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What are the demographic consequences of a seed bank stage for columnar cacti?

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Abstract

The dynamics of plant populations are often limited by the early stages in their life cycles. However, information regarding seed bank dynamics and how these may influence the whole life cycle of plant species is remarkably scarce or not considered explicitly. This lack of knowledge is due mainly to the challenges in quantifying seed vital rates. Studies of arid land plant species have historically been focused on the drivers of sporadic recruitment. However, little attention has been given to the demographic consequences of early developmental stages, and how seed banks affect their dynamics. Here, we evaluate the effects of seed bank survival and seedling recruitment vital rates on the population dynamics and viability of 12 columnar cacti species. Recent evidence suggests that cacti seeds may remain viable for the short-term. We assess how changes in the vital rates of these processes and the inclusion of a seed bank affect population growth rate (λ). We found that a seed bank in the examined matrix population models significantly increased λ as well as the vital rate elasticities of λ to growth and fecundity, whereas that of overall survival decreased. Our numerical simulations showed that seed survival had a more considerable effect on λ than seedling recruitment and establishment. We suggest that the seed bank may explain the structure and population dynamics.

Thus, we reconsider that this early stage in demographic models will generate more informed decisions on the conservation and management of columnar cacti.

1 | INTRODUCTION

In plant populations, seeds and seedlings often act as primary constraints to population size and demographic viability (Crawley, 1990; Ågren, 1996), particularly true for short to mid-lived species (Silvertown et al., 1993; Franco and Silvertown, 2004). On the one hand, seed limitation, whereby the number of individuals increases following seed addition (Turnbull et al., 2000), occurs when insufficient amounts of seeds are produced (Ågren, 1996), when these are not viable (Bell et al., 1993) or when their dispersal is limited (Clark et al., 2007). On the other hand, the establishment of those seeds as seedlings may be limited by factors such as environmental stress, cross-pollination, pollinator limitation (Bell et al., 1993), or microsite availability (Turnbull et al., 2000), regardless of seed limitation (Clark et al., 2007). Seedling recruitment is understood as the process by which new individuals are added to a population, including seed germination, seedling survivorship, and seedling growth (Eriksson and Ehrlén, 2008).

Seedling recruitment in cactus species is primarily recognized as a critical process in their life cycles and thus as an essential restriction to population growth rate λ (Godínez-Álvarez et al., 2003; Arroyo-Cosultchi et al., 2016). While several studies have examined the mechanisms limiting recruitment in the Cactaceae, these have predominantly assessed establishment limitation (Steenbergh and Lowe, 1977; Godínez-Álvarez et al., 2003; Mandujano et al., 2007; Holland and Molina-Freaner, 2013). However, the demographic consequences of seed and seedling limitation in this diverse taxon have been largely overlooked (Godínez-Álvarez et al., 2003). Studies in Cactaceae show a high potential germination rate in laboratory conditions, which contrasts with the high seedling mortality rates reported in the field (Esparza-Olguín et al. 2002; Holland and Molina-Freaner 2013; Pierson et al. 2013; Zepeda-Martínez et al. 2013). Together, this research group suggests that demographic processes at the interface of seed limitation and seedling recruitment are crucial to life cycles and population dynamics in Cactaceae.

An essential trait for plant species inhabiting unpredictable environments such as arid lands is generating seed banks (Gutterman, 1994). This strategy is thought to be a fundamental component for population persistence in variable environments (Pake and Venable, 1996), and it is a critical factor that affects seed and seedling limitation (Venable, 2007). However, estimating seed bank dynamics is challenging as seed longevity depends on morphological and physiological traits such as seed size, dormancy, and photoblastism (Baskin and Baskin, 1989; Rojas-Aréchiga and Batis, 2001; Rojas-Aréchiga, 2014) as as well as on mortality by biotic drivers such granivores and (Álvarez-Espino et al., 2014). So obtaining accurate estimates for survival and germination of seeds (often of a more few millimeters) in the soil can be an arduous task (Adams et al., 2005; Nguyen et al., 2019).

Even though the presence/absence of a seed bank can be significant in demographic terms (Kalisz and McPeek, 1992; Doak et al., 2002), these are not always included in plant demographic models (Nguyen et al., 2019). These are so albeit evidence of their presence in numerous species (Doak et al., 2002; Nguyen et al., 2019). Still, this life stage is commonly assumed to be non-existent or short-lived, or the origin of seedlings is not differentiated. Seeds residence time in the soil determines if the species may generate a transient (<1 year), short-term (≥ 1 but <5 years) or long-term persistent seed bank (≥ 5 years) *sensu* (Bakker et al., 1996; Thompson et al., 1997). The presence of seed banks is often correlated with a short mean life expectancy of established individuals (Cohen, 1966); however, seed dormancy and the formation of a seed bank are potentially costly features (Rees, 1994). Additionally, seed banking in long-lived organisms can hedge against recruitment failure from periodical fluctuations in seed production and/or seedling recruitment (Rees, 1994).

The inclusion - or not - of seed banks in population models can affect population dynamics (Doak et al., 2002; Nguyen et al., 2019). In existing population models in the Cactaceae, seed banks are rarely explicitly considered (Godínez-Álvarez et al., 2003; Zepeda-Martínez et al., 2013). Indeed across columnar cacti, most demographic studies do not include seed banks (Godínez-Alvarez et al., 1999; Esparza-Olguín et al., 2005; Rojas-Sandoval and Meléndez-Ackerman, 2013), except in *Cephalocereus polylophus* (Arroyo-Cosultchi et al., 2016). Assuming the absence of a seed bank would suggest seed viability decreases after dispersal (seed limitation; Rojas-Aréchiga and Batis, 2001; Méndez et al., 2004), or granivore pressure is high such that seeds are rapidly depleted after dispersal (dispersal limitation; Valiente-Banuet and Ezcurra, 1991; Sosa and Fleming, 2002; Clark-Tapia et al., 2005). However,

growing evidence suggests that cactus seeds may remain viable for significant periods (e.g., 1-2 years) (Mandujano et al., 1997), leading to a potential short-term seed bank (Godínez-Álvarez et al., 2003; Bowers, 2005; Cano-Salgado et al., 2012; Álvarez-Espino et al., 2014; Ordoñez-Salanueva et al., 2017; Lindow-López et al., 2018). Matrix population models are helpful tools in plant population ecology, as they provide a common conceptual framework for comparative research (Silvertown et al., 1993; Salguero-Gómez and de Kroon, 2010; Salguero-Gómez and Plotkin, 2010; Nguyen et al., 2019). The growing number of studies using comparative approaches with matrix population models (Salguero-Gómez et al., 2015) has allowed linking specific vital rates (Franco and Silvertown, 2004; Adler et al., 2014) and stages in ecological successional gradients (Silvertown et al., 2002), life history evolution (Burns et al., 2010), population dynamics of native *vs.* invasive plant species (Ramula et al., 2008), or senescence (Jones et al., 2014), among others. We focused on the vital rates of seed bank survival and seedling recruitment to examine their relative effects on the overall population growth rates (λ). A total of 12 columnar cacti species have been published and analyzed through the use of population-projection matrices. For this study, we compiled, modified, and compared their matrices. We apply matrix population models to assess (i) the role of seed banks and related dynamics (e.g., recruitment of from seed bank) as opposed to recruitment from direct reproduction, *i.e.* without seed banks, on the vital rate elasticities and population growth rate (λ) and, (ii) evaluate the potential effects on λ of an increase in the vital rate of seed banks, the seed-seedling transition, and seedling survival on λ.

2 | MATERIALS AND METHODS

2.1 | The Database

We used a comparative approach to determine the effects of a seed bank stage on the population dynamics of columnar cacti using published matrix population models. We searched the ISI Web of Science and Scopus electronic databases using the following combination of keywords *"cacti"*, *"Cactaceae"*, *"cactus"*, and *"population growth rate"* since September 1993. We included studies that explicitly used a matrix population model for columnar cacti belonging to the taxonomic tribe

Pachycereeae and Trichocereeae (Anderson, 2001). Additional studies were obtained by studying the latest issues of ecological journals and by including data from (`http://www.dgbiblio.unam.mx/index.php/catalogos` Accessed 30 July 2015), the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015, see Table 1), as well as part of collaborative, ongoing unpublished research. Our criteria for study selection included at least one matrix population model (Caswell, 2001) to estimate the population growth rate (λ). If the study had more matrices (*i.e.*>1 annual transition or populations), matrices were averaged across years or sites to obtain a single, representative matrix model per species (see Supplementary Appendix A for all original mean matrices). The final sample size contained 12 matrices, one matrix for each columnar cacti species (Table 1).

2.2 | Reduction of matrix dimensions

A critical step in comparative stage-structured demographic studies is selecting the dimension (stage or size classes) as dimensionality affects λ and derived metrics (Enright et al., 1995; Ramula and Lehtilä, 2005; Salguero-Gómez and Plotkin, 2010; Picard and Liang, 2014). To overcome potential biases in our comparative inference on the role of seed bank survival and seedling recruitment for population dynamics, we standardized the variable matrix dimensions in our study, ranging originally from 15×15 for *Carnegiae gigantea* to 6×6 for *Harrisia fragrans* (Table 1). To test whether changes in matrix dimension significant changed vital rates, we chose matrix dimensions of 6×6, 5×5, and 4×4 without a seed bank stage (hereafter WOSB) and the inclusion of a seed bank resulted in 7×7, 6×6, and 5×5 matrix dimensions respectively (hereafter WSB, see Supplementary Appendix A for all original and reduced matrices). We used the algorithm developed by Salguero-Gómez and Plotkin (2010) for size/stage-based matrices, adapted from Hooley (2000) for age-based models. This algorithm allows the reduction of a given matrix population model of $n \times n$ dimensions into $m \times m$, where $m < n$. There are naturally different ways of reducing a matrix population model of interest of $n > 2$; here, we followed the recommendation by Salguero-Gómez and Plotkin (2010), whereby early life cycle stages (e.g., Figure 1) were left unaltered as they were also the life stages of interest for this study. This method

preserves population growth rates, stable class distributions, and reproductive output through the assumption of stationary stability (Salguero-Gómez and Plotkin, 2010).

Matrix population models in our study were reduced by n -1 dimensions by merging the two adjacent size categories with the lowest number of individuals as reported by the population vector $n(t)$ while leaving the remaining stages unaltered. Here, we did not reduce reproductive and non-reproductive stages into the same class, and the stage corresponding to seedlings was kept unaltered (Table 1).

The number of stages for each matrix was reduced by combining information for adjacent stages to generate new estimates of survival in a given stage class j (σ_j), negative growth (ρ_{ij}), positive growth (γ_{ij}), individual fecundity (ϕ_{ij}), and individual ramet production (κ_{ij}) (Franco and Silvertown, 2004). Fecundity entries were estimated from the information found in the original source (see Section 2.1) as the *per capita* number of seeds in each reproductive size category (Table 2). The seed to seedling transition was reported as the number of seeds × seed germination. When seed germination was calculated from laboratory and experiments under natural conditions in different sources, we averaged both germination percentages as germination in natural conditions usually includes factors that affect or limit germination (granivory, drought, and fungal attack) (Table 2). Seedling survival was calculated by the survival of seedlings in field or laboratory conditions reported in each study (Table 2).

2.3 | The importance of the seed bank

In the species that fulfilled our criteria, we included a hypothetical short-term seed bank (≥ 1 year) with an initial survival value of 0.05, except in *C. polylophus* where the transient seed bank is known (Arroyo-Cosultchi et al., 2016). In the WSB model individuals in an unstructured seed bank assumed no senescence and are thus potentially immortal. Since a seed bank is a discrete stage class and did not involve categorization, transition rates for the other stages should remain unaffected by its inclusion (Nguyen et al., 2019), however as a consequence, a temporal component in terms of longer life cycles was added. After that, the finite rate of population increase (λ), the stable structure of each stage (w), and the specific reproductive value per stage (v) were calculated using the WOSB (6×6) (Fig-ure 1a) or WSB (7×7) (Figure 1b) models for each species (Caswell, 2001). To test for the significance of a seed bank on the population dynamics of our examined species, we used a paired *t*-test ($\alpha = 0.05$) using the values of λ obtained from the WOSB and WSB models. The elasticity (e_{ij}) and sensitivity (s_{ij}) matrices were calculated using the v and w vectors (Caswell, 2001) and finally, 95 % confidence intervals for λ were estimated in order to use the analytic method suggested by Alvarez-Buylla and Slatkin (1991).

We explored the effect of the following variables: species, the dimension of the matrix, and the seed bank on the vital rates for the WOSB and WSB models. Elasticities were previously calculated, obtaining the following vital rates: survival in a given stage class (σ), negative growth (ρ), positive growth (γ), and individual fertility (ϕ) (Silvertown et al., 1993; Franco and Silvertown, 2004) for both the WOSB (6×6, 5×5, and 4×4) and WSB models (7×7, 6×6, and 5×5). A PCA was used to determine the linear combination of vital rate elasticities with the presence/absence of a seed bank and whether this relationship was consistent between species. PCA scores were extracted from the first four principal components (PC1 to PC4) for all variables (species, seed bank, and vital rates), and the most important of them were identified based on the loadings factor and the percentage of explained variance and eigenvalues (Digby and Kempton, 2012). Finally, we performed a one-way ANOVA ($\alpha = 0.05$) for the PC scores of the principal components (PC1-PC4). *Post hoc* Tukey tests ($\alpha = 0.05$) were performed using the matrix dimension as a factor and each principal component's values as the response variable. The PCA's were performed with the prcomp function of the R library "stats" (R Core Team, 2017).

2.4 | Numerical simulations

The relative importance of seed bank survival and seedling recruitment from the seed bank was evaluated through numerical simulations (Adams et al., 2005; Nguyen et al., 2019). As seedling recruitment was reported in studies, the average probability of germination and fecundity were used as a proxy for the transition from seed to seedling. No clonal reproduction into the seedling stage happened such that the observed seedlings only consisted of two components: the individuals that germinated immediately between year t and $t + 1$ and those

TABLE 1 Species used in this study for which matrix population models are available, showing the original dimension of the matrices (in gray), and the adjacent life cycle classes that were reduced (in black) to produce matrices with the same dimension: 6 × 6. Stage 1 was always kept unaltered because it contains the seedling stage. *Note that all matrices lack seed bank (stage 0), except for *Cephalocereus polylophus* (stage 0, Figure 1b). [1]Silvertown et al. (1993), [2]Esparza-Olguín et al. (2002), [2,3,5]Esparza-Olguín et al. (2005), [2,5]Godínez-Alvarez and Valiente-Banuet (2004), [4](Arroyo-Cosultchi et al., 2016),[5]Godínez-Alvarez et al. (1999), [6]Ortega (2001),[7]Rae and Ebert (2002), [8]Rojas-Sandoval and Meléndez-Ackerman (2013),[9]Méndez et al. (2004), [10]Morales-Romero et al. (2012), [11]Silva (1996), and [12]Clark-Tapia et al. (2005).

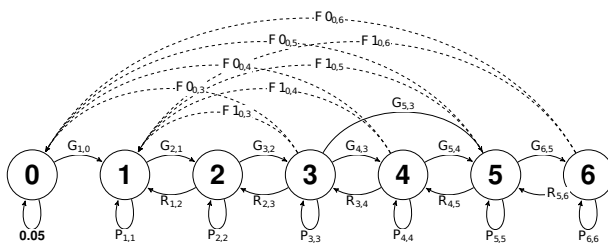| Species/original stages	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Carnegiae giganteae[1]		░	█	░	█	█	█	█	░	░	░	░	█	█	█	█
Cephalocereus macrocephalus[2]		░	█	█	░	█	░	█	█	█	█					
C. mezcalaensis[3]		░	█	░	█	█	░	█	█	█	█					
C. polylophus[4,*]	█	░	█	░	█	░	█	█	█	█	█	█				
C. tetetzo[5]		░	█	░	█	█	░	█	█	█	█	█	█			
Escontria chiotilla[6]		░	█	░	█	█	░	█	░	█	█	█	█	█		
Harrisia fragrans[7]		░	█	░	█	░	█	░	█							
H. portoricensis[8]		░	█	█	█	░	█	█	░	█	█					
Pachycereus gaumeri[9]		░	█	░	█	█	█	█	░	█	█					
P. pecten-aboriginum[10]		░	█	░	█	█	░	█	█	█	█					
P. pringlei[11]		░	█	░	█	█	░	█	█	█						
Stenocereus eruca[12]		░	█	░	█	█	░	█	█							

(a)
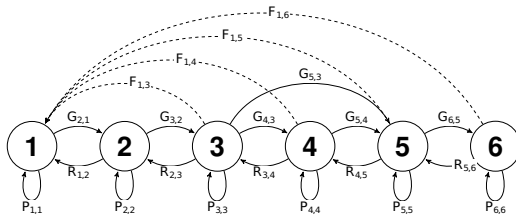
(b)

FIGURE 1 Life cycle diagrams of the matrix population models used: (a) WOSB, and (b) WSB models. Six and seven stages of individuals are possible: seeds (0), seedling (1), juvenile (2), and reproductive adults (3-6). The arrows represent the following demographic elements: stasis (P), retrogression (R), growth (G), and fecundity (F; dashed lines). The transition rate (F0) gives the fecundity into the seed bank and (F1) gives the fecundity into the seedling stage.

that germinated from the dormant seed bank from prior years (Figure 1b). The probability of germinating within the census year is equal to the probability of germinating from the seed bank (Kalisz and McPeek, 1992).

We conducted simulation experiments to explore the influence on λ when vital rate probabilities during the first life stages were modified. With these simulations, we assessed the possible effects of a seed bank on columnar cacti populations during rare but potentially important events with exceptionally high or low seedling recruitment and establishment. Despite their rarity, these types of events can have substantial impacts on long-term population dynamics (Morris and Doak, 2002). The frequency and effects of these events are highly uncertain for columnar cacti, so we covered a wider range of seed survival potential, seedling recruitment and establishment probabilities and, impacts on the simulations to highlight recruitment events that are likely to be important for population growth rates. All simulations were performed independently for the WOSB (6 × 6), and WSB (7 × 7) models. We, therefore, modified the following entries depending on the presence/absence of a seed bank: seed bank (σ_{sb}), seedling survival (σ_{se}), recruitment of seedlings from the seed bank (γ_{sb-se}), the transition from seedling to juvenile (γ_{se-ju}), and juvenile survival (σ_{ju}). These entries of the vital rates were modified during each simulation and λ was calculated keeping all other vital rates constant but checking that the stage-specific survival would not exceed 1. All demographic analyses and numerical simulations were done in R (R Core Team, 2017) using popbio (Stubben and Milligan, 2007).

3 | RESULTS

3.1 | Population dynamics

Original matrices of the columnar cacti concentrated individuals in juvenile and young adult size categories except in *Cephalocereus tetetzo* and *C. polylophus*. The former had the highest proportion of individuals in the seedling stage from experimental data (no seedlings under natural conditions) and the latter quantified natural recruitment in natural conditions. *Harrisia fragrans* and *H. portoricensis* had consistently large proportions of individuals in adult size categories. Values of λ were not different from equilibrium for most species (Table 2);

except for *Carnegiea gigantea*, *C. polylophus*, *H. fragrans*, and *H. portoricensis* which were below unity, and only in one species (*Pachycereus pecten-aboriginum*) was it slightly larger than unity. The inclusion of a seed bank (WSB) changed (Table 2) and increased λ across eleven species (*C. macrocephalus*, *C. mezcalaensis*, *C. polylophus*, *C. tetetzo*, *E. chiotilla*, *H. fragrans*, *H. portoricensis*, *P. gaumeri*, *P. pecten-aboriginum*, *P. pringlei*, and *S. eruca*), where values (and confidence intervals) were larger than unity (>2.0 % increase of λ) and *C. gigantea* that was originally below unity (Table 2). Including a hypothetical seed bank (WSB) yielded systematic significant increases in λ (*t*-test = 4.48, *df* = 11, *P* = 0.001).

3.2 | The importance of the seed bank

The PCA showed that four components accounted for 92.25% of the total variance. PC-1 explained 33.98% of the total variance with two vital rates: positive growth (γ) and individual fecundity (ϕ) with high loadings. PC-2 explained 27.10% of the residual variance with positively correlated retrogression (ρ) and negatively correlated with species. PC-3 explained 18.86% of the residual variance due to the presence/absence of a seed bank. PC-4 explained 12.21% of the residual variance and positively correlated with survival (σ) (Supplementary Appendix B). In all but PC3 matrix dimensions had no significant effects ($F_{5,66}= 0.84$; $P=0.52$, $F_{5,66}= 0.76$; $P=0.58$, $F_{5,66}= 1.49$; $P=0.20$). For PC3, there was a significant difference given by the presence of a seed bank (Figure 2) regardless of matrix dimension ($F_{5,66}= 41.44$; $P<0.001$; Figure 3).

3.3 | Numerical simulations

The numerical simulations of the vital rates showed a significant effect on λ by seedling survival (σ_{se}) (Figure 4 a and f) in both SWB and WOSB models, as well as in the seed bank (σ_{sb}) (Figure 4 d) for the WSB model. Although survival in the seed bank is unknown under field conditions, simulations suggest λ changes significantly, even with a relatively small shift in the survival probability. Small changes in the seedling to juvenile (γ_{se-ju}) and juvenile survival (σ_{ju}) transitions for the WOSB (Figure 4 b and c) and the seed to seedling (γ_{sb-se}) in WSB model (Figure 4 e) were particularly important. The recruitment of seedlings and their survival of the seed bank seems to

TABLE 2   Data for the 12 columnar cacti species used in the study. Seed *per* fruit, germination (mean proportion) and matrix size corresponds to the original (no reduced dimension) matrix reported in each study, and the value of λ CI 95 % for WOSB model (6 × 6) and WSB model (7 × 7) with a hypothetical short-term seed bank (=0.05; Figure 1b). Change in λ between models for each species ($\Delta\lambda$ %). *a* = natural *in situ* estimates, *b* = experimental *in situ* estimates, *c* = experimental *ex situ* estimates, and *d* = combined *ex* and *in situ* estimates.

| Columnar cacti species	Seed/fruit mean	Germination (mean proportion)	Original matrix size	WOSB 6 × 6 mean λ (95 % CI)	WSB 7 × 7 mean λ (95 % CI)	$\Delta\lambda$ %
Carnegiea giganteae	244	0.0041*b*	15	0.5404 (0.4178–0.6630)	0.5410 (0.4302–0.6518)	0.06
Cephalocereus macrocephalus	509	0.0280*d*	10	1.0474 (0.9193–1.1754)	1.0659 (0.9245–1.2073)	1.85
C. mezcalaensis	496	0.1760*b*	10	1.0875 (0.9586–1.2164)	1.1148 (0.9679–1.2616)	2.73
C. polylophus	976	0.0002*a*	10	0.9827 (0.9414–1.0239)	0.9997 (0.9991–1.0200)	1.70
C. tetetzo	933	0.0360*d*	12,10	1.0486 (0.9887–1.1085)	1.0647 (0.9963–1.1331)	1.61
Escrontria chiotilla	149	0.0118*d*	12	1.0187 (0.9285–1.1089)	1.0331 (0.9323–1.1339)	1.44
Harrisia fragrans	1,400	0.6400*c*	6	0.9450 (0.8713–1.0188)	0.9470 (0.8738–1.0201)	0.20
H.portoricensis	1,272	0.0255*b*	9	0.9519 (0.8625–1.0413)	0.9984 (0.8974–1.0994)	4.65
Pachycereus gaumeri	350	0.1770*d*	10	1.0029 (0.8971–1.1086)	1.0398 (0.9313–1.1482)	3.69
P. pecten-aboriginum	539	0.0522*b*	9	1.1035 (0.8443–1.3626)	1.1301 (0.8251–1.4351)	2.66
P. pringlei	1,330	0.0010*b*	10,9	1.0139 (0.9074–1.1204)	1.0252 (0.9074–1.1431)	1.13
Stenocereus eruca	336	0.3500*d*	7	1.0253 (0.9774–1.0731)	1.0275 (0.9679–1.0871)	0.22
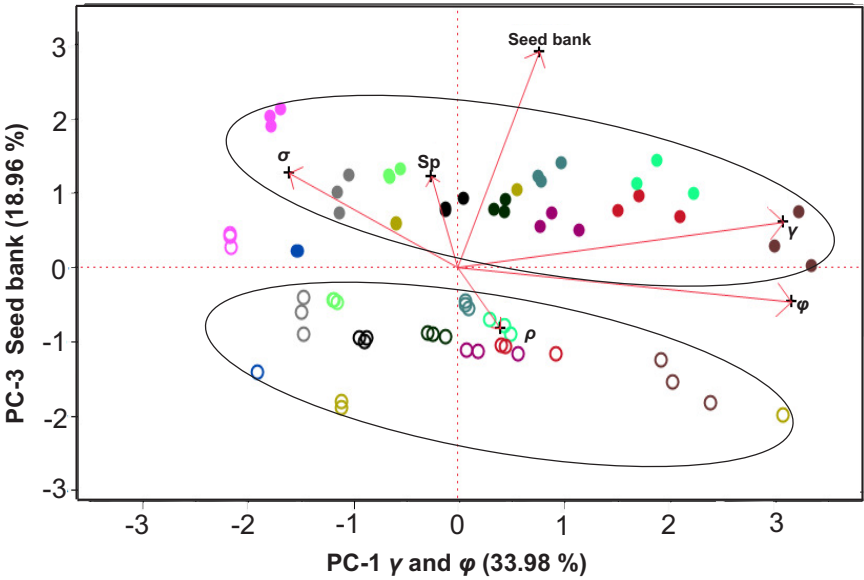
FIGURE 2   Biplot resulting from principal components analysis (PC 1-3) was used to evaluate elasticities of vital rates: survival in a given stage class (σ), negative growth (ρ), recruitment or positive growth (γ), individual fecundity (ϕ), seed bank models, and species effect (Sp). Different colors showed each species of 12 columnar cacti and each ellipse clustered two groups: WOSB (open circles) and WSB models (solid circle).
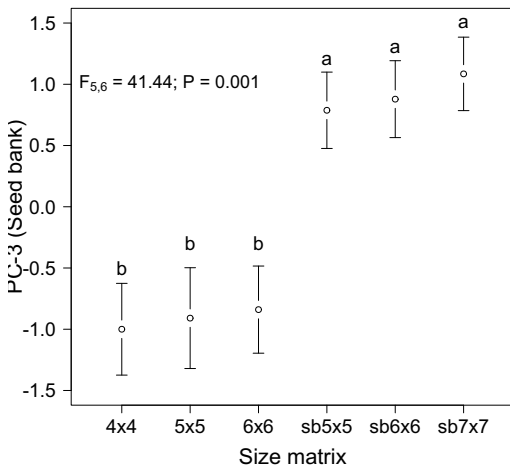
FIGURE 3 Average (± 95 CI) of PC-3 (seed bank model) against matrix dimension (WOSB = 6×6, 5×5 and 4×4; WSB = sb7×7, sb6×6, and sb5×5). Different letters indicate differences between matrix dimensions with and without seed bank (*P*<0.05).

be crucial processes for the population dynamics of columnar cacti except in (*C. gigantea*) and (*H. fragrans*), where changes transition from seed to seedling had a negligible impact on λ.

4 | DISCUSSION

There is very little information in arid environments about what are believed to be the most limiting factors for population dynamics: seed banks and seedling dynamics. This is surprising as several studies have highlighted the importance of seed banks for the persistence of populations over time in unpredictable environments (Gutterman and Venable, 2014) and the extremely limiting conditions for seedlings imposed by abiotic and biotic conditions. However, even though there is growing evidence that seed banks can be found in columnar cacti, they have been mainly overlooked despite the importance of population dynamics, especially so in the early life stages. Thus, the presence of a seed bank and its exclusion from demographic models continues to be a hindrance to understand and

model population dynamics. No explicit consideration of the seed bank in a population can generate fluctuating degrees of uncertainty in the estimation of growth rates and the accuracy of the estimated vital rates (Nguyen et al., 2019).

Most studies of columnar cacti have values of λ that are not significantly different from equilibrium (Godínez-Álvarez et al., 2003), with relatively large confidence intervals, suggesting that populations of these species are either stable or close to equilibrium (Rae and Ebert, 2002; Méndez et al., 2004; Morales-Romero et al., 2012). Unfortunately, confidence intervals are sufficiently large that any management decision should be taken with caution, if at all. The decrease of λ in two species (*C. gigantea*, and *H. fragrans*) may be caused by species or even population-specific factors and inter-annual variations in climatic factors. External factors are commonly determinants of the endangered status for cacti species (Goettsch et al., 2015) including some columnar species (*Carnegiea gigantea*, *P. gaumeri*, *S. eruca*, *H. fragrans* and *H. potoricensis*). The drivers of declining populations are usually associated to fragmentation and habitat loss (urbanization, road construction, cattle ranch management and agriculture, Esparza-Olguín et al., 2002; Méndez et al., 2004; Rojas-Sandoval and Meléndez-Ackerman, 2013) as well as interannual variation in climatic factors (Esparza-Olguín et al., 2002, 2005; Arroyo-Cosultchi et al., 2016).

Overall, the phenomenon of λ close to unity is not surprising and is expected for long-lived species such as cacti, in which relevant population processes may occur at the scale of decades (Pierson et al., 2013). The slow growth, late maturity, low fecundity, and high survival probabilities are common life-history traits (Esparza-Olguín et al., 2002; Godínez-Álvarez et al., 2003). Results in this study indicate that columnar species of cacti are at equilibrium with structures mainly composed of juvenile and young adults and consistent low numbers of seedling numbers (except for *Cephalocereus polylophus* (Arroyo-Cosultchi et al., 2016) and *C. tetetzo* (Godínez-Alvarez and Valiente-Banuet, 2004)). A limitation of this study was the minimization of interannual and interpopulation variability by averaging matrices and ignoring episodic interannual recruitment. However, these were out of the scope of our research.

An increase in λ followed the addition of a hypothetical transient seed bank. Seed banks seem to be more widespread than previously thought as evidence suggests short term seed
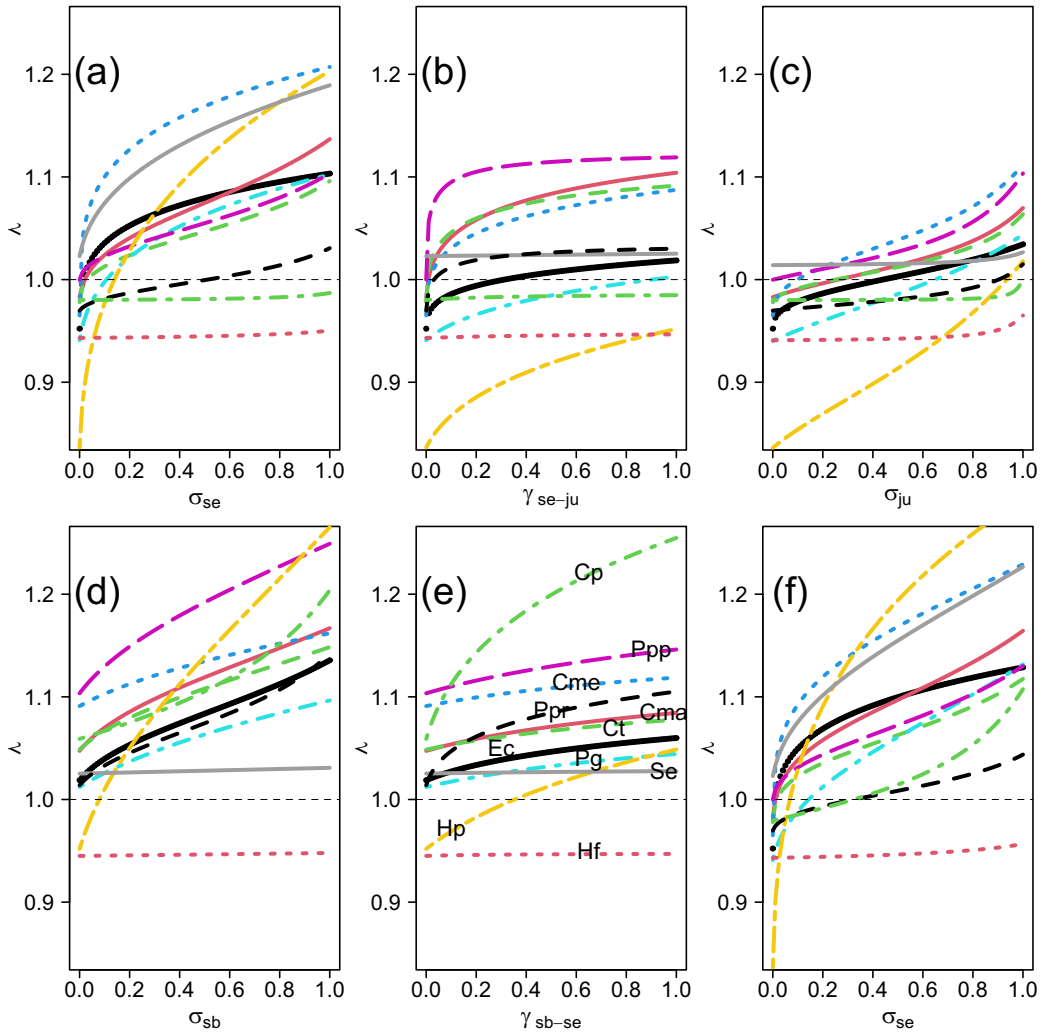
FIGURE 4 Population growth rates (λ) as a function of seedling survival (σ_{se}) (a), seedling to juvenile (γ_{se-ju}) (b), juvenile survival (σ_{ju}) (c), seed bank (σ_{sb}) (d), germination (γ_{sb-se}) (e) and seedling survival (σ_{se}) (f). Eleven columnar cacti were using the WOSB model 6×6 (a-c) and WSB model 7×7 (d-f) and simulated by changing the values, between 0 and 1 at intervals of 0.01, from each vital rates. The grey dotted line is equilibrium, λ = 1. It was not included *Carnegiea gigantea* to present small values of $\lambda \approx 0.50$. Different line colors showed each species of 11 columnar cacti, and figure 4(e) showed the acronyms of each species: (Cma = *C.macrocephalus*, Cme = *C.mezcalaensis*, Cp = *C.polylophus*, Ct = *C.tetetzo*, Ec = *E.chiotilla*, Hf = *H.fragrans*, Hp = *H.portoricensis*, Pg = *P.gaumeri*, Ppp = *P.pecten-aboriginum*, Ppr = *P.pringlei*, and Se = *S.eruca*.

banks in the subtribe Stenocerinae (*Myrtillocactus geometrizans*, *Polaskia chende*, *Stenocereus* sp. and *Stenocereus stelatus*) (Ordoñez, 2008; Cano-Salgado et al., 2012; Álvarez-Espino et al., 2014; Ordoñez-Salanueva et al., 2017) and the tribe Trichocereeae (*Harrisia fragrans*) (Goodman et al., 2012). Even though adult longevity in the Cactaceae is high and seed banks would not be theoretically expected, seed banks decouple reproduction from other life stages, which buffer against environmental variation. A clearer understanding of age-dependent germination rates of seeds, age-dependent survival of non-germinated seeds, and the production of new seeds by reproductive plants (Doak et al., 2002) are needed to determine the specific factors (e.g., environmental, physiological) that contribute to their formation. The presence of seed banks changes the life history of species and has a small but positive consequence of population growth rates that may compound population dynamics in variable environments.

The population dynamics of the majority of the studied species strongly depends on the survival of adult individuals and the growth of intermediate stages in the life cycle, a pattern similar to that reported for many long-lived plants including succulents, shrubs, and trees (Silvertown et al., 1993; Enright et al., 1995; Franco and Silvertown, 2004). Arid and semi-arid environments pose important challenges for plant persistence, and species rely on recruitment whereby the lack of recruitment at any given time gives the impression of a slowly decreasing population that depends on survival (Holland and Molina-Freaner, 2013). In the case of *C. gigantea*, *H. portoricensis* and *C. polylophus*, the recurring presence of freezing and ENSO is phenomena that strongly impacted populations by either high mortality or recruitment (Pierson et al., 2013; Rojas-Sandoval and Meléndez-Ackerman, 2013; Arroyo-Cosultchi et al., 2016). The lack of recruitment in the studies on columnar and other cacti species points towards a limiting demographic stage and has often been associated with seed predation (seed limitation) and/or high seedling mortality (seedling limitation) (Mandujano et al., 2001; Esparza-Olguín et al., 2002, 2005; Ferrer et al., 2011; Rojas-Sandoval and Meléndez-Ackerman, 2013; Zepeda-Martínez et al., 2013).

Low water availability and the quantity of solar radiation that characterize arid and semi-arid environments impose severe limitations on population growth, mainly because they induce high seedling mortality and limit the establishment of new individuals (Steenbergh and Lowe, 1977). The PCA allowed us to identify that the vital rates corresponding to positive growth and fecundity were higher, so these vital rates significantly affected population dynamics. The results of the analysis variance of the seed bank inclusion were shown essential, and the effect of the matrix size was negligible. Thus, adding a seed bank increased the importance of the vital rates (positive growth and fecundity) for the early life stages, and our results from numerical simulations showed that changes in seedling survival and seed bank could have significant effects on the population dynamics of columnar cacti and therefore protecting the seed bank is essential to the persistence of these species.

The simulations suggest that the seedling limitation has a larger effect than seed limitation in the population dynamics of cacti in most cases. Columnar cacti are strongly seed-limited by the variable reproduction of adults and the high predation of seed. Still, they are also seedling-limited even when enough seeds are produced and seedlings do not survive. The early stages are a possible option for the management of cacti species which should consider manipulations to enhance/reduce recruitment by either active introduction/elimination of juveniles or by increasing/decreasing the survival probabilities of naturally established plants. For example, several species of *Harrisia* (*H. balansae*, *H. martinii*, *H. pomanensis* and *H. tortuosa*) are considered highly invasive (Novoa et al., 2015) and control of early stages could help manage these populations. On the other hand, four species (*H. fragrans*, *H. portoricensis*, *P gaumeri* and *C. polylophus*) have some degree of endangered status so increasing the seed-seedling transitions can provide solutions for conservation strategies. The cost-efficient management of cacti would indicate that for conservation purposes, the reintroduction by transplanting nursery reared seedlings or juveniles (reducing seedling limitation) be a better strategy than sowing seeds (seed augmentation) directly into the wild (Birnbaum et al., 2011; Reemts et al., 2014).

Seed banking may increase seedling recruitment of columnar cacti by increasing seedling opportunities when conditions are favorable for survival. Their effect would also suggest that several columnar cacti populations are not threatened in demographic conditions under the assumptions used in this study. This by no means indicates that other contributing factors to their decline should not be considered for conservation (see

Goettsch et al., 2015). If we assume that Rojas-Aréchiga (2014) found positive photoblastism and seed size as phylogenetically associated to the subtribe Stenocerinae, at least the physiological component of seed bank formation is favored in this group (Rojas-Aréchiga and Batis, 2001). We need to determine the presence and longevity of seeds for many cacti species and untangle the factors behind seed and seedling limitation to portray this taxonomic group's life cycle adequately.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

APPENDIX SUPPLEMENTARY DATA

Supplementary material related to this article can be found, in the online version, at doi:.

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REFERENCES

Adams, V. M., Marsh, D. M. and Knox, J. S. (2005) Importance of the seed bank for population viability and population monitoring in a threatened wetland herb. *Biol. Conserv.*, **124**, 425–436.

Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C. and Franco, M. (2014) Functional traits explain variation in plant life history strategies. *PNAS*, **111**, 740–745.

Ågren, J. (1996) Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology*, **77**, 1779–1790.

Alvarez-Buylla, E. and Slatkin, M. (1991) Finding confidence limits on population growth rates. *Trends Ecol Evol*, **6**, 221–224.

Álvarez-Espino, R., Godínez-Álvarez, H. and De la Torre-Almaráz, R. (2014) Seed banking in the columnar cactus *Stenocereus stellatus*: distribution, density and longevity of seeds. *Seed Sci Res*, **24**, 315–320.

Anderson, E. F. (2001) *The Cactus Family*. Portland, Oregon, USA: Timber Press.

Arroyo-Cosultchi, G., Golubov, J. and Mandujano, M. (2016) Pulse seedling recruitment on the population dynamics of a columnar cactus: Effect of an extreme rainfall event. *Acta Oecol*, **71**, 52–60.

Bakker, J. P., Poschlod, P., Strykstra, R. J., Bekker, R. M. and Thompson, K. (1996) Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot Neerl*, **45**, 461–490.

Baskin, J. M. and Baskin, C. C. (1989) Physiology of dormancy and germination in relation to seed bank ecology. In *Ecology of soil seed banks* (eds. M. A. Leck, V. T. Parker and R. L. Simpson), 53–66. San Diego, USA: Academic Press.

Bell, D. T., Plummer, J. A. and Taylor, S. K. (1993) Seed germination ecology in southwestern Western Australia. *Bot Rev*, **59**, 24–73.

Birnbaum, S. J., Poole, J. M. and Williamson, P. S. (2011) Reintroduction of star cactus *Astrophytum asterias* by seed sowing and seedling transplanting, Las Estrellas Preserve, Texas, USA. *Conserv Evid*, **8**, 43–52.

Bowers, J. E. (2005) New evidence for persistent or transient seed banks in three Sonoran Desert cacti. *Southwest Nat*, **50**, 482–487.

Burns, J. H., Blomberg, S. P., Crone, E. E., Ehrlén, J., Knight, T. M., Pichancourt, J. B., Ramula, S., Wardle, G. M. and Buckley, Y. M. (2010) Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. *J Ecol*, **98**, 334–344.

Cano-Salgado, A., Zavala-Hurtado, J. A., Orozco-Segovia, A., Valverde-Valdés, M. T. and Pérez-Rodríguez, P. (2012) Composición y abundancia del banco de semillas en una región semiárida del trópico mexicano: patrones de variación espacial y temporal. *Rev Mex Biodivers*, **83**, 436–446.

Caswell, H. (2001) *Matrix population models: construction, analysis and interpretation*. Sunderland, Massachusetts, USA: Sinauer Associates, 2nd edn.

Clark, C. J., Poulsen, J. R., Levey, D. J. and Osenberg, C. W. (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *Am Nat*, **170**, 128–142.

Clark-Tapia, R., Mandujano, M. C., Valverde, T., Mendoza, A. and Molina-Freaner, F. (2005) How important is clonal recruitment for population maintenance in rare plant species?: the case of the narrow endemic cactus, *Stenocereus eruca*, in Baja California, México. *Biol Conserv*, **124**, 123–132.

Cohen, D. (1966) Optimizing reproduction in a randomly varying environment. *J Theor Biol*, **12**, 119–129.

Crawley, M J.and Ross, G. J. S. (1990) The population dynamics of plants [and discussion]. *Philos T Roy Soc B*, **330**, 125–140.

Digby, P. and Kempton, R. (2012) *Multivariate Analysis of Ecological Communities*. Population and Community Biology Series. Springer Netherlands.

Doak, D. F., Thompson, D. and Jules, E. S. (2002) Population viability analysis for plants: understanding the demographic consequences of seed banks for population health. In *Population Viability Analysis* (eds. S. R. Beissinger and D. R. Mc Cullough), 312–337. University of Chicago Press.

Enright, N. J., Franco, M. and Silvertown, J. (1995) Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. *Oecologia*, **104**, 79–84.

Eriksson, O. and Ehrlén, J. (2008) Seedling recruitment and population ecology. In *Seedling Ecology and Evolution* (eds. M. A. Leck, V. T. Parker and R. L. Simpson), 239–254. Cambridge University Press.

Esparza-Olguín, L., Valverde, T. and Mandujano, M. C. (2005) Comparative demographic analysis of three *Neobuxbaumia* species (Cactaceae) with differing degree of rarity. *Popul Ecol*, **47**, 229–245.

Esparza-Olguín, L., Valverde, T. and Vilchis-Anaya, E. (2002) Demographic analysis of a rare columnar cactus (*Neobuxbaumia macrocephala*) in the Tehuacan Valley, Mexico. *Biol Conserv*, **103**, 349–359.

Ferrer, M., Durán, R., Méndez, M., Dorantes, A. and Dzib, Y. (2011) Dinámica poblacional de genets y ramets de *Mammillaria gaumeri* Cactácea endémica de yucatán. *Bol Soc Bot Mex*, **89**, 83–105.

Franco, M. and Silvertown, J. (2004) A comparative demography of plants based upon elasticities of vital rates. *Ecology*, **85**, 531–538.

Godínez-Alvarez, H. and Valiente-Banuet, A. (2004) Demography of the columnar cactus *Neobuxbaumia macrocephala*: a comparative approach using population projection matrices. *Plant Ecol*, **174**, 109–118.

Godínez-Alvarez, H., Valiente-Banuet, A. and Banuet, L. V. (1999) Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley, Mexico. *Can J Bot*, **77**, 203–208.

Godínez-Álvarez, H., Valverde, T. and Ortega-Baes, P. (2003) Demographic trends in the Cactaceae. *Bot Rev*, **69**, 173–201.

Goettsch, B., Hilton-Taylor, C., Cruz-Piñón, G., Duffy, J., Frances, A., Hernández, H., Inger, R., Pollock, C., Schipper, J., Superina, M., Taylor, N., Tognelli, M., Abba, A., Arias, S., Arreola-Nava, H., Baker, M., Bárcenas, R., Barrios, D., Braun, P., Butterworth, C., Búrquez, A., Caceres, F., Chazaro-Basañez, M., Corral-Díaz, R., Del Valle Perea, M., Demaio, P., Duarte De Barros, W., Durán, R., Yancas, L., Felger, R., Fitz-Maurice, B., Fitz-Maurice, W., Gann, G., Gómez-Hinostrosa, C., Gonzales-Torres, L., Patrick Griffith, M., Guerrero, P., Hammel, B., Heil, K., Hernández-Oria, J., Hoffmann, M., Ishihara, M., Kiesling, R., Larocca, J., León-De La Luz, J., Loaiza S., C., Lowry, M., MacHado, M., Majure, L., Ávalos, J., Martorell, C., Maschinski, J., Méndez, E., Mittermeier, R., Nassar, J., Negrón-Ortiz, V., Oakley, L., Ortega-Baes, P., Ferreira, A., Pinkava, D., Porter, J., Puente-Martinez, R., Gamarra, J., Pérez, P., Martínez, E., Smith, M., Manuel Sotomayor M Del C, J., Stuart, S., Muñoz, J., Terrazas, T., Terry, M., Trevisson, M., Valverde, T., Van Devender, T., Véliz-Pérez, M., Walter, H., Wyatt, S., Zappi, D., Alejandro Zavala-Hurtado, J. and Gaston, K. (2015) High proportion of cactus species threatened with extinction. *Nature Plants*, **1**.

Goodman, J., Walters, D., Bradley, K., Maschinski, J. and Salazar, A. (2012) Seeds of endangered *Harrisia fragrans* form persistent soil seed banks and withstand orthodox storage conditions. *Haseltonia*, **18**, 85–94.

Gutterman, Y. (1994) Strategies of seed dispersal and germination in plants inhabiting deserts. *Bot Rev*, **60**, 373–425.

Gutterman, Y. and Venable, D. (2014) Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. *Ecology Letters*, **17**, 380–387.

Holland, J. N. and Molina-Freaner, F. (2013) Hierarchical effects of rainfall, nurse plants, granivory and seed banks on cactus recruitment. *J Veg Sci*, **24**, 1053–1061.

Hooley, D. E. (2000) Collapsed matrices with (almost) the same eigenstuff. *Coll Math J*, **31**, 297–299.

Jones, O. R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C. G., Schaible, R., Casper, B. B., Dahlgren, J. P., Ehrlén, J., García, M. B., Menges, E. S., Quintana-Ascencio, P. F., Caswell, H., Baudisch, A. and Vaupel, J. W. (2014) Diversity of ageing across the tree of life. *Nature*, **505**, 169–173.

Kalisz, S. and McPeek, M. (1992) Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology*, **73**, 1082–1093.

Lindow-López, L., Galíndez, G., Sühring, S., Pastrana-Ignes, V., Gorostiague, P., Gutiérrez, A. and Ortega-Baes, P. (2018) Do cacti form soil seed banks? An evaluation using species from the Southern Central Andes. *Plant Biol*, **20**, 1053–158.

Mandujano, M. C., Golubov, J. and Huenneke, L. (2007) Effect of reproductive modes and environmental heterogeneity in the population dynamics of a geographically widespread clonal desert cactus. *Popul Ecol*, **49**, 141–153.

Mandujano, M. C., Golubov, J. and Montaña, C. (1997) Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the southern Chihuahuan Desert. *J Arid Environ*, **36**, 259– 266.

Mandujano, M. C., Montaña, C., Franco, M., Golubov, J. and Flores-Martínez, A. (2001) Integration of demographic annual variability in a clonal desert cactus. *Ecology*, **82**, 344–359.

Méndez, M., Durán, R., Olmsted, I. and Oyama, K. (2004) Population dynamics of *Pterocereus gaumeri*, a rare and endemic columnar cactus of Mexico. *Biotropica*, **36**, 492–504.

Morales-Romero, D., Godínez-Álvarez, H., Campo-Alves, J. and Molina-Freaner, F. (2012) Effects of land conversion on the regeneration of *Pachycereus pecten-aboriginum* and its consequences on the population dynamics in northwestern Mexico. *J Arid Environ*, **77**, 123–129.

Morris, W. and Doak, D. (2002) *Quantitative conservation biology: theory and practice of population viability analysis.* Sinauer, Sunderland.

Nguyen, V., Buckley, Y., Salguero-Gómez, R. and Wardle, G. (2019) Consequences of neglecting cryptic life stages from demographic models. *Ecol Model*, **408**.

Novoa, A., Le Roux, J. J., Robertson, M. P., Wilson, J. R. U. and Richardson, D. M. (2015) Introduced and invasive cactus species: a global review. *AoB Plants*, **7**, plu078.

Ordoñez, S. C. (2008) *Características ecológicas y fisiológicas del banco de semillas de Polaskia chende.* Master's thesis, UNAM, México.

Ordoñez-Salanueva, C. A., Orozco-Segovia, A., Canales-Martínez, M., Seal, C. E., Pritchard, H. W. and Flores-Ortiz, C. M. (2017) Ecological longevity of *Polaskia chende* (Cactaceae) seeds in the soil seed bank, seedling emergence and survival. *Plant Biol*, **19**, 973–982.

Ortega, B. (2001) *Demografía de la cactácea columnar Escontria chiotilla.* Master's thesis, UNAM, México.

Pake, C. E. and Venable, D. L. (1996) Seed banks in desert annuals: Implications for persistence and coexistence in variable environments. *Ecology*, **77**, 1427–1435.

Picard, N. and Liang, J. (2014) Matrix models for size-structured populations: Unrealistic fast growth or simply diffusion? *PLoS ONE*, **9**, e98254.

Pierson, E. A., Turner, R. M. and Betancourt, J. L. (2013) Regional demographic trends from long-term studies of saguaro (*Carnegiea gigantea*) across the northern Sonoran Desert. *J Arid Environ*, **88**, 57–69.

R Core Team (2017) *R: a language and environment for statistical computing.* R Foundation for Statistical Computing. URL: http://www.R-project.org.

Rae, G. J. and Ebert, A. T. (2002) Demography of the endangered fragrant prickly apple cactus, *Harrisia fragrans*. *Int J Plant Sci*, **163**, 631–640.

Ramula, S., Knight, T. M., Burns, J. H. and Buckley, Y. M. (2008) General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. *J Appl Ecol*, **45**, 1124–1133.

Ramula, S. and Lehtilä, K. (2005) Matrix dimensionality in demographic analyses of plants: when to use smaller matrices? *Oikos*, **111**, 563–573.

Reemts, C. M., Conner, P., Janssen, G. K. and Wahl, K. (2014) Survival of planted star cactus, *Astrophytum asterias*, in southern Texas. *Southwest Nat*, **59**, 122–125.

Rees, M. (1994) Delayed germination of seeds: A look at the effects of adult longevity, the timing of reproduction and population age/stage structure. *Am Nat*, **144**, 43–64.

Rojas-Aréchiga, M. (2014) *Patrones de respuesta fotoblástica en las semillas de cactáceas: un enfoque ecológico y filogenético*. Ph.D. thesis, Universidad Autónoma Metropolitana.

Rojas-Aréchiga, M. and Batis, A. I. (2001) Las semillas de cactáceas...¿forman banco en el suelo? *Cact Suc Mex*, **46**, 76–82.

Rojas-Sandoval, J. and Meléndez-Ackerman, E. (2013) Population dynamics of a threatened cactus species: general assessment and effects of matrix dimensionality. *Popul Ecol*, **55**, 479–491.

Salguero-Gómez, R. and de Kroon, H. (2010) Matrix projection models meet variation in the real world. *J Ecol*, **98**, 250–254.

Salguero-Gómez, R., Owen, R. J., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D. A., Brinks, E., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., Wille, J., Zeh, S., Davison, R., Vieregg, D., Baudisch, A., Altwegg, R., Colchero, F., Dong, M., de Kroon, H., Lebreton, J.-D., Metcalf, C. J. E., Neel, M. M., Parker, I. M., Takada, T., Valverde, T., Vélez-Espino, L. A., Wardle, G. M., Franco, M. and Vaupel, J. W. (2015) The COMPADRE Plant Matrix Database: an open online repository for plant demography. *J Ecol*, **103**, 202–218.

Salguero-Gómez, R. and Plotkin, J. B. (2010) Matrix dimensions bias demographic inferences: Implications for comparative plant demography. *Am. Nat*, **176**, 710–722.

Silva, P. (1996) *Demografía comparativa de Pachycereus pringlei en dos unidades geomórficas contrastantes del paisaje en Baja California Sur, México*. Master's thesis, UNAM.

Silvertown, J., Franco, M., Pisanty, I. and Mendoza, A. (1993) Comparative plant demography–relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J Ecol*, **81**, 465–476.

Silvertown, J., McConway, K. J., Hughes, Z., Biss, P., Macnair, M. and Lutman, P. (2002) Ecological and genetic correlates of long-term population trends in the park grass experiment? *Am Nat*, **160**, 409–420.

Sosa, V. J. and Fleming, T. H. (2002) Why are columnar cacti associated with nurse plants? In *Columnar Cacti and their Mutualists. Evolution, Ecology and Conservation* (eds. T. H. Fleming and A. Valiente-Banuet), 306–323. Tucson, USA: The University of Arizona Press.

Steenbergh, W. F. and Lowe, C. H. (1977) *Ecology of the saguaro II: reproduction, germination, establishment, growth, and survival of the young plant*. 8. National Park Service Scientific Monograph.

Stubben, C. and Milligan, B. (2007) Estimating and analyzing demographic models using the popbio package in R. *J Stat Softw*, **22**, 1–23. URL: http://www.jstatsoft.org/v22/i11.

Thompson, K., Bakker, J. P. and Bekker, R. M. (1997) *The soil seed banks of North West Europe: Methodology, density and lonvegity*. Cambridge University Press.

Turnbull, L. A., Crawley, M. J. and Rees, M. (2000) Are plant populations seed-limited? a review of seed sowing experiments. *Oikos*, **88**, 225–238.

Valiente-Banuet, A. and Ezcurra, E. (1991) Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. *J Ecol*, **79**, 961–971.

Venable, D. L. (2007) Bet hedging in a guild of desert annuals. *Ecology*, **88**, 1086–1090.

Zepeda-Martínez, V., Mandujano, M. C., Mandujano, F. J. and Golubov, J. K. (2013) What can the demography of *Astrophytum ornatum* tell us of its endangered status? *J Arid Environ*, **88**, 244–249.