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Demographic Effects of Seedling Reintroduction on the Viability of a Vulnerable Columnar Cactus of the Chihuahuan Desert

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ABSTRACT

Reintroduction is a crucial step in the conservation efforts aiming to restore ecosystems and protect threatened species. However, studies that incorporate and evaluate the effect of plant reintroduction are scarce. A study on a population of *Cephalocereus polylophus*, a vulnerable cactus endemic to the southern Chihuahuan Desert, allowed us to evaluate the effect of seedling reintroduction and protection on the viability of this population. An integral projection model was used on a 5-year dataset to forecast population size over a century and to simulate scenarios of seedling survival and protection. The study revealed an asymptotic population growth rate (λ) of 0.97 (95% CI = 0.96–0.99). Simulating seedling survival and an increase in the seedling bank translated into a λ that showed only a slight increase but remained below one, mainly because the recruitment and survival of small individuals were insufficient to compensate for the population decline. Protecting seedlings against herbivores and increasing their survival to 96.5% resulted in a larger population size (~8% average increase) and delayed extinction in comparison with an unmanaged scenario with a 60% survival rate. This demonstrates that increasing seedling survival rates through protection and reintroduction efforts can only be conceived as a complementary conservation strategy to those focused on preserving existing individuals. Effective reintroduction strategies can help delay the extinction of the population of this cactus, but the conservation of the current population and its habitat is pivotal for its future survival.

1 | Introduction

Research on the reintroduction of plants in their natural habitats has increased in the last two decades (Maschinski and Duquesnel 2006; Menges 2008; Godefroid et al. 2011; Albrecht et al. 2019; Fenu et al. 2020), with several studies demonstrating increased biodiversity and species persistence due to these reintroduction efforts (Armstrong et al. 2019). Reintroduction of endemic and threatened species, which involves the reestablishment of an extirpated population or the reinforcement (also called supplementation, enhancement, augmentation, or restocking) of a small and vulnerable population, may be essential for increasing population size and guaranteeing their conservation (Godefroid et al. 2011). However, limited evidence exists on the success of these programs in improving the viability and self-sustainability of populations (Knight 2012). Thus, when performing a reinforcement program, it is essential to propose appropriate strategies that ensure that the dynamics of such populations will be able to guarantee their viability in the medium to long term. In addition, reintroduction efforts must

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be followed up with demographic studies to track their performance (Maschinski and Duquesnel 2006; Godefroid et al. 2011; Knight 2012; Albrecht et al. 2019).

Population viability analyses can provide valuable insights into the potential success of reinforcement. Such analyses involve gathering demographic data (e.g., survival, growth, fecundity, seedling recruitment, dispersal of individuals) to project future population size, stage structure, and population growth rates (Menges 2000). Moreover, population models use demographic data to predict changes in abundance in the middle and long term (Caswell 2001), and population responses to natural and human disturbances, such as future climate change (Quintana-Ascencio et al. 2021). In addition, the effect of reintroduction or reinforcement plans on vital rates and population dynamics can be incorporated into vital rate analysis to help us determine how plant populations will likely respond to the different strategies (Knight 2012).

Unfortunately, for precise population dynamics to be determined, long-term surveys are needed (Menges 2000). However, the time and resources required to gather these data are not often available, even for endemic or threatened species. This leads to a trade-off between the need to collect data on vital rates in the long term to provide accurate estimates and the need to provide timely and data-driven advice on species management in the short term (Frye 1996). This trade-off can in part be solved by using data gathered over short- or medium-term periods as a starting point in combination with modeling procedures that can simulate hypothetical scenarios of species management (Zepeda-Martínez et al. 2013). Demographic modeling can thus provide insight into short- and middle-term possible directions for reintroduction and management of vulnerable plant species.

The Cactaceae is one of the most threatened plant families and more than 30% of its species are categorized as being at risk (Goettsch et al. 2015), and the entire family is listed in Appendix II of the CITES (CITES. Convention on International Trade in Endangered Species of Wild Fauna and Flora 2022). The main reason for their threatened status is largely due to their vulnerability to disturbance, their narrow habitat specificity, which limits their ability to recover after natural or anthropogenic disturbance, and their low population sizes, population growth rates, and recruitment rates, and their high mortality during their seedling phase (Esparza-Olguín et al. 2005; Martínez et al. 2010; Zepeda-Martínez et al. 2013; Ortiz-Martínez et al. 2021).

Ecologically, cacti are fundamental for the maintenance of the arid and semiarid ecosystems which the family Cactaceae characteristically inhabit (Guerrero et al. 2019). The population dynamics of many members of the cactus family are often determined by the survival of adults, the survival at vulnerable early stages of development, and the infrequent recruitment of seedlings (Godínez-Álvarez et al. 2003; Zepeda-Martínez et al. 2013; Arroyo-Cosultchi et al. 2016; Jiménez-Guzmán et al. 2024). Survivorship is generally the vital rate that mostly contributes to the population growth rate, being the adults the most important stage for the maintenance of cacti populations (Godínez-Álvarez et al. 2003; Zepeda-Martínez et al. 2013). Recruitment is a critical process in the life cycles of cactus species and thus constitutes an essential restriction to population growth rate (Godínez-Álvarez et al. 2003; Arroyo-Cosultchi et al. 2016, 2022; Jiménez-Guzmán et al. 2024). Studies on the population dynamics of columnar and other cacti species suggest that a lack of recruitment is often associated with high seedling mortality, a phenomenon known as seedling limitation (Esparza-Olguín et al. 2005; Ferrer-Cervantes et al. 2012; Zepeda-Martínez et al. 2013). These high seedling mortality rates and limited establishment of new individuals are due mainly to low water availability and high solar radiation characteristic of arid and semi-arid environments (Godínez-Álvarez et al. 2003), with some studies suggesting the additional effects of herbivory and predation of these individuals (Valiente-Banuet and Ezcurra 1991; Mandujano et al. 1998).

Although several studies have involved the construction of population models for cactus species (Jiménez-Guzmán et al. 2024) and some have simulated conservation scenarios (e.g., Ferrer-Cervantes et al. 2012), to our knowledge, no study has yet attempted to project population dynamics under management (e.g., reintroduction or reinforcement) and/or conservation scenarios. Long-term demographic studies of *Mammillaria gaumeri* (Ferrer-Cervantes et al. 2012) and *Echinomastus erectocentrus* (Larios et al. 2020) have demonstrated that populations of these cactus species tend to decrease in most of the studied years due to adverse climatic conditions and human disturbance.

Seedling survivorship and seedling growth are considered the highest measures of success of a natural population (Sutter 1996) and indicate its self-sustainment through the development of successive generations (Primack 1996). In perennial plants, it is primarily the seedling and adult survival of individual plants that influence the year-to-year population dynamics (Jongejans et al. 2006); but reproduction can markedly increase population growth rate in some cases (Silvertown et al. 1993). Moreover, sexual reproduction offers advantages beyond simply bolstering the population of local plants: it preserves genetic diversity, facilitates the formation of seed and seedling banks, and enables the population to inhabit regions outside the range of vegetative growth (Crawley 1997).

Efficiently managing the reintroduction of cacti would significantly contribute to their conservation. Reinforcement of populations through transplants of nursery-reared seedlings or juveniles, rather than direct seed sowing, has proven to be a more effective strategy, as it reduces seedling limitation (Knight 2012; Reemts et al. 2014; Ortiz-Martínez et al. 2021). This approach is particularly successful in protected sites (Godefroid et al. 2011), though its long-term impact on natural population viability remains understudied. Given current environmental changes, a cost-effective conservation strategy involves propagating seedlings *ex situ* for future reintroductions when needed (Arroyo-Cosultchi et al. 2016). Seedling reinforcement not only addresses recruitment bottlenecks but is also more reliable than seed augmentation, as suggested by Reemts et al. (2014). Thus, managed propagation and reintroduction could serve as a viable tool for cactus conservation. This approach involves actively introducing and protecting seedlings to increase the chances of survival, in comparison with naturally established plants, and thus enhance recruitment. Under this scenario, reintroduced seedlings no longer have cotyledons and have primordial thorns that reduce their chances of predation (Ortiz-Martínez et al. 2021).

Furthermore, larger young plants can hold more water in their tissues, which allows them to endure longer periods of dry weather conditions (Jordan and Nobel 1981). One way to reintroduce a cactus population is to reinforce it through the reintroduction of seedlings from the same site (Reemts et al. 2014).

Here, we provide evidence of the role of seedling reinforcement and protection in improving the demographic status of an endangered columnar cactus. Our study uses a 5-year demographic dataset and information from field management experiments on seedling survival to assess how this crucial step impacts the population dynamics of the golden saguaro, *Cephalocereus polylophus*, an endemic and vulnerable cactus, dominant of the semi-desert in the southern Chihuahuan Desert, Mexico, as an essential first step toward reintroduction and conservation programs. We model the population dynamics to (1) assess the effect of annual environmental variability on the middle-term dynamics of the population, (2) estimate the contribution of new and preexistent individuals, and of the different vital rates, on the population's growth rate, (3) determine the effectiveness of seedling reinforcement, targeting seedling survival, a strategy that has been previously shown to improve reinforcement (Ortiz-Martínez et al. 2021), and (4) simulate changes in population size over time under two seedling survival scenarios (with and without reinforcement and protection) as potential conservation strategies for the species.

2 | Methods

2.1 | Study Species

The golden saguaro, *Cephalocereus polylophus* (DC.) Britton & Rose, is a monopodial columnar cactus, with ~15% of its populations consisting of branched individuals, reaching up to 13 m in height (Arroyo-Cosultchi et al. 2016). This columnar cactus occurs naturally in canyon regions covered with deciduous forest and calcareous soils. It is distributed in an area of approximately 6000 km^2, constrained to few isolated locations in the southern Chihuahuan Desert, Mexico (IUCN 2017). Populations are dispersed, but some have high densities (6700 ± 2800 ind/ha mean ± SD; Arroyo-Cosultchi et al. 2016). The flowering season is between May and July; flowers are hermaphroditic with nocturnal anthesis and last for one or rarely two nights; they are large (4–6 cm), with dark-red or pink perianth (Anderson 2001). Flowers are nectariferous and are visited by bats and hummingbirds. Fruits contain a high number of seeds (976 ± 80; Arroyo-Cosultchi et al. 2016) whose dimensions lie between 2.68 × 1.85 mm (Arroyo-Cosultchi et al. 2016) and are dispersed by bats, birds, and ants during July and August (Arroyo-Cosultchi et al. 2016). Seedling establishment is constrained by drought, sun exposure (Godínez-Álvarez et al. 2003), granivory and herbivory, and is favored by the presence of nurse plants (Ortiz-Martínez et al. 2021), mainly microphyllous scrubs, such as *Croton mazapensis* Lundell and *Hoverdenia speciosa* Nees.

The species is listed as vulnerable by the IUCN Red List of Threatened Species (IUCN 2017) and is found in Appendix II of the CITES (CITES. Convention on International Trade in Endangered Species of Wild Fauna and Flora 2022). Arroyo-Cosultchi et al. (2016), using matrix projection models, with height (cm) as the state variable and assuming the presence of a seed bank, reported for the population studied here two transitions (2012–2013 and 2013–2014) with an asymptotic population growth rate (λ) at equilibrium and another with an increasing rate. Individuals are valued in the horticultural industry, and biogeographically the species is one of the northernmost representatives of the genus *Cephalocereus* (Anderson 2001). In addition, within the semi-desert of the southern Chihuahuan Desert in Mexico, columnar cacti like *C. polylophus* provide important ecosystem services such as the provision of nectar, pollen, fruits, seeds and shade, particularly during the dry season, as well as increasing soil fertility, and maintaining biodiversity through their interaction with pollinators and seed dispersers (Cruz and Pavón 2013; Arroyo-Cosultchi et al. 2016; Ortiz-Martínez et al. 2021).

2.2 | Study Sites

The study was carried out in the Barranca de Metztitlán Biosphere Reserve (BMBR), in the vicinities of the town of San Miguel Almolón (20°43′32.8″ N and 98°54′56.9″ W), in the state of Hidalgo, Mexico. BMBR, with an extension of 96,042 ha, is characterized by an intertropical semiarid environment that is biologically important because of its high number of endemisms and functions as a corridor between the northern Nearctic and southern Neotropical vegetation (CONABIO 2003). This area has a high biological richness and is considered one of the most important zones in Mexico for cacti, with around 70 species (CONABIO 2003). However, different anthropogenic factors are present in the BMBR, including the presence of roads, goat grazing, and a small village close to the studied population (~1 km).

The climate of the study area is dry, semi-warm with summer rains (BS0hw), with a mean temperature of 20.7°C (range = 14.1°C–27.3°C; $n = 61$ years) and a mean annual precipitation of 411 mm (range = 184–810 mm) (Ortiz-Martínez et al. 2021), with nearly 85% of the annual precipitation occurring during summer and fall (CONAGUA. Comisión Nacional del Agua 2022). The vegetation is classified as xerophytic scrub (CONABIO 2003), with predominant vegetation types the microphyllous scrub, dominated by *Croton mazapensis* and *Hoverdenia speciosa* (Ortiz-Martínez et al. 2021), and the deciduous forest, dominated by the columnar cactus *Cephalocereus senilis* (Haw.) Pfeiff. Allg. and *Isolatocereus dumortieri* (Scheidw.) Backeb (Cruz and Pavón 2013), as well as shrubby legumes such as *Mimosa leucaenoides* Benth (Herce et al. 2013).

2.3 | Field Methods

In 2012, a permanent observation plot (with an area of 1100 m^2) was established in a population of *C. polylophus* and was censused until 2016 (four transitions). In April 2012, 722 individuals were mapped, tagged, and their main stem width (cm) and height (cm) were measured. Width and height were measured with a caliper or a tape, or with a level staff (for plants taller than 200 cm). The stem of each individual was marked at a fixed length from the apex, such that subsequent censuses (2013–2016) would quantify the relative increments in stem height (Esparza-Olguín et al. 2005). When adult individuals were multibranched (13%), the length of each branch was measured from the tip to the point of attachment to the main stem and then added to the length of the highest stem to provide a measure of the cumulative individual length. With these measurements, we approximated plant volume through a cylinder model.

During the reproductive season, from April to August of each year, we registered the mortality and the number of reproductive structures (floral buds, flowers, and fruits) produced per plant, and counted and measured newly recruited individuals in the population with a digital vernier caliper to the nearest 0.01 mm. We collected three mature fruits from 30 different *C. polylophus* individuals during the 2012, 2013 and 2014 reproductive seasons to estimate the mean number of seeds produced per fruit. According to the demographic study by Arroyo-Cosultchi et al. (2016), the natural survival rate after 1 year for established seedlings was 63.3% ($n = 210$) for the 2012–2013 period and 57.9% ($n = 142$) for the 2013–2014 period, yielding an overall average of 60%.

In 2014, we performed a field controlled experiment to evaluate seedling survival. One hundred 1-year-old seedlings were reintroduced, each contained in a jiffy pot filled with soil from the study site and placed under the canopy of a *C. mazapensis* or *H. speciosa* individual; we did not conduct the experiment in open spaces because we observed a high mortality rate under these conditions (Ortiz-Martínez et al. 2021). These seedlings were placed inside small wire mesh boxes (10 cm^3 in size, with a 1-mm mesh aperture) in groups of ten seedlings, with 10 replicates, and were monitored and measured daily for the first 12 days and then 1, 2, 5, and 12 months following their reintroduction (Ortiz-Martínez et al. 2021). Survival of these 100 reintroduced and protected seedlings was 96.5% after 1 year after their reintroduction.

2.4 | Modeling the Population Dynamics

Demographic data on *C. polylophus* were used to construct models of the vital rates as a function of plant size (volume, cm^3); however, to achieve linearity, individual volume was transformed by its cubic root (cm). In a previous work, Arroyo-Cosultchi et al. (2016) used plant height (cm) as the state variable; however, a preliminary comparative analysis (not shown) demonstrated that plant volume was a better predictor of plant performance. The modeled vital rates were: survival probability; growth, that is, change in size from 1 year to the next; reproduction probability; and fecundity, that is, the number of reproductive structures produced by a reproductive individual. These models consisted of generalized linear mixed models (GLMMs) and generalized additive mixed models (GAMMs), thus exploring linear and non-linear relationships between plant size and the vital rates. In these models we included year as a random effect, and the probability distributions used to describe survival, growth, reproduction, and fecundity were binomial, normal, binomial, and negative binomial, respectively. We performed model selection using the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002) to choose the most plausible model among those considered for each vital rate (Table 1). Model construction and selection were performed in R (v. 4.2.0; R Development Core Team 2021) using packages AICcmodavg (Mazerolle 2020), gamlss (Rigby and Stasinopoulos 2005) and lme4 (Bates et al. 2015).

Integral projection models (IPMs) are extensions of matrix models that return identical outputs (i.e., population growth rate, elasticities, sensitivities, etc.), but employ relations between vital rates (survival, growth, and fecundity) and continuous state variables (e.g., diameter, height, volume, DBH, or age) as input, instead of categorical ones as matrix models do (Easterling et al. 2000; Ellner et al. 2016; Doak et al. 2021). IPMs benefit from being robust to small data sets compared with matrix models (Doak et al. 2021) and are able to include explanatory drivers as covariates (Quintana-Ascencio et al. 2021). IPMs have been employed recently and widely for demographic analyses (e.g., Easterling et al. 2000; Ellner et al. 2016; González et al. 2021), including the evaluation of population viability for threatened and endemic species (e.g., Ferrer-Cervantes et al. 2012; Tye et al. 2016).

Using the selected vital rate models described above, the random effect of year, and estimates from the field observations without reinforcement and protection, the average and annual IPMs were

$$n_{t+1}(z') = \int k_{\text{avg}}(z, z') \cdot n_t(z) \mathrm{d}z, \tag{1}$$

and

$$n_{t+1}(z') = \int k_t(z, z') \cdot n_t(z) \mathrm{d}z, \tag{2}$$

respectively, where z is the size of an individual at time t, z' is the size at time $t+1$, n is the distribution of individuals across sizes, k_{avg} is the average kernel and k_t year-specific kernels. The year-specific kernels were obtained by including in the vital rate functions the random effects of each year.

A kernel is usually decomposed into seven functions describing survival, $s(z')$, the expected survival probability at size z; growth, $g(z, z')$, the expected probability of an individual of size z to have a size z' at time $t+1$; $p_b(z)$, the expected probability of reproduction; $b(z)$, the expected number of reproductive structures produced by an individual; s_f, the estimated mean number of seeds produced per fruit; p_g, the mean seed germination probability estimated from the field experiment; p_s, the mean seedling survival probability estimated from the field experiment; and C_0, the size distribution of newborns. Thus, the kernel can be decomposed as.

$$k(z, z') = s(z) \cdot g(z, z') + p_b(z) \cdot b(z) \cdot s_f \cdot p_g \cdot p_s \cdot C_0(z'). \tag{3}$$

To simulate the effect of an initial, single reinforcement of 100 1-year-old seedlings and their protection, we added a second term to Equation (1) at time 0 as.

$$n_1(z') = \int k_{\text{avg}}(z, z') \cdot n_0(z) \mathrm{d}z + \int s_r \cdot g(z, z') \cdot n_r(z) \mathrm{d}z, \tag{4}$$

where s_r is the mean survival probability of the introduced seedling, estimated from the field experiment;

$$n_r(z) = N_r \cdot C_r(z) \tag{5}$$

$$C_r(z) \sim \text{Normal}(\mu_r, \sigma_r) \tag{6}$$

where N_r is the number of reintroduced seedlings (100); $C_r(z)$ is the size of introduced seedlings at time 0; and μ_r and σ_r are the mean and standard deviation of the introduced seedlings sizes. Subsequent years were modeled following Equation (1). A similar procedure was followed to simulate reinforcement and protection using the year-specific kernels.

We modeled the change in the population size (N) and population growth rates (λ) of *C. polylophus* with and without reinforcement and protection. This involved considering both the iteration of the average kernel, k_{avg}, and the use of year-specific kernels, k_t.

We calculated the population growth rates (λ) and stable size-class distributions (w), and their 95% confidence intervals (with and without reinforcement and protection conditions) through bootstrapping (1000 iterations; Li et al. 2015).

2.5 | Projection of Population Size Under Seedling Survival Scenarios With and Without Protection

To project the future population size of *C. polylophus*, we used the average IPM using two different seedling survival rate conditions: without ($p_s = 60\%$; Arroyo-Cosultchi et al. 2016) and with reinforcement and protection ($s_r = 96.5\%$, based on the 100 1-year-old seedlings described above; Ortiz-Martínez et al. 2021). We are assuming that the population receives reinforcement and protection annually in the projection. Thus Equation (4) was substituted by:

$$n_{t+1}(z') = \int k_{avg}(z, z') \cdot n_t(z) dz + \int s_r \cdot g(z, z') \cdot n_r(z) dz + n_r(z') \tag{7}$$

We used this information to predict the population size of *C. polylophus* for 100 years starting from 2012 using only the average kernel, as year-specific kernels capture environmental variation of which we have no evidence in the future. We chose this timespan because *C. polylophus* is a long-lived species, and changes in its demographic patterns require long projection periods.

TABLE 1 | Selection of the most plausible generalized linear and additive mixed models predicting survival probability, growth, reproduction probability, and fecundity (number of reproductive structures produced) for *Cephalocereus polylophus* as a function of individual size (CRT_t, cubic root of volume at time *t*, cm).

Model	df	AICc	ΔAICc
Survival (binomial distribution)			
Survival~CRT_t, random = ~(1|year)	**2343.0**	**1462.34**	**0.00**
Survival~s(CRT_t), random = ~(1|year)	2342.0	1464.34	2.00
Growth (normal distribution)			
CRT_{t+1}~CRT_t + re(random = ~1|year)	1939.0	−369.55	823.14
CRT_{t+1}~cs(CRT_t) + re(random = ~1|year)	1936.0	−442.27	750.42
CRT_{t+1}~CRT_t + re(random = ~1|year), sigma. formula = ~ CRT_t	1938.0	−1075.45	117.24
CRT_{t+1}~cs(CRT_t) + re(random = ~1|year), sigma. formula = ~CRT_t	1935.0	−1094.28	98.41
CRT_{t+1}~CRT_t + re(random = ~1|year), sigma. formula = ~cs(CRT_t)	1935.0	−1169.36	23.33
CRT_{t+1}~cs(CRT_t) + re(random = ~1|year), sigma. formula = ~cs(CRT_t)	**1932.0**	**−1192.69**	**0.00**
Reproduction probability (binomial distribution)			
Reproduction~CRT_t, random = ~(1|year)	2640.0	1029.90	7.98
Reproduction~s(CRT_t), random = ~(1|year)	**2639.0**	**1021.92**	**0.00**
Fecundity (PO or NBI distributions)			
Fecundity~CRT_t + re(random = ~1|year) (*PO*)	180.7	1232.51	240.64
Fecundity~cs(CRT_t) + re(random = ~1|year) (*PO*)	177.4	1205.82	213.95
Fecundity~CRT_t + re(random = ~1|year) (*NBI*)	179.7	995.80	3.93
Fecundity~cs(CRT_t) + re(random = ~1|year) (*NBI*)	**176.3**	**991.87**	**0.00**

Note: The selected model is in bold. Survival and reproduction probability models were fitted with the gamm4 package, whilst growth and fecundity were fitted with the gamlss package because we wanted to consider heteroscedastic models (i.e., with a sigma formula) and a negative binomial distribution (NBI) in addition to a Poisson distribution (PO), respectively.

Abbreviations: ΔAICc, difference between the AICc of the model and the minimum AICc value; AICc, Akaike Information Criterion corrected for small sample sizes; cs, cubic spline (gamlss); df, degrees of freedom; re, random effect (gamlss); s, thin-plate spline (gamm4).

3 | Results

In the 1100 m^2 we studied, we found 722 individuals of *C. polylophus* in 2012 with a density of 0.66 ind/m^2. In the 2013–2016 censuses, we found 658, 746, 526, and 486 plants, respectively, with a final density of 0.44 ind/m^2. During the period between 2014 and 2016, there was a significant reduction in the number of individuals within the plot, with a 34.86% drop from 746 to 486 individuals, which represents the most pronounced decrease in this time frame. However, during the period 2013–2014, there was a significant increment in the number of individuals within the plot (13.37%). The number of recruited seedlings between 2012 and 2013 was eight (mean ± SE: 6.90 ± 0.59 cm length); in 2013–2014 it was 130 (2.69 ± 0.12 cm length); in 2014–2015 it was four (3.94 ± 1.02 cm length); and in 2015–2016 it was 96 (3.39 ± 0.18 cm length).

3.1 | Modeled Vital Rates and Population Dynamics, Structure and Size

The survival of *C. polylophus* individuals increased with volume (Figure 1a), with the probability of seedling (i.e., an individual having a cubic-root volume < 0.23 cm) survival being very low, going from 37% in the 2013–2014 period to 8% in 2014–2015. In turn, juveniles (i.e., those with a cubic-root volume of 10 cm) and adults (i.e., having >28 cm) had higher survival probabilities (~78% and ~90%, respectively). Adult mortality was caused by rot during the rainy year and by desiccation during the dry year. In seedlings, the main mortality factors were herbivory and desiccation. In all years, stems grew very slowly (Figure 1b), with larger individuals even decreasing in their size, due to a loss of branches or stem apex necrosis. Reproductive probability was above 0 at ~30 cm in (cubic-root) volume and increased with volume up to ~70 cm from where it decreased (Figure 1c). A similar pattern was obtained for the number of reproductive structures (i.e., fecundity) (Figure 1d), but with some variation between years.

The kernel represents the aggregation of all the investigated vital rates of *C. polylophus* (survival, growth, probability of reproduction, and fecundity). The resulting kernel, describing the dynamics of the studied population, is depicted in Figure 1e. The kernel surface was almost flat over the majority of its range, except for the ridge running near its diagonal (or central region), which is determined by $P(z, z')$, and the wall close to the z-axis, determined by $F(z, z')$.

The observed size distribution, and the size distributions projected with the average kernel and the year-specific kernels, were unimodal and skewed more heavily toward small sized individuals in the predicted than in the observed distributions (red, blue and black lines in Figure 2a–e, respectively).

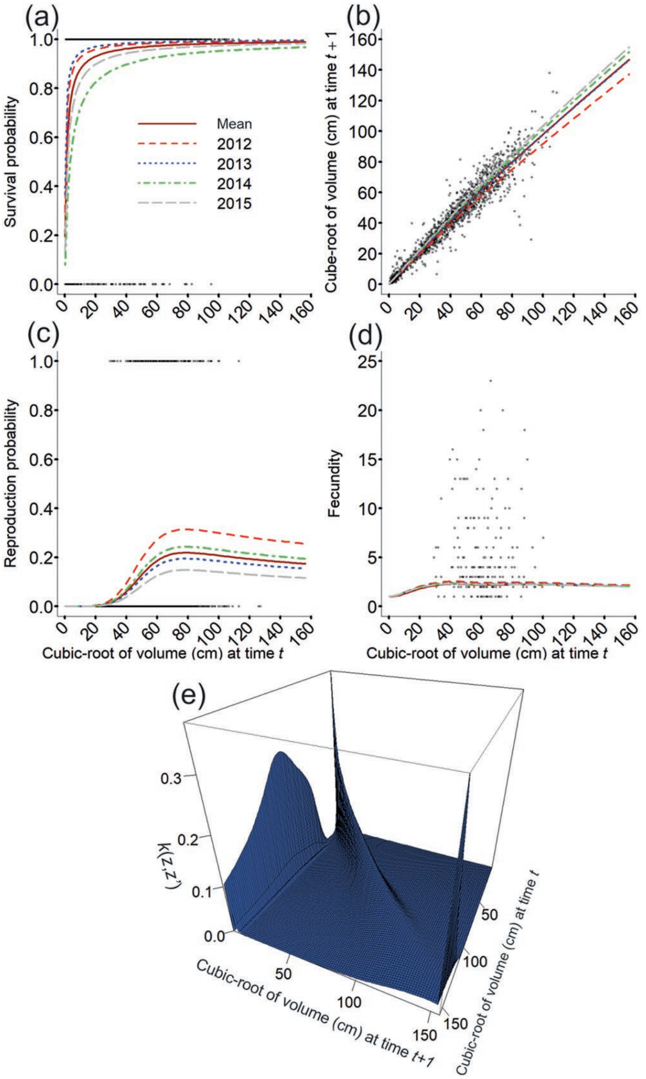

FIGURE 1 | Modeled vital rates and kernel of the *Cephalocereus polylophus* population (unmanaged condition) as a function of the cubic root of plant volume at time *t* (*z*, cm). (a) Probability of survival, (b) plant volume at time $t + 1$ (z', cm), (c) probability of reproduction, (d) fecundity (number of reproductive structures) and (e) kernel (*k*) associated with the integral projection model.

Projecting population size with the average kernel and the year-specific kernels from 2014 to 2016 resulted in a slight decline that corresponds to the actual decline observed in the population (Figure 3a), with, as expected, the year-specific estimates fitting more closely the observed pattern. However, projecting population size with the average kernel with the reinforcement and protection scenario (seedling survival 0.965) from 2013 to 2016 resulted in a larger population size (8.1% average increase) compared to the scenario without reinforcement and protection (Figure 3a), while projecting population size with year-specific kernels with reinforcement from 2014 to 2016 resulted in a sharp decline that corresponds to the actual decline observed in the population.

The estimate of the population growth rate (λ) derived from the average kernel was 0.9769 (95% CI = 0.9667–0.9915) without reinforcement and protection from 2012 to 2015. In this context, λ refers to the asymptotic growth rate, which is a measure of the population growth rate under stable, long-term conditions. Therefore, based on the estimated λ, the population remained below one with and without reinforcement and protection from 2014 to 2016, whereas it was above one from 2012 to 2014 (Figure 3b). This pattern is also reflected in the individual counts of columnar cacti within the plot.

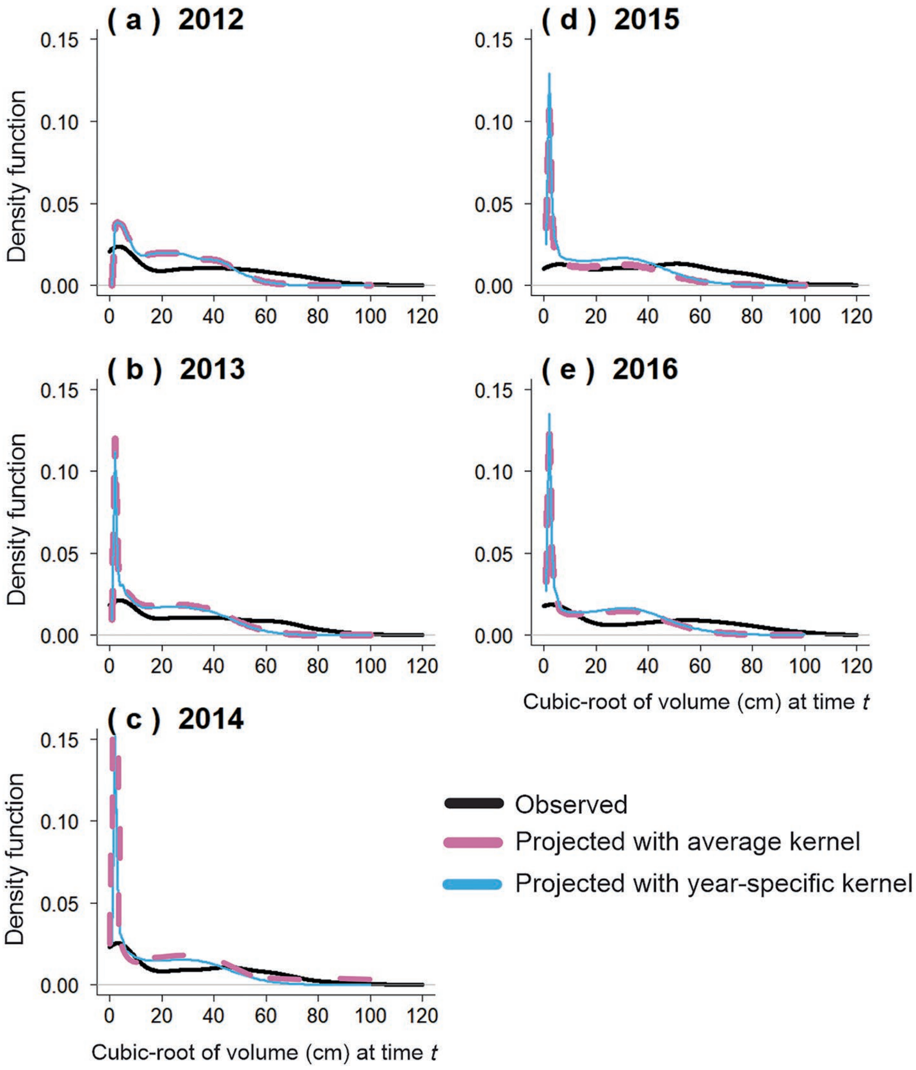

FIGURE 2 | Density functions of the size distributions over the study period (2012–2016). Observed size distributions (black) without reinforcement and protection, projected size distributions obtained with the average kernel (red), and projected size distributions obtained with the year-specific kernels (blue).

For the population growth rate (λ) estimated from the year-specific kernels, it was above one for half of the study periods, with the exception of the 2014–2015 and 2015–2016 periods (Figure 3b). Specifically, without reinforcement and protection, estimates were above one for the 2012–2013 and 2013–2014 periods but below one for all remaining periods. With reinforcement and protection, λ values exceeded one during 2012–2013 and 2013–2014, while remaining below one for all other periods.

3.2 | Projection of Population Size Under Seedling Survival Scenarios With and Without Reinforcement and Protection

Projecting population size from 2012 to 2111 using two seedling survival conditions, without reinforcement and protection (with a 0.60 survival probability) and the annual reinforcement and protection condition (0.965) resulted in sharp declines (Figure 4) that correspond to the current observed pattern (Figure 3a). However, the decline for the reinforcement and protection condition was less pronounced than without reinforcement and protection (Figure 4); nonetheless, under both conditions the population declines over time.

4 | Discussion

We found differences in the projected population structures and sizes with and without seedling reintroduction and protection for *Cephalocereus polylophus*, threatened columnar cactus. Simulations under two seedling survival conditions showed that increasing the seedling survival rate to 96.5% resulted in a higher population size (N) and growth rate (λ) and a delayed local extinction compared to conditions without treatment with a seedling survival rate of 60%.

Our demographic analyses in *C. polylophus* suggest that the population will continue to decline under current conditions, with a population structure dominated by juvenile individuals and a high number of seedlings. In our study, the values of λ lied slightly above one during the first two time transitions and below it in the last two transitions, which is a pattern that has also been observed

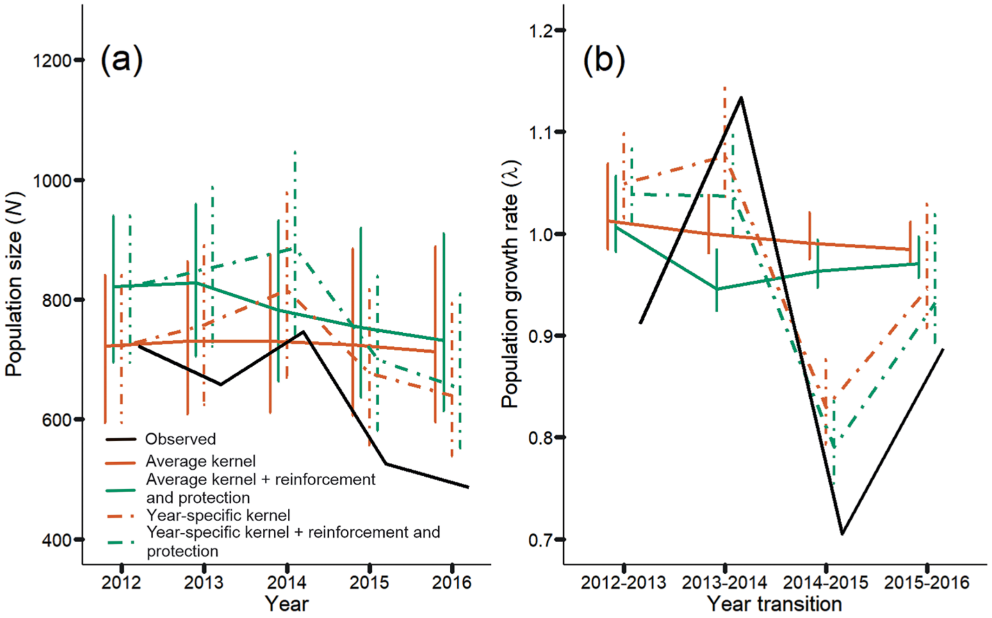

FIGURE 3 | Observed and projected population sizes (a) and growth rates (b) over the study period (2012–2016). Observed values (black), projected values using the average kernel without reinforcement and protection (red, solid) and with reinforcement and protection condition (green, solid) and projected values using the year-specific kernels without reinforcement and protection (red, dash-dot) and with reinforcement and protection condition (green, dash-dot). Vertical bars represent 95% confidence intervals.

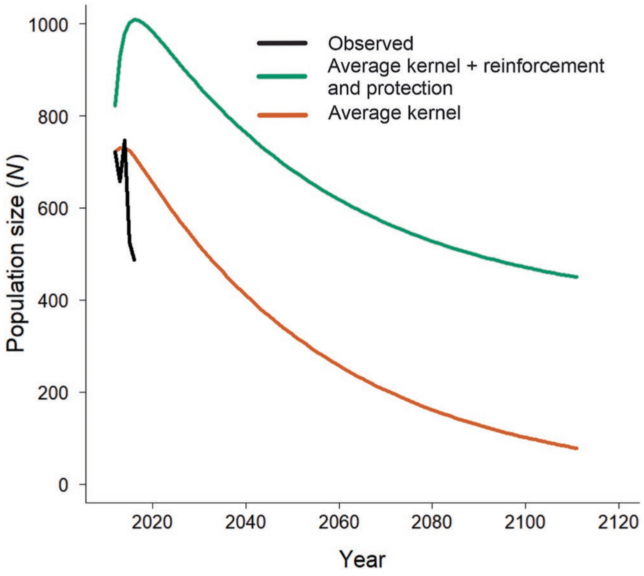

FIGURE 4 | Observed and projected population sizes (N) over the 2012–2111 period. Observed population sizes over the study period (2012–2016) (black) and projected population sizes using the average kernel without reinforcement and protection (red), and with annual reinforcement and protection scenario (green).

in other columnar cacti species of the genus *Cephalocereus* and *Pachycereus* (Esparza-Olguín et al. 2005; Arroyo-Cosultchi et al. 2022). Several studies using matrix projection models to examine columnar cacti dynamics have found that their λ values are not significantly different from equilibrium (Arroyo-Cosultchi et al. 2016, 2022; Jiménez-Guzmán et al. 2024).

Furthermore, these studies report relatively wide confidence intervals, indicating that populations of these cacti may be below, at, or close to equilibrium. Potential reasons for these contrasting conclusions between our results and those obtained by Arroyo-Cosultchi et al. (2016) and other studies could be due to the different modeling procedures: (1) here we used an IPM to model the population dynamics, in contrast to previous studies that relied on matrix projection models (Arroyo-Cosultchi et al. 2016, 2022), (2) we structured the population through a continuous variable, cubic-root of volume (cm), which we found to be a better predictor of individual performance than plant height (cm), used by these studies, (3) we calculated short-term growth rates, whilst others report long-term (asymptotic) growth rates (Arroyo-Cosultchi et al. 2016), and (4) Arroyo-Cosultchi et al. (2016, 2022) included a hypothetical seed bank in the model, an assumption that we did not do in the present study; such a lack of seed bank represents a more conservative scenario in the design of conservation and management strategies.

Numerous studies on cacti have shown that recruitment is a significant limiting factor of population dynamics (Zepeda-Martínez et al. 2013; Arroyo-Cosultchi et al. 2016, 2022), with the bottleneck occurring more at the seed-to-seedling transition than in seed production itself (Zepeda-Martínez et al. 2013; Arroyo-Cosultchi et al. 2022). Large-size cacti mortality is generally low in long-lived species and may not be affected to any great extent by environmental variation (Godínez-Álvarez et al. 2003), in stark contrast to seedlings which are far more susceptible to mortality caused by adverse environmental conditions (Godínez-Álvarez et al. 2003; Ortiz-Martínez et al. 2021). The occurrence of wet and dry seasons and other natural cycles in the environment is also believed to play a significant role for species inhabiting semi-arid environments (Holmgren et al. 2006). The notable increase in the number of seedlings and population growth rate observed during 2013–2014 can probably be attributed to the La Niña phenomenon (Arroyo-Cosultchi et al. 2016). However, it is also possible that this increase is linked to hurricanes or sporadic periods of high moisture levels (Arroyo-Cosultchi et al. 2016). In 2015–2016, there was a significant reduction in the number of individuals within the plot, representing the most pronounced decrease during this time frame due to a severe ENSO event. Future climate change scenarios could add to the loss of individuals due to prolonged drought periods that would further reduce seedling survival.

Our population-size projection results suggest that, by the end of the century, the population, either with or without reinforcement, is expected to decrease significantly. We are still in need of decreasing the mortality of adult individuals so as to reverse the decline of the population. It is particularly dramatic as this population benefits from being isolated and protected within a nature preserve, a condition that is not found in all populations, making the status of the species even more dire.

Conservation attempts generally aim to increase the rate of population growth (Ureta and Martorell 2009) or avoid or delay local extinction (Martínez et al. 2010). The increase in seedling survival suggests that it has a significant and long-term impact on the population dynamics of *C. polylophus*. Certainly, long-term demographic surveying and monitoring of reintroduction effects will be of paramount importance to make informed decisions for conservation management. Our results suggest that the interpretation of the demographic monitoring results will benefit from a focus on mechanisms such as causes of seedling survival and growth, as well as from further analysis as long-term data accrue.

Our research provides strong evidence supporting the need to prioritize the survival, reinforcement, and protection of *C. polylophus* seedlings as a key conservation strategy. Successfully reintroducing seedlings into their natural habitats can not only be a viable approach for the conservation of other vulnerable species, particularly cacti, but also give a significant push to the population, allowing it to remain viable in the long term. By delaying extinction, the population is given the opportunity to better adapt to environmental change (Arroyo-Cosultchi et al. 2016; Larios et al. 2020), thus increasing its long-term viability. To maximize these possibilities, it is essential to develop a reinforcement plan that addresses seedling limitation and increases seedling survival by reducing predation—measures that have proven effective in other threatened species.

Seedling reinforcement or reintroduction is meticulously carried out to enhance survival rates and reduce the risk of extinction in plant species. Moreover, the effectiveness of such management strategies in aiding the recovery of threatened populations increases significantly when implemented as part of a comprehensive conservation strategy that combines both in situ and *ex-situ* methodologies (Maschinski and Duquesnel 2006; Godefroid et al. 2011; Fenu et al. 2020).

However, introducing only seedlings may not be sufficient to ensure rapid and sustained recovery of columnar cactus populations, as these plants must undergo additional developmental stages (juvenile and adult) to achieve effective reproduction and contribute to population stability. According to this research, plants in juvenile and adult stages exhibit significantly higher survival rates than seeds or early-stage seedlings, facilitating their establishment and reproduction in the target habitat. Furthermore, plants in more mature phases are capable of reproducing with greater probability, which is essential for species facing extreme threats and limitations to their natural reproduction. Therefore, introducing plants at more advanced developmental stages represents a strategy that accelerates recovery and increases the success probability of reintroduction efforts compared to simply sowing seeds or establishing young seedlings (Fenu et al. 2020) that will take longer to reach reproductive stages and consequently ensure future population sustainability.

Furthermore, ensuring the survival of adult individuals within the *C. polylophus* population is equally crucial (Esparza-Olguín et al. 2005; Zepeda-Martínez et al. 2013). The survival of adult individuals in the Cactaceae family, in particular, has been identified as the process with the greatest contribution to population growth rates (Godínez-Álvarez et al. 2003; Jiménez-Guzmán et al. 2024). Adult plants play a significant ecological role in seed production, as larger individuals produce more flowers, fruits, and seeds, which are vital for sustaining the population. Protecting these adult cacti is not only necessary for their direct contribution to population stability (Martínez et al. 2010; Larios et al. 2020) but also for their role as seed sources for nurseries and repopulation efforts. This approach has been shown to improve establishment success in other species (Maschinski and Duquesnel 2006; Menges 2008; Godefroid et al. 2011; Albrecht et al. 2019).

Finally, the long-term conservation of *C. polylophus* requires preserving its habitat and the broader ecological community in which it exists. Protecting the germplasm through seed collection, propagation, and cultivation in greenhouses, whether for natural habitat reinforcement or commercial sale, will help reduce the exploitation of this species. Moreover, conserving the microhabitats where *C. polylophus* thrives is essential for maintaining the community structure that supports the survival and growth of both seedlings (Ortiz-Martínez et al. 2021) and adult individuals. Maintaining these habitats could mitigate the impact of factors that threaten their survival, increase population growth rates, and ensure the sustainability of these populations. Therefore, conservation efforts should integrate habitat preservation as a critical component, supporting the broader ecological network essential for the species' long-term survival.

5 | Conclusions

Reinforcement with seedlings alone is insufficient to guarantee population maintenance; ensuring adult survival is equally or more critical for population preservation. Effective conservation of *Cephalocereus polylophus* requires a dual focus on enhancing both seedling and adult survival while preserving critical habitat. Increasing the survival rates of seedlings and juveniles is essential for population growth and delaying extinction, particularly when paired with active habitat protection and reinforcement. In addition to these efforts, mature individuals play a crucial role in population stability due to their substantial contribution to reproduction and long-term viability. Integrating these strategies into conservation plans—by implementing targeted in situ measures and establishing protocols for controlled seed collection—can mitigate pressures on natural populations. Specifically, maintaining and reinforcing microhabitats that are crucial for seedling establishment can help ensure higher survival rates in these vulnerable early stages, ultimately supporting both short-term viability and long-term resilience. Furthermore, the impacts of climate change, such as prolonged drought periods, underline the urgency of these measures, suggesting that adaptive conservation practices will be necessary to address future environmental stresses. Our findings underscore that successful reintroduction and reinforcement efforts for *C. polylophus* can serve as a model for other vulnerable and threatened cactus species facing similar challenges. By ensuring that microhabitats remain intact and reducing external threats, we can facilitate a sustainable path forward that not only enhances the persistence of *C. polylophus* populations but also strengthens the broader ecosystem they support.

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Conflicts of Interest

The authors declare no conflicts of interest.

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