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Original article

The impact of seed extraction on the population dynamics of *Pinus maximartinezii*

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ABSTRACT

Pinus maximartinezii is a rare, endemic, threatened species known from a single small population in the state of Zacatecas, Mexico. Among the pine species that produce edible nuts, it produces one of the largest and most nutritious seeds. The seeds of *P. maximartinezii* have historically been used for human consumption. The cones are harvested directly from the trees, and the seeds are sold illegally in local, national and international markets. However, the effects of seed extraction must be thoroughly evaluated to determine the potential impacts on population stability. To assess the impact of different rates of seed harvesting on the demography of this species, a 2-yr study of population dynamics was conducted in three 0.1-ha plots. A 9 × 9 size-structured matrix model was used to simulate changes in population growth over time in conjunction with increasing stepwise reductions in fecundity. The population growth rate (λ) of *P. maximartinezii* was 1.1175, with a 95% confidence interval (CI) from 1.1008 to 1.1321, and it was relatively insensitive to changes in fecundity and growth. Under a seed extraction intensity of 99%, λ decreased to 1.0241, with a CI from 1.0177 to 1.0361. Elasticity analysis was then performed to identify the combined effects of proportional changes in fecundities and the largest stasis elements on λ. The results suggest that a sound conservation strategy should focus on improving the survival of juveniles and adults during their first reproductive events and on the largest adults, as well as on protecting the habitat of this threatened endemic species.

1. Introduction

Habitat loss and fragmentation due to contemporary changes in land use represent major critical threats to biodiversity because remnant populations of species are decreased in size and increased in isolation (Ledig et al., 2001; Groom et al., 2005; Hunter and Gibbs, 2007). For species with highly restricted geographic ranges, high habitat specificity, and small population sizes, the risk of extinction is expected to be extremely high due to local demographic and environmental stochasticity and loss of genetic variability (Menges, 2000a; Groom et al., 2005). The most extreme cases of isolation are those of species having only one known population in a restricted area. In many cases, these species are especially prone to extinction because they are traded or consumed by humans. This is the case for the blue pine, or Mexican maxipiñon, *Pinus maximartinezii* Rzedowski, a pinyon pine species restricted to one population in central Mexico. Several authors have noted the major ecological (Donahue and Mar-López, 1995; López-Mata, 2001) and genetic challenges (Ledig et al., 1999) facing the Mexican maxipiñon. From an ecological standpoint, there are three major threats to the long-term persistence of *P. maximartinezii*: 1) recent land-use changes resulting in soil erosion, habitat fragmentation and range reduction (López-Mata, unpublished data); 2) overgrazing and human-induced forest fires, which prevent seedling and sapling recruitment; and 3) seed harvesting for illegal trade (López-Mata, 2001) and local consumption. From a genetic standpoint, Ledig et al. (1999) have shown that *P. maximartinezii* may have undergone an extreme genetic bottleneck.

Donahue and Mar-López (1995) estimated the total number of mature *P. maximartinezii* to be 2000–2500 individuals. However, seedling and sapling recruitment is relatively scarce over its fragmented range. Mature cones of the Mexican maxipiñon are harvested directly from trees to extract the seeds, which are sold in local, national, and international markets. No life-history stage of the blue pine other than the seeds (i.e., seedlings, saplings, or trees) is used, harvested, extracted or commercialized. *Pinus maximartinezii* seeds are among the largest (17.5–27.4 mm in length, 9–13 mm in width, 7–10 mm thick and 0.95–1.46 g fresh mass) and most nutritious of the edible pine nuts (López-Mata,

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2001). Seed extraction would seem to represent yet another challenge to the persistence and long-term viability of this small population. However, a lack of knowledge about the population ecology of *P. maximartinezii* has hindered the development of recommendations for a sustainable level of seed extraction. It is thought that seed harvesting and seasonal, human-induced forest fires may negatively affect natural regeneration of its population.

The Mexican maxipiñon belongs to the endangered category in the IUCN Red List of threatened plants (www.iucnredlist.org) and in the Mexican norm NOM-059-ECOL-2010 (SEMARNAT, 2010). Effective conservation of *P. maximartinezii* requires estimates of current and future population sizes obtained from demographic data. For this purpose, population projection matrices are a valuable analytical tool for generating conservation recommendations, as well as for gaining insights into population status, management and conservation strategies (Silvertown et al., 1996; Heppell et al., 2000b; Menges, 2000b; Crone et al., 2011).

This study addresses the following questions: 1) is the blue pine population declining, growing or stable, and 2) under the current regime of seed extraction from trees, which size-specific vital rates (survival, growth or reproduction), if any, should be the priorities for a conservation strategy? Our objectives were to evaluate the demographic status and population growth rate of *P. maximartinezii*, to assess the effects of seed extraction on population growth rate and to identify which demographic vital rates have the greatest impact on its population growth rate. The results of this population ecology study provide *in situ* recommendations for effective conservation of the Mexican maxipiñon.

2. Materials and methods

2.1. The study species

Pinus maximartinezii is a rare endemic species known from a single population occurring over fewer than 720 ha (López-Mata, unpublished data) in the state of Zacatecas, Mexico. It is found on the Sierra de Morones at approximately 21°20′–21°22′ N and 103°12′–103°15′ W at elevations of 1650–2500 m. The blue pine grows sparsely on flat terrain and more densely on low to steep slopes (30–55°). Its trees are small, with an average height $\leq$18 m and a diameter at breast height (dbh) $<$70 cm (mostly 10–40 cm). However, in humid, protected ravines scattered individuals may be as tall as 25 m and present a dbh of up to 110 cm. Using tree cores, Passini (1985) estimated the oldest trees of this species to be 200–250 years old; trees 9 m in height with a 50 cm dbh were found to be approximately 130–150 years old; and 4.5 m tall pines were estimated to be 20–25 years old.

2.2. Field data

This study was conducted in a stand of interspersed individuals of *P. maximartinezii* with representation of all size classes. I set up three 0.1-ha (20 m × 50 m) permanent plots on gently sloping terrain. On each plot, all stems of blue pines $>$40 cm in height with $\geq$1 cm dbh were located, tagged, measured and qualitatively assessed for condition (healthy, damaged, broken, or dying). The determination of the population structure was based on an inventory of all tallied trees in these permanent plots, in which the tallest trees were $\leq$18 m. The measurements were repeated on each stem at six-month intervals for two consecutive years to examine changes in dbh and height and to monitor mortality. The height of saplings, juveniles and mature trees was measured either with an expandable measuring stick or by visual estimation for trees taller than 10 m.

2.3. Fecundity

Taking advantage of the fact that cones remain attached to branches for up to four years after seed dispersal, the total numbers of cones per tree were counted in the three permanent plots. Additionally, cones from mature trees outside the plots were counted and measured for their dbh and height. Five to ten cones were harvested from over 50 randomly selected mature trees from the permanent plots and outside the plots and dried under the sun for two to three weeks. Then, 250 cones were randomly selected and opened to count the total number of seeds. Per-tree fecundity was calculated as the average number of seeds per cone multiplied by the total number of cones produced by each tree in the permanent plots. Seed release occurs from early September through October, and germination occurs soon after, 2–10 weeks post-dispersion.

2.4. Seedling survivorship

Seedlings (individuals $\leq$40 cm tall) were monitored in one 150-m^2 (30 m × 5 m) transect per plot to obtain detailed information on seedling survivorship, mortality, growth, and likely causes of mortality at six-to-eight-week intervals for two years. In these tree transects, I recorded the height (mm) and condition (healthy, dead, missing, or damaged) of seedlings. The causes of damage, such as falling branches, broken stems, fungal pathogens, herbivores and drought (desiccation), were also recorded.

2.5. The model

The projection matrix model used here is an extension of the Lefkovitch matrix model (Caswell, 2001). The basic structure is given by the equation $\mathbf{n}\,(t+1) = \mathbf{An}\,(t)$, where $\mathbf{n}\,(t)$ is a column vector in which the elements n_i are the number of individuals in each stage at time t, and $\mathbf{n}\,(t+1)$ is the vector for the population in the next time period. **A** is a square non-negative matrix in which the entries a_{ij} define the transition probabilities among life cycle stages in one time interval. Each element in the first row represents the average fecundity of an individual at stage j and defines the contribution of each stage j to the seedling stage.

Repeatedly multiplying **A** by the column vector will eventually yield the dominant eigenvalue (λ) and its associated right ($\boldsymbol{w}$) and left ($\boldsymbol{v}$) eigenvectors. These are measures of the population growth rate (λ), the stable size distribution ($\boldsymbol{w}$), and the size-specific reproductive values ($\boldsymbol{v}$). Additionally, elasticity analysis was performed to identify the relative effects of proportional changes in a particular vital rate (i.e., survival, growth or reproduction) on λ (de Kroon et al., 1986; Benton and Grant, 1999; Heppell et al., 2000a; Caswell, 2001) and to explore the potential applications of the results of this analysis to species management and conservation (Silvertown et al., 1996; Dixon et al., 1997; Heppell et al., 2000b; Menges, 2000b; Crone et al., 2011). The elasticity of each matrix parameter is defined as: $(\mathbf{A}/\lambda)\,(\boldsymbol{vw}/\lambda\boldsymbol{v}|\boldsymbol{w})$. Furthermore, I estimated the 95% confidence intervals (CI) for λ by running 10,000 bootstrap samples from original data. These analyzes were performed using the popbio package in R (R Development Core Team, 2009).

2.6. Projection matrix construction

There have been two types of approaches for definition of classes or stage categories, the numerical (Vandermeer, 1978; Moloney, 1986), based on maximizing sample size within classes while errors of growth or survival estimators are minimized, and the biological (Lefkovitch, 1965; Werner, 1975), based on size, sex or developmental stages. I chose the biological approach combining the reproduction with the size criteria, because the reproduction

Table 1
Size-structured population of *Pinus maximartinezii*, defined by both height (ht) and diameter at breast height (dbh).

Category	Category description	Size category (cm)	Density (plants/3000 m^2)
S_1	Seedlings	≤40 ht	2520
S_2	Small Saplings	41–134 ht	173
S_3	Large Saplings	≥135 ht and ≤2 dbh	133
S_4	Juveniles	2.1–7.0 dbh	36
S_5	Adults 1	7.1–20.0 dbh	19
S_6	Adults 2	20.1–30.0 dbh	15
S_7	Adults 3	30.1–40 dbh	16
S_8	Adults 4	40.1–50 dbh	10
S_9	Adults 5	>50 dbh	8

varied much more with the size that the survival. The population of *P. maximartinezii* was structured into nine different size classes (Table 1) to describe its complete life cycle (Fig. 1). The model describes a developmental progression (G_{ij}, straight arrows in Fig. 1) from seedlings (S_1) to adults (S_5–S_9). The pre-reproductive sizes include S_1, seedlings (≤40 cm in height); S_2, small saplings (41–134 cm in height); S_3, large saplings (≥135 cm in height and ≤2 cm dbh) and S_4, juveniles (2.1–7 cm dbh). Reproductive trees were classified into five categories because they differed remarkably with respect to dbh and fecundity: S_5, adults 1 (7.1–20 cm dbh); S_6, adults 2 (20.1–30 cm dbh); S_7, adults 3 (30.1–40 cm dbh); S_8, adults 4 (40.1–50 cm dbh) and S_9, adults 5 (>50 cm dbh). The S_5 size class was selected as the initial class of reproductive trees because in the observational plots, the minimum dbh of trees observed in their first reproductive event was 7.2 cm ($n = 2$), whereas smaller trees were not recorded to produce cones in field observations made inside or outside the plots. Individuals of *P. maximartinezii* in size class i may survive and grow into stage class $i + 1$ with a probability of G_i, survive and remain in size class i with probability of R_i, or die. Size-dependent numbers of cones and seeds (fecundity, F_i) are produced during reproduction and transition into the smallest size class. The seed stage was omitted from the model because *P. maximartinezii* does not develop a seed bank, and seeds germinate within 2–10 weeks of dispersion. Overall seed germination is as high as 96–98%, and a small proportion of the remaining fraction of seeds germinate within 6–10 weeks after dispersion, with the rest dying.

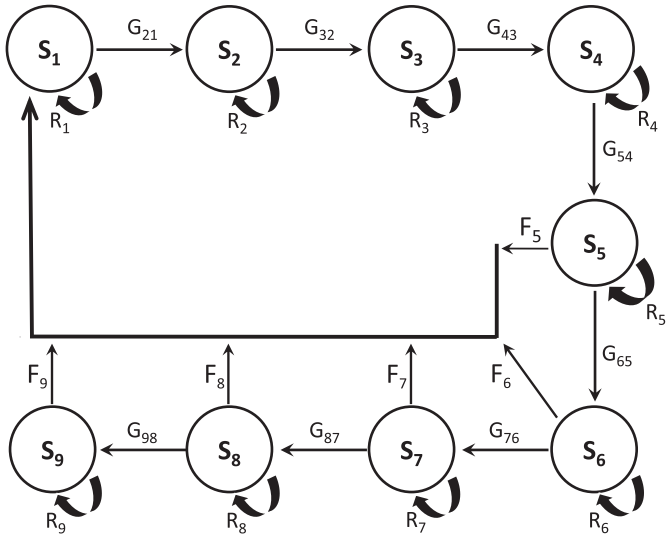

Fig. 1. Diagrammatic benchmark size structured model of the life-history of *Pinus maximartinezii* population.

Fecundity entries are located in the upper row of the projection matrix, except for the four top left elements. The change in population structure and size over time was simulated using a calibrated transition matrix model based on data from the nine life-history categories. By selectively varying the fecundity coefficients in the projection matrix, simulations were performed to examine the demographic impact of increasing percentages of seed extraction on the population growth rate and on the vital rates at each time step. To simulate seed harvesting prior to dispersion, fecundity entries in the transition matrix were reduced in a stepwise fashion for all adult stages accordingly. I used the elasticity analysis to identify the life-history vital rates of *P. maximartinezii* at which to target conservation efforts for improving population viability.

3. Results

The population of *P. maximartinezii* ($n = 2930$) showed a decrease in individuals from seedling to large adult sizes (Table 1). The frequencies of the life-history size categories presented an inverted *J*-shaped distribution, indicating an exponential decline in absolute density from small to large diameter sizes. This distribution suggests that mortality in all size categories is compensated by the growth of trees from smaller categories. Although the observed size distribution curve shows a steady decrease from seedling to final adult sizes, even on a log scale, the lack of peaks at any size category suggests that recruitment is a process occurring almost continually at the study site. Thus, 86% of the population consisted of seedlings; 5.9% and 4.5% consisted of small and large saplings, respectively; and 1.2% consisted of juveniles. Adult size categories comprised only 2.3% of the population. Based on observations of individual trees in the study plots, the smallest size at first reproduction was 7.2 cm dbh, but consistent reproduction occurred from 11 cm dbh onward. Reproductive trees were 5.5–15 m tall, and reproductive status was strongly related to tree diameter: 100% of trees ≥20 cm dbh were reproductive ($n = 47$), while only 43% of trees with a 7.1–20 cm dbh were reproductive ($n = 14$). Reproductive trees showed a significant correlation between dbh and the number of seeds produced ($r = 0.75$, $P < 0.0001$, $n = 53$), suggesting that fecundity increases with diameter. During the two years of the study, seedling survival was approximately 4%, and most seedlings died during the summer dry season, presumably due to desiccation or heavy cattle grazing. In contrast, small and large sapling survival was as high as 95% and 98%, respectively. Juveniles and mature trees (S_5–S_9) exhibited 100% survivorship. Table 2 shows the transition probabilities for individuals in each size category of the structured population model, as well as the size-specific average fecundity values per year.

Assuming linearity, time invariance, and density independence in the matrix model, the population growth rate was $\lambda = 1.1175$ (Fig. 2), with a 95% CI from 1.1008 to 1.1321, suggesting that the

Table 2
Population projection matrix for the *Pinus maximartinezii* population studied at Juchipila, Zacatecas. Fecundity values correspond to average of seed set per adult category per year. All other probability matrix entries are rounded off to three digits.

Category	S_1	S_2	S_3	S_4	S_5	S_6	S_7	S_8	S_9
S_1	0.032	0	0	0	48	483	1467	2803	3047
S_2	0.008	0.844	0	0	0	0	0	0	0
S_3	0	0.110	0.880	0	0	0	0	0	0
S_4	0	0	0.098	0.972	0	0	0	0	0
S_5	0	0	0	0.028	0.947	0	0	0	0
S_6	0	0	0	0	0.053	0.800	0	0	0
S_7	0	0	0	0	0	0.200	0.875	0	0
S_8	0	0	0	0	0	0	0.125	0.900	0
S_9	0	0	0	0	0	0	0	0.100	0.990
q_x	0.960	0.046	0.022	0.000	0.000	0.000	0.000	0.000	0

population of *P. maximartinezii* is growing. A log-likelihood ratio test (Zar, 1999) of the stable size distribution (**w**) of the projected population (Table 3) showed a significant difference from the observed size distribution ($G = 4116.53$; d.f. $= 8$; $P << 0.001$). The model predicts a stable size distribution with more seedlings, fewer saplings and juveniles and even fewer adult trees than observed in the study plots (Table 3).

The reproductive value (**v**) or the expected contribution of each size category to future population growth became progressively higher at larger diameters. Table 3 shows that the highest proportion of reproductive value was concentrated almost exclusively in adult categories. Only a small percentage (~1.5%) was shared among the four non-reproductive diameters, with the seedling category presenting the lowest contribution to future population growth. The contribution of the three largest adult categories (S_7–S_9) accounted for 21.6%, 28.1% and 28.2% of total reproductive value, respectively (Table 3). The two remaining adult stages ($S_5 + S_6$) accounted for approximately 20.5% of total reproductive value (Table 3).

The largest elasticity was found for the probability of individuals remaining in the same juvenile category (a_{44}), suggesting that this category has the strongest impact on the projected population growth rate (Table 4). The projected λ value was also highly sensitive to the stasis of adult trees in the first reproductive category (a_{55}) and, to a lesser extent, to the stasis of large saplings (a_{33}), whereas the lowest elasticity was observed for seedling stasis (a_{11}).

Given that the population is increasing ($\lambda > 1.0$), I asked the question what would happen to the population of *P. maximartinezii* if different proportions of the seed crop were consistently harvested from mature trees? To simulate seed extraction before seed dispersal, fecundity elements in the transition matrix were reduced incrementally for all adult size categories. Population growth rates were then calculated for each new matrix to find the maximum level of seed extraction allowable to maintain population stability ($\lambda = 1$). Population growth rates greater than 1.0 were consistently obtained under all levels of seed extraction (Fig. 2). For instance, the population growth rate with 99% seed extraction was 1.0241, with a 95% CI from 1.0177 to 1.0361, suggesting that even under extreme seed extraction conditions, the population is expected to continue to grow. Under these particular seed harvesting conditions, the stable size distribution of the projected population (**w_{99}**) is composed mostly of seedlings, which represent nearly 83% of the population, while the remaining 17% is distributed irregularly in categories S_2–S_9 (Table 3). The stable size distribution projected for this seed harvest regime was significantly different from the observed size distribution ($G = 3892.49$; d.f. $= 8$; $P << 0.001$). In this case, the stable size distribution (**w_{99}**: S_2–S_9) showed an increment of nearly 12% over that of the non-harvested population (**w_u**: S_2–S_9; Table 3). The biggest changes resulted in increases in the juvenile category (S_4) and in the largest adults (S_9); the other categories showed smaller increments (Table 3).

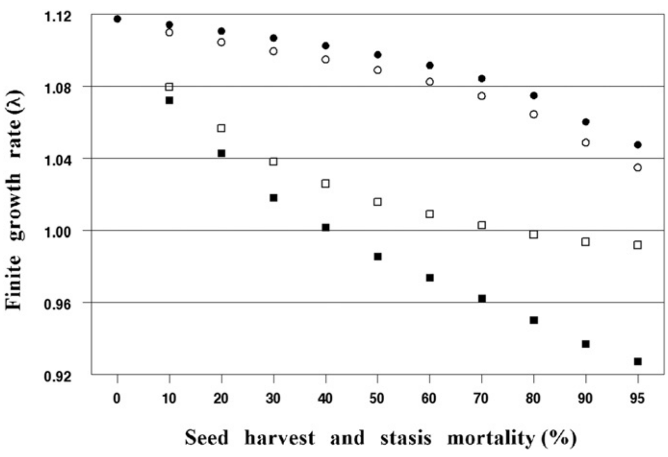

Fig. 2. Population growth rates (λ) of the observed population and decreased λ for *Pinus maximartinezii* after a range of simulated seed harvesting and stasis mortalities (i.e., reductions of: ● = fecundities (F); ○ = F and stasis of largest adult trees (a_{99}); □ = F, stasis of juveniles (a_{44}) and stasis of trees undergoing their first reproduction (a_{55}); and ■ = F, a_{44}, a_{55} and stasis of largest trees (a_{99})).

Table 3
Observed size distribution (w), stable size distribution for unharvested population (w_u) and for population with 99% seed harvested (w_{99}), and reproductive value for unharvested (v_u), and 99% seed harvested population (v_{99}).

Category	w	w_u	v_u	w_{99}	v_{99}
S_1	0.8600	0.9492	1.1762×10^{-5}	0.8301	2.1086×10^{-4}
S_2	0.0590	0.0275	1.6090×10^{-3}	0.0366	2.6366×10^{-2}
S_3	0.0454	0.0127	4.0077×10^{-3}	0.0278	4.3261×10^{-2}
S_4	0.0122	0.0086	9.7497×10^{-3}	0.0523	6.3927×10^{-2}
S_5	0.0064	0.0014	5.0985×10^{-2}	0.0189	1.1947×10^{-1}
S_6	0.0051	0.0002	1.5407×10^{-1}	0.0044	1.7233×10^{-1}
S_7	0.0055	0.0002	2.1617×10^{-1}	0.0060	1.8785×10^{-1}
S_8	0.0034	0.0001	2.8130×10^{-1}	0.0060	1.9882×10^{-1}
S_9	0.0027	0.0001	2.8210×10^{-1}	0.0178	1.8776×10^{-1}

Reproductive values increased considerably from seedlings (S_1) to adults 2 (S_6), after which they remained relatively constant in the remaining adult categories (S_7–S_9). The contribution of the four largest adult categories (S_6–S_9) to future population growth accounted for nearly 75% of the total reproductive value, compared to 11.9% being contributed by adults in category S_5 and 13.4% by non-reproductive size categories (Table 3).

Reductions in fecundity had little impact on the population growth rate (Fig. 2; closed circles). Under the highest regime of seed extraction, changes in stasis and transition probabilities had the most significant effects on λ (Table 5). The stasis of the largest adult size (a_{99}) is the largest contributor to λ, followed by stasis of the juvenile category (a_{44}) and stasis of the first reproductive size (a_{55}). With the exception of seedlings and small saplings, the elasticity values for stasis were higher than those for transitions (Table 5). Pooling the stasis of a_{99}, a_{44}, and a_{55} accounted for 59% of λ, while growth accounted for 2.3% and total fecundity for only 1.18% (Table 5).

Because stepwise reductions in fecundities were irrelevant to λ, as predicted by the elasticity analysis (Fig. 2), I concentrated the analyzes on those matrix elements with the highest elasticities (i.e., stasis a_{44}, a_{55}, and a_{99}) to assess their impact on λ. Therefore, I progressively and simultaneously decreased fecundities and stasis by 10% increments and solved each new matrix for λ. Fig. 2 shows the impact of concomitant reductions in fecundity and stasis on λ; for example, note that 95% reductions in fecundities and a_{99} (open circles) had no important impact on population growth rate ($\lambda = 1.0348$). Furthermore, stepwise reductions of fecundities and a_{44} and a_{55} (open quadrats) of 80% and above had a significant impact on λ ($\lambda = 0.9977$); moreover, the highest impact on λ was caused by the combined reductions in fecundities, a_{44}, a_{55}, and a_{99} (closed quadrats) of approximately 40% and above ($\lambda = 1.0016$).

4. Discussion

The observed survivorship, size structure, and reproduction throughout the life-history of *P. maximartinezii* revealed that the current recruitment levels and projected structure are sufficient to maintain the population. However, the shape of the stage distribution curve suggests that much higher levels of mortality occur in the seedling and small sapling sizes than in any other size category. The high seedling mortality found in this population was strongly influenced by cattle grazing and desiccation, suggesting that under such strong mortality pressure, seedling density alone is an unreliable indicator of regeneration potential. The population growth

Table 4
Elasticity matrix for *P. maximartinezii* population without seed extraction.

Categories	S_1	S_2	S_3	S_4	S_5	S_6	S_7	S_8	S_9
S_1	0.000806	0	0	0	0.001788	0.003004	0.007552	0.008222	0.007029
S_2	0.027570	0.085056	0	0	0	0	0	0	0
S_3	0	0.027570	0.101997	0	0	0	0	0	0
S_4	0	0	0.027570	0.184524	0	0	0	0	0
S_5	0	0	0	0.027570	0.153537	0	0	0	0
S_6	0	0	0	0	0.025776	0.064950	0	0	0
S_7	0	0	0	0	0	0.022782	0.082208	0	0
S_8	0	0	0	0	0	0	0.015283	0.063243	0
S_9	0	0	0	0	0	0	0	0.007047	0.054941

rate was not significantly impacted by seedling survival, although most of the stable size distribution was represented by this category. For all simulations, the elasticities of λ for harvested and non-harvested populations associated with seedling stasis were consistently much smaller than the elasticities related to the stasis of other categories. Such a pattern has also been recorded for other species, especially tropical rainforest trees (Peters, 1991; Alvarez-Buylla et al., 1996; Bernal, 1998).

In *P. maximartinezii*, the highest survivorship occurred after the juvenile stage, and λ was more sensitive to changes in juvenile stasis and the stage of first reproduction than to changes in growth and fecundity throughout the entire life cycle. The juvenile stage contains trees that are starting to become reproductive but have not yet contributed to future population growth. However, these are the most valuable individuals in the population in terms of the number of seeds required to produce an individual in that stage. The reproductive value of *P. maximartinezii* increased with progressively increasing sizes, which is expected for long-lived, size-structured species.

The λ value obtained for *P. maximartinezii* is one of the highest reported for trees, particularly for conifers. For instance, the λ values compiled by Silvertown et al. (1993) for conifer species (e.g., *Araucaria cunninghamii*, $\lambda = 1.009$; *A. hunsteinii*, $\lambda = 1.020$; *Pinus palustris*, $\lambda = 0.998$; *Nothofagus fusca*, $\lambda = 1.006$; and *Sequoia sempervirens*, $\lambda = 0.992$) and those reported by van Mantgem and Stephenson (2005) for six conifer tree species (e.g., *Abies concolor*, $\lambda = 0.999–1.094$; *A. magnifica*, $\lambda = 0.935–1.039$; *Calocedrus decurrens*, $\lambda = 1.011–1.045$; *Pinus jeffreyi*, $\lambda = 0.945$; *Pinus lambertiana*, $\lambda = 0.973–1.058$; and *Pinus ponderosa*, $\lambda = 0.990$) appear to be at or near demographic stability and differ from the values observed for actively growing populations, such as that of the blue pine. It is even more surprising that under any seed extraction scenario, matrix projections for the blue pine always yielded $\lambda > 1$. These results suggest that extremely high percentages of seed extraction may be sustained without substantially reducing the population growth rate of *P. maximartinezii*. Heppell et al. (2000a,b) suggested that such a pattern should be considered with caution because the low reduction in λ partially depends on extremely high survival probabilities of the largest trees, especially for long-lived species.

Therefore, assuming that current environmental conditions remain constant, the population will increase, and even under the heaviest seed extraction regimes, *P. maximartinezii* will continue to grow demographically. The observed population growth rate of the blue pine could be advantageous for the management of this species. The simulations addressing fecundity alone imply that, as long as all other matrix elements remain unchanged, the population could tolerate more than 99% of seeds being harvested without causing a decline in the population growth rate below 1.0. This suggests that the seeds being set and natural regeneration are sufficient to balance natural mortality rates, provided that the seeds remaining at the site are located in safe sites for germination, seedling establishment, and growth to mature stages.

On the other hand, it is clear that the population growth rate of *P. maximartinezii* declined more rapidly under conditions of simultaneous stepwise reductions of three stasis parameters and fecundities than under any other combination of these factors (Fig. 2). The value of λ larger than 1.00 found for the extreme 95% seed harvest conditions combined with adult mortality (a_{99}) suggests that under these regimes, the population of *P. maximartinezii* will continue to grow after attaining stable size distributions. This result indicates that the seed extraction and mortality regimes of the largest and most fecund trees have a low impact on λ, and therefore, they are of small concern for the long term population viability.

Employing 70% stepwise reductions of fecundity along with mortality of juveniles (a_{44}) and adults undergoing their first reproduction (a_{55}) can support a λ of nearly 1.00. Nevertheless, the population growth rate is drastically affected by simultaneous 40% reductions in fecundity and in the three stasis elements (a_{44}, a_{55} and a_{99}) of the projection matrix. Therefore, simultaneous harvest intensities of greater than 40% would cause λ to decay below 1.0. This suggests that an increase in juvenile mortality would have an important impact on λ that would be magnified by additive effects of mortality occurring in the first reproductive stage along with the largest and most fecund trees. This finding indicates that special concern must be given to the survival and stasis of these life-history stages to assure the lowest impact on the population growth rate. Therefore, an *in situ* conservation strategy for *P. maximartinezii* should concentrate on increasing the survivorship and stasis of these three stages. An important step in reaching this objective is to avoid permanent overgrazing and human-induced forest fires, especially those that promote regrowth of pastures during the dry season.

Table 5
Elasticity matrix for *P. maximartinezii* population with 99% of seed extraction.

Categories	S_1	S_2	S_3	S_4	S_5	S_6	S_7	S_8	S_9
S_1	0.000377	0	0	0	0.000130	0.000318	0.001281	0.002408	0.007658
S_2	0.011796	0.055242	0	0	0	0	0	0	0
S_3	0	0.011796	0.071844	0	0	0	0	0	0
S_4	0	0	0.011796	0.220914	0	0	0	0	0
S_5	0	0	0	0.011796	0.145572	0	0	0	0
S_6	0	0	0	0	0.011666	0.041638	0	0	0
S_7	0	0	0	0	0	0.011347	0.066576	0	0
S_8	0	0	0	0	0	0	0.010066	0.072982	0
S_9	0	0	0	0	0	0	0	0.007658	0.225138

5. Conclusions

Matrix population models provided a useful means of investigating the population dynamics of *P. maximartinezii* under different seed harvesting regimes and stasis mortality rates. The results of this study have important implications for conservation and forest restoration and emphasize the value of a demographic approach for analysis of the exploitation of a non-timber forest resource, such as has been highlighted by Menges (2000a,b) and more recently by Crone et al. (2011). Based on the obtained demographic information alone, the population of *P. maximartinezii* should not become extinct or even threatened as a result of seed extraction *per se*. Seed extraction may be considered sustainable given that the population was not predicted to decline below the critical value of $\lambda = 1.0$ as a result of any regime of seed harvesting. Nevertheless, when making conservation and management decisions, the aim of assuring the maximization of juvenile categories, as well as adults undergoing their first reproductive event and the largest adult trees should be considered as a major priority. Sound management of *P. maximartinezii* requires employing a comprehensive perspective on conservation and an integrated approach to decision making. Conservation proposals should integrate research on the social, economic, and political aspects involved in protecting the habitat of this endemic rarity. Beginning approximately 50 years ago, the habitat of *P. maximartinezii* became fragmented due to changes in local land use, overgrazing and induced forest fires resulting in soil erosion (Lorenzo Magallanes, *personal communication*). The lack of seedlings and small saplings throughout most of the habitat of this species suggest poor habitat quality for seed germination and seedling establishment. This poor habitat quality is mainly the consequence of permanent overgrazing and seasonally induced forest fires. These two local land-use activities have resulted in a major reduction of the distribution of *P. maximartinezii* (López-Mata, *unpublished data*). Although its population is healthy and growing, the effects of low genetic diversity are unhealthy over the long term due to the potential for inbreeding to expose deleterious genes. The population of the Mexican maxipiñon may be vulnerable to deleterious genetic effects because the rate at which genetic variability is lost depends on the effective number of mature trees in the population. This effective number is central to determining the magnitude of detrimental genetic effects and is also a key parameter in designing strategies for conservation and management. Therefore, it is imperative that any conservation and management strategy for the *P. maximartinezii* population should include the protection of juveniles and adults in their first reproductive stage, as well as the largest adult trees, as these are the most important stages for population maintenance. Conservation practices should prevent overgrazing in selected areas to enhance seedling and juvenile tree growth. Finally, in spite of the fact that *P. maximartinezii* was found to be a self-maintaining population, even under high levels of seed harvesting, it is suggested that its endangered status should be retained in both the Mexican norm and in the IUCN red list.

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