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5 **Demography and habitat associations of the basalt cactus: *Pediocactus nigrispinus***
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7 Running footer: Cactus Demography and Habitat Associations
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9 4 tables, 11 figures, 2 supplementary figures
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Accepted Article

18 **Abstract**

19 Cacti are iconic members of arid ecosystems. *Pediocactus nigrispinus* is a species of cactus
20 endemic to the Pacific Northwest and has been listed as a sensitive species due to its
21 vulnerability to habitat loss. Best conservation methods for this species are poorly understood,
22 due in part to a limited understanding of its demography and habitat associations that may help
23 define its occurrence. A demographic study in Washington state was implemented in 2016 to
24 provide a baseline of the population dynamics for *P. nigrispinus* and to enhance conservation
25 efforts for this sensitive species. Five years of size, fecundity, and survival information for the
26 cactus were recorded. A stochastic analysis was performed to assess survival and fecundity rates
27 for different climatic variables. To better understand the cacti's limited habitat, biotic and abiotic
28 associations were assessed in an additional 16 plots throughout Washington and Oregon by
29 spatial analysis of soil and climatic variables and in situ assessment of vegetation and ground
30 cover associations. These variables were then compared with population density, overall size of
31 the individuals, and number of fruits to assess how changes in associations may correlate with
32 changes in these population traits. The demographic study found no juvenile recruitment and a
33 declining population over the four years of analysis regardless of variation in annual
34 precipitation. The association analysis found no correlation between population density or
35 fecundity with associations but indicated higher fruit production in Oregon than in Washington.

36
37 **Key Points**

38 □ Plant community and microbial associations were similar for *P. nigrispinus* throughout its
39 range in Oregon and Washington.

40 □ No juvenile recruitment and a declining population size was observed for *P. nigrispinus* over
41 a four-year study.

42 ● A small increase in survival of the medium size class adult population could lead to
43 stabilization of the *P. nigrispinus* population

44
45 **Keywords:** Cactaceae, demography, habitat associations, matrix model, Washington

46 47 **Introduction**

48 Native to only the Americas, cacti are an iconic plant family that provide important
49 ecosystem functions. Cactus fruits and flowers provide food and water to wildlife (Wolf et al.
50 2002) and their roots stabilize soil (Le Honérou 1996). Many species also provide food and
51 medicine to humans (Shetty et al. 2011). Cacti are currently the fifth most threatened taxonomic
52 group throughout all plant and animal taxa with 75% of species declining and 31% currently
53 threatened or endangered (Goettsch et al. 2015, Hultine et al. 2016).

54 Because they are often rare, beautiful and charismatic, cacti are frequently targets of
55 illegal poaching, with 47% of species impacted by illegal harvesting (Goettsch et al. 2015). In
56 addition, because of their often extreme endemism, cacti are heavily impacted by habitat loss,
57 invasive species, and changes in temperature or precipitation due to climate change (Benavides
58 et al. 2020, Hultine et al. 2023). However, each species of cactus may be uniquely impacted by
59 these threats, emphasizing the need to monitor and conserve declining cacti populations and to
60 understand the dynamics of each species within its habitat.

61 Conservation efforts for endemic species can be enhanced through an understanding of
62 typical population dynamics and of the habitat associations and specificity of the species. One

63 common way to understand population dynamics is through transition matrix models, which can
64 assess the relative importance of different vital rates and life stages in a population (Caswell
65 2001). Such models can help researchers and land managers prioritize species for conservation
66 depending on the overall population survival year to year. These models can also help
67 researchers compare vital rate changes over time with changes in climatic variables, and project
68 future changes in population size through different environmental scenarios (Caswell 2001). This
69 is of particular importance for cacti because their survival and reproduction has often been tied to
70 climatic variables. For example, high winter temperatures and high annual precipitation
71 generally have been found to drive recruitment (Shyrock 2014, Félix-Burrel et al. 2021) whereas
72 high summer temperatures may increase mortality (Aragón-Gastélum et al. 2016).

73 Understanding habitat variation through a species' range allows researchers to assess the
74 endemism of the species, which in turn can give them insight into how susceptible the species of
75 concern may be to habitat disturbance or loss. Cacti are particularly likely to exhibit clumped
76 spatial distributions, indicating specific site resources or community associations that are of
77 particular importance to the species (Godínez-Alvarez et al. 2003, Butler et al. 2012). Some
78 species of cacti benefit from nurse plants or nurse rocks that help their seedlings establish in
79 harsh environments (Franco and Nobel 1989, Godínez-Alvarez et al. 2003). However, an
80 overabundance of grasses or shrubs can out-compete cacti and make it difficult for the
81 populations to persist (McAuliffe and Janzen 1986, Rojas-Sandoval et al. 2016). The difficulty
82 cacti have at competing with vigorously growing plants can make them very susceptible to
83 population loss in the face of invasive species (Hultine et al. 2023). In addition to these macro
84 community characteristics, cacti have been shown to have symbiotic relationships with
85 microorganisms. Mycorrhizal associations have been linked with improved nutrient uptake in

86 cacti (Cui and Nobel 1992), while bacteria in the soil and on cacti seeds have been shown to be
87 important associates that allow cacti seedlings to germinate and survive in harsh environments
88 (Puente et al. 2009, Lopez et al. 2012). Understanding each of these unique community
89 relationships can be a key for determining potential suitable cacti habitat, as well as best
90 practices for restoration of known habitat that has been degraded.

91 Many studies have addressed these questions of demographic trends and habitat
92 specificity for threatened species throughout South America, Central America and the Southwest
93 United States, where the majority of cactus species occur (Godínez-Álvarez et al. 2003,
94 Jiménez-Guzmán et al. 2024). However, there appears to be very limited information addressing
95 these questions in relation to cactus species that occur throughout the semi-arid lands further
96 north, perhaps related to the reduced number of cactus species at higher latitudes (Thompson et
97 al. 2024). *Pediocactus nigrispinus* is one such species of cacti that is endemic to only the drier
98 regions of the Pacific Northwest. *P. nigrispinus* is known to be locally abundant in Washington,
99 Idaho, and Oregon, but occurs in limited habitats, and is currently listed as a sensitive species in
100 Washington State by the United States Bureau of Land Management and the Washington Natural
101 Heritage Program (Bureau of Land Management 2021, Fertig et al. 2021, Miller et al. 2024).
102 Current threats to the species include habitat loss and illegal collection (Fertig & Kleinknecht
103 2020). Like many other cacti species (Arroyo-Cosultchi et al. 2016, Godínez-Álvarez et al.
104 2003), members of the genus *Pediocactus* have been shown to require years with high
105 precipitation events for populations to produce new recruits (Phillips et al. 1996, Hreha et al.
106 2001, Shyrock et al. 2014, Clark et al. 2015). As precipitation patterns change in the coming
107 years, understanding this potential demographic pattern in *P. nigrispinus* will be important for
108 conservation efforts for *Pediocactus* species. As well as having specific recruitment patterns,

109 members of this genus are often extremely narrowly endemic with both small ranges, and high
110 habitat specificity (Hochstätter, 2008). This study endeavored to enhance conservation efforts for
111 *P. nigrispinus* by building a baseline understanding of the cacti's demography and habitat
112 associations. To do this, the following research questions were addressed:

- 113 □ What are the abiotic associations found with *P. nigrispinus* and how do they change
114 throughout the cacti's range?
- 115 □ What are the plant community associations found with *P. nigrispinus* and how do they
116 change throughout the cacti's range?
- 117 □ Does *P. nigrispinus* have any bacterial specialists associated with its soil crust that may
118 assist in its survival?
- 119 □ What demographic vital rates or cactus size classes are the biggest contributors to overall
120 population survival and growth, how do these change with changes in annual
121 precipitation, and what is the quasi-extinction probability?

122

123 **Methods**

124 Study species

125 *Pediocactus nigrispinus* (Hochstätter) Hochstätter is a small, globose cactus endemic to
126 Washington, Oregon and Idaho. It is listed secure at a federal level, but as a sensitive species by
127 the Department of Natural resources in Washington State due to its extreme endemism (Fertig,
128 2021, Miller 2024). It has been found throughout Columbia Plateau scrubland with low sage
129 (*Artemisia rigida*), grasslands (*Poa secunda* and *Pseudoroegneria spicata*), and juniper forests
130 (*Juniperus occidentalis*). This cactus can grow up to 30 cm in diameter as solitary stems or in
131 clumps (Heil and Porter 2004). Like many other species of *Pediocactus*, *P. nigrispinus* has dry,

6

132 tough fruits that are unlikely to be dispersed by birds. Because *P. nigrispinus* seeds are extremely
133 small like the other members of the genus, they are likely dispersed by wind or water flow (Heil
134 et al. 1981).

135

136 Study Locations and Sampling Methods

137 Climatic information from the PRISM climate group (Oregon State University) 4 km time series
138 was used for all climate variables. Annual precipitation and temperature measurements were
139 defined as the 12 months preceding data collection to assess survival (June–June).

140 Seventeen sites of known *P. nigrispinus* occurrence, based on internet-accessible
141 herbarium (www.burkeherbarium.org) and iNaturalist (www.inaturalist.org) reports, were
142 sampled across Washington and Oregon; within each site, a single location was randomly chosen
143 on a gridded map to sample for habitat associations. All habitats had similar United States
144 Department of Agriculture (USDA) seed zone classifications with 152-304 mm average annual
145 precipitation and average winter minimum temperatures of -6 °C to -1 °C (Figure 1). Due to the
146 limited dispersal mechanisms of *P. nigrispinus*, the typical presence-absence method for
147 determining habitat preference may unreliably indicate some habitats were unsuitable. To
148 account for this, no attempt was made to describe habitat preference for *P. nigrispinus*. Instead,
149 habitats where it was known to occur were selected (Airi et al. 2000, Burkhart 2013) and percent
150 cover and number of fruits were used to compare characteristics of the different known
151 populations in relation to their associations.

152 Line point intercept plots were established as three 15 m transects running at 0°, 120° and
153 240° from the center of each location established for habitat association measurements with a 2
154 m buffer around each line to prevent trampling. Plot diameter was 34 meters. Measurements of

155 percent cover by species were made for each transect and species inventory was conducted
156 within the entire plot. To assess if there were any differences in cactus populations among the
157 seventeen sites, three metrics were used: (1) percent cover, determined by measuring the
158 diameter of every cactus within the plot using ImageJ software (Schneider et al. 2012) from
159 digital photographs of a square meter quadrat, (2) the number of fruits produced per plot,
160 counted as fruits and fruit scars, and (3) cactus size class distribution of plots.
161
162 Habitat association and population structure data analysis
163 To assess the number of distinct communities that *P. nigrispinus* occurs within, a habitat
164 similarity analysis was performed on a species presence-absence matrix for each plot through
165 R's Vegan package (Oksanen 2022). Genera that did not reliably have the elements required for
166 in-field identification to species were only identified to genus. Because sampling occurred
167 throughout the summer, ephemeral wildflowers that may not have been present in the plots
168 throughout the entire summer were not used in the analysis. While these less common species
169 could be potential indicators of *P. nigrispinus* habitat, no absence plots were recorded and using
170 indicator species without presence/absence sampling would be unreliable. Differences in species
171 composition were assessed using the Bray-Curtis method and the cluster analysis was done with
172 the Ward method (Bray and Curtis 1957, Ward 1963, Pakgohar et al. 2021). Species used for this
173 analysis were any that occurred in more than two sites or in one site with at least 5% cover. A
174 follow-up silhouette width measurement on the cluster analysis was used to determine how many
175 different communities should be described. Jaccard beta diversity was chosen as a beta diversity
176 analysis method that has low sensitivity to potential undersampling errors and works well for

177 presence/absence data (Jaccard 1912, Schroeder and Jenkins 2018). Jaccard beta diversity was
178 calculated across all sites, and across all identified communities.

179 To assess specificity of habitat type, species found on plots were grouped based on their
180 similar characteristics (functional groups). Functional group classifications were: annual grass,
181 perennial grass, forb, shrub, or tree. Percent cover of each canopy layer was added, resulting in a
182 total cover that could exceed 100%, and an ANOVA was used to assess differences in cover of
183 each functional group between the communities as well as for total cover. Slope, aspect,
184 elevation, and rock cover were also compared between communities using an ANOVA (Fisher
185 1925).

186

187 Soil crust associations

188 Half the sites of known *P. nigrispinus* occurrence were sampled for soil microbial composition.

189 At nine randomly chosen plots, a 1 cm deep soil crust sample was collected from the base of two
190 cacti that occurred closest to the plot center and mixed to constitute a single sample. An

191 additional soil crust sample was also taken, near *Poa secunda* or *Pseudoriginaria spicata*,

192 whichever species was most abundant and nearest the plot center (although two samples were

193 lost). DNA from 250 mg of each soil sample was extracted with the Qiagen soil power pro kit

194 and sent to Mr. DNA (Shallowater, Texas) for analysis using the 16s rRNA primer for associated

195 bacteria and archaea. Sequences were analyzed using Qiime2 (Bolyen et al. 2019). The primers

196 on the demultiplexed samples were removed using Cutadapt. This was followed by DADA2

197 filtering and denoising with a trim length of 120 (Callahan et al. 2016). Amplicon sequence

198 variant (ASV) clustering at 99% into taxonomic groups was through Qiime2's Greengenes Naive

199 Bayesian classifier. Rarefaction of sequences by mean sequencing depth did not noticeably

200 change abundances, or trends between groups. All results shown are from non-rarefied data.
201 Simpson's and Shannon diversity indices were calculated to assess differences in diversity
202 (Shannon and Weaver 1949, Simpson 1949), and a Multinomial Species Classification (CLAM)
203 test was run in R's Vegan package to find any species that may specialize with *P. nigrispinus*
204 (Chazdon et al. 2011, Oksanen et al. 2022).

205

206 Demographic data collection

207 Demographic data was collected at The Wild Horse Wind and Solar Facility (Wild Horse)
208 located between the cities of Ellensburg and Vantage, Washington (47° 1' N, 120° 10' W). Wild
209 Horse is a 10,000 acre site owned by Puget Sound Energy and most of the land is protected
210 under a conservation easement agreement and is open to recreation. The area is sagebrush-steppe
211 and classified as semi-arid with 152–304 mm of precipitation per year and average winter
212 minimum temperatures reaching about -6 °C.

213 One 2 m × 50 m plot and three 2 m × 40 m plots were established in June 2016 at Wild
214 Horse by students in a Central Washington University Biological Field Techniques class. Each
215 cactus in the plots was tagged with a unique ID number (n = 418 individuals). Size was measured
216 with diameter to be consistent with past studies on *Pediocactus* cacti (Shyrock et al. 2014,
217 Sivinski & McDonald 2007, Clark et al. 2015), and because diameter has been shown to be an
218 accurate measurement of flower production in another globose cacti species (McIntosh et al.
219 2019). The diameters were measured with a ruler, and the number of fruits were counted.

220 Clumped cacti, where it was impossible to distinguish between branches or clonal ramets versus
221 closely neighboring individuals, were given only one tag, and the average diameter of the clump
222 was applied to each individual in the clump. Normal fruit counts were still used for these stems,

223 as averaging the fruits biased the clumped fruit counts towards zero. Data for each cactus was re-
224 collected during the same class, with different students in June 2017, 2018, 2019 and 2022. Due
225 to the COVID-19 global pandemic, no data were collected in 2020 or 2021.

226

227 Matrix models

228 The population was divided into five classes based on diameter, to reflect how different sizes
229 may contribute to vital rates: seedlings (< 1 cm), non-fruiting adults (1–4 cm), small fruiting
230 adults (4–7 cm), medium fruiting adults (7–10 cm), and large fruiting adults (>10 cm). The non-
231 fruiting adult size class was based on the size at which fruiting was observed to occur, and
232 subsequent size classes were set to match the bin size for the non-fruiting adults. From 5 years of
233 data, four annual matrices were built to assess differences in transitions. The model was built
234 using the style of the Lefkovitch stage-classified model (Lefkovitch 1965, Godínez–Álvarez et
235 al. 2003). The equation used was:

236
$$n(t+1) = An(t)$$

237 where A is the population matrix and $n(t)$ is a vector of the number of individuals in each size
238 class at time t , in years (Caswell 2001). This matrix output has the dominant eigenvector λ as the
239 population growth rate. If λ is above 1, the population is considered increasing and if it is below
240 1 the population is declining (Caswell 2001). Percentile bootstraps were used to estimate
241 confidence intervals for λ . For each set of yearly transitions, 1000 bootstrapped iterations were
242 used. The 2.5th and 97th percentile of all the generated λ values were used as the confidence
243 intervals (Caswell 2001, Scheiner and Gurevitch 2001). No recruitment was seen during the
244 study period, so recruitment was estimated through greenhouse germination experiments. Seeds
245 were sown in a desert soil mix consisting of 50% equal amounts of perlite, vermiculite, and small

246 gravel mixed with 50% potting soil. Air temperature was kept between 21–38 °C and irrigated
247 three times a week for the first two months and subsequently once a month. The final greenhouse
248 germination rate (79%) was calculated by counting the seedlings that germinated and survived
249 after six months. The greenhouse germination rate was then multiplied by 0.1% to estimate field
250 recruitment (Martínez et al. 2010). Field recruitment was multiplied by the average number of
251 seeds produced by cactus in experimental plots each year to determine seedling establishment.
252 Because no seedling to juvenile transition rate was observed, this had to be estimated as well. To
253 do this, simulations with different values for the seedling to non-fruiting adult transition were
254 evaluated. A static seedling to juvenile transition rate of 0.1 was used in the final matrix and
255 subsequent simulations because values ranging from 1% to 100% did not significantly affect the
256 estimate of λ .

257 June fruit counts were used to estimate fecundity (no new fruits or fruit scars were found
258 in fall surveys) and the category of “seed” was not included in the transition matrix because
259 while long-term seed viability is unknown for *P. nigrispinus*, other studies have found that
260 globose and rupicolous cactus seeds don’t tend to retain viability in the soil for more than two
261 years (Martinez et al. 2010, Contreras and Valverde 2002). The matrix model was subsequently
262 used to determine the elasticity, or proportional contribution of each vital rate to overall
263 population growth and survival, between years. All demographic analysis was done using the
264 popbio package in R (Stubben and Milligan 2007, R Core Team 2022).

265

266 Quasi-extinction probability

267 The quasi-extinction probability over the next 75 years was estimated stochastically with quasi-
268 extinction defined as the population reaching less than 10 individuals (Shyrock et al. 2014).

269 Three scenarios were used for the probabilities and each scenario was iterated 500 times. The
270 first scenario modeled the probability of quasi-extinction based on current observed climate
271 conditions. Each yearly transition matrix had an even probability of being chosen for this model.
272 The second scenario modeled the probability of quasi-extinction if drought conditions become
273 more common. Transition values from years with less annual precipitation than average were
274 given 2× probability of being chosen for this simulation. Finally, we simulated a scenario with
275 years of increased precipitation given 2x probability. The missing sampling years of 2020 and
276 2021 made it impossible to assess survival based on climatic variables in 2022, so this last year
277 was not used in the quasi-extinction projection.

278

279 **Results**

280 Abiotic and habitat associations

281 Two different plant community associations were apparent from the cluster analysis: Washington
282 and Oregon. The two communities also separate by different USDA seed zones, which are based
283 on winter minimum temperature and average annual precipitation and are useful for
284 understanding to which climatic zones a native plant species is adapted (Bower et al. 2014). The
285 Washington and Oregon USDA seed zones had the same limited precipitation, but the
286 Washington seed zone had colder average winter temperatures than Oregon. Soil complexes
287 were similar between all sites, with all the sites being on volcanically derived soil, typically
288 basalt (Figure 1).

289 *Pediocactus nigrispinus* was commonly associated with *Artemisia rigida* in Washington
290 state, and with *Juniperus occidentalis* in Oregon (supplementary Figure 1). However, the
291 bunchgrass communities were similar between the two states, with *Poa secunda* and

292 *Pseudoroegneria spicata* present on every plot. The invasive annual grass *Bromus tectorum* was
293 also seen on every site (supplementary Figure 1) and did not have any significant impact on the
294 population metrics of either percent cover or fecundity.

295 Beta diversity was similar through Washington and Oregon, but there was three times
296 more replacement than richness contribution to the beta diversity in Oregon, while Washington
297 had a balanced distribution of effects of the two (Table 1). ANOVA analysis of all the habitat
298 associations indicated that slope and canopy height were the only variables that significantly
299 differed between Washington and Oregon (Table 2). The slope and canopy height in Oregon
300 were both double what was observed in Washington. While most of the cacti plots were on
301 southern facing slopes, cacti also occurred on northern slopes in both states, and there was no
302 significant difference in the aspect between states (Table 2).

303 304 Microbial associations

305 Twenty-two different microbial phyla were found throughout the study, and abundance was
306 slightly higher in *P. nigrispinus* than the bunchgrasses (Figure 2). This increase in abundance
307 was seen in both the raw data and rarified data. The most abundant phyla in the samples were
308 Actinobacteria, Cyanobacteria, Proteobacteria and Bacteroides (Figure 2). On average, these four
309 phyla comprised about 90% of the abundance for samples both from cactus and from
310 bunchgrasses. When comparing relative abundance for the most common phyla, Cyanobacteria
311 and Bacteroides trended higher in the crust of *P. nigrispinus* (Figure 3). Actinobacteria and
312 Proteobacteria were lower in *P. nigrispinus* than in the crust of the bunchgrasses. However, a
313 permanova test found that there was no significant difference in the relative abundance between
314 the cacti-associated crust and the bunchgrass-associated crust in any of these most common

315 phyla (Figure 3). There was no difference in either Simpson's diversity or Shannon diversity
316 between the soil crusts of *P. nigrispinus* and the soil crusts of the bunchgrasses.

317 A multinomial species classification (CLAM) test found that most of the taxa were
318 shared between the crust of the bunchgrasses and *P. nigrispinus* (Figure 4). However, 12% of
319 organisms were found only in crusts at the base of the cacti (Figure 4). None of these were
320 identified to species, but the majority of the bacteria found only on *P. nigrispinus* belonged to the
321 family Acetobacteraceae.

322

323 Demography

324 The mean cactus diameter throughout all the plots was 5.8 cm, but diameters up to 20 cm were
325 observed. There was no difference in size, number of individuals, or percent cover between the
326 two states, but the Oregon cacti had significantly more fruits (supplementary Figure 2). The
327 median number of fruits in Oregon was twice that of what was seen in Washington. The lowest
328 number of fruits observed in a single plot in Oregon was 47, whereas the lowest number of fruits
329 in Washington in a plot was 17. None of the population or fecundity metrics assessed were
330 significantly impacted by the biotic or abiotic associations characteristics assessed (elevation,
331 slope, aspect, canopy height, percent canopy cover, or percent rock cover).

332 Of the 415 cacti tagged during the study, 344, or 83% of the cacti survived at the end of
333 the six years (Figure 5). The small size class (4–7 cm) was the most abundant size class at the
334 beginning of the study, comprising just over half of all the cacti in the site. By the end of the six
335 years, the medium size class (7–10 cm) was the most abundant, and the large size class (>10cm)
336 had more than doubled in the number of individuals compared to 2016 (Figure 5).

337 The overall λ for the population was below one for every year of the study. Yearly
338 lambda values fluctuated between 0.93 and 0.97 with the bootstrapped confidence intervals never
339 reaching unity (Table 3). Reversion to smaller sizes was observed in every class, particularly in
340 the large size class where it was the dominant vital statistic for that size class for the first three
341 years of the study (Table 3). Greenhouse germination resulted in a germination rate of 79%. The
342 greenhouse germination rate was reduced by a factor of 1000 to reflect poor seedling survival in
343 the field (Martínez et al. 2010) and then multiplied by the average seed output on the site (12
344 seeds), resulting in the reproductive values of each size class. The medium and large size classes
345 had much higher reproductive output than the small size class (Table 3) such that the median
346 number of fruits produced by the medium size class was double that of the small size class. A
347 generalized linear model using a negative binomial distribution indicated no significant
348 difference in the number of fruits produced by size class between multi-stem cacti and single
349 stem cacti (Figure 6).

350 The average matrix derived from all the years showed that stasis was the primary vital
351 rate for every size class (Figure 7). Only the non-fruiting adults had a balanced proportion of
352 individuals that remained the same size between years and individuals that grew to the next size
353 class (Figure 7). Similarly, stasis had the highest elasticity value (proportional contribution to
354 overall population growth and survival) both overall and for every size class except for non-
355 fruiting adults. When combined between all size classes, the elasticity of stasis was nearly three
356 times that of the elasticity for growth rate, which had the second highest elasticity value. The
357 medium size class had the overall highest elasticity values, which was nearly double the
358 elasticity value of small fruiting and large fruiting individuals (Table 4).

359 A quasi-extinction projection indicated that the population is very likely to hit quasi-
360 extinction levels within the next 75 years (Figure 8). While all three projections indicate a
361 potential for reaching 100% probability of quasi-extinction, there is a delay in the probability
362 change for the increased precipitation projection. Quasi-extinction probability for the observed
363 climate and increased drought projections at year 65 is 20 percent, while the probability for the
364 increased precipitation projection lags behind at 10 percent. Modeling changes in the lambda
365 value with different levels of stasis found that increased stasis for the medium size class led to
366 the biggest increase in overall population survival. Stasis of the medium size class increasing to
367 69% from the average 54% gave a lambda value high enough for the population to begin
368 increasing (Figure 9). Any values below this 15% increase were not enough to stabilize the
369 population (Figure 9)

370

371 **Discussion**

372 Habitats for known populations of *P. nigrispinus* in Washington and Oregon were generally
373 similar, differing in shrub and tree associations, canopy heights, and slope. These differences did
374 not affect cactus mean diameter, number of individuals, coverage, or fecundity. Because absence
375 plots were not measured, however, we cannot be certain that the observed habitats are optimal
376 for the species or optimal for restoration efforts. The median number of fruits produced per plot
377 was higher for plots in Oregon, although the observed population in Washington was declining,
378 with no recruitment observed in over four years.

379

380 Abiotic and habitat associations

381 The two main objectives of both the abiotic and the habitat association assessments in this study
382 were to describe associations found within known populations and describe the differences
383 between them. Describing differences in population metrics between community types was
384 accomplished using a presence-only sampling approach. Such an approach must be interpreted
385 with care because the subjective nature of only sampling known populations may introduce bias.
386 Because absence plots were not measured, we cannot be certain that the observed habitats are the
387 ideal habitats for the cactus and may not be appropriate for use to predict suitable habitat.
388 However, because the small seeds of *P. nigrispinus* have been suggested to be dispersed by
389 moving with the soil, not independently, through strong winds or water (Heil et al. 1981), and
390 have limited movement potential, presence-absence data would likely have generated bias by
391 overestimating poor habitat suitability, rather than an inability to disperse into the area.

392 Plant associations were generally very similar throughout the distribution of *Pediocactus*
393 *nigrispinus*, with plots dominated with the bunchgrasses *Poa secunda* and *Pseudoroegneria*
394 *spicata*. The differences observed throughout the two states were in the shrub and tree
395 associations. In Washington, *Artemisia rigida* was found in every plot except one that may have
396 had unusual associations due to a fire that had burned the area two years prior. *Juniperus*
397 *occidentalis* was observed with the cacti in Oregon, as well as shrub species much taller than
398 what has been found in association with *P. nigrispinus* in Washington.

399 Oregon's habitat associations with *P. nigrispinus* were much more varied. While both
400 Oregon and Washington had similar overall beta diversity, the primary driver of diversity in
401 Oregon was one species being replaced by another throughout the sites (replacement), whereas
402 the beta diversity in Washington was evenly influenced by replacement and differences in
403 species richness. It is possible that the prominence of replacement as the driver of beta diversity

404 was partially due to the large spatial spread of points throughout Oregon because replacement is
405 often seen across wide latitudinal gradients (Soininen et al. 2017). However, this cannot be the
406 sole reason for the high turnover seen in Oregon, because the sites that primarily displayed high
407 beta diversity were spatially close together.

408 In addition to the spatial spread, there may be high abiotic and biotic heterogeneity
409 between these sites (Soininen et al. 2017), indicating that *P. nigrispinus* has multiple potential
410 community associations throughout Oregon. It is possible that the Washington *P. nigrispinus*
411 populations had lower site variability because they are at the Northern edge of their range, and
412 the difficulty surviving colder winters may make them less flexible to habitat variation. Studies
413 on the cold tolerance of some cacti species have found that having more specific associations
414 with nurse plants and rocks are key for the cacti to survive at the northern edge of their range
415 (Parker 1987, Fleming and Valiente-Banuet 2002). This study did not assess particular
416 associations that *P. nigrispinus* may have with any nurse plants or rocks, but this could be an
417 important part of future studies in Washington, where *P. nigrispinus* is at the edge of its range. In
418 addition to showing an increased variability of habitat, the Oregon cacti populations produced
419 more fruits than Washington populations. Fruit production in Oregon may have been partially
420 influenced by higher precipitation levels and higher winter minimum temperatures that occurred
421 the spring prior to sampling, a phenomenon reported in prior studies (Parker 1989).

422 The only two habitat variables that were significantly different between the two states
423 were canopy height and slope, however neither of these variables had a significant impact on
424 fruit production between the sites so it is unlikely either of these factors contributed to the
425 difference in fecundity. This difference in slope and canopy height between the two states may

426 indicate, however, that the specificity of these environmental variables are less important to the
427 cacti than the other variables that did not differ between states.

428

429 Microbial associations

430 Cyanobacteria, Actinobacteria, Proteobacteria, and Bacteroidetes were the most common phyla
431 in the crust of both *P. nigrispinus* and the bunchgrasses. This is consistent with patterns found
432 from other studies in arid systems (Maier et al. 2014). *Pediocactus nigrispinus* was associated
433 with a generally higher abundance of microbes in the soil, and the relative abundance was
434 slightly different between *P. nigrispinus* and the bunchgrasses. Cyanobacteria were slightly
435 higher in the crusts of *P. nigrispinus* and slightly more Actinobacteria were associated with the
436 bunchgrasses, however these were not significant differences. Actinobacteria and Cyanobacteria
437 proportionality changes based on soil moisture content (Rego et al. 2019); therefore, these
438 differences may be indicators of the different moisture content at the base of these plants.
439 Additionally, 12% of the organisms found were only associated with *P. nigrispinus*. Many of
440 these were in the family Acetobacteraceae (Tang et al. 2021). This is a unique microbial family
441 that are often nitrogen fixers and have been recommended as potential inoculants for soil crust
442 restoration. Cacti have previously been shown to be associated with bacteria that can fix nitrogen
443 and allow seedlings to establish (Puente et al. 2009). Therefore, it is possible that *P. nigrispinus*
444 has some unique associations with members of Acetobacteraceae that can aid the growth and
445 survival of seedlings.

446

447 Demography

448 The population of *P. nigrispinus* was declining throughout the entire duration of the study with
449 lambda values consistently above 0.9 but below 1. No new recruitment was observed on the site
450 during the study, which is a common result from cacti demographic studies and is often
451 attributed to not seeing years with high enough precipitation levels to either induce seed
452 germination or maintain seedling survival (Contreras and Valverde 2002, Martínez et al. 2010,
453 Mandujano et al. 2015). While some studies have found species of cacti that may have improved
454 population growth in the face of climate change, many cactus population studies have found λ
455 that are much lower than 1, particularly in endemic species (Godínez-Álvarez et al. 2003).
456 Stasis, defined as the persistence of individuals within a size class between years, was the vital
457 rate with the highest elasticity, and the medium size class had highest elasticity. Thus, adults
458 surviving between years is most important for overall population survival, consistent with
459 findings from other demographic studies on cacti, particularly those for endemic and globose
460 rupicolous cacti (Contreras and Valverde 2002, Godínez-Álvarez et al. 2003, Martínez et al.
461 2010, Shyrock et al. 2014, Mandujano et al. 2015). Every size class older than the juvenile stage
462 showed some amount of reversion to a smaller size class between years. This is common in cacti
463 and is considered a response to drought (Martínez et al. 2010, Shyrock et al. 2014). However, it
464 is also true that a year of intense precipitation may lead to a period of high recruitment that could
465 both increase the population growth rate to a λ above 1 and potentially improve population
466 projections (Shyrock 2014, Arroyo-Cosultchi et al 2016, Antonini et al. 2020, Félix-Burrel et al.
467 2021).

468 The quasi-extinction projection indicated that the population may decrease to fewer than
469 10 individuals within the next 75 years. While all three climate scenarios were very similar, there
470 was a lag in the simulation with higher precipitation years that may reflect a correlation between

471 precipitation and survival in these cactus populations. Precipitation projections from the National
472 Oceanic and Atmospheric Administration (NOAA) indicate that we may see a 5% decrease in
473 summer precipitation in Washington state, and a 70% decrease in average snowpack by the mid
474 21st century (Kunkel et al. 2022). However, this may also be coupled with more frequent extreme
475 precipitation events, and the specific impact each of these precipitation variables may have on *P.*
476 *nigrispinus* is largely uncertain. Accounting for additional climatic variables, looking at
477 precipitation by season, and assessing how these climatic variables interact on these sites would
478 make our demographic models more robust (McIntosh et al. 2019, Shyrock et al. 2014, Larios et
479 al. 2020). We were unable to model how changes in annual temperature would affect populations
480 because average, high, and low temperatures were relatively consistent between years observed.

481 While the demographic projection indicates the possibility for a steep decline in the
482 numbers of *P. nigrispinus* within the next 75 years, the simulated increase in stasis of the
483 medium size class indicated that a relatively small increase in survivorship could lead to an
484 increasing population. The importance of stasis for the persistence of these cacti populations in-
485 between recruitment events suggests that protection of the habitat of adult populations is critical
486 for the continued existence of this species.

487

488 **Conclusions**

489 *Pediocactus nigrispinus* occurs in a relatively narrow habitat, particularly in Washington State
490 where it is at its most northern range. Overall survival of adult *Pediocactus nigrispinus*,
491 particularly middle size classes, is critical for population maintenance. Any habitat restoration
492 efforts for disturbed *P. nigrispinus* sites may be aided by the addition of inoculating the soil with
493 the four prominent bacterial phyla that comprise the cacti's soil crust, with particular focus on

494 the bacterial family Acetobacterace, which may be of particular importance. Future studies using
495 presence-absence sampling may improve habitat association information and enable drawing
496 more specific conclusions about plant association preferences. The declining population numbers
497 and narrow endemism support the importance that this species should be monitored and studied
498 for future conservation efforts.

499

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505

506 **Conflict of Interest**

507 The authors declare that the research was conducted in the absence of any commercial or
508 financial relationships that could be construed as a potential conflict of interest.

509

510 **Author Contributions**

511 **Zarha S. Dillon-Zuppelli:** Conceptualization, Methodology, Investigation, Formal Analysis,
512 Resources, Software, Writing-Original draft preparation, Visualization, Funding acquisition.

513 **Mary E. Poulson:** Conceptualization, Methodology, Investigation, Formal Analysis, Resources,
514 Writing -Reviewing and Editing, Supervision, Project administration.

515 **Eric A. Graham** Conceptualization, Methodology, Investigation, Formal Analysis, Resources,
516 Writing -Reviewing and Editing, Supervision, Project administration.

517 **References Cited**

- 518 Airi S, Rawal RS, Dhar U, Purohit AN. 2000. Assessment of availability and habitat preference
519 of Jatamansi – a critically endangered medicinal plant of west Himalaya. *Current Science*
520 79:1467–1471. <http://www.jstor.org/stable/24105109>
- 521 Antonini Y, Dirzo R, de Cassia Quitete Portela, R. 2020 Are protected populations of two
522 globular cactus species facing a demographic explosion or just a “bonanza” year? *Journal of*
523 *Arid Environments*. 179:104192. DOI: 10.1016/j.jaridenv.2020.104192
- 524 Aragón-Gastélum JL, Badano E, Yáñez-Espinosa L, Ramírez-Tobías HM, Rodas-Ortiz JP,
525 González-Salvatierra C, Flores J. 2016. Seedling survival of three endemic and threatened
526 Mexican cacti under induced climate change. *Plant Species Biology*. 32:92–99.
527 DOI:10.1111/1442-1984.12120
- 528 Arroyo-Cosultchi G, Golubov J, Mandujano MC. 2016. Pulse seedling recruitment on the
529 population dynamics of a columnar cactus: Effect of an extreme rainfall event. *Acta*
530 *Oecologica*, 71: 52-60. DOI: 10.1016/j.actao.2016.01.006
- 531 Benavides E, Breceda A, Anadón JD. 2020. Winners and losers in the predicted impact of
532 climate change on cacti species in Baja California. *Plant Ecology* 222:29–44. DOI:
533 10.1007/s11258-020-01085-2
- 534 Bolyen E, Rideout JR, Dillon MR, Bokulich NA, Abnet CC, Al-Ghalith GA, Alexander H, Alm
535 EJ, Arumugam M, Asnicar F, Bai Y, Bisanz JE, Bittinger K, Brejnrod A, Brislawn CJ,
536 Brown CT, Callahan BJ, Caraballo-Rodríguez AM, Chase J, Cope EK, Da Silva R, Diener C,
537 Dorrestein PC, Douglas GM, Durall DM, Duvall C, Edwardson CF, Ernst M, Estaki M,
538 Fouquier J, Gauglitz JM, Gibbons SM, Gibson DL, Gonzalez A, Gorlick K, Guo J, Hillmann
539 B, Holmes S, Holste H, Huttenhower C, Huttley GA, Janssen S, Jarmusch AK, Jiang L,

Dillon-Zuppelli ZS, Poulson ME, Graham EA. 2024. Demography and habitat associations of the basalt cactus: *Pediocactus nigrispinus*. Northwest Science 98(1): *in press*.

540 Kaehler BD, Kang KB, Keefe CR, Keim P, Kelley ST, Knights D, Koester I, Kosciolk T,
541 Kreps J, Langille MJI, Lee J, Ley R, Liu Y-X, Loftfield E, Lozupone C, Maher M, Marotz C,
542 Martin BD, McDonald D, McIver LJ, Melnik AV, Metcalf JL, Morgan SC, Morton JT,
543 Naimey AT, Navas-Molina JA, Nothias LF, Orchanian SB, Pearson T, Peoples SL, Petras D,
544 Preuss ML, Pruesse E, Rasmussen LB, Rivers A, Robeson II MS, Rosenthal P, Segata N,
545 Shaffer M, Shiffer A, Sinha R, Song SJ, Spear JR, Swafford AD, Thompson LR, Torres PJ,
546 Trinh P, Tripathi A, Turnbaugh PJ, Ul-Hasan S, van der Hooft JJJ, Vargas F, Vázquez-Baeza
547 Y, Vogtmann E, von Hippel M, Walters W, Wan Y, Wang M, Warren J, Weber KC,
548 Williamson CHD, Willis AD, Xu ZZ, Zaneveld JR, Zhang Y, Zhu Q, Knight R, Caporaso
549 JG. 2019. Reproducible, interactive, scalable and extensible microbiome data science using
550 QIIME 2. Nature Biotechnology 37:852–857. DOI: 10.1038/s41587-019-0209-9
551 Bower AD, St Clair JB, Erickson V. 2014. Generalized provisional seed zones for native plants.
552 Ecological Applications Ecological Society of America 24:913–919. DOI: 10.1890/13-
553 0285.1
554 Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of Southern
555 Wisconsin. Ecological Monographs 27:325–349. DOI: 10.2307/1942268
556 Bureau of Land Management. 2021. Final State Director’s Special Status Species List. OR-P-
557 IM-2021-004. United States Department of the Interior, Bureau of Land Management,
558 Oregon State Office, Portland OR, August 3, 2021. Available online at
559 <https://www.blm.gov/policy/or-p-im-2021-004>
560 Burkhart EP. 2013. American ginseng (*Panax quinquefolius* L). floristic associations in
561 Pennsylvania: guidance for identifying calcium-rich forest farming sites. Agroforestry
562 Systems 87: 1157–1172. DOI: 10.1007/s10457-013-9627-8

Dillon-Zuppelli ZS, Poulson ME, Graham EA. 2024. Demography and habitat associations of the basalt cactus: *Pediocactus nigrispinus*. Northwest Science 98(1): *in press*.

- 563 Butler CJ, Wheeler EA, Stabler LB. 2012. Distribution of the threatened lace hedgehog cactus
564 (*Echinocereus reichenbachii*) under various climate change scenarios. Journal of the Torrey
565 Botanical Society. 139:46–55. <https://www.jstor.org/stable/41475121>
- 566 Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson AJA, Holmes SP. 2016. DADA2:
567 High-resolution sample inference from Illumina amplicon data. Nature Methods. 13:581–
568 583. DOI: 10.1038/nmeth.3869
- 569 Caswell H. 2001. Matrix population models. Sinauer Associates, Incorporated.
- 570 Chazdon RL, Chao A, Colwell RK, Lin S-Y, Norden N, Letcher SG, Clark DB, Finegan B,
571 Arroyo JP. 2011. A novel statistical method for classifying habitat generalists and specialists.
572 Ecology. 92:1332–1343. DOI: 10.1890/10-1345.1
- 573 Clark DJ, Clark TO, Duniway MC, Flagg C. 2015. Effects of ungulate disturbance and weather
574 variation on *Pediocactus winkleri*: Insights from long-term monitoring. Western North
575 American Naturalist. 75:88–101. DOI: 10.3398/064.075.0110
- 576 Contreras C, Valverde T. 2002. Evaluation of the conservation status of a rare cactus
577 (*Mammillaria crucigera*) through the analysis of its population dynamics. Journal of Arid
578 Environments. 51:89–102. DOI: 10.1006/jare.2001.0926
- 579 Cui M, PS Nobel. 1992. Nutrient status, water uptake and gas exchange for three desert
580 succulents infected with mycorrhizal fungi. New Phytologist. 122:643-649.
581 <https://www.jstor.org/stable/2557432>
- 582 Félix-Burrueel RE, Larios E, González EJ, Búrquez A. 2021. Episodic recruitment in the saguaro
583 cactus is driven by multidecadal periodicities. Ecology DOI: 102.e03458
- 584 Fertig W. 2021. Washington vascular plant species of conservation concern. Washington Natural
585 Heritage Program Report 2021-05 Washington State Department of Natural Resources,

- 586 Olympia WA August 31, 2021. Available online at:
587 https://www.dnr.wa.gov/publications/amp_nh_vascular_r1_r2.pdf.
- 588 Fertig W, J Kleinknecht. 2020. Conservation status and protection needs of priority plant species
589 in the Columbia Plateau and East Cascades ecoregions. Washington Natural Heritage
590 Program Report 2020-02. Washington Natural Heritage Program, Washington State
591 Department of Natural Resources, Olympia WA. January 27, 2020. Available online at
592 https://www.dnr.wa.gov/publications/amp_nh_priority_species_cp_ec_ecoregions.pdf
- 593 Fisher RA. 1925. Statistical methods for research workers. Oliver and Boyd, Edinburgh.
- 594 Fleming TH, Valiente-Banuet A. 2002. Columnar cacti and their mutualists: evolution, ecology,
595 and conservation. University of Arizona Press, Tucson.
- 596 Franco AC, Nobel PS. 1989. Effect of nurse plants on the microhabitat and growth of cacti.
597 *Journal of Ecology*. 77:870. DOI:10.2307/2260991
- 598 Godínez-Álvarez H, Valverde T, Ortega-Baes P. 2003. Demographic trends in the Cactaceae.
599 *Botanical Review* 69:173–203. DOI: 10.1663/0006-8101(2003)069[0173:dtitc]2.0.co;2
- 600 Goettsch B, Hilton-Taylor C, Cruz-Piñón G, Duffy JP, Frances A, Hernández HM, Inger R,
601 Pollock C, Schipper J, Superina M, Taylor NP, Tognelli M, Abba AM, Arias S, Arreola-
602 Nava HJ, Baker MA, Bárcenas RT, Barrios D, Braun P, Butterworth CA, Búrquez A,
603 Cáceres F, Chazaro-Basañez M, Corral-Díaz R, del Valle Perea M, Demaio PH, Duarte de
604 Barros WA, Durán R, aúndez Yancas L, Felger RS, Fitz-Maurice B, Fitz-Maurice WA, Gann
605 G, Gómez-Hinostrosa C, Gonzales-Torres LR, Griffith MP, Guerrero PC, Hammel B, Heil
606 KD, Hernández-Oria JG, Hoffmann M, Ishihara MI, Kiesling R, Larocca J, León-de la Luz
607 JL, Loaiza CR, Lowry SM, Machado MC, Majure LC, Guadalupe Martínez Ávalos J,
608 Martorell C, Maschinski J, Méndez E, Mittermeier RA, Nassar JM, Negrón-Ortiz V, Oakley

Dillon-Zuppelli ZS, Poulson ME, Graham EA. 2024. Demography and habitat associations of the basalt cactus: *Pediocactus nigrispinus*. Northwest Science 98(1): *in press*.

- 609 LJ, Ortega-Baes P, Pin Ferreira AB, Pinkava DJ, Porter JM, Puente-Martinez R, Roque
610 Gamarra J, Saldivia Pérez P, Sánchez Martínez E, Smith M, Sotomayor JM, Stuart SN, Tapia
611 Muñoz JL, Terrazas T, Terry M, Trevisson M, Valverde T, Van Devender TR, Véliz-Pérez
612 ME, Walter HE, Wyatt SA, Zappi D, Zavala-Hurtado JA, Gaston KJ. 2015. High proportion
613 of cactus species threatened with extinction. Nature Plants. 1:1–7. DOI:
614 10.1038/nplants.2015.142
- 615 Heil KD, Porter JM. *Pediocactus*. In Flora of North America Editorial Committee (editors),
616 Flora of North America [Online]. New York and Oxford. Vol. 4.
617 http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=124250. (accessed 30 May
618 2023).
- 619 Heil KD, Armstrong B, Schleser D. 1981. A review of the genus *Pediocactus*. Cactus and
620 Succulent Journal 53:17-39. Hochstätter F. 2008. The genus *Pediocactus*. Cactus World.
621 26:141–150. <https://www.jstor.org/stable/42794941>
- 622 Hochstätter F. 2008. The genus *Pediocactus*. Cactus World. 26(3):141–150
623 <https://www.jstor.org/stable/42794941>
- 624 Hreha, A, Meyer M, Therese B. 2001. Five-year monitoring study of Siler's Pincushion Cactus
625 (*Pediocactus sileri*) in Kane County, Utah. In: J Maschinski, L Holter, (technical editors),
626 Southwestern rare and endangered plants: Proceedings of the Third Conference; 2000
627 September 25-28; Flagstaff, AZ. Proceedings RMRS-P-23. Fort Collins, CO: U.S.
628 Department of Agriculture, Forest Service, Rocky Mountain Research Station. Pp. 83-94.
- 629 Hultine KR, Majure LC, Nixon VS, Arias S, Búrquez A, Goettsch B, Puente-Martinez R,
630 Zavala-Hurtado JA. 2016. The role of botanical gardens in the conservation of Cactaceae.
631 BioScience. 66:1057–1065. DOI:10.1093/biosci/biw128

Dillon-Zuppelli ZS, Poulson ME, Graham EA. 2024. Demography and habitat associations of the basalt cactus: *Pediocactus nigrispinus*. Northwest Science 98(1): *in press*.

- 632 Hultine KR, Hernández-Hernández T, Williams DG, Albeke SE, Tran N, Puente R, Larios E.
633 2023. Global change impacts on cacti (Cactaceae): current threats, challenges and
634 conservation solutions. *Annals of Botany* 132:671–683. DOI: 10.1093/aob/mcad040
- 635 Jaccard P. 1912. The distribution of the flora in the alpine zone. *New Phytologist*. 11:37–50.
636 DOI: 10.1111/j.1469-8137.1912.tb05611.x
- 637 Jiménez-Guzmán G, Arroyo-Cosultchi G, Martorell C, Martínez-Ramos M, Vega-Peña EV.
638 2024. What do we know about the demographic modeling of cacti? A systematic review of
639 current knowledge. *Journal of Arid Environments* 224. DOI:
640 10.1016/j.jaridenv.2024.105226.
- 641 Kunkel, K.E., R. Frankson, J. Runkle, S.M. Champion, L.E. Stevens, D.R. Easterling, B.C.
642 Stewart, A. McCarrick, and C.R. Lemery (editors). 2022: State Climate Summaries for the
643 United States 2022. NOAA Technical Report NESDIS 150. NOAA/NESDIS, Silver Spring
644 MD.
- 645 Larios E, González EJ, Rosen PC, Pate A, Holm P. 2020. Population projections of an
646 endangered cactus suggest little impact of climate change. *Oecologia*. 192:439–448. DOI:
647 10.1007/s00442-020-04595-y
- 648 Le Houérou HN. 1996. The role of cacti (*Opuntia* spp). in erosion control, land reclamation,
649 rehabilitation and agricultural development in the Mediterranean Basin. *Journal of Arid*
650 *Environments*. 33:135–159. DOI: 10.1006/jare.1996.0053
- 651 Lefkovich LP. 1965. The study of population growth in organisms grouped by stages.
652 *Biometrics*. 21:1–18. DOI: 10.2307/2528348
- 653 Lopez BR, Tinoco-Ojangure C, Bacilio M, Mendoze A, Bashan Y. 2012. Endophytic bacteria of
654 the rock-dwelling cactus *Mammillaria fraileana* affect plant growth and mobilization of

Dillon-Zuppelli ZS, Poulson ME, Graham EA. 2024. Demography and habitat associations of the basalt cactus: *Pediocactus nigrispinus*. Northwest Science 98(1): *in press*.

- 655 elements from rocks. Environmental and Experimental Botany. 81:26-36. DOI:
656 10.1016/j.envexpbot.2012.02.014
- 657 McIntosh ME, Boyd AE, Arnold AE, Steidl RJ, McDade LA. 2019. Growth and demography of
658 a declining, endangered cactus in the Sonoran Desert. Plant Species Biol. 35:6–15.
- 659 Maier S, Schmidt TSB, Zheng L, Peer T, Wagner V, Grube M. 2014. Analyses of dryland
660 biological soil crusts highlight lichens as an important regulator of microbial communities.
661 Biodiversity and Conservation. 23:1735–1755.
- 662 Mandujano MC, Bravo Y, Verhulst J, Carrillo-Angeles I, Golubov J. 2015. The population
663 dynamics of an endemic collectible cactus. Acta Oecologia. 63:1–7. DOI:
664 10.1016/j.actao.2014.12.004
- 665 Martínez AF, Medina GIM, Golubov J, Montaña C, Mandujano MC. 2010. Demography of an
666 endangered endemic rupicolous cactus. Plant Ecology. 210:53–66. DOI: 10.1007/s11258-
667 010-9737-6
- 668 McAuliffe, JR FJ Janzen. 1986. Effects of intraspecific crowding on water uptake, water storage,
669 apical growth and reproductive potential in the sahuaro cactus, *Carnegiea gigantea*.
670 Botanical Gazette. 147:334-341. <https://www.jstor.org/stable/2474402>
- 671 McIntosh ME, Boyd AE, Arnold AE, Steidl RJ, McDade LA. 2019. Growth and demography of
672 a declining, endangered cactus in the Sonoran Desert. Plant Species Biology. 35(1):6–15.
- 673 Miller JED, Wessel S, Fertig W. 2024. Washington Vascular Plant Species of Conservation
674 Concern. Washington Natural Heritage Program Report 2024-07. Washington Natural
675 Heritage Program, Washington State Department of Natural Resources, Olympia WA. July 3,
676 2024. Available online at
677 https://www.dnr.wa.gov/publications/amp_nh_vascular_ets.pdf?4jnufw6

Dillon-Zuppelli ZS, Poulson ME, Graham EA. 2024. Demography and habitat associations of the basalt cactus: *Pediocactus nigrispinus*. Northwest Science 98(1): *in press*.

- 678 Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P,
679 Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G,
680 Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B,
681 Hannigan G, Hill M, Lahti L, McGlenn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A,
682 Ter Braak C, Weedon J. 2022. Vegan: Community Ecology Package_. R package version
683 2.6-4, <https://CRAN.R-project.org/package=vegan>
- 684 Pakgohar N, Eshaghi Rad J, Gholami G, Alijanpour A, Roberts DW. 2021. A comparative study
685 of hard clustering algorithms for vegetation data. Journal of Vegetation Science. 32:e13042.
686 DOI: 10.1111/jvs.13042
- 687 Parker KC. 1989. Height structure and reproductive characteristics of *Senita*, *Lophocereus*
688 *schottii* (Cactaceae), in Southern Arizona. Southwestern Naturalist. 34:392–401. DOI:
689 10.2307/3672168
- 690 Phillips, BG. Phillips, AM. 1996. Results of an eleven-year monitoring study of the endangered
691 *Pediocactus peeblesianus* (Croizat) LD Benson var. *peeblesianus*. In Maschinski J,
692 Hammond HD (editors) Southwestern Rare and Endangered Plants: Proceedings of the
693 Second Conference, USDA Forest Service General Technical report RM-GTR-283. Pp. 27–
694 38).
- 695 PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu> (accessed 30
696 March 2023).
- 697 Puente ME, Li CY, Bashan Y. 2009. Endophytic bacteria in cacti seeds can improve the
698 development of cactus seedlings. Environmental and Experimental Botany. 66:402–408.
699 DOI: 10.1016/j.envexpbot.2009.04.007.
- 700 R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for

- 701 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 702 Rego A, Raio F, Martins TP, Ribeiro H, Sousa AGG, Séneca J, Baptista MS, Lee CK, Cary SC,
703 Ramos V, Carvalhot RF, Leão P, Magalhães C. 2019. Actinobacteria and cyanobacteria
704 diversity in terrestrial Antarctic microenvironments evaluated by culture-dependent and
705 independent methods. *Frontiers in Microbiology*. 10. DOI: 10.3389/fmicb.2019.01018
- 706 Rojas-Sandoval J, EJ Meléndez-Ackerman, D Anglés-Alcázar. Assessing the impact of grass
707 invasion on the population dynamics of a threatened Caribbean dry forest cactus. *Biological*
708 *Conservation*. 196:156-164. DOI: 10.1016/j.biocon.2016.02.015
- 709 Scheiner SM, Gurevitch J. 2001. *Design and analysis of ecological experiments*. Oxford
710 University Press.
- 711 Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image
712 analysis. *Nature Methods*. 9:671–675. DOI: 10.1038/nmeth.2089
- 713 Schroeder PJ, DG Jenkins. 2018. How robust are popular beta diversity indices to sampling
714 error? *Ecosphere* (2):e02100. DOI: 10.1002/ecs2.2100
- 715 Shannon CE, Weaver W. 1949. *The mathematical theory of communication*. University of
716 Illinois Press, Urbana, Illinois.
- 717 Shetty AA, Rana MK, Preetham SP. 2011. Cactus: a medicinal food. *Journal of Food Science*
718 *and Technology*. 49:530–536. DOI: 10.1007/s13197-011-0462-5.
- 719 Shryock DF, Esque TC, Lee Hughes. 2014. Population viability of *Pediocactus bradyi*
720 (Cactaceae) in a changing climate. *American Journal of Botany* 101:1944–1953. DOI:
721 10.3732/ajb.1400035.
- 722 Simpson EH. 1949. Measurement of diversity. *Nature*. 163:688–688.
- 723 Sivinski RC, C McDonald. 2007. Knowlton’s cactus (*Pediocactus knowltonii*): Eighteen years of

- 724 monitoring and recovery actions. In Barlow-Irick, P, J Anderson, C McDonald, tech eds.
725 Southwestern rare and endangered plants: Proceedings of the Fourth Conference; March 22-
726 26, 2004; Las Cruces, New Mexico. Proceedings. RMRS-P-48CD. Fort Collins, CO: U.S.
727 Department of Agriculture, Forest Service, Rocky Mountain Research Station. Pp. 98-107.
728 Soil Survey Staff, Natural Resources Conservation Service, United States Department of
729 Agriculture. Web soil survey. <http://websoilsurvey.sc.egov.usda.gov> (accessed 12 February
730 2022).
- 731 Soininen J, Heino J, Wang J. 2017. A meta-analysis of nestedness and turnover components of
732 beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*. 27:96–
733 109. DOI: 10.1111/geb.12660.
- 734 Stubben C, Milligan B. 2007. Estimating and analyzing demographic models using the popbio
735 Package in R. *Journal of Statistical Software*. 22. DOI: 10.18637/jss.v022.i11
- 736 Tang K, Yuan B, Jia L, Pan X, Feng F, Jin K. 2021. Spatial and temporal distribution of aerobic
737 anoxygenic phototrophic bacteria: key functional groups in biological soil crusts. *Environ*
738 *Microbiol*. 23(7):3554–3567. DOI: 10.1111/1462-2920.15459
- 739 Thompson J.B., Hernández-Hernández T., Keeling G, Vásquez-Cruz M, Priest NK. 2024.
740 Identifying the multiple drivers of cactus diversification. *Nature Communications* 15, 7282.
741 DOI: 10.1038/s41467-024-51666-2
- 742 Ward JH. 1963. Hierarchical grouping to optimize an objective function. *J. American. Statistical*
743 *Assoc.* 58:236–244. DOI: 10.1080/01621459.1963.10500845
- 744 Wolf BO, Martínez del Rio C, Babson J. 2002. Stable isotopes reveal that saguaro fruit provides
745 different resources to two desert dove species. *Ecology*. 83:1286–1293. DOI: 10.1890/0012-
746 9658(2002)083[1286:sirtsf]2.0.co;2

Dillon-Zuppelli ZS, Poulson ME, Graham EA. 2024. Demography and habitat associations of the basalt cactus: *Pediocactus nigrispinus*. Northwest Science 98(1): *in press*.

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748 *Submitted 16 May 2024*

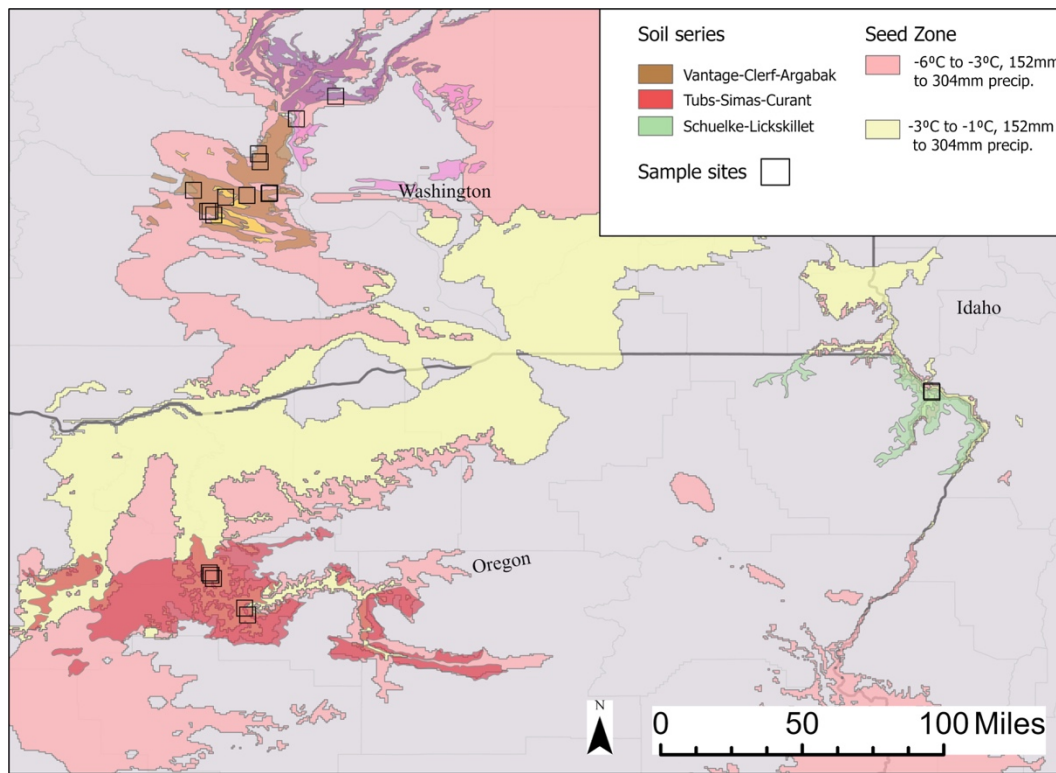
749 *Accepted 5 November 2024*

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751 **Figures**

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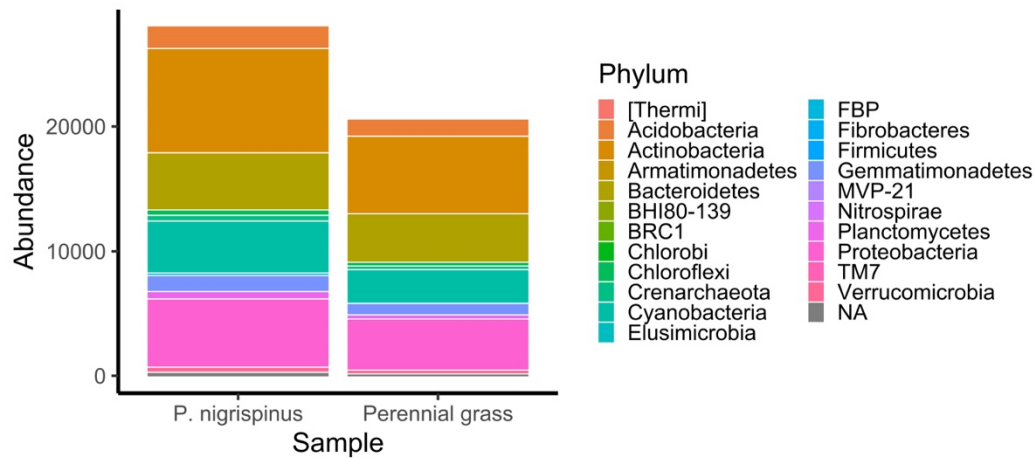
753

754 Figure 1 Generalized rectangles of *Pediocactus nigrispinus* site locations. USDA seed zone
755 associations, and soil complex associations of all the sites depicted. Seed zones are based on data
756 from average winter minimum temperature and average annual precipitation (Bower 2014). Soil
757 complexes from Web Soil Survey (soil survey staff).

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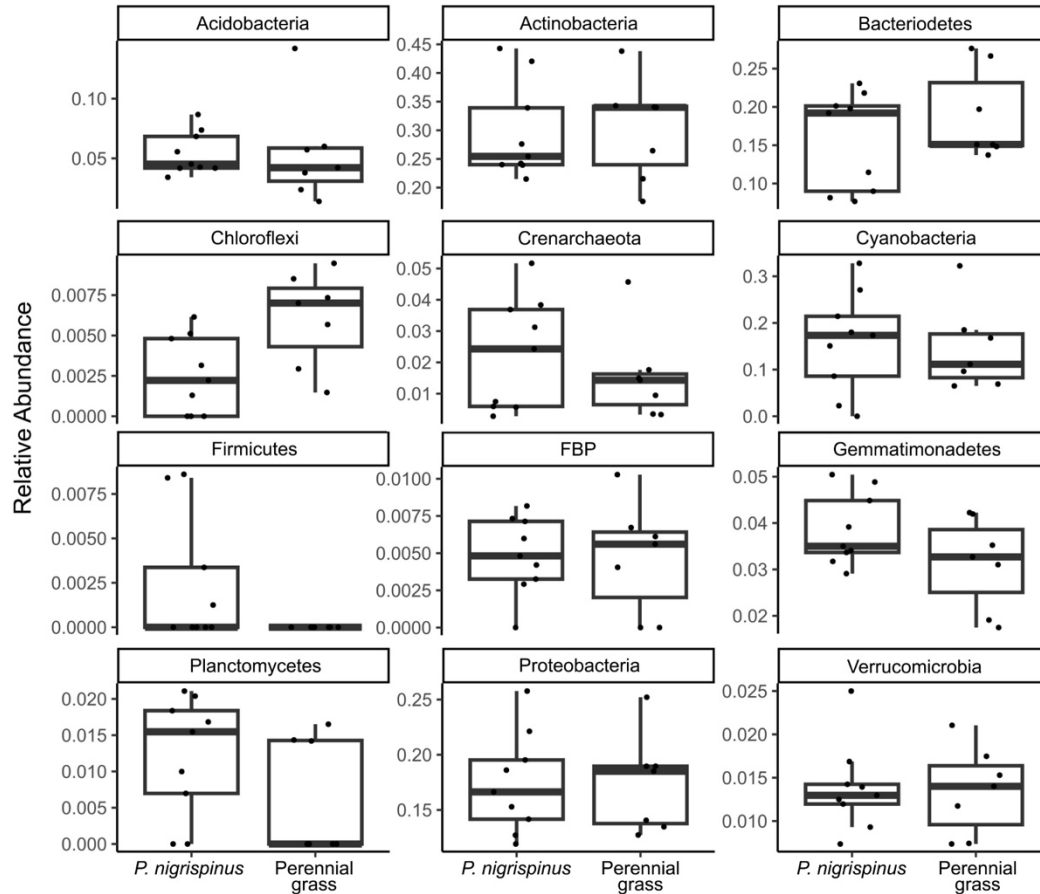
760

761 Figure 2 Total bacterial abundance by phyla for *Pediocactus nigrispinus*, ($n = 9$) and
762 bunchgrasses ($n = 7$). Bunchgrasses were either *Poa secunda*, or *Poa spicata* depending on
763 which had highest density on the plot.

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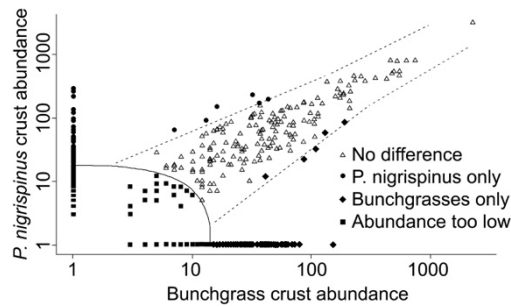
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767 Figure 3 Relative abundance of the most common bacterial phyla for *Pediocactus*
768 *nigrispinus*, ($n = 9$) and bunchgrasses ($n = 7$). Bunchgrasses were either *Poa secunda*, or
769 *Pseudoriginaria spicata* depending on which had highest density on the plot. No significant
770 difference was observed in the relative abundance between *P. nigrispinus* or the bunchgrasses for
771 any of the phyla.

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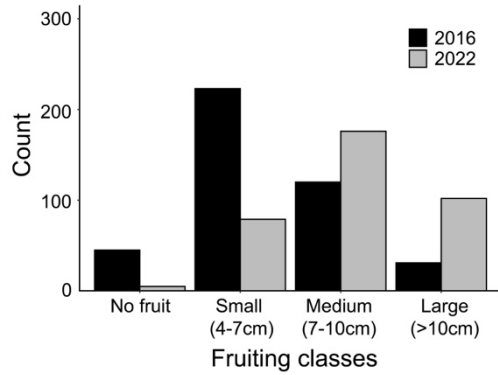
775 Figure 4 Multinomial species classification (CLAM) test to assess specialist crust
776 associates of *Pediocactus nigrispinus*, (circles, $n = 9$) and bunchgrasses (diamonds, $n = 7$).

777 Bunchgrasses were either *Poa secunda*, or *Poa spicata* depending on which had highest density
778 on the plot. Generalist between the species are shown with triangles, and squares indicate taxa
779 with abundance values too low to determine if they were generalists or specialists.

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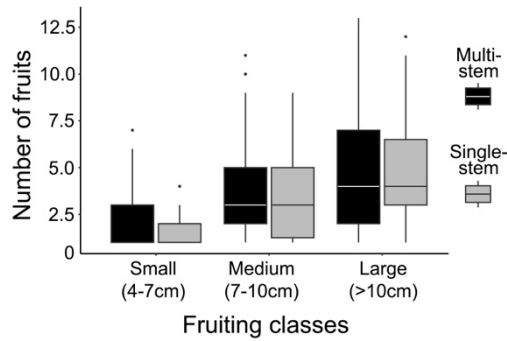
783 Figure 5 The number of individuals in each size class in 2016 ($n = 415$) and 2022 ($n =$

784 344). The average individual size for a clump was used instead of individual sizes.

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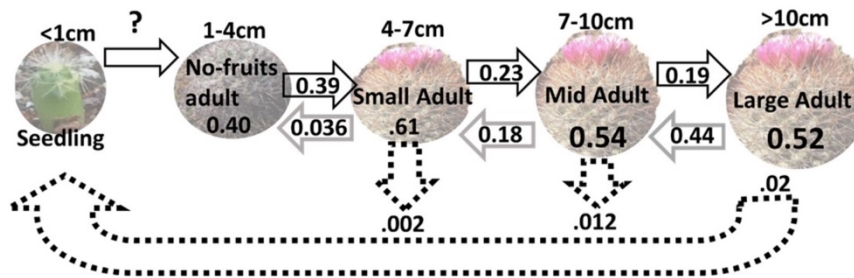
787

788 Figure 6 The number of fruits produced in each size class that produced fruits. For the
789 clumped cacti, each individual was given the average size of all individuals within the clump for
790 analysis, as each individual within the clump did not have their own tag to monitor size
791 transitions between years. Fruits of cacti in clumps were still counted on an individual basis.

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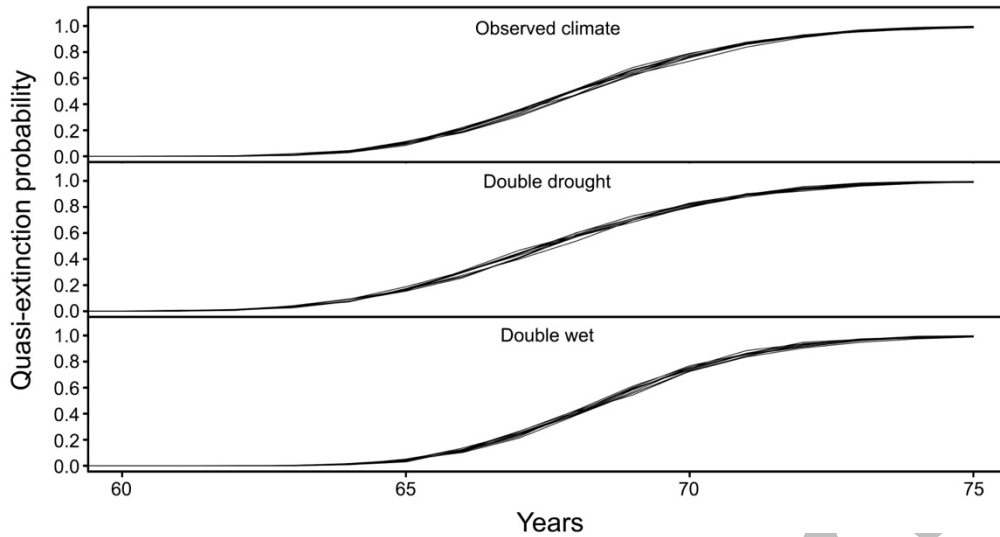
794

795 Figure 7 Average stage transitions for *Pediocactus nigrispinus*. All stages can interact year
796 to year, but those proportions are all very small (< 5%; Table 4) Values within circles indicate
797 stasis. Dotted arrows indicate fecundity.

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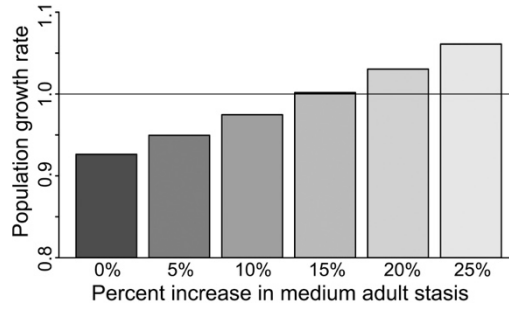
800

801 Figure 8 The projected probability of quasi-extinction after 75 years based on 500
802 iterations of running the stochastic population model with no added recruitment. Upper panel:
803 projection based on the observed climatic variables, with the assumption of no future change in
804 precipitation. Middle panel: Probability of years with drought doubled for projection. Lower
805 panel: Probability of high precipitation years doubles.

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809 Figure 9 Modeled changes in the population growth rate for different rates of stasis of

810 medium sized (7–10 cm) individuals

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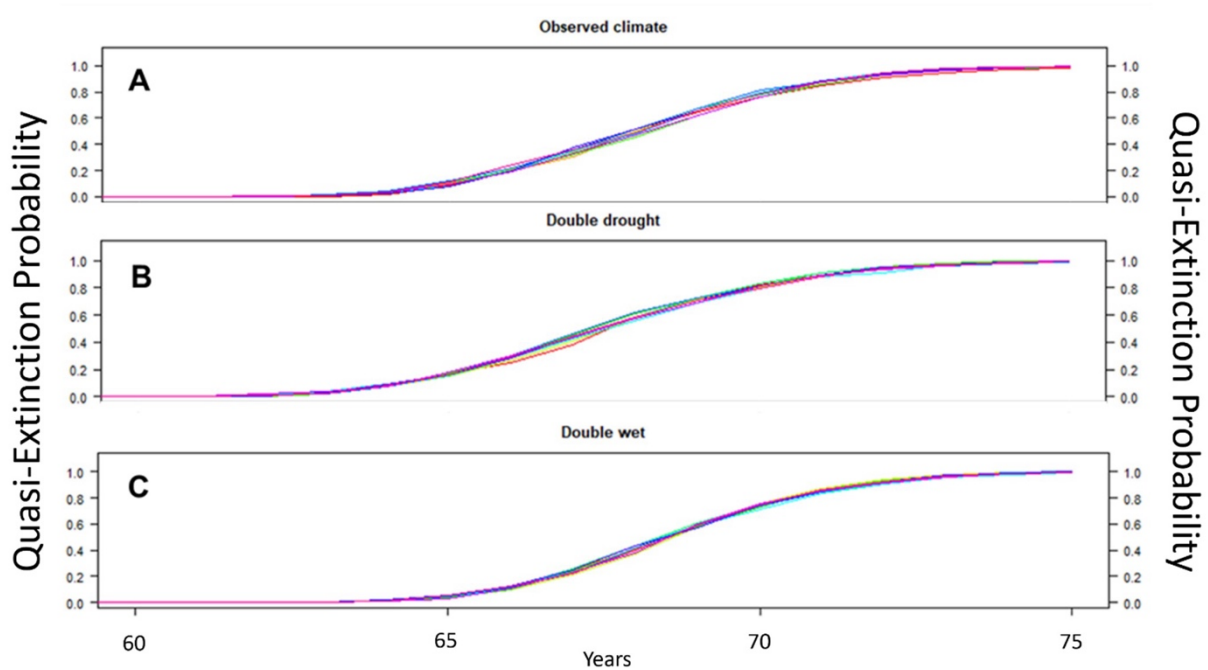


Figure 12 The projected probability of quasi-extinction after 75 years based on 500 iterations of running the stochastic population model with no added recruitment. A: projection based on the observed climatic variables, with the assumption of no future change in precipitation. B: Probability of years with drought doubled for projection. C: Probability of high precipitation years doubles.

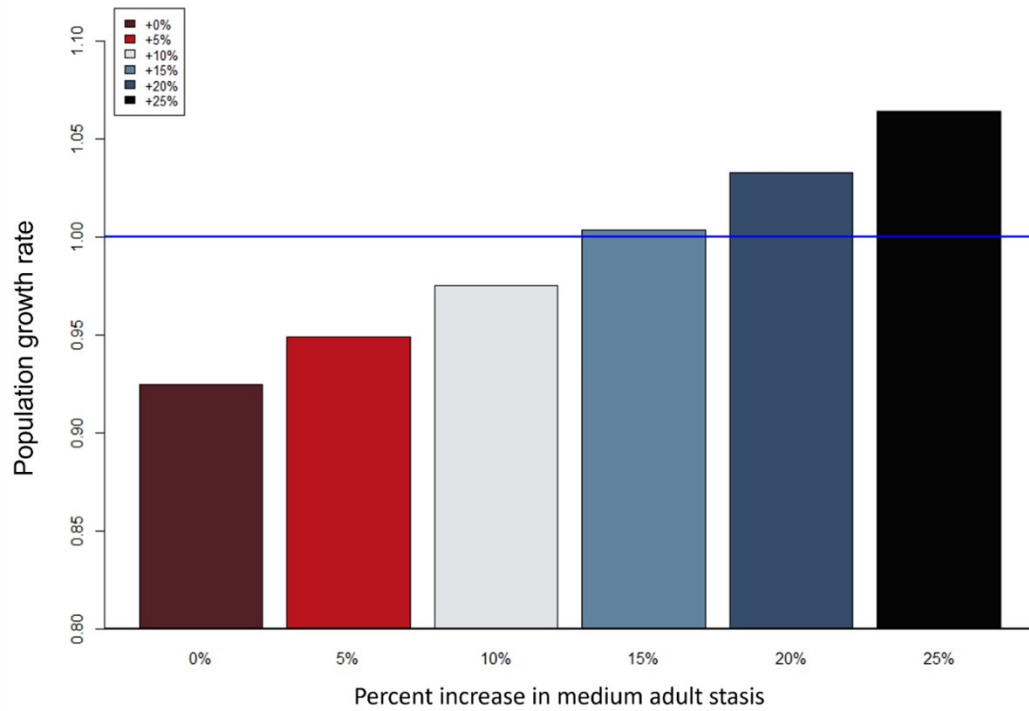
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814 Figure 10

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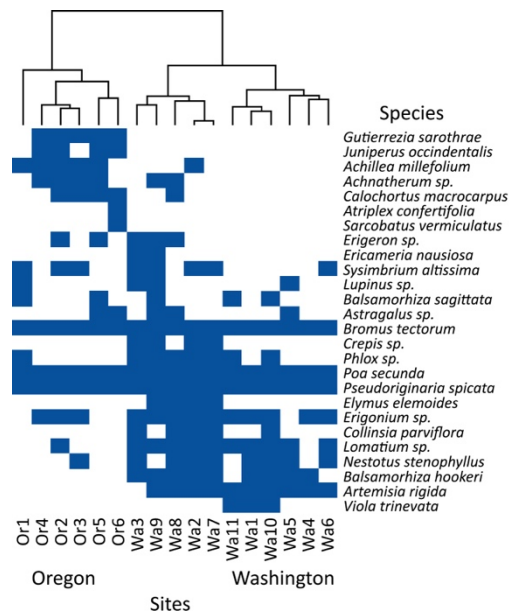
818 Figure 11

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820 **Supplementary Materials: Figures**

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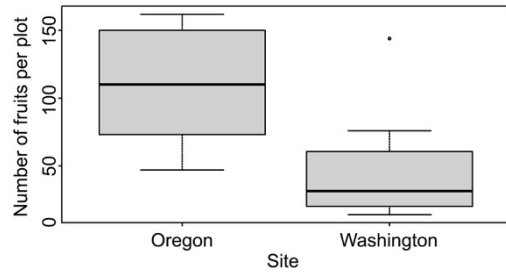
822

823 Supplementary Figure 1 Presence absence matrix for the common plant species found in
824 each plot throughout Oregon ($n = 6$) and Washington ($n = 11$).

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828 Supplementary Figure 2 Number of fruits per plot in Oregon ($n = 6$) as compared to

829 Washington ($n = 8$). $P = 0.03$.

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831 **Tables**

832

833 Table 1. Jaccard dissimilarity index showing beta diversity of all sites, and then broken

834 down by just the Washington community, and just the Oregon community

Region	Beta Diversity	Proportion of diversity due to replacement	Proportion of diversity due to richness difference
Washington	0.24	0.424	0.576
Oregon	0.26	0.713	0.287
Overall	0.29	0.620	0.370

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837 Table 2. Habitat characteristics compared between Washington and Oregon. Values are
838 means \pm confidence intervals (ci). n.s = not significant

Measurement	Washington	Oregon	<i>P</i> -value (ANOVA)
Number of Sites	11	6	
Elevation (m) \pm ci	723 \pm 143	725 \pm 145	n.s
Slope (%) \pm ci	13 \pm 6	26 \pm 12	0.01
Aspect ($^{\circ}$) \pm ci	230 \pm 42	188 \pm 90	n.s
Canopy height (cm) \pm ci	25 \pm 9	50 \pm 37	0.04
Total canopy cover (%) \pm ci	47 \pm 7	50 \pm 6	n.s
Rock cover (%) \pm ci	50 \pm 12	37 \pm 20	n.s

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841 Table 3 *Pediocactus nigrispinus* transition matrices by year.
842

2016-2017		$\lambda=0.946 \pm 0.021$				
	Seedling	Non-fruiting	Small Fruiting	Medium Fruiting	Large Fruiting	
Seedling (a1)	0.000	0.000	0.001	0.011	0.016	
Non-fruiting	0.100	0.415	0.055	0.000	0.000	
Small Fruiting	0.000	0.463	0.799	0.216	0.000	
Medium Fruiting	0.000	0.000	0.064	0.621	0.556	
Large Fruiting	0.000	0.000	0.009	0.147	0.444	
2017-2018		$\lambda=0.935 \pm 0.033$				
	Seedling	Non-fruiting	Small Fruiting	Medium Fruiting	Large Fruiting	
Seedling (a1)	0.000	0.000	0.000	0.000	0.000	
Non-fruiting	0.100	0.538	0.066	0.025	0.037	
Small Fruiting	0.000	0.231	0.725	0.322	0.111	
Medium Fruiting	0.000	0.000	0.153	0.496	0.630	
Large Fruiting	0.000	0.038	0.000	0.116	0.222	
2018-2019		$\lambda=0.974 \pm 0.019$				
	Seedling	Non-fruiting	Small Fruiting	Medium Fruiting	Large Fruiting	
Seedling (a1)	0.000	0.000	0.003	0.019	0.027	
Non-fruiting	0.100	0.567	0.020	0.000	0.000	
Small Fruiting	0.000	0.200	0.620	0.140	0.000	
Medium Fruiting	0.000	0.067	0.233	0.661	0.476	
Large Fruiting	0.000	0.000	0.012	0.198	0.524	
2019-2022		$\lambda=0.938 \pm 0.048$				
	Seedling	Non-fruiting	Small Fruiting	Medium Fruiting	Large Fruiting	
Seedling	0	0.000	0.005	0.019	0.024	
Non-fruiting	0.1	0.087	0.005	0.000	0.000	
Small Fruiting	0	0.652	0.293	0.034	0.000	
Medium Fruiting	0	0.043	0.500	0.381	0.098	
Large Fruiting	0	0.000	0.027	0.318	0.878	

Stages are: seedlings = < 1cm, non-fruiting = 1-4 cm, small fruiting = 4-7 cm, medium fruiting = 7-10 cm, large fruiting = >10 cm. Top row of the matrix represents contributions of the stage to new seedlings the following year (estimated). Bolded values are stasis, values above stasis are reversions to previous size classes. Values below stasis are growth to larger classes

843

844 Table 4 Average elasticity values for the four years of a demographic study for
845 *Pediocactus nigrispinus*.

	Seedling (a1)	Non-fruiting	Small Fruiting	Medium Fruiting	Large Fruiting
Seedling (a1)	0.0000	0.0000	0.0001	0.0005	0.0003
Non-fruiting	0.0008	0.0103	0.0088	0.0022	0.0016
Small Fruiting	0.0000	0.0120	0.1794	0.0753	0.0059
Medium Fruiting	0.0000	0.0010	0.0796	0.2599	0.1056
Large Fruiting	0.0000	0.0004	0.0047	0.1083	0.1434
Contribution to population elasticity by vital rate		Contribution to population elasticity by class			
Stasis	0.5930	Seedling	0.0008		
Growth	0.2068	Non-fruiting	0.0237		
Reversion	0.1993	Small Fruiting	0.2726		
Fecundity	0.0008	Medium Fruiting	0.4461		
		Large Fruiting	0.2567		

Stages are: seedlings = < 1cm, non-fruiting = 1-4 cm, small fruiting = 4-7 cm, medium fruiting = 7-10 cm, large fruiting = >10 cm. Top row of the matrix represents contributions of the stage to new seedlings the following year (estimated). Bolded values are stasis, values above stasis are reversions to previous size classes. Values below stasis are growth to larger classes

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