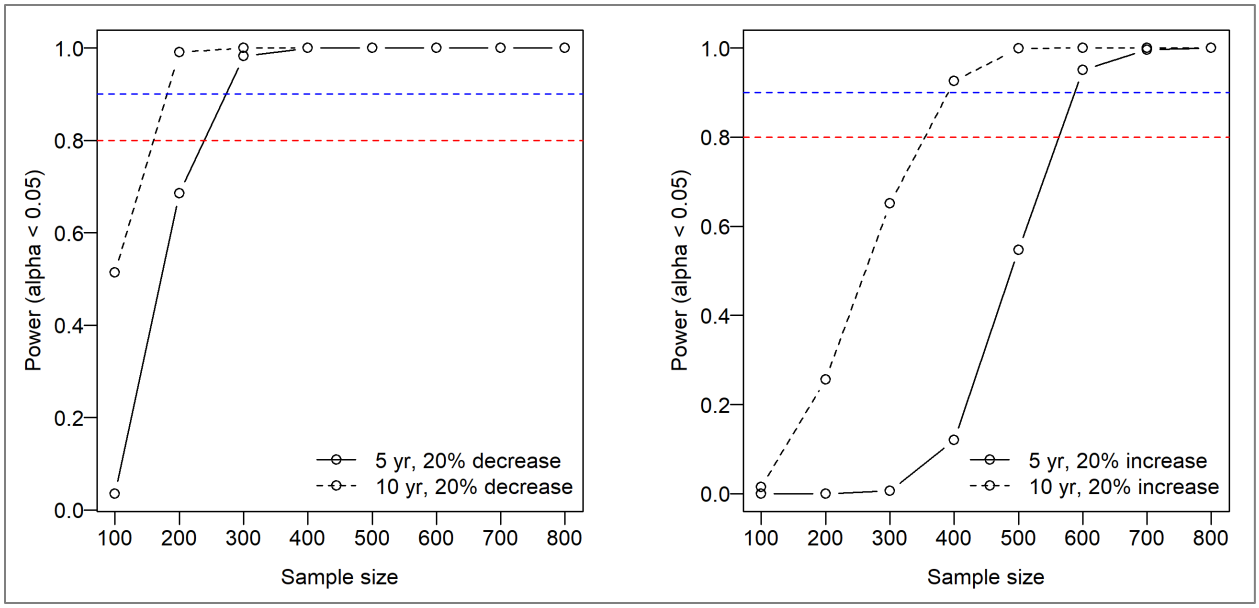

Figure 13. Power analysis for balanced-stratified subsampling (i.e., repeat sampling on same grid cells that represent equal number of grid cells across density classes) for *Swallenia alexandrae* illustrating number of grid cells needed (i.e., sample size) to achieve sufficient power to detect 20% decrease (left panel) and increase (right panel) in populations over 5- and 10-yr periods. The 80% and 90% probability of correctly detecting a true trend are indicated by the horizonal red and blue dashed lines, respectively. *USGS / DANIEL SHRYOCK*

Discussion

Survey efforts for *S. alexandrae* have ranged from photographic points and localized density measurements in the 1970s–1990s to more recent quantitative surveys during the 2000s. The establishment of a population-wide grid system by Michèle Slaton (2008) was instrumental in providing the basis for tracking trends in *S. alexandrae* abundance and distribution; however, changes in subsampling methods among surveys conducted throughout the 2000s make direct comparisons challenging. The approach has shifted from surveying the same subsample of grid cells across the three dunes each year for demography with periodic whole-population presence/absence surveys (Slaton 2008; 2007/08–2011), to surveying all grid cells using an abundance category approach and omitting demography (Kaiser 2015; 2011–2015), and most recently to surveying a different 10% random subsample of grid cells (including never occupied cells) using the abundance categories and adding demography as a count of stage classes on different individuals each year (2017–2019). The rationale for repeatedly shifting survey methods was not fully detailed in NPS reports, although reducing the labor for surveys, which is largely volunteer-based, was cited as one consideration (Hoines and Ellis, unpublished).

Our analyses using proportional odds logistic regressions on density and stage classes demonstrate population fluctuations during the 2007–2019 period, which were correlated with precipitation and temperatures during the summer/fall and winter/spring seasons prior to spring surveys. Spatially modeled climate data that are publicly available (PRISM) correlated well with data collected by local weather stations temporarily maintained on each dune (USGS) and the single long-term station installed in Eureka Valley (NPS). These climate data provided an accurate representation of seasonal precipitation and temperatures to use in our analyses, particularly after adjustment using regression equations.

Greater densities of *S. alexandrae* were related to antecedent summer maximum temperatures that were warmer than normal, suggesting either increased establishment of new individuals (seedling recruitment) or expansion of existing individuals through rhizomes (clonal growth), both of which would be detected during subsequent spring surveys. The C_4 photosynthetic strategy of *S. alexandrae* and other warm season grasses allows this species to assimilate carbon dioxide at high temperatures and support growth during May–September while maintaining low water stress on the dunes (Pavlik 1980). Hummocks of *S. alexandrae* can persist for many years (Pavlik and Barbour 1988), and similar to other C_4 psammophytic grasses, *S. alexandrae* likely allocates resources toward rhizome and ramet growth to withstand burial from shifting sands (Brown and Zinnert 2018; Liu et al. 2012; Pavlik 1980). It is unclear whether an increase in *S. alexandrae* densities during years with prior warmer than normal summer temperatures could reflect recruitment because seedlings were rare overall (0–15 total seedlings found across years and dunes), and summer rainfall amounts resembling the events that induce mass germination (e.g., Pavlik and Barbour 1988; coinciding with 2× long-term average for April–September rainfall in our Figure 6) were largely absent during years of grid cell surveys (Figure 6). Furthermore, annual surveys can only estimate the abundance of *S. alexandrae* seedlings that survived from prior summer emergence to the following spring (Pavlik and

Barbour 1988). Seedling mortality is typically high before spring (89% from October through March for a 1975 cohort, Henry 1979) or seedlings may grow in size and transition beyond the seedling stage by the time grid cells are subsequently surveyed in spring (seedlings from fall 1984 cohort became juveniles by April in Pavlik and Barbour 1986, 1988).

Proportionally fewer reproductive adults and more non-reproductive plants were correlated with cooler, wetter winter/spring conditions prior to survey. This result suggests that mild conditions during this season cue plants to invest in plant growth with the onset of spring and delay reproduction, which is in contrast to arid antecedent winter/spring conditions that can accelerate onset of reproduction and senescence for adults of perennial grasses (Munson and Long 2017). Early spring surveys for *S. alexandrae* may not distinguish between plants that are non-reproductive in a given year (e.g., suboptimal conditions for flowering) from those that delay reproduction due to seasonal weather conditions. Importantly, the snapshot-in-time approach to measure demography during density surveys may not capture the dynamics of plant establishment (i.e., seedlings emerging after summer rains) and the transition from non-reproductive adult to reproductive adult for parameterizing population viability analysis.

Effective rare plant monitoring is a balance between the benefits of a sound statistical design that informs managers of population declines and the labor costs of efficiently surveying range-wide distribution and abundance with NPS employees and volunteers. We present the following scenarios for sampling *S. alexandrae* moving forward that consider these costs and benefits while still incorporating aspects of previous work. Efforts may be maximized with a strategy that staggers subsampling grid cells for each monitoring goal (distribution, population changes, and demography) across years, rather than attempting to subsample to meet all three goals in every year. We acknowledge that planning for censuses is also dependent on two other rare species that NPS monitors but whose habitats are inversely distributed compared with that of *S. alexandrae* (Kaiser 2015)–Eureka Dunes evening primrose (*Oenothera californica* ssp. *eurekensis*) and shining milkvetch (*Astragalus lentiginosus* var. *micans*). Evaluation of the monitoring for these species may also demonstrate where sampling effort can be conserved while maximizing the information for analyzing trends in these rare dune endemics.

Distribution

The most recent whole-population survey of *S. alexandrae* distribution was conducted in 2015 and included measuring abundance classes across the entire grid system. Given the contraction in distribution documented by NPS surveys from 2011 to 2015 (Kaiser 2015), an updated whole-population survey is certainly warranted at this time. The consistently clustered nature of *S. alexandrae,* based on whole-population surveys conducted 2007–2015 (Figures 2B, 3B, 4B), and limited seed dispersal distances (Pavlik and Barbour 1985) indicate that future distribution surveys can be focused on previously occupied grid cells (573 cells at Main, Figure 2B; 114 cells at Marble, Figure 3B; 134 cells at Saline, Figure 4B) with adjacent grid cells searched following an adaptive cluster analysis to document any potential expansion in distribution (Philippi 2005). With the total number of grid cells for survey reduced to those previously occupied, the effort to characterize whole-population distribution using abundance classes would take approximately half the person-

days required to complete surveys compared with years when all grid cells on each dune were surveyed (i.e., 60–75 person-days in 2011, Cipra and Fuhrmann 2012; 50+ person-days in 2014 and 2015, derived from data sheets). Based on past surveys, contractions or shifts in the distribution of *S. alexandrae* are expected to be captured by a whole-population survey of previously occupied plus adjacent grid cells every 5–7 years. This repeated whole-population survey using abundance classes not only documents species distribution, but also allows comparison of whole-population change to inform adaptive capacity for the species (e.g., percent of whole-population decline over 5–10 years, Thurman et al. 2020) and provides the basis for more frequent population surveys (i.e., weighted-stratified subsampling, see below). In contrast, measuring only presence/absence on the previously occupied plus adjacent grid cells for distribution—while requiring even less time to execute—does not provide a population size estimate but can still be the basis for population change surveys in subsequent years (i.e., occupied-only subsampling, see below).

Population Changes

Random selection of grid cells from the entire grid system—with many unoccupied by *S. alexandrae* (i.e., 2017–2019 field efforts, Figures 2–4)—biases the estimate of abundance downward and increases uncertainly in the estimate. Our analysis of density trends indicates decreasing (Main Dune) or increasing (Marble Canyon and Saline Spur dunes) density during 2011–2015 whole-population surveys, but no detectable changes during 2007/08–2011 or 2017–2019 subsample surveys. We cannot conclude whether the latter outcome reflects true absence of a trend in density or a lack of power to detect meaningful change during these two time periods.

Our analysis suggests two related subsampling scenarios moving forward that would provide the power to detect a 20% decrease or increase in population numbers over 5 years by selecting from known occupied grid cells, as determined from the whole-population surveys in 2015. Both scenarios involve subsampling 300 1-ha grid cells across the three dune sites and categorizing them into the same density classes used from 2011 onward (0 = no plants, 1 = 1–10 plants, 2 = 11–60 plants, and 3 = >60 plants). Although this subsampling scenario requires 20% more grid cells per year than were sampled during 2017–2019 survey efforts, either approach will require similar or fewer person-days (56–65 person-days for 231–256 grid cells, derived from data sheets). Adjacent grid cell searches, as conducted in 2017–2019, would not be needed under these scenarios because the whole-population distribution survey would be conducted separately (as described in *Distribution* above). Furthermore, because demography needs to be measured consistently on the same plots/plants over time, categorization and canopy measurements of plants within the randomly-sampled grid cells would also be eliminated.

For both subsampling scenarios, the selected grid cells would be stratified over the three dune sites based on *S. alexandrae* presence–209 grid cells at Main, 42 grid cells at Marble Canyon, and 49 grid cells sampled at Saline Spur dunes. The difference between the two scenarios is in how the grid cells are selected–the first ("occupied-only subsampling") is a different random selection of grid cells from known occupied grid cells to survey each year, while the second ("weighted-stratified subsampling") is an initial random selection and repeated survey from known occupied grid cells with proportionally more grid cells in the 0 and 1 density classes to capture their greater variability.

Although the whole-population distribution survey using abundance classes (as described in *Distribution* above) provides a population size estimate, these more frequent subsampling surveys allow population changes to be correlated with weather variables on an annual basis, which may be useful for forecasting future population trends.

Demography

Changes in demography are classically measured by revisiting the same marked individual plants (yearly, at minimum; monthly to seasonally, optimally) to estimate the likelihood of moving from one life stage to another and then projecting this model into the future to assess population viability (Brigham and Schwartz 2003; Harper 1977; Solbrig 1980). This classical approach was used to monitor demography of *S. alexandrae* on one 50 m × 50 m plot at the northwest end of Eureka Dune in the mid-1980s (Pavlik and Barbour 1988). The two recent survey periods when *S. alexandrae* life stages were recorded at all three dune sites used a different approach to estimate demographic structure. Although the likelihood of plants moving from one life stage to another (e.g., seedlings to juveniles to reproductive adults) cannot be estimated with these more recent surveys, monitoring the change in demographic structure may be more sensitive to detecting declining populations than measuring density alone (Elzinga et al. 1998). We could not directly estimate the time required to collect stage class data from provided reports and databases. Gathering such detailed data is a large time investment, as indicated by the subsampling of total grid cells (all plants on same grid cells during 2007/08–2011, up to 26 plants per random grid cell during 2017–2019), and no demographic data recorded during 2011–2015 when time was devoted to whole-population surveys. This time investment during density surveys is still far less than that needed to conduct a classical demography study, as evidenced by the subsampling strategy employed by Pavlik and Barbour on their single much smaller study plot (Pavlik and Barbour 1988).

Optimally, demography monitoring should capture the important transitions of a species' life table for understanding population viability through time. This can be done by measuring individual size and growth (possibly using density/counts as a proxy if using marked quadrats for an integral projection model, where growth can be fit with a Poisson GLM; Ellner and Rees 2006), annual reproductive effort per individual (estimated through the allometry between individual plant size and number of tillers or seeds, as per Pavlik and Barbour 1988), seedling count (during late fall/early winter census), and survival/mortality (such as by using logistic regression on plants in quadrats). This monitoring is best conducted on, at minimum, an annual or seasonal basis over multiple years of varied conditions, given the need to account for variable fecundity, episodic seedling emergence, and the previously estimated lifespan of adult plants. For a long-lived species such as *S. alexandrae*, important considerations about the life stage transitions can inform the design of demography studies for managing the species into the future. We summarize information gleaned from the reports that can help inform such considerations in Appendix A for future reference.

Acknowledgments

Swallenia alexandrae survey and demography data from 2007–2019 were provided to USGS in multiple ArcGIS and Excel files and Microsoft Access databases by NPS. Published and unpublished reports were also provided by NPS upon request. At the time of publication, survey data were not publicly available from NPS. We thank Andrew Kaiser and Alison Ainsworth (NPS) for assistance with rectifying disagreements between files of survey and demography data. We thank Mary Crawford (USFWS) and Marie Denn (NPS) for providing valuable feedback to improve this manuscript. This work was supported through an agreement between Death Valley National Park and USGS, Western Ecological Research Center. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Appendix A. Considerations for Life Stage Transitions for *Swallenia alexandrae*

Classically, a demography model estimating the likelihood of moving from one life stage to another is developed by revisiting the same marked individuals through time. This model is then projected into the future to assess population viability (Brigham and Schwartz 2003; Harper 1977; Solbrig 1980). For *S. alexandrae*, estimates of life stage transitions best coincide with seasonal population visits including annual survival (spring), reproductive status and fecundity (late spring/summer), and seedling emergence (late summer/early fall). The local NPS weather station in Eureka Valley can identify in real time the above-average late summer rainfall that is likely to trigger *S. alexandrae* mass germination events so seedlings can be tagged and revisited over multiple years to measure seedling survival and transition into juvenile and adult stage classes. In contrast, it is important to assess survival and reproduction of adult plants across a variety of annual weather conditions, meaning that plants can be marked or mapped without waiting for a year of exceptional summer rainfall to trigger seedling emergence. For *S. alexandrae*, the important considerations about the life stage transitions mentioned below can inform the design of demography studies for managing the species into the future.

Seedling to Juvenile

The demographic study of *S. alexandrae* on northwest Main Dune found that approximately 60% of seedlings established in fall 1984 survived into the following spring to become juveniles (Pavlik and Barbour 1988), while only 11% of seedlings established in October 1975 survived into spring during a separate study (Henry 1979). These estimates are at one dune location during years with exceptionally high and slightly above-average summer rainfall, respectively (Figure 6), illustrating how variable conditions following seedling emergence can influence seedling survival over different cohorts, and expectedly, across dune locations. In the demographic study, 24% of the fall 1984 seedling cohort were hummock-forming juveniles after nearly 2 years. A few *S. alexandrae* seedlings were recorded during the 2007–2011 spring surveys when the same grid cells across all three dunes were consistently surveyed (1–5 seedlings across years and dunes), but because the individuals within the grid cells were neither tagged nor mapped, the fate of these seedlings is unknown.

Juvenile to Reproductive Adult

The mid-1980s demographic study indicated that *S. alexandrae* juveniles must survive more than 20 months to reach reproductive maturity, although the study ended before any juveniles transitioned to reproductive adults (Pavlik and Barbour 1988). Based on survival to the hummock-forming juvenile stage, we can only infer that no more than 24% of the 1984 cohort of seedlings became reproductive adults (Pavlik and Barbour 1988). As with seedling survival, this estimate is limited to the years and location of the study and cannot be generalized to the entire population. *S. alexandrae* is known to produce rhizomes with roots growing vertically or horizontally from nodes extending 50 cm from the plant (Henry 1979, but see Pavlik and Barbour 1988), but no estimate has been made of the relative contributions of sexual and asexual reproduction for this species. Confirmation of the parameters of

asexual reproduction during demography studies can also help refine plant density counts as conducted during distribution and population change surveys.

Reproductive Adult to Seed

Swallenia alexandrae is thought to maintain a soil seed bank from which seedlings establish following above average summer rainfall (Pavlik and Barbour 1988), making annual seed production by reproductive adults an important measure for assessing population viability. Seed production was estimated as a linear function of *S. alexandrae* plant canopy volume in both 1985 and 1986 on the northwest end of the Main Dune, with the slopes of the predictive equations varying by a multiple of 4 between years (Pavlik and Barbour 1988). Such large variation at a single location illustrates the importance of measuring reproductive output at all dunes over multiple years of varied conditions to elucidate how annual seed production is influenced by antecedent climatic conditions or other factors.

Seed to Seedling

Although soil seed bank longevity has not been directly measured for *S. alexandrae*, seeds are known to survive for some time in the soil based on seasonal seed bank sampling where germinable seeds were found in soils collected 10 months after seed dispersal (Pavlik and Barbour 1988). The only other attempt to estimate seed longevity was a germination and viability trial (100% viable, Pavlik and Barbour 1988), although the conditions were not analogous to soil seed bank conditions in habitat because seed was stored in a laboratory for 8 years. The lack of knowledge about soil seed bank dynamics complicates estimating the seed to seedling transition because an estimate of seed production from the current year does not represent soil storage of multiple generations of seeds. Estimating the likelihood of moving from seed to seedling is further complicated by the highly episodic nature of *S. alexandrae* germination (varying from 0 to 52 seedlings per 100 m^2 per year, Pavlik and Barbour 1988), as demographic modeling requires reliable estimates between stages.

Reproductive Adult to Senescence

Over the 600-day course of the 1980s *S. alexandrae* demography study, 8% of adult plants died, resulting in an estimated half-life of 16 years for established individuals at that time and place (Pavlik and Barbour 1988). An accurate estimate of senescence through time over the entire population is vital to determine if recruitment is exceeding or falling behind replacement. As with all other transitions, the estimate from the 1985–86 study is limited to the years and location of that study and cannot be generalized to the entire *S. alexandrae* population.

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