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ORIGINAL PAPER

Extinction risk of *Zamia inermis*: a demographic study in its single natural population

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Abstract Demographic studies of endemic and threatened plant species are essential for establishing effective conservation strategies. This paper aims to determine the structure and dynamics of the only natural population reported for *Zamia inermis*. All individuals were mapped to determine the spatial structure and patterns of association between categories and sexes. Matrix analysis were conducted to determine the population dynamics based on three on-site visits. The population is distributed randomly, although seedlings were found to be aggregated at all scales, juveniles are aggregated in smaller radii up to 4.5 m and males at radii above 3.5 m. Seedlings and juveniles are associated with males over greater radii of 3 m, the dependence of adults from earlier categories and females is less than 1.5 m. The population growth rate confirms that the population is in decline ($\lambda = 0.963 \pm 0.011$). Although few juveniles were identified and no seedling survival was observed in the field, also the amount of viable seeds per female cone is low. However, inhabitants of the region are cultivating the species by germinating seeds in backyard nurseries with 92 of 954 seeds reaching the juvenile category to date. It is clear that the population has lost its regenerative potential and is simply holding on to persistence of adults, this implies a great risk to the species. Ex situ propagation is encouraged.

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Introduction

Matrix models used in demographic studies are a powerful tool to describe the life history of a species, establish persistence of a population and compare dynamics between populations (Silvertown et al. 1993; Caswell 2001). This has already been used to assess the potential extinction risk for different species of Mexican cycads such as *Dioon edule* Lindl. (Vovides 1990; Octavio-Aguilar et al. 2008) *Ceratozamia mexicana* Brongn. (Alejandre-Rosas et al. 1990) *C. matudae* Lundell (Pérez-Farrera et al. 2000; Pérez-Farrera and Vovides 2004), *C. mirandae* Vovides, Pérez-Farrera and Iglesias (Pérez-Farrera et al. 2006) and *Zamia loddigesii* Miq. (González-Astorga et al. 2006). It is therefore necessary to establish how plants are spatially distributed, since patterns of spatial distribution represent an indirect measure of population functionality in response to environmental changes (Rzedowski 1978; Rivera-Fernández et al. 2012).

Zamia inermis Vovides, Rees and Vazq.-Torres (Fig. 1) is an understory cycad with a grayish trunk up to 30 cm high or more and 30 cm in diameter and branched in older plants. Leaves are pinnate with up to 20 leaves per crown. Leaflets are light green, linear-lanceolate with entire margins. Cones are light beige in color and up to six cones per crown have been recorded in males. A full taxonomic description can be seen in Vovides et al. (1983) and Whitelock (2002). It is a rare and critically endangered cycad species with only one known population, divided into three subpopulations, originally collected by Ms. Zenaida Lopez Romero in 1973 and formally described by Vovides et al. (1983). Before and after its description many plants have been illegally removed for the ornamental plant trade. Vovides et al. (2010a) its current population is estimated between 300 and 500 individuals, with extremely poor recruitment, due to absence of the natural beetle pollinator.

Deforestation and agricultural expansion in the area has been responsible for habitat decimation (Osborne and Vovides 2007; Donaldson 2003). The *Z. inermis* population is on private land dedicated to livestock and agriculture, where burning to control weeds and encourage pasture may have led to the possible extinction of the pollinator whose diapauses larval stages are in cone bagasse that form part of the humus litter (Vovides et al. 1997). The cycad is highly appreciated as an ornamental plant, and adult specimens have been located in several yards and gardens in the local town (Fig. 1). Seeds can be obtained via the Internet since this species is cultivated in commercial nurseries in the USA and to a lesser extent in Mexico. It is classified under the IUCN Red List as Critically Endangered (CR: A4abcd; B2ab: i, ii, iii, iv) with population declining. It is also protected by Mexican legislation under the Norma Oficial 059 (IUCN 2015; SEMARNAT 2010; Diario Oficial de la Federación 2010).

National efforts to conserve cycads (INE-SEMARNAP 2000) suggest five key points for management: (i) propose species protection measures; (ii) encourage in situ nurseries incorporating local communities to propagate and obtain benefits through plant sales thus creating an initiative to conserve natural habitats (Vovides et al. 2002); (iii) training authorities responsible for monitoring and protection of wildlife; (iv) create awareness of the importance of cycads among the general public through outreach and extension of conservation project, and (v) to increase our scientific knowledge of these plants.

The aim of this study covers part of the point (v) to generate demographic information on the current status of the only wild population of the species and to estimate the potential

Fig. 1 *Zamia inermis*. **a** Male cones, **b** Adult plants in a private garden (Photos: Octavio-Aguilar)

risk its extinction. The study will also be crucial for planning specific protection measures and management for *Z. inermis* as indicated in point (i).

Materials and methods

Study site

This research was conducted in two of the three natural sub-populations of *Z. inermis* located in two hills in central Veracruz. Both locations totaling 9.7 km^2, distributed in small isolated and fragmented patches. Extensive explorations in the area have not uncovered new locations or isolated populations. All this region is severely deteriorated due to periodic fires, deforestation to establish pastures and agricultural activities using fertilizers, weed-killers and pesticides. Exact geographical locality is omitted in order to prevent illegal extraction of plants.

Population structure

Four permanent plots (70 × 70) were placed and individuals mapped on XY coordinates and labeled. The plants were classified into the following categories: (1) Seedling: individuals who had one or two leaves with up to six leaflets per leaf; (2) Juvenile: non-reproductive plants with more than three leaves but less than 12; (3) Adult: non-reproductive and reproductive, with minimum of 12 leaves. Reproductive adults were identified not only by the cones present but also previous traces of reproductive structures on and at the bases of the plants. Owing to the non-consistent presence of reproductive structures throughout the year, sampling for gender determination was done over two periods; the first in February and the second in August.

Spatial distribution

To determine the spatial distribution, as well as spatial association or independence between categories and gender, the *K12* and *Kt* functions were used according to Ripley (1981) with the *Spatial Analysis* program (Duncan 1990). These functions considered an independent random distribution (Poisson) of individuals with respect to random points. In the case of *Z. inermis* 99 simulations in ascending distances of intervals of 0.5 m were put forward until a radius of 15 m was reached. This being the limit proposed by De la Cruz (2006) that corresponds to less than a third of the quadrant lengths in order to diminish border effects. If the data does not match the expected values generated by the *Kt* and *K12* functions, then an aggregated pattern and dependency between groups of individuals are presented respectively (Peter 1995).

Transition, sensibility and elasticity matrices

Transition matrices were calculated considering the probability of retention, transition and regression from the reproductive stage to the non-reproductive, according to Octavio-Aguilar et al. (2008). Fertility was determined as the product of females × coning females × mean number of seeds per cone × viability and germination ratio. This was calculated from germination experiments with 10 cones according to Raimondo and Donaldson (2003). With these data three Lefkovich matrices (*L*) were constructed for years 2012, 2013 and 2014. The finite population growth rate (λ), survival curve, confidence interval, temporal projection, sensitivity and elasticity matrices were estimated from the *L* matrices using the BRANCHES/stage program (Ferson 1990) based on the guidelines established by Caswell (1989, 2001), Caswell and Trevisan (1994), Silvertown et al. (1995) and Álvarez-Buylla and Slatkin (1991, 1994).

Results

Population structure

The total number of plants in the two subpopulations was 654 individuals (554 in the first subpopulation and 100 in the second), 83 seedlings, 26 juveniles, 311 reproductive adults

(130 males and 181 females, sex ratio 1:1.39) and 234 non-reproductive adults. Throughout the study period a mortality of 69 seedlings, twelve juveniles and six adults was observed. A total of 954 seeds were obtained from 10 cones (collected in 2005, mean of 53 ± 27.57 seeds per cone, with a viability 10 ± 0.1%), but survival was only 9.6% (92 plants). Thanks to the efforts of the local people participating in sowing the seeds we managed to reach are productive stage within 3 years for three females, although most plants remained in the juvenile category for at least 8 years. The proportion of females with respect to the population was 23.8% while the proportion of females coning per period was only 7%. The survival curve based on lx (survival percentage) showed a type I tendency (Fig. 2a) according to Deevey's criterion (linear regression coefficient $= -0.8895$, $F_{(1,3)} = 11.37$, $p = 0.0433$, $b = -0.89$, $a = 19.7$). The linear model had a better fitting than negative exponential regression ($r = -0.8031$, $F_{(1,3)} = 4.16$, $p = 0.1017$, $b = -0.1031$, $a = 11.15$) proper to a type III survival curve. The survival curve based on LnN (natural logarithm of number of individuals per class) didn't show any adjustment (Fig. 2b).

Spatial distribution

Total population density is 0.035 ± 0.027 ind/m^2 and is randomly distributed (Fig. 3). However, when the analysis is done by categories, seedlings and juveniles (<4.5 m) and males (>3.5 m) an aggregated distribution pattern is observed (Table 1). Regarding between groups association the early life-cycle categories (seedlings and juveniles) are spatially aggregated with respect to adults, males as well as females, atradii less than 1.5 m. However, no spatial association exists between sexes. Furthermore, early life-cycle categories are associated with respect to males in groups with radii greater than 3.5 m (Table 2).

Transition, sensibility and elasticity matrices

No transition, recruitment or reproductive events for at least one study period has been observed for the second population. Owing to the distance between the two sites being less than 2 km, it was decided to unify the data from the two subpopulations for a better approach.

The average population growth rate was 0.963 ± 0.011, corresponding to an annual loss of less than 3.7%. There is the possibility of a natural retrogression of adults back into juveniles (field observation where a naturally segmented crown through gravity re-rooted close by as a juvenile) (Table 3a). Sensitivity analysis showed that the category explaining the highest importance for permanence of the population were non-breeding adults, while seeds and seedlings practically do not contribute to population growth (Table 3b). Finally, the elasticity analysis showed that population fertility and transition are virtually nil (E: 0.991, T: 0.009, F: 1×10^{-6}).

Discussion

Population structure

Long-lived plants usually have a population distribution dominated by young individuals, with high mortality in the early categories and a gradual accumulation of adults by

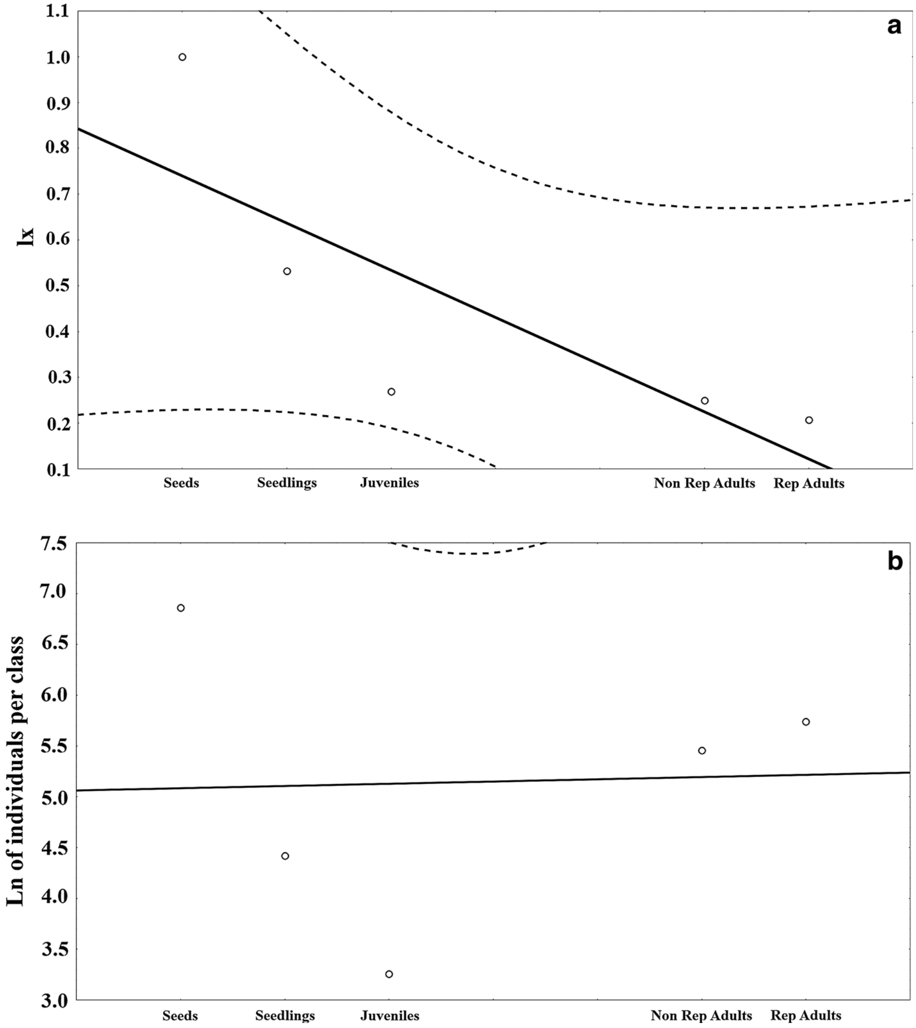

Fig. 2 Survival curves for a *Zamia inermis* natural population with linear regression model and confidence interval (95%). **a** based on survival percentage lx, **b** based on natural logarithm of individual number per class. Rep: reproductive

incorporating few individuals in each generation (Chamberlain 1935). Most cycads follow this pattern and population structure corresponds to an inverse J type III survival curve according to Deevey (1947). This has been previously reported for *Ceratozamia matudae* (Pérez-Farrera et al. 2000), *C. mirandae* (Pérez-Farrera et al. 2006), *D. edule* (Vovides 1990), *D. purpusii* (Yáñez-Espinosa and Sosa–Sosa 2007) and *Zamia loddigesii* (Aguirre-Fey 2004) . It is notable that *Z. inermis* does not follow this pattern since its population is dominated by adults (83.33%), with only 12.69% for seedlings and 3.98% for juveniles, showing very low natural recruitment, but not zero (Fig. 2b). This has also been reported for *Encephalartos ghellinckii* (Scott-Shaw 1995), *Cycas armstrongii* (Watkinson and Powell 1997), *Dioon holmgrenii* (Velasco-García et al. 2016) and *D.* sonorense (Álvarez-Yépiz et al. 2011) in all cases the increased mortality of seeds and seedlings and

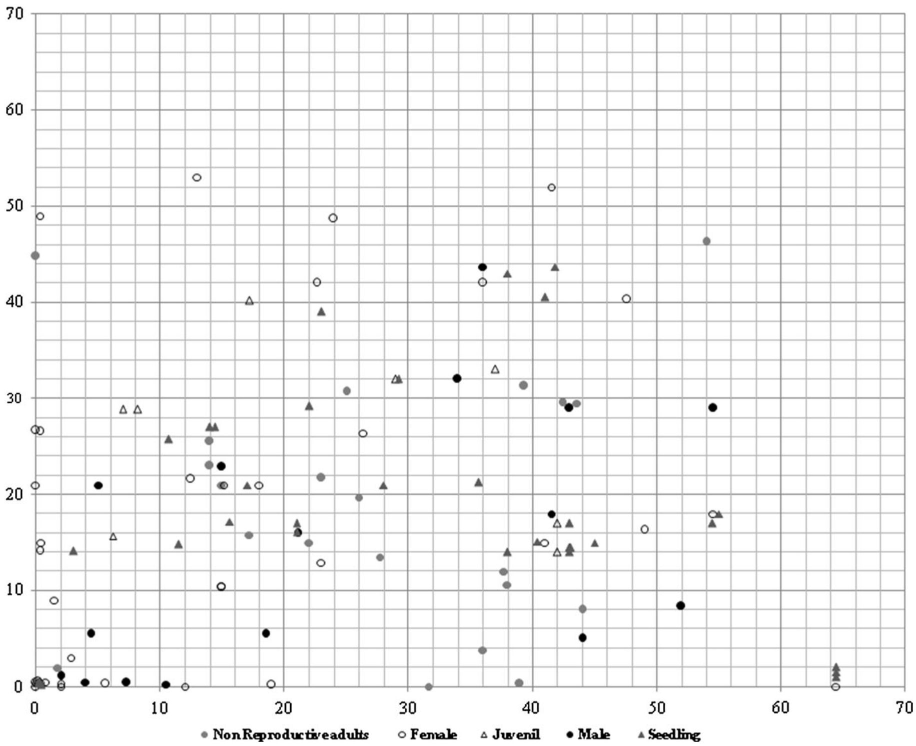

Fig. 3 Spatial distribution of *Zamia inermis* population in a random quadrat of 70 m^2

differences on adults survival was related to environmental factors and disturbing giving rise to adult dominance, thus changing the survival pattern to type I survival curve.

In the case of *Z. inermis*, even considering high seedling mortality (>80%) it is more likely that this population structure has arisen through absence of recruitment. This is suggested by observation that ovule abortion is about 90%, being a product of inefficient pollination (Vovides et al. 1997, 2010) owing to the probable reduction or extinction of the beetle pollinators. This may be due to the application of pesticides in areas close to the study site devoted to growing crops or by fires burning the humus litter where the pollinator diapauses larvae overwinter. This loss of pollinator is confirmed by the decrease in ex situ germination of field collected seeds, since only 9.6% of these made it to the juvenile stage, contrasting sharply with previous results (Gilbert 1984; Vovides 1989). Reports that in situ field germination is virtually nonexistent, while in nurseries and botanic gardens after hand pollination, germination almost 100%. The absence of pollinators has generated a serious problem on recruitment and fertility, and has accelerated over the past 30 years. It is worth mentioning that in subpopulation 2 none of the female cones found presented viable seeds, in spite of regular and ample presence of both male and female cones.

Spatial analysis

Zamia inermis shows a decreased density (0.035 ± 0.027 ind/m^2) compared to other cycads (0.32 ± 0.12 ind/m^2 for *D. edule*, Octavio-Aguilar et al. (2008); 1.96 ± 1.68 ind/

Table 1 Ripely's $K(t)$ for *Zamia inermis* a population; using 95% confidence interval (99 simulations) with a 0.5 m step

Class	N	Distance (m)																
		0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5
Adults	75*																	
Females	36																	
Males	16							+	+	+	+	+	+	+	+	+	+	+
Juveniles	8			+			+	+	+	+								
Seedlings	36	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Total	120																	

Class	N	Distance (m)												
		9	9.5	10	10.5	11	11.5	12	12.5	13	13.5	14	14.5	15
Adults	75*													
Females	36													
Males	16	+	+	+	+	+	+	+	+	+	+	+	+	+
Juveniles	8													
Seedlings	36	+	+	+	+	+	+	+	+	+	+	+	+	+
Total	120													

* Including non reproductive adults

\+ Indicates a clumped distribution

Empty cell indicates a non class interaction

N Number of plants

Table 2 Ripely's *K*(12) for *Zamia inermis* populations; using 95% confidence interval (99 simulations) with a 0.5 m step

Interaction	Distance (m)																
	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5
Adults* versus seedlings	+	+	+														
Female versus seedlings	+	+	+														
Males versus seedlings	+	+	+				+	+	+	+	+	+	+	+	+	+	+
Females versus males																	
Adutls* versus juveniles	+	+	+														
Females versus juveniles	+	+	+														
Males versus juveniles				+										+	+	+	+
Juveniles versus seedlings	+	+	+														

Interaction	Distance (m)													
		9	9.5	10	10.5	11	11.5	12	12.5	13	13.5	14	14.5	15
Adults* versus seedlings														
Female versus seedlings														
Males versus seedlings		+	+	+	+	+	+	+	+	+	+	+	+	+
Females versus males														
Adutls* versus juveniles														
Females versus juveniles														
Males versus juveniles		+	+		+	+	+		+					
Juveniles versus seedlings	+													

* Including non reproductive adults

\+ Indicates a spatial association

Empty cell indicates a non class interaction

Table 3 Matrix analysis for the unified populations of *Zamia inermis*. a) Mean Lefkovich Matrix, b) Mean sensibility Matrix, c) Mean elasticity Matrix

	Seeds	Seedlings	Juveniles	Non reproductive adults	Reproductive adults
a					
Seeds					0.0029
Seedlings	0.5325	0.4643			
Juveniles		0.0403	0.9023	0.0010	
Non reproductive adults			0.0257	0.9543	0.3627
Reproductive adults				0.0140	0.3300
b					
Seeds	1.2E–06	1.3E–06	3.0E–04	1.8E–02	4.0E–04
Seedlings	2.2E–06	2.4E–06	5.7E–04	3.4E–02	7.4E–04
Juveniles	2.7E–05	2.9E–05	7.0E–03	4.2E–01	9.2E–03
Non reproductive adults	6.5E–05	6.9E–05	1.7E–02	9.8E–01	2.2E–02
Reproductive Adults	3.7E–05	4.0E–05	9.5E–03	5.6E–01	1.2E–02
c					
Seeds	0	0			
Seedlings		0	0		
Juveniles			0.0066	0.0004	
Non reproductive adults			0.0004	0.9720	0.0082
Reproductive adults				0.0082	0.0042
N	954	83	26	234	311

m^2 for *D. spinulosum*, Salomé-Castañeda (2009); 0.52 ± 0.37 ind/m^2) for *Ceratozamia mexicana* Rivera-Fernández et al. (2012) and 0.68 ± 0.52 ind/m^{2}for *Ceratozamia fuscoviridis*, Pulido et al. (2015) and a previous report for *Z. inermis* the largest subpopulation 0.12 ind/m^2, that could be an effect of the size of the area analyzed. Sosa et al. (1998) carried out the registration of individuals *Z. inermis* in an area of 600 m^2, while this study was performed in a total area of 19,600 m^2. However, other studies in similar areas (24,000 m^2 for *D. edule* Octavio-Aguilar et al. (2008); 3600 m^2 for *D. spinolosum*, Salomé-Castañeda 2009) show densities between 10 to 50 times higher. Considering this situation, the result suggests a reduction of up to 70.8% in the density of individuals of *Z. inermis* over the last 20 years. According to Vovides et al. (1983), these results could be due to illegal logging and change in land use, also plant extraction, corroborated by direct observations of adult individuals planted in private backyards in the city of Veracruz.

Spatial distribution showed a clumping of seedlings around the seed sources (mother plants) such as in *Zamia floridana* before *Z. pumila* (Eckenwalder 1980; Tang 1988). This may be linked to the absence of dispersers due to the presence of toxins in the seeds or low slopes that do not favor the dispersion (Tang 1988; Schneider et al. 2002). However, the density independent mortality, associated mainly to seed desiccation (Octavio-Aguilar et al. 2008) and environmental changes (Velasco-García et al. 2016), has generated a randomly aggregated pattern in subsequent life-cycle stages. The fact that males show a clustered distribution suggests the existence of neighborhoods with related individuals from 3.5 to 15 m. This observation is reaffirmed by the spatial dependence of early life-cycle categories with the presence of reproductive males, as has been reported for many plant species (Ellstrand and Antonovics 1985). Considering decreased pollinator activity, males may be a limiting resource for the populations of *Z. inermis*. However, the spatial distribution pattern of early stages with males is important only in relatively large radii, which has generally been correlated with pollination by wind for most plant species whereas smaller radii are related to insect pollination events (Scwendemann et al. 2007), such as in cycads (Hall and Walter 2011). The pollination range has been reported as 17 m for *Dioon merolae* (Cabrera-Toledo et al. 2012), 30 m for *Z. furfuraceae* (Norstog et al. 1986) and 46 m for *Dioon caputoi* (Cabrera-Toledo et al. 2012), which renders the range observed for *Z. inermis* within that considered for insect pollination. However, there is a low probability of isolated pollination events independent of insect pollination in radii greater than 3.5 m, resulting in low inefficiency in viable seed production with respect to that observed for other plants.

Transition, sensibility and elasticity matrices

Transition matrices show a high mortality in seeds and seedlings, consistent with those reported by Silvertown et al. (1995) for long-lived trees in tropical forests. High seedling mortality has also been observed in other species of cycads (Raimondo and Donaldson 2003; Pérez-Farrera and Vovides 2004; Pérez-Farrera et al. 2006; Octavio-Aguilar et al. 2008; Rivera-Fernández et al. 2012). The main problem lies in low or nil seed production and adult mortality in *Z. inermis* contrasting from that reported for other cycads. The elimination of the transition and fertility stages would have negative effects on growth rate and significant declination in population. Previous studies have shown similar patterns in response to disturbance (Pérez-Farrera et al. 2006; Rivera-Fernández et al. 2012) but without a substantial loss of individuals. These results highlight the presence of adults as elements that guarantee population persistence, placing *Z. inermis* in a really disturbing scenario considering that no other Mexican cycad so far studied has reported such high mortality rates in adults. Moreover, the sex ratio is reversed with respect to that reported for over 20 years (1:1.39 vs. 1.16:1, Sánchez-Tinoco et al. 1993). This makes an increase in reproductive females relative to males, allowing a major transition from the non-reproductive adult category to reproductive adults. Notwithstanding, a greater presence of female cones is not reflected in fertility increase since most ovules are aborted without being pollinated. Field et al. (2013) suggests that differences in the sex ratio depends on the life-history characteristics of the populations, in that variation in reproductive events is dependent on reproductive cost. The reproductive cost appears to be higher in males than in females of *Z. inermis* contrary to what is expected considering the energy cost of seed production (Cipollini and Stiles 1991) but we must take into account that most ovules are aborted in *Z. inermis.*

According to our results *Z. inermis* is a species that still exists thanks to the persistence of adult plants. However, there is a significant reduction in fertility and seed viability due to pollinator absence, which results in decreased recruitment and declining population. The few seedlings and juveniles which are incorporated into the population depends on the presence of reproductive females in radii less than 1.5 m and the availability of males in radii greater than 3.5 m.

In general, conservation programs of cycads have had better results with in situ or *inter situ* (close nurseries of natural populations) propagation programs, which guarantees the presence of pollinators (Vovides et al. 2010b). However, previous experiences have shown than within inter specific crops of *Zamia* there is a risk of cross-pollination (Vovides pers. comm.) thus the need to consider particular studies on each case. The lack of sufficient pollinators has given rise to population growth values of less than unity, with a reduction of at least 3.7% annually. It is therefore necessary to take concrete conservation actions such as ex situ propagation as a life-boat policy, identification and conservation of the pollinating insects and conservation of its only known habitat. Failing this the continuing panorama in situ will lead to the extinction of *Z. inermis* in the wild in less than 100 years.

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