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NOTES AND INSIGHTS

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Current topics on cycad biology: Deciphering the Rosetta Stone of plant evolution

Spatial distribution pattern of the endangered endemic cycad *Ceratozamia fuscoviridis* (Zamiaceae) in central Mexico

María Teresa Pulido Silva[1] | **Juan Carlos Flores-Vázquez**[2] | **Maricela Vargas-Zenteno**[1] | **Aurelia Vite Reyes**[1] | **Andrew P. Vovides**[3]

[1]Laboratorio de Etnobiología, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, Mexico

[2]Facultad de Ciencias UNAM, Universidad Nacional Autónoma de México, Mexico City, Mexico

[3]Departamento de Biología Evolutiva, Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico

Correspondence
María Teresa Pulido Silva, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Carr. Pachuca-Tulancingo, Km 4.5 s/n. Pachuca, Hidalgo, C.P. 42184, México.
Email: mtpulido@yahoo.com; mtpulido@gmail.com

Abstract

Spatial distribution pattern was studied for *Ceratozamia fuscoviridis*, an endangered species in Mexico. The conservation importance of this species lies in the fact that it is endemic to a relatively small geographic area in which changes in land use negatively impact the populations. Based on Ripley's *K (t)* and *K (12)* analysis, the spatial distribution patterns of five populations of *C. fuscoviridis* were studied as follows: (a) the population as a whole (*K (t)* function); (b) by each size class (*K (t)* function); and (c) between pairs of categories (*K (12)* function). For *C. fuscoviridis*, the distribution pattern of the group of individuals was aggregated. Cluster patterns are related to a lack of dispersal and/or indicate places more suitable for cycads. Comparison between categories (Ripley's *K (12))* indicated that they were mainly independent but sometimes dependent and, at certain distances, there was inhibition. It is the first record of inhibition in cycads in Mexico, suggesting intraspecific competition. The value of Ripley's *K (t)* and *K (12)* for conservation purpose is discussed. The results of the spatial distribution analysis can be applied to restoration strategies to facilitate conservation of the species.

KEYWORDS

cloud forest, endemic plant species, population biology, Ripley's function *K (t)* and *K (12)*, Sierra Madre Oriental

1 | INTRODUCTION

In the case of plants, the spatial distribution pattern can illustrate important ecological aspects of the species such as: life habits of the organisms, habitat preferences, use of resources and dispersal capacity of the species (Valverde-Valdés et al., 2005). This is particularly important for documenting species of conservation concern or those with a particular interest in their conservation and restoration. Cycads are one of the most endangered plant group in the planet (Donaldson, 2003). The spatial distribution patterns of cycad populations have been studied for some species.

Because plants are sessile organisms, detailed knowledge of the spatial distribution pattern can illustrate how

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seeds are dispersed, seedlings are established, potential consort crosses are carried out between adult individuals, and the neighborhood arrangement of different size categories in populations. Particularly in dioecious plants, where interbreeding is obligatory, the spatial arrangement illustrates how crosses and the establishment of propagules, whether seeds or seedlings, are carried out near the mother plants. This establishes a spatial correlation between individuals of different age categories, which determines the population neighborhood (Vekemans & Hardy, 2004). In the case of cycads, this is very important because all species are dioecious and, in many cases, the adult reproductive stages have few individuals (Donaldson, 2003; Vovides, 1990). So, interbreeding takes place between few individuals and the seed and seedling stages tend to be aggregated at short distances from the parent plants. Therefore, there has been observed a degree of spatial autocorrelation and a neighborhood defined by a small distance between individuals (Cabrera-Toledo et al., 2012; López-Gallego & O'Neil, 2010).

A spatial distribution analysis provides information on the effects of both biotic and abiotic factors on the distribution patterns. Spatial distribution can be altered in different ways by biotic factors such as competition, herbivory, pollination, dispersion (Nathan & Muller-Landau, 2000) and human disturbance, while the abiotic factors such as microclimate and edaphology can contribute to another scale (Rivera-Fernández et al., 2012). For example, the tree *Tilia mexicana* Schltdl. shows different spatial patterns according to the degree of disturbance of its ecosystem, varying from an aggregate pattern in preserved habitats to being randomly distributed in those disturbed by human activities (Pavón & Rico-Gray, 2004).

In general, studies that have explored the pattern of spatial distribution in cycad species have recorded certain patterns, in which the first stages of development (seedlings and infants) tend to present an aggregate distribution, mainly due to the low dispersal of seeds caused by low levels of interaction with predators/disperser and/or presence of neurotoxins in the seeds. For example, in *Macrozamia miquellii*, 97% of the marked seeds remained at a distance of no more than 1 m from the parent plant (Hall & Walter, 2013); *Cycas megacarpa* presented an aggregate pattern, regardless of the gender and height of the individuals in question (Etherington et al., 2018). Likewise, for the African cycad *Encephalartos latifrons*, an aggregate spatial pattern was found, particularly among the seedlings (Swart et al., 2019). Finally, for the genus *Ceratozamia*, *C. matudae* (Pérez Farrera & Vovides, 2004), *C. fuscoviridis* (Rubio-Tobón et al., 2023) and *C. zaragozae* (Castillo-Lara et al., 2018) are also reported to exhibit an aggregate distribution pattern.

This work focused on the study of the spatial distribution patterns of wild populations of *Ceratozamia fuscoviridis* W. Bull. Studying the species of *Ceratozamia* is particularly important because it is the second largest cycad genus in Mesoamerica, with many endemic to Mexico, including *C. fuscoviridis* (Calonje et al., 2023; Haynes, 2023). *Ceratozamia fuscoviridis* is one of the few cycad species in Mexico with ecological and demographic studies (García-Montes et al., 2020; Pulido et al., 2015; Rubio-Tobón et al., 2023). Additionally, it is included in the only conservation strategy at State level that is available for Mexico (Vite et al., 2013). Only two decades ago it was thought that there were very few populations and individuals of *C. fuscoviridis* and therefore it was considered as critically endangered by Osborne et al. (2006). Thanks to the extensive fieldwork of Vite et al. (2013) it is now known that the species is further distributed in municipalities of the state of Hidalgo. Hidalgo is the fourth State of Mexico richest in cycads (Pulido et al., 2017), in spite of it represents 1.1% of the country.

Pulido et al. (2015) calculated that the distribution of the species covers approximately 2075 km^2, therefore, we recommended a change in the conservation status from Critically Endangered (CR) to Endangered (EN). Subsequently, Martínez-Domínguez et al. (2021)—employing ecological niche modeling—reported that the predicted distribution area of *C. fuscoviridis* is 6674 km^2; however, they emphasize that 3596 km^2 has been transformed by human activities. Moreover, another study reported that the demographic parameters of *C. fuscoviridis* populations are negatively affected by human activities such as grazing, logging, and soil degradation (Rubio-Tobón et al., 2023). According to the IUCN criteria (A2c; B1ab [i, ii, iii, iv, v]), *C. fuscoviridis* is currently categorized as an Endangered Species (EN). Criterion A pertains to a decline in population size, while Criterion B relates to geographical range. An extent of occurrence of less than 5000 km^2 is consistent with the species' categorization made by Pulido et al. (2015). The size, density, population structure, and static life table was studied by Pulido et al. (2015). In general, the recruitment of new individuals is common, with 0.523 individuals/m^2 to 0.945 individuals/m^2, suggesting healthy populations. Rubio-Tobón et al. (2023) studied two conserved and two disturbed populations and reported that disturbance increased spatial aggregation. The same authors reported that seedlings show a more aggregate pattern in the proximity of juveniles in areas affected by human disturbance, which could be attributed to the lack of dispersers in these disturbed sites. This species is mainly used for traditional purposes (Vite et al., 2013), which could threaten its conservation when harvested destructively.

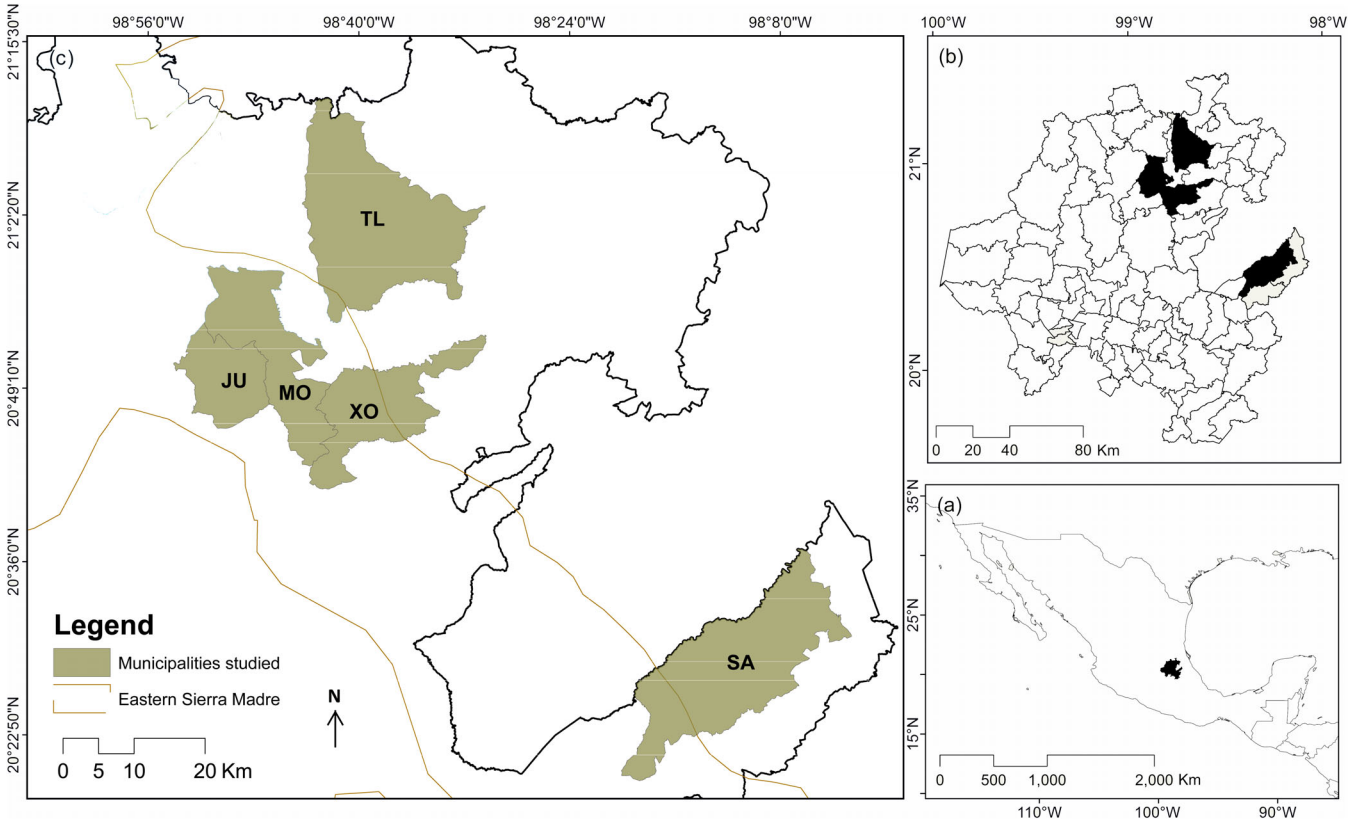


FIGURE 1 (a) Map highlights the state of Hidalgo within Mexico, (b) zoom in on Hidalgo and the municipalities where sampling took place and, (c) detailed view of the municipalities, clearly indicating their corresponding acronyms: municipalities: Juárez Hidalgo (JU), Molango (MO), San Bartolo Tutotepec, (SA), Tlanchinol (TL) and Xochicoatlán (XO).

The purpose of this study was to provide insight into the spatial pattern of stage classes within natural populations for which there is limited information. The spatial pattern analyzed included both the population as a whole and the interaction between pairs of size classes. The study should also contribute to conservation strategies for the species and support efforts to preserve these threatened plants in their natural habitats.

2 | METHODS

2.1 | *Study plots*

The study was based on the populations studied previously by Vite et al. (2013) who found 29 new populations of *C. fuscoviridis* across the biogeographical region Sierra Madre Oriental in Mexico. The currently spatial pattern analysis was made in five populations selected to represent geographical variation (in terms of latitude, longitude, and elevation) of *C. fuscoviridis*. Native guides helped us to locate specific populations that represent dense populations (populations located close to each other and those with sparse individuals were avoided). Sampling took place in five municipalities located in Hidalgo state, the following refers to their respective acronym in parenthesis: Juárez Hidalgo (JU), Molango (MO), San Bartolo Tutotepec (SA), Tlanchinol (TL) and Xochicoatlán (XO) (Figure 1). Vouchers were collected according to the collector number of Aurelia Vite Reyes (AVR) and Maricela Vargas Zenteno (MVZ) and deposited at HGOM and XAL herbaria. The collections were as follows: Juárez Hidalgo (7 MVZ, 8 MVZ, 9 MVZ), Molango (5 AVR, 6 AVR), San Bartolo Tutotepec (35 MVZ), Tlanchinol (10 MVZ) and Xochicoatlán (3 AVR, 17 MVZ).

In each plot and surrounding area, the vegetation type was recorded, disturbance evidence including wood extraction, garbage, roads or tracks, fences and plantations. The use of the plot in the last five decades was recorded and obtained by the local guides (e.g., grazing, timber extraction, fires, agriculture). The characterization of the studied plots is available in Table 2 of Pulido et al. (2015). The surrounding area around the plots included a patch matrix including forest fragment, roads and deforested area.

A 400 m^2 (20 × 20 m) plot was measured in each population, then subdivided into four 10 × 10 m sub-quadrats with ropes marking one-meter intervals and wooden stakes at each corner. Geographical location, slope, altitude, and tree cover percentage were measured in all sub-quadrats in every plot.

Every individual in each plot was sampled, and spatially located with the use of a measuring tape with respect to a reference coordinate. The following information was taken: number of live leaves, number of leaflets found in the longest leaf and sex whenever there was a cone or remnants.

2.2 | *Size categories*

Size categories were made according to the number of leaflets on the longest leaf as a criterion following Pulido et al. (2015). Plants were considered adults if they had ≥70 leaflets on the longest leaf. Individuals were classified in eight size categories: Seedling, Infantile 1, Infantile 2, Juvenile 1, Juvenile 2, Adult 1, Adult 2 and Adult 3 following table 1 of Pulido et al. (2015).

2.3 | *Spatial distribution*

The map of the plant's spatial location in each plot was created using the coordinates (*x*, *y*). A Kernel density map was made using PAST software (Hammer et al., 2001). The Spatial Analysis Program (Duncan, 1990) software, developed by Richard Duncan (Department of Plant Science, Canterbury, New Zealand) was subsequently used to determine the spatial distribution of the individuals in each population, enabling us to calculate functions *K t* and *K 12* (Haase, 1995). Categories were grouped for the analysis, that is, seeding, infantile (1 & 2), juvenile (1 & 2), adult (1, 2, & 3).

Function *K (t)* calculates the distribution (random, aggregate, or uniform) of a single group of data, through a series of repetitions (99 simulations) that counts the number of individuals present around a randomly chosen point, varying the ratio (distance *t*) and comparing it to that of theoretical function *K* of a Poisson pattern. The H_0 (null hypothesis) is that the distribution pattern of individuals is random. The *K (t)* function has a confidence interval (CI) such that values greater than the CI indicate spatial aggregation, while values less than the CI indicate a uniform distribution, and values within the CI are interpreted as a random distribution. *K (t)* function was used for all individuals of each plot, and separately with the group of seedlings, infantile (1 & 2), juveniles (1 & 2) and adults (1, 2 & 3).

K (12) analysis compares the degree of association between the distribution of two sets of data (which results in dependency, independency, or inhibition). The H_0 indicates the distribution patterns of the two data sets are independent. In the *K (12)* analysis, resulting values greater than CI indicate dependence (association) between the sets of data being compared. Values below CI indicate inhibition between them, and values that fall within CI indicate no dependence between them. The *K (12)* function was used to do every possible comparison between pairs of sets: seedlings, infantile, juveniles and adults.

Functions *K (t)* and *K (12)* were calculated with 95% confidence interval and for a maximum radius of 660 cm. This being the distance that is less than a third of the length of the shortest side of the study area (2000 cm), as recommended by De la Cruz to decrease the error associated with Border Effect (De la Cruz, 2006).

3 | RESULTS

3.1 | *Spatial distribution*

The levels of aggregation of the individuals in each population (Figure 2), plants are clustered and distributed in the five populations based on the Ripley's *K* (*t*) analysis (Table 1). Ripley's *K* (*t*) function showed that in general seedlings were spatially clustered. However, seedlings in San Bartolo population exhibit a random distribution at radii between 550 and 660 cm (Table 1). Adults show in general a random distribution, with some exceptions (Table 1), including Molango (MO) with adults aggregated in radii >190 cm and Tlanchinol (TL) where adults are aggregated. Therefore, depending on radius and plot, the distribution of each size category was aggregated or random but never uniform (Table 1).

A *K (12)* Ripley's function analysis done to compare the distribution of pairs of categories (e.g., dependence, independence or inhibition between seedlings and adults or any pair of categories) showed that distribution was mainly independent, sometimes dependent, and inhibition case was rare (Table 2). Generally, seedlings showed independence with regards to other categories, even adults. However, in some cases, there was dependence (association) between seedlings and infants for example in the Juárez Hidalgo (JU) plot considering shorter radius (10 to 250 cm); in contrast seedlings and infants are independent at radius between 260 and 660 cm (Table 2). Seedlings and adults showed independence (not association) in three populations. In contrast, there was dependence between seedlings and adults in Tlanchinol (TL) particularly at high radius, while Juárez Hidalgo

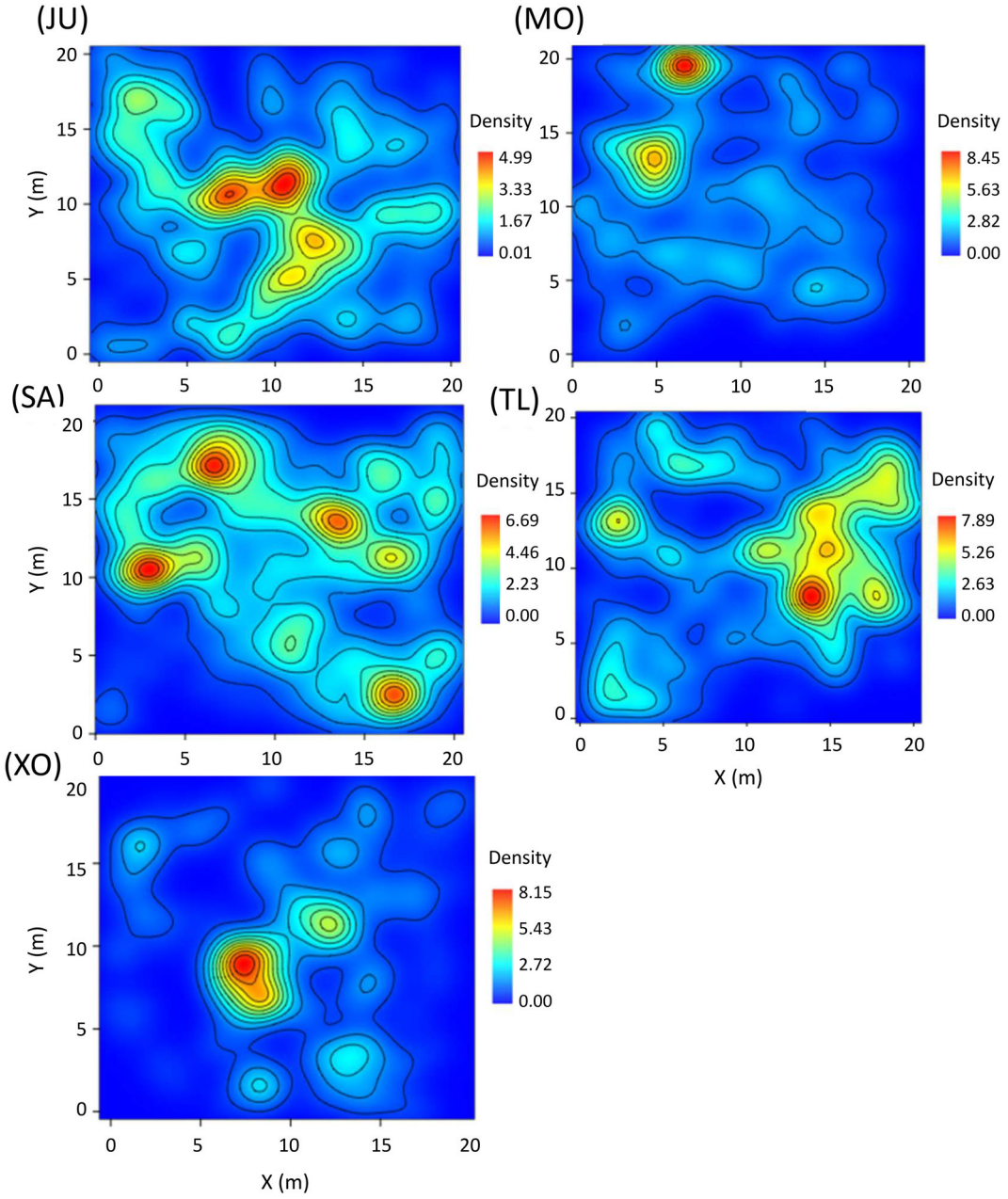


FIGURE 2 The studied localities, each represented by squares for 20 × 20 m (400 m^2) plots, showing the levels of aggregation of the individuals of *Ceratozamia fuscoviridis* across five populations. Juárez Hidalgo (JU), Molango (MO), Tlanchinol (TL), San Bartolo Tutotepec (SA) and Xochicoatlán, (XO). For detailed values of: dependence, independence and inhibition among different size categories, see Tables 1 and 2.

(JU) population exhibited at low radius (10–20 cm). Other examples in Table 2. Infantile and adult plants, as well as juveniles and adults, tended to be independent from each other at different distances while, frequently, infantile and juveniles showed dependency at short distances (Table 2). Although inhibition between plants of different size categories was rare, it did occur between infantile and adults in Molango (MO) and Juárez Hidalgo (JU), and between seedlings and juveniles in Molango (MO) at particular radius (Table 2).

4 | DISCUSSION

4.1 | *Spatial distribution*

According to Ripley's *K (t)* function, the distribution pattern of the group of individuals found in five populations in cloud forest was of the aggregate type for all distances measured. Cycads with an aggregate spatial distribution are *C. matudae* (Pérez-Farrera et al., 2000), *C. mirandae* (Pérez-Farrera et al., 2006), *Dioon edule*

TABLE 1 Abstract of the results of the *K (t)* analysis which evaluated the pattern of spatial distribution of *Ceratozamia fuscoviridis*.

Population	Class	*n*	Radii (cm)	100									200										300										400
Xochicoatlán	Seedling	136	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	26	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x									
	Juvenile	21																																	
	Adult	26																																x	
	Total	209	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Molango	Seedling	84	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	53																				x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Juvenile	72												x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Adult	63																		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Total	272	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Júarez Hidalgo	Seedling	130	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	76	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Juvenile	34						x				x	x	x	x	x																			
	Adult	19																																	
	Total	259	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Tlanchinol	Seedling	226	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	29																																	
	Juvenile	52	x	x	x	x											x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Adult	67	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Total	374	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
San Bartolo	Seedling	98	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	82	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Juvenile	189	x	x	x	x							x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Adult	9																																	
	Total	378	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

Population	Class	*n*	500																600														660
Xochicoatlán	Seedling	136	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	26																																	
	Juvenile	21																																	
	Adult	26																																	

(Continues)

TABLE 1 (Continued)

Population	Class	*n*	500										600															660
	Total	209	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Molango	Seedling	84	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	53	x										x	x										x				
	Juvenile	72	x	x																								
	Adult	63	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Total	272	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Júarez Hidalgo	Seedling	130	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	76	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Juvenile	34																										
	Adult	19																										
	Total	259	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Tlanchinol	Seedling	226	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Infantile	29																										
	Juvenile	52	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Adult	67	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Total	374	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
San Bartolo	Seedling	98	x	x	x	x	x	x	x	x	x	x	x	x	x	x												
	Infantile	82	x	x					x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Juvenile	189	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Adult	9																										
	Total	378	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

Note: The distribution type was calculated at 10 cm by 10 cm intervals up to 666 cm, using 95% confidence interval. Numbers in the table indicate the radius (in cm) used to evaluate the Ripley function. X indicate clumped distribution. Empty cells indicate random distribution. Uniform distribution was not found.

TABLE 2 Abstract of the results of the bivariate Ripley's *K (12)* analysis which evaluated radius (distances) to which there is dependency (numbers values), independence (empty cell) or inhibition (bold numbers) between groups of *Ceratozamia fuscoviridis* individuals in five populations.

		Class		
Population	**Class**	**Seedling**	**Infantile**	**Juvenile**
Xochicoatlán	Infantile			
	Juvenile		90, 100	
	Adult			400–460
Molango	Infantile			
	Juvenile	**400–510**	50,90 150, 370, 430–640	
	Adult		**80, 90, 110–150, 170–180, 200, 240–370**	
Júarez Hidalgo	Infantile	10–250		
	Juvenile		10, 30	
	Adult	10, 20	**410, 480, 490**	
Tlanchinol	Infantile			
	Juvenile		10–120, 140–150, 170–190	
	Adult	10, 30, 440–510, 560–660	10, 80, 100, 110, 130–170, 190–200, 240–320, 360	10–70, 150–170, 190–200, 460, 480–490, 520, 550–560, 580–610, 630, 650
San Bartolo	Infantile			
	Juvenile	80–100, 190–210	10–70, 110–180, 200, 220, 660	
	Adult			310–350, 450, 610–620

Note: The distribution type was calculated at 10 cm by 10 cm intervals up to 666 cm using Ripley function. For example, in Xochicoatlán there are independence between pairs of categories (therefore empty cell), but there is dependency between infantile and juvenile at 90 and 100 cm of radius.

(Octavio-Aguilar, 2009; Vovides, 1990), *D. holmgrenii* (Velasco-García et al., 2016, but adults have a random pattern), *D. spinulosum* (Castañeda, 2009), *Zamia furfuracea* (Octavio-Aguilar, Iglesias-Andreu, et al., 2017) and *Z. loddigesii* Miq. (Aguirre, 2004). According to these papers mentioned earlier, aggregation can be the result of a series of factors such as topographic characteristics, soil depth, and seed dispersers. Cycads also exhibit a random spatial pattern, that is the case of *C. zaragozae* (Castillo-Lara et al., 2018), *C. zaragozae* has been heavily collected in the past (IUCN Category Endangered B1ab(v)), and *Zamia inermis* (Octavio-Aguilar, Rivera-Fernández, et al., 2017; and sometimes aggregated pattern in seedlings and males) *Z. inermis* is Critically Endangered A2acd + 4acd; B1ab(i,ii,iii,v). However, the same authors reported that in general seedlings and adults have a clumped distribution, different to juveniles (randomly). The Chinese *Cycas panzhihuaensis* shows a clustered distribution, but the aggrupation tendency decreased with the increase in the age of individuals (Yonhua & Chaoluan, 1999).

Ripley's *K (t)* function shows that, with some exceptions, seedlings and infants of *C. fuscoviridis* tend to be aggregated. Most juveniles are aggregated or random, while adults mainly present a random distribution (Table 1). In the present case study, this pattern could be due to the lack of dispersers and/or intraspecific competition for suitable places for establishment, a factor that was not evaluated experimentally.

Ripley's *K (12)* function provides another window for understanding the fine interactions between categories, including dependence, independence or inhibition. In general, for *C. fuscoviridis*, Ripley's *K (12)* function shows independence (no association) between the spatial patterns of pairs of size categories (i.e., seedling and juvenile). However, dependence between pairs of categories was found at specific radiuses in particular cases, as explained in the results and presented in Table 2. Inhibition was not common but is still relevant considering it is the first time reported for cycads in Mexico. Inhibition occurred between infant and adults at specific radiuses in the Molango (MO) and Juárez Hidalgo (JU) populations (Table 2). Inhibition also was found between seedlings versus juveniles at Molango (MO); that is the population with the lower number of seedlings and the second highest number of juveniles in our study plots. This finding suggests the presence of an important intra-specific competition at least in two populations. Long-term

demographic studies can indicate whether the vital rates of infants are different, close to, or far from adults.

The slope of the terrain could be affecting seed dispersal through gravity in *C. fuscoviridis*, and highly influencing distribution. Distribution could also be modified by competition from angiosperms which root in the deepest soils, leaving the shallower and more inhospitable niches to the cycads, as mentioned by Vovides (1990), and by seed dispersers like the rodent *Peromyscus mexicanus* (Vovides, 1990) as well peccaries (*Tayassu tajacu*) (Pérez-Farrera et al., 2000). Local people report peccaries and rodents eat and disperse the cycad seeds in the area of *C. fuscoviridis* (field information). In addition, the intervention of dispersers is necessary for these plants, since the sarcotesta of the seeds contain auxins that inhibit germination, therefore, the dispersers, usually rodents, fulfill the function of facilitators of germination since they feed on the sweet sarcotesta, allowing germination to take place. Although we did not measure soil depth, or potential dispersers, we do not discount the possibility that they play a fundamental role in the spatial distribution of *C. fuscoviridis* and should be studied more thoroughly in future research. Additionally, aggregation can be the result of old mast seedling events, promoted by fires, as reported by Grove et al. (1980) in an Australian *Macrozamia* habitat where minerals, particularly N was released in the soil after fire resulting in exceptional cone production in the cycads the following year.

Ripley's *K* (12) function has been evaluated in *Zamia inermis* finding independence between pairs of categories (however, dependence was found between seedlings vs. males and juveniles vs. males). Also *Z. furfuraceae* has association between males and females at <3 m; for distance <5 m there is dependence between seedlings and both female and adults (Octavio-Aguilar, Iglesias-Andreu, et al., 2017; Octavio-Aguilar, Rivera-Fernández, et al., 2017).

Rubio-Tobón et al. (2023) studied the spatial aggregation in four populations of *C. fuscovoridis* in Tlahuiltepa municipality using Ripley's *K (t)* and *K (12)* function, similar to the current work. However, it is hard comparing our results with that paper. There are big methodological differences between both studies: for example, plots of 50 m × 50 m; authors considered as adults those with >19 pairs of leaflets, while Pulido et al. (2015) and the current study >35 pairs (70 leaflets) was considered, based on field observations of many fertile individuals. The discrepancy in the number of leaflets may be due perhaps to the possibility that they are different species, since for Chapulhuacán, a neighbor of Tlahuiltepa, a new species of cycad was later described (Martínez-Domínguez et al., 2017). Herbarium voucher comparison may be useful.

Seedlings in some species tend to be close to adults (mother plants), that is, *C. matudae* (Pérez-Farrera & Vovides, 2004), *C. mirandae* (Pérez-Farrera et al., 2006), *D. holmgrenii* (Velasco-García et al., 2016) and *D. spinulosum* (Castañeda, 2009) found in relatively flat areas. Current study indicated that although the seedlings had a tendency to group, they were not distributed near adults (except for Juárez Hidalgo (JU) and Tlanchinol (TL) plots at specific radius (Table 2)), which could be related to gravity, owing to the slope of the terrain and rocky outcrops which influence seed dispersal, as reported for *D. spinulosum* (Castañeda, 2009). Nevertheless, some other size categories did have a tendency to group together, avoid each other, or were independent. For example, inhibition between category pairs was uncommon, but did occur between infantile and adults, as well as between seedlings and juveniles, which suggested a strong intraspecific competition between the youngest, but only where density was relatively high.

4.2 | *Conservation implications*

In general, the results of this study show that the evaluated populations of *C. fuscoviridis* maintain a good level of regeneration since the first stages of development are very well represented. However, in the San Bartolo population there are very few adults, which has direct implications for propagule regeneration. Unlike other cycad species, the populations of *C. fuscoviridis* studied show a high number of individuals within a relatively small area, which guarantees good regeneration and a good health status in most populations. This is contrary to that found for *C. zaragozae*, in which the populations are small (Castillo-Lara et al., 2018). Moreover, restricted geographical distributions are associated with conservation problems, although this is not the case for *C. fuscoviridis* since we now know that the geographic distribution range of this species is wide (Pulido et al., 2015). The data obtained in that study showed that populations are locally abundant, with a high number of seedlings and juveniles, so populations do not appear to be at risk as a result of intrinsic factors. However, deforestation is the main threat to these populations in the study region (field obs.). Vite et al. (2013) included the species in the conservation strategy of Hidalgo's state.

The spatial distribution pattern in cycads, particularly those of *Ceratozamia* is aggregated (Ripley's *K t* function). This seems to be related to seed size and dispersal by gravity, where the secondary dispersal associated with any type of fauna is scarce. In this sense, the evidence suggests that the spatial distribution of species that have been studied in Mexico—*D. edule* (Vovides, 1990) *C. matudae*

(Pérez Farrera & Vovides, 2004) *C. mirandae* (Pérez-Farrera et al., 2006), *C. zaragozae* (Castillo-Lara et al., 2018) and *C. fuscoviridis* (current study)—present the same aggregated pattern regardless of their threat level. Currently, the latter four species are listed as Endangered (EN) according to the IUCN criteria (IUCN, 2010), each one in different geographical regions and different environmental conditions. This indicates that aggregation is a condition associated with dispersal constraints rather than an indicator of the degree of threat. Nevertheless, high levels of aggregation tell us that, at short distances, individuals in a population share more alleles than would be expected by chance, presenting a high spatial autocorrelation (Cabrera-Toledo et al., 2012; López-Gallego & O'Neil, 2010). In this case, it is possible that, for the *C. fuscoviridis* populations in this study, many of the seedlings that grow in an aggregate distribution share a high degree of kinship, since it is very likely that they are descendants of the same mother plant. This implies that, when they grow, crosses could potentially be between relatives and thus cause a degree of inbreeding that results in low seed production in the future.

Ripley's *K (12)* function provides another window in the light of ecological applications. Because this analysis compares the dependence (association), independence or inhibition between pairs of size categories (or pairs of datasets), the results have implications for example in restauration, reforestation and horticulture. However, Ripley's *K (12)* function has been evaluated only in a handful of Mexican cycad species, including *C. fuscoviridis* (current study and Rubio-Tobón et al., 2023), *C. zaragozae* (Castillo-Lara et al., 2018), *Zamia inermis* (Octavio-Aguilar, Rivera-Fernández, et al., 2017) and *Z. furfuraceae* (Octavio-Aguilar, Iglesias-Andreu, et al., 2017).

Like all cycads, *C. fuscoviridis* is charismatic and is a potentially sought-after ornamental that can be managed in small family back-yard nurseries through harvesting seeds and cultivation. The sale of plants would thus create an incentive to conserve the cycads´ habitat, coupled with reintroduction back into habitat of nursery established seedlings or juveniles (Vovides et al., 2010). Though the genus *Ceratozamia* is listed in Appendix I of CITES for international trade (CITES 2025), there are provisions for artificially propagated species listed. The Norma Oficial Mexicana 059 (SEMARNAT, 2010) covers permits for collecting and establishment of sustainable management nurseries for native flora within Mexico.

5 | CONCLUSIONS

Regarding the conservation, Ripley's *K (t) and K (12)* functions provide complementary information about the spatial distribution pattern. Clumped spatial distribution patters was found in individuals of all populations as well as common in seedlings (*K (t)* function). That suggest low interaction with predators/dispersers and/or evidence of microsites where gymnosperms are favored over angiosperms. In contrast, *K (12)* function showed spatial independence between pairs of categories, suggesting low intraspecific competition. However, evidence of inhibition pattern was reported for the first time between infants and adults (in two populations) indicating that, the smaller classes seek to establish themselves where there is suitable microhabitat, suggesting intraspecific competition. Despite the high density found in the studied populations, competition does not appear to be strong. In this context, sustainable management nurseries have great potential for the conservation of this species and, when combined with application of the spatial patterns, can contribute to the development of effective restoration strategies and horticulture.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ORCID

María Teresa Pulido Silva https://orcid.org/0000-0003-1307-9574

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