

# Moderate anthropogenic disturbance does not affect the demography of *Magnolia schiedeana*, an endangered species from Mexico



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## ABSTRACT

Among the many *Magnolia* species that are endangered by anthropogenic disturbance, some are known to have the capacity to produce new shoots. Demographic studies are an important tool to evaluate the impact of disturbances as well as the resilience and resistance of endangered species. Our study looked at the demographic dynamics of two *Magnolia schiedeana* populations, with an aim to determine the role played by disturbances. The questions were: 1) what demographic trends characterize this species? 2) What differences are there between disturbed and undisturbed populations? 3) Is *M. schiedeana* a disturbance-resilient species in general? 4) How important is the contribution of the resprouting trait to  $\lambda$  in a population under anthropogenic disturbance? The demographic attributes evaluated were: elasticity, population growth rate ( $\lambda$ ), and sensitivity to concrete disturbances (LTRE, Life Table Response Experiment). The results indicated that the  $\lambda$  of the two populations did not differ significantly. The transitions that contributed the most to  $\lambda$  and presented the largest variation were similar in both populations under study. More than 90% of the contribution came from those individuals measuring  $\leq 5$  cm in diameter. Surprisingly, *M. schiedeana* is not sensitive to moderate anthropogenic disturbance. Resprouting contributed to  $\lambda$  with less than 0.2%.

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## 1. Introduction

Demographic studies in natural habitats are an important tool to evaluate both the extent to which endemic and endangered species are impacted by disturbance, and their demographic resilience and resistance (Caswell, 2001; Wiehle et al., 2016). The general condition of a population, its vulnerability or resistance through different life-cycle stages, and the extent to which all this is impacted by disturbance, can be determined by demographic attributes, such as population growth rate ( $\lambda$ ), elasticity and life table response (Li and Zhang, 2015). It is therefore important to take these indica-

tors into account when defining conservation strategies and other courses of action (Cf. de Kroon et al., 2000; Sánchez-Velásquez et al., 2002; Ninot et al., 2008; Lázaro-Zermeño et al., 2011). An extension of sensitivity analysis, the Life Table Response Experiment (LTRE) incorporates a vital index and its variation (Mills and Lindberg 2002) for the analysis of the total contributions of each life-cycle transition and the variations among them (Ehrlén and van Groenendael, 1998).

The resprouting trait represents the ability of some woody plants to generate secondary stems after the main stem or tree trunk is severed or broken; a common process in forests subjected to different types of disturbances, such as fires, storms, hurricanes, the harvesting of timber and the felling of trees and branches (Mwavu and Witkowski, 2008). Resprouting is an adaptive resilient response to disturbances among various species at both early (e.g. *Liquidambar styraciflua* L., *Alnus acuminata* Kunth; Kormanik 1990; Avendaño-Yáñez et al., 2014) and late successional stages (e.g. *Magnolia dealbata* Zucc and *Acer rubrum* L.; Sánchez-Velásquez and Pineda-López, 2006; Sánchez-Velásquez

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and Pineda-López, 2010; Keyser and Loftis, 2015). Within the transition matrix, resprouting may indicate either permanence or a shift to smaller-size classes. Effective management, conservation or restoration of tropical forests require an understanding of how plants respond to natural and anthropogenic disturbance events (Mwavu and Witkowski, 2008).

The Magnoliaceae family has a worldwide distribution, comprising about 314 species (Rivers et al., 2016), 228 of which are listed under some protection category (IUCN, 2015). In Mexico, 30 species of the Magnoliaceae family, including *Magnolia schiedeana* Schltl., have been listed as endangered species (Semarnat, 2010; González-Espinosa et al., 2011; Rivers et al., 2016). Populations of *Magnolia schiedeana* are sparsely distributed throughout the country, often replaced by other plants or threatened by urban expansion. *Magnolia schiedeana* is endemic to tropical cloud forest, a vegetation type and a threatened ecosystem (Hamilton et al., 1995) now covering only the central portion of the Gulf of Mexico drainage basin (Jiménez-Ramírez et al., 2007).

Demographic studies of *Magnolia* species are scarce (Sánchez-Velásquez et al., 2016). Among the species most studied are *M. dealbata* (now referred to as *M. vovidesii* A. Vázquez, Domínguez-Yescas & L. Carvajal) and *M. schiedeana*. Whereas the entire life cycle of the former has been described (Sánchez-Velásquez and Pineda-López, 2010; Vázquez-García et al., 2013), the latter has been the object of studies concerned with one stage of its life cycle and one of its vegetative structures (namely the leaves) (Williams-Linera, 2000). There are also seed ecology studies of *M. dealbata* (seed pool and germination treatments) (Corral-Aguirre and Sánchez-Velásquez, 2006) and *M. schiedeana* (Vásquez-Morales and Sánchez-Velásquez, 2011). Aside from these species, studies have been published on the production of polyfollicles in *M. macrophylla* Michx., *M. schiedeana* and *M. praecocissima* Koidz v. *borealis* (Doyle, 1989; Dieringer and Espinosa, 1994; Yasaka et al., 2008), and on the roots of *M. obovata* Thunb. (Satomura et al., 2006). Although the *Norma Oficial Mexicana* (Semarnat 2010) lists *Magnolia schiedeana* as a threatened species, and some authors consider it a vulnerable species (Rivers et al., 2016) or an endangered species (González-Espinosa et al., 2011), the current status of its populations and their demographic attributes are unknown.

In our study, we set out to identify the demographic attributes of two populations of *M. schiedeana* living under contrasting conditions (i.e., moderate anthropogenic disturbance, and no disturbance). The attributes were: size structure, population growth rate ( $\lambda$ ), transition variations and the life-cycle transitions that contribute the most to  $\lambda$ . The questions to be explored were: 1) what demographic trends characterize this species? 2) What differences are there between disturbed and undisturbed populations? 3) Is *M. schiedeana* a disturbance-resilient species in general? 4) How important is the contribution of the resprouting trait to  $\lambda$  in a population under anthropogenic disturbance?

## 2. Materials and methods

### 2.1. Species under study

*Magnolia schiedeana* is a perennial tree that can grow as tall as 25 m. It flowers from April to June, and its fruit is a pollyfollicle measuring between 4 and 8 cm in length. The seeds measure 5–7 mm in length, with a succulent red sarcotesta and a light brown testa, abundant endosperm and a rudimentary embryo. Pollyfollicle production occurs during the months of June to August (Hernández-Cerda, 1980), under a temperature of 12–22 °C, and an annual rainfall of 1500 to 2500 mm, distributed along an altitudinal interval of 1000 to 2000 m (Rzedowski, 1996 Zulueta and Soto, 1993). *M. schiedeana* has a persistent seed pool (Vásquez-

Morales and Sánchez-Velásquez, 2011) and seeds can be dispersed by birds (Watanabe et al., 2002). The main pollinator is *Cyclocephala jalapensis* Casey (Scarabaeidae: Dynastinae) (Dieringer and Espinosa, 1994).

### 2.2. Study area

In order to compare the demographic attributes of the two populations of *Magnolia schiedeana* in question, two contrasting sites were selected in the state of Veracruz, Mexico, with the largest possible number of individuals in each of them. The site with disturbance (La Martinica) was crisscrossed by three paths, and it was defined basically by the presence of tree stumps and accumulated branches and timber pieces resulting from the illegal felling of trees by machete or ax. The undisturbed site (Acatlán volcano), on the other hand, presented no paths and no evidence of these activities. Both sites are located in the biogeographic province known as Transversal Neovolcanic Axis, at a distance of 15 kilometers from each other. The predominant type of soil in these sites is the andosol, and their mean annual temperature ranges between 16 and 20 °C. At La Martinica site, 37 stumps of *M. schiedeana* were identified at the beginning of the study. This area is part of an Ecological Reserve adjacent to the town of Banderilla, Veracruz, Mexico (19° 34' 55" N; 96° 56' 55" W), with a mean annual rainfall of 1451 mm. Young trees of *M. schiedeana* are valued here for their straight vertical trunks, and employed as racks to lay logs traded in the nearby markets. The Acatlán site sits high up on the slope of the Acatlán volcano, in the municipality of Acatlán, Veracruz (19° 41' 0.8" N; 96° 51' 14" W), where the mean annual rainfall is 1570 mm. Its lofty location near to the volcano's summit keeps this population free from anthropogenic impact.

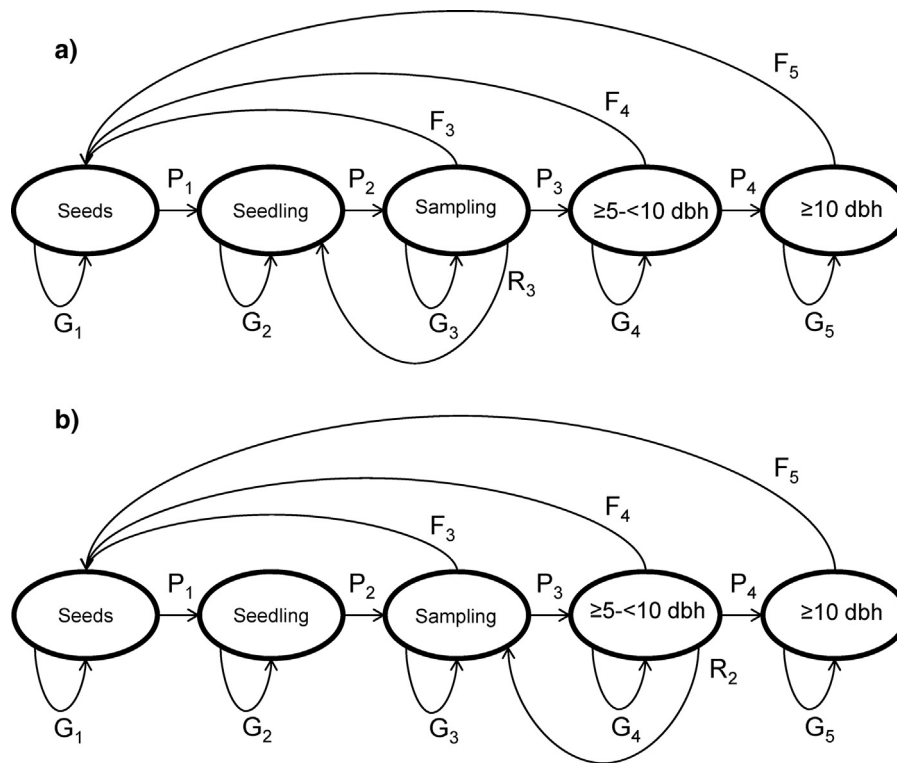
Both sites present a similar community composition that includes *Clethra mexicana* D. C., *Fagus grandifolia* var. *mexicana* Martínez, *Liquidambar macrophylla* L., *Oreopanax xalapensis* Decne and Planch. *Quercus xalapensis* Humb and Bonpl. and *Q. germana* Cham and Schlecht (Rzedowski, 1996; Williams-Linera, 2002).

### 2.3. Field data

A census was carried out at both sites for four years (2010–2013) during the early rainy season (when fruits and seeds are produced), and three annual cycles were obtained. At each population, the diameter at breast height (dbh) was registered every year on individuals >1.3 m high, and all other individuals ( $\leq 1.3$  m high) were counted up. Each individual was then geo-referenced (UTM) and tagged with an aluminum label. The number of polyfollicles was randomly assessed using a sample of 10 trees per reproductive life cycle (Fig. 1), and the number of seeds produced every year by each reproductive tree was also assessed (each polyfollicle having  $25 \pm 0.03$  seeds; Vásquez-Morales and Sánchez-Velásquez, 2011). This information allowed for the extrapolation and application of average values to the remainder of the populations. The presence and absence of new individuals and shoots in *M. schiedeana* stumps was also recorded. New individuals from seeds were easily spotted on the field, as they presented only one stem and sometimes even the sarcotesta. Also, these sprouts were different from the rest in that they stemmed from a stump. When one stump produced more than one shoot, the square root of the addition of the square dbh of all shoots was calculated, and this value was included in their respective population data (dbh size class).

### 2.4. Data analysis

In comparing the size structure of both populations according to size, a Wilcoxon matched pairs test with Statistic 6.1 (StatSoft,



**Fig. 1.** Life cycles of two *M. schiedeana* populations divided into five size classes: a) with disturbance and b) undisturbed. *dbh* is diameter at breast height (1.3 m); *P* is the probability that an individual passes from one size class to the next; *G* is the probability that an individual remains in its size class; *R* is the proportion of stumps sprouting anew and going back to the previous size class; and *F* is the average number of seeds produced.

1999) was used. Stump resproutings were included in their respective class size.

The yearly transition probabilities ( $a_{ij}$ ) of each population were estimated by dividing the life cycle into five stages: 1) seed; 2) seedling (individuals  $\leq 1.3$  m tall); 3) samplings (individuals from  $>0$  to  $<5$  cm *dbh*); 4) juvenile (individuals from  $\geq 5$  to  $<10$  cm *dbh*); and 5) adult (individuals  $\geq 10$  cm *dbh*) (Fig. 1). All seedlings proceed from seeds, and the role of stumps is represented by the lines marked with an *R* (Fig. 1). The  $a_{ij}$  value represents the probability of annual transition, from one size class to another in the transition matrix (Caswell, 2001). At both sites, the probability that seeds remain in the next annual cycle in the seed pool ( $P=0.08 \pm 0.06$ ) was taken from Vásquez-Morales and Sánchez-Velásquez (2011), who placed seeds where natural populations of *M. schiedeana* develop, recorded the remaining number after a year, and evaluated seed survival using a chloride tetrazolium test. A total of six annual transition matrixes were obtained, three for each site. The size-structure demography data was analyzed by a transition matrix model of the form  $\mathbf{n}(t+1) = \mathbf{A} \cdot \mathbf{n}(t)$  (Caswell 2001). Matrix **A** describes how individuals of each size class in the vector  $\mathbf{n}(t)$  contribute to the size classes in  $\mathbf{n}(t+1)$ . It yields information on stable size distribution and population growth rate ( $\lambda$ , which is also the dominant eigenvalue in the transition matrix). The annual population growth rate was estimated for each population and each annual cycle, using the RAMAS/stage (Ferson, 1990).

The confidence interval for  $\lambda$  in each treatment was calculated using the program SIM.VAR.BAS (<http://www.sci.sdsu.edu/Cornered.Rat/>; Ebert 1999), which calculates the  $\lambda$  mean (with confidence intervals of 95%) through the Bootstrap process, i.e., choosing any of the three matrices of transition (from each treatment) to calculate  $\lambda$  a thousand times randomly.

Transitions matrixes were explored by a Log-linear analysis (based on CATMOD; SAS, 2003), which allows for comparison between years and treatments, starting from the null hypothesis

that the fate of an individual is independent of the time and treatment. The response variable was fate (**F**, i.e., the counts value or number of individuals at each stage), and the explanatory variables were stage (**S**), time (**T**), and treatment (**L**), and their interactions. The general log-linear model is defined by:

$$\log m_{ijkl} = \mu + u_{F(i)} + u_{S(j)} + u_{T(k)} + u_{L(l)} + u_{FS(ij)} + u_{ST(ik)} \\ + u_{SL(il)} + u_{TL(kl)} + u_{STL(ikl)}$$

Where the logarithm of  $m_{ijkl}$  is the cell count,  $\mu$  is the log of the total number of observation of the contingency table,  $u_{F(i)}$  is the effect of the  $i_{th}$  fate class, and  $u_{S(j)}$  is the effect of the  $j_{th}$  stage class, and so on. Likelihood ratio tests were used to select submodels (Bierzychudek, 1982).

The sensitivity analysis explores the dependence of  $\lambda$  on the stage-specific vital rate by calculating the effect of infinitesimally small changes in the elements of the matrix ( $a_{ij}$ ) over  $\lambda$ , that is,  $S_{ij} = (\delta\lambda/\delta a_{ij})$  (Caswell 2001). The sensitivity analysis was estimated for each cycle in both populations. The elasticity analysis explored the proportional contribution of the elements of the transition matrix ( $a_{ij}$ ) in  $\lambda$ , i.e.,  $e_{ij} = (a_{ij}/\lambda) S_{ij}$  (Caswell, 2001). The sum of the elasticity values of a matrix is equal to 1. Elasticity is used to evaluate the relative importance of the elements in the matrix and to select those that are more appropriate for devising conservation and management measures (Caswell, 2001; Link and Doherty, 2002).

The analysis of the Life Table Response Experiments (LTRE) proceeded by breaking up the total effects that contributed to variations among populations in lambda. The LTRE analysis measures the response to those changes that are proportional to the past variation in the transition rate to variation in  $\lambda$  (Ehrlén and van Groenendael, 1998). The LTRE analysis was used to estimate the

sensitivity of the growth rate of each population to actual disturbance using the following equation:

$$LTRE_{ij} = \sqrt{V_{ij}} \times \delta\lambda / \delta a_{ij}|_{mean}$$

Where  $\sqrt{V_{ij}}$  is the standard variation of the transition index, and  $\delta\lambda / \delta a_{ij}|_{mean}$  is the sensitivity of the mean matrix (n=3 for each population) (Ehrlén and van Groenendael, 1998).

The LTRE analysis was also used to determine how the treatments contribute to differences in  $\lambda$ . Following Caswell (2001), this method considers  $T_1 \cdot \dots \cdot T_N$  treatments with population growth rates  $\lambda^{(1)}, \dots, \lambda^{(N)}$ . In this study the treatments were applied to populations with and without disturbance. A reference matrix  $A^{(r)}$  was chosen as a baseline to compare treatment effects, where  $A^{(r)}$  is the mean matrix  $A^{(.)} = \frac{1}{N} \sum_i A^{(i)}$ , i.e., the mean annual matrix from

the treatment to the undisturbed population (“control”). With the mean matrix  $A^{(r)}$ ,  $\lambda^{(r)}$  was estimated. Similarly, with the annual mean matrix  $A^{(m)}$  from the treatment to the disturbed population, we estimated  $\lambda^{(m)}$ .

Expanding  $\lambda$  as a function of the  $a_{ij}$  around  $A^{(r)}$  results in the growth rate in treatment  $m$  as follows:

$$\lambda^{(m)} \approx \lambda^{(r)} + \sum_{i,j} (a_{ij}^{(m)} a_{ij}^{(r)}) (\delta\lambda / \delta a_{ij})|_{A^E}, \quad m = 1, \dots, N$$

Where  $A^E = (A^{(m)} + A^{(r)})/2$ . The terms in the summation ( $\Sigma$ ) are the contributions of  $a_{ij}$  to the effect of treatment  $m$  on population growth. The difference between  $\lambda^{(m)}$  (estimated from the matrix  $A^{(m)}$ ), and  $\lambda^{(r)}$  (estimated as a function of the  $a_{ij}$ , around  $A^{(r)}$ ), determine how the treatments contribute to the differences in  $\lambda$  (Caswell, 2001).

### 3. Results

#### 3.1. Structure and growth rate of each population

The number of individuals per hectare was similar in both populations ( $X^2 = 0.695$ ,  $P > 0.05$ ), while their size structure was significantly different ( $Z = 2.5205$ ,  $P = 0.0117$ ) (Fig. 2). At the end of the study, 43 *M. schiedeana* stumps cut with an axe or machete were recorded at the disturbed population site, whereas none was recorded at the site of the undisturbed population. Aside from this, throughout the three years of the study, five trees were severed at the trunk by falling branches, three of them at the disturbed site, and two at the undisturbed site. All stumps produced new shoots. The average production of polyfollicles per individual was  $8.26 \pm 8.99$  for the disturbed population, and  $2.61 \pm 1.73$  for the undisturbed one. The sprouts from stumps did not produce polyfollicles during the time of the study.

Mean population growth rates (and 95% confidence limits) were 1.342 (1.069–1.91) and 1.154 (1.074–1.306) at the disturbed and the undisturbed populations, respectively. In the former, a decrease in the growth rate was observed from 51% at the time of the first census to 6%, while the undisturbed population showed a less significant decrease, from 42% to 37% (Table 1).

#### 3.2. Population matrix differences

The transition matrices were significantly different in terms of treatment (T) (log linear analysis, S is stage) (S–ST,  $\Delta G^2 = 12619$ ,  $P < 0.00001$ ), time (t) (S–St,  $\Delta G^2 = 7926$ ,  $P < 0.00001$ ), treatment and time (ST–STt,  $\Delta G^2 = 12618$ ,  $P < 0.00001$ ), and the interaction treatment  $\times$  time (STt–STtT  $\times$  t,  $\Delta G^2 = 685$ ,  $P < 0.00001$ ).

#### 3.3. Elasticity analysis

In both populations, the size classes that contributed the most to  $\lambda$  were the transitions from seed to seedlings to samplings and the stasis (individuals that remain in the same loop after an annual cycle, i.e. seedlings to seedlings and samplings to samplings) (Table 2). In both populations, stasis was the demographic process that contributed the most to  $\lambda$  (almost 50%). The transitions with the highest elasticity values (i.e., those contributing the most to  $\lambda$ ) were similar in both populations. Over 90% of the contribution came from <5 cm dbh individuals (Table 2).

#### 3.4. Analysis of the Life Table Response Experiments (LTRE)

In the disturbed population, the transitions from seed to seedling, from seedling to sampling and fecundity (seed produced by juvenile individuals), were the ones that contributed the most to variations in  $\lambda$ , whereas in the undisturbed population variations in  $\lambda$  came mostly from the transition from seedlings to samplings and fecundity (Table 3).

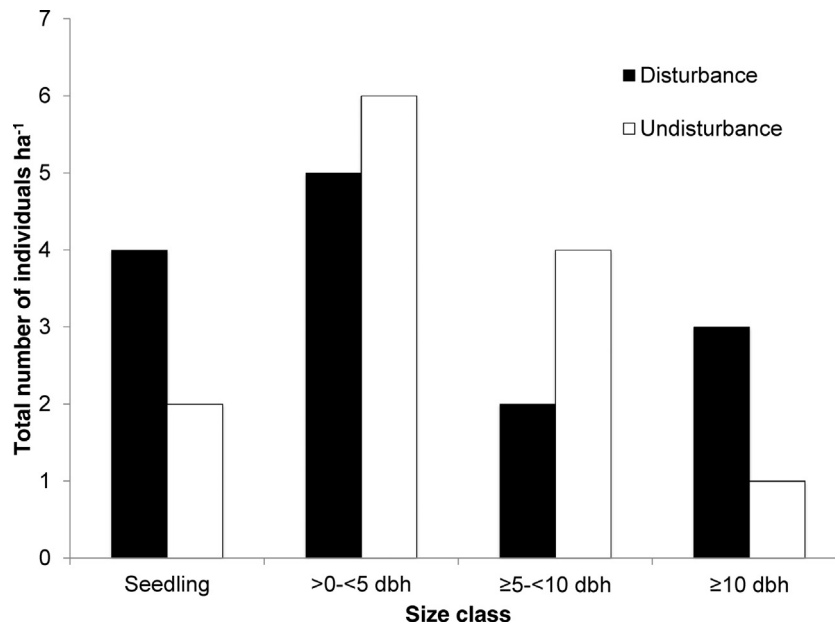
A comparative LTRE analysis revealed that the contribution of the disturbed population treatment to the differences in  $\lambda$  between the two treatments was 3.67%.

### 4. Discussion

In both *M. schiedeana* populations, the size structure is not the typical inverted 'J' or 'J' shape curve, a fact that suggests the presence of regeneration pulses caused by mast seeding (Kelly, 1994). These structures are very different from those encountered among other *Magnolia* species. For example, in *M. dealbata* (Sánchez-Velásquez and Pineda-López, 2006, 2010), *M. macrophylla* (Doyle 1989), *M. sharpii* (Ramírez-Marcial et al., 2001), *M. splendens* (Weaver, 1997) and *M. obovata* (Hoshino et al., 2002), the size structure presented an inverted 'J' shape, which indicates a constant regeneration and a high probability that the existing number of individuals in each class may be sustained through time by those in their preceding classes. However, a J-shaped structure has been also found in, for example, *Magnolia sinica* in China, indicating a low regeneration and a scarcity of individuals at the early stages of life (Wang et al., 2016). This suggests that *Magnolias* respond differently to environmental constraints, and their regeneration strategies may differ.

In both populations, the number of individuals of *M. schiedeana* per hectare was similarly scarce ( $P > 0.05$ : 14 at the disturbed population, and 12 at the undisturbed one). This is clearly an effect of resprouting, which contributes to keep mortality rates low. However, with other *Magnolia* species this was not the case. For example, with *M. officinalis* subsp. *biloba*, Rehder and Wilson obtained an interval of 0.15–5 individuals per hectare in China (He et al., 2009), whereas in Coyopolán, Ver., Mexico, with *M. dealbata*, a 1137 ind ha<sup>-1</sup> value was obtained in secondary tropical cloud forest, and 300 ind ha<sup>-1</sup> in grasslands (Sánchez-Velásquez and Pineda-López, 2006). Furthermore, in Nuevo León, Mexico, 30 ind ha<sup>-1</sup> were registered for *M. nuevoleonensis* (formerly *M. dealbata*) in a pine and oak forest, mainly in ravines (Velazco-Macías et al., 2008; Vázquez-García et al., 2016). Finally, there are also cases of extremely poor regeneration, as that of *M. zenii*, whose entire population consists of only 18 individuals, a fact that places this species at the “very critical” entry of conservation lists (Rivers et al., 2016).

Although in places with disturbance individuals tend to produce a larger number of polyfollicles than those at undisturbed sites (the average production of polyfollicles per individual at the disturbed population was between  $42 \pm 87$ , whereas at the undisturbed one



**Fig. 2.** Size structure of two *M. schiedeana* populations in Veracruz, Mexico. *dbh* is diameter at breast height; <1.3 h are individuals less than 1.3 m high (seedlings); >0<5 are individuals higher than 1.3 m and with a diameter at breast height (*dbh*) larger than 0 cm, and less than 5 cm (samplings); ≥5–<10 are individuals with a *dbh* from 5 to less than 10 cm (juveniles); and ≥10 are individuals with a *dbh* above 10 cm (adults).

**Table 1**

Transition matrices of two *M. schiedeana* populations (with and without disturbance) in Veracruz, Mexico. >0–<5 = individuals with a diameter at breast height (*dbh*) larger than 0 cm and less than 5 cm (samplings); ≥5–<10 = individuals with a *dbh* from 5 to less than 10 cm (juveniles); and ≥10 = individuals with a *dbh* above 10 cm (adults).

La Martinica (disturbed)						Volcán de Acatlán (undisturbed)				
2010–2011	λ = 1.510					λ = 1.427				
	Seeds	Seedlings	>0–<5	≥5–<10	≥10	Seeds	Seedlings	>0–<5	≥5–<10	≥10
Seeds	0.08	0	27.5	12.5	135	0.08	0	12.5	15	12.5
Seedlings	0.618181	0.9775	0	0	0	0.133333	0.8333	0	0	0
>0–<5	0	0.0229	0.98387	0	0	0	0.2	0.956521	0.18181	0
≥5–<10	0	0	0.016393	0.96078	0	0	0	0.045454	0.78571	0
≥10	0	0	0	0.04081	0.98	0	0	0	0.09090	0.8
N	27.5	89	124	51	68	30	6	23	14	5
2011–2012 λ = 1.431						λ = 1.306				
Seeds	0.08	0	22.5	22.5	77.5	0.08	0	5	5	12.5
Seedlings	0.120006	0.8965	0.008403	0	0	0.1500375	0.6	0	0	0
>0–<5	0	0.1153	0.975409	0	0	0	0.333333	0.954545	0	0
≥5–<10	0	0	0.008403	0.97959	0	0	0	0.047619	0.90909	0
≥10	0	0	0	0.02083	0.98	0	0	0	0.1	0.8
N	58.33	87	122	49	67	13.33	5	22	11	4
2012–2013 λ = 1.069						λ = 1.372				
Seeds	0.08	0	5	2.5	175	0.08	0	5	5	10
Seedlings	0.010975	0.8846	0	0	0	0.133333	0.666666	0	0	0
>0–<5	0	0.1304	0.957983	0	0	0	0.5	0.95238	0	0
≥5–<10	0	0	0.017543	0.97916	0	0	0	0.05	0.9	0
≥10	0	0	0	0.02127	0.98	0	0	0	0.11111	0.8
N	273.33	78	119	48	66	7.5	3	21	10	4

**Table 2**

Average vital rates (elasticity) matrix of two *M. schiedeana* populations (with and without disturbance) from Veracruz, Mexico. >0–<5 = individuals higher than 1.3 m and with a diameter at breast height (*dbh*) larger than 0 cm and less than 5 cm (samplings); ≥5–<10 = individuals with a *dbh* from 5 to less than 10 cm (juveniles); and ≥10 = individuals with a *dbh* above 10 cm (adults). \* It is from resprouting.

La Martinica (disturbed)						Volcán de Acatlán (undisturbed)				
Mean	Seeds	Seedlings	>0–<5	≥5–<10	≥10	Seeds	Seedlings	>0–<5	≥5–<10	≥10
Seeds	0.00840	0	0.14211	0.0026	0.0041	0.0091075	0	0.1329	0.01319	0.003991
Seedlings	<b>0.14887</b>	<b>0.23708</b>	0.00012	0	0	<b>0.1501819</b>	<b>0.1503</b>	0	0	0
>0–<5	0	<b>0.14899</b>	<b>0.27595</b>	0	0	0	<b>0.1501</b>	<b>0.3263</b>	0.00184*	0
≥5–<10	0	0	0.00676	0.0125	0	0	0	0.0190	0.03081	0
≥10	0	0	0	0.0041	0.0082	0	0	0	0.00399	0.007996
Σ	0.15727	0.38608	0.42495	0.0193	0.0123	0.1592894	0.3005	0.4783	0.04984	0.011987

**Table 3**  
Effects of the Life Table Response Experiments (LTRE) on the average life cycle of two *M. schiedeana* populations in Veracruz, México. <1.3 h = individuals less than 1.3 m high (seedlings); >0–<5 = individuals higher than 1.3 m and with a diameter at breast height (dbh) larger than 0 cm and less than 5 cm (samplings); ≥5–<10 = individuals with a dbh from 5 to less than 10 cm (juveniles); and ≥10 = individuals with a dbh above 10 cm (adults). Pwd is population with disturbance and Pud is population undisturbed.

La Martinica (Pwd)						Volcán de Acatlán (Pud)				
2010–2013	Seeds	Seedlings	>0–<5	≥5–<10	≥10	Seeds	Seedlings	>0–<5	≥5–<10	≥10
Seeds	0	0	<b>0.137140</b>	0.00312	0.00616	0	0	<b>0.1074</b>	0.01278	0.000690
Seedlings	<b>0.288993</b>	0.019517	0.000319	0	0	<b>0.0145898</b>	0.0361	0	0	0
>0–<5	0	<b>0.144869</b>	0.005609	0	0	0	<b>0.0916</b>	0.0009	0.00448	0
≥5–<10	0	0	0.003571	0.00020	0	0	0	0.0012	0.00342	0
≥10	0	0	0	0.00256	0.00010	0	0	0	0.00056	0.001384
Σ	0.288993	0.164386	0.146640	0.00589	0.00626	0.0145898	0.1278	0.1096	0.02125	0.002075

it was  $6 \pm 3.7$ , i.e., seven times lower), this higher seed production makes little difference in terms of the population growth rate (see Table 2). This might be explained by the unpredictability of different vital strategies (fertility in this case, and its possible evolutionary implications; Aragón, 2014), or simply as a result of changing environmental factors, such as nutrient availability, quality and quantity of light, and successional habitat (Johnson, 2007). This needs to be explored in further studies. The fact is that other populations of *M. schiedeana* (such as those of Naranjillo, La Mesa and Otilpan in the state of Veracruz, Mexico) produce a very small quantity of polyfollicles per individual (one or two) (Dieringer and Espinosa, 1994).

In spite of similar population growth rates, transition matrices vary significantly between populations and from one year to another. This suggests that populations have different life histories, which may be reflected in their genotype, something that genetic-ecological studies could help to confirm.

Interestingly, the disturbed population maintained always a growth rate above one, and there were no significant differences in relation to the undisturbed population. In both populations, the size classes that contributed the most to the population growth rate were the ones with less than 5 cm in dbh (over 90% contributed to  $\lambda$ ). They include seeds, seedlings and samplings (Tables 2). Resprouting contributed only 0.012% in the disturbed population, and 0.184% in the undisturbed one (Table 2). These life cycle stages were also the ones presenting the highest variation (Table 3).

The resprouting trait has been registered for other *Magnolia* species, such as *M. dealbata* (Sánchez-Velásquez and Pineda-López, 2006), *M. obovata* (Yamamoto, 1989), *M. splendens* (Weaver, 1997), and *M. tomentosa* (Setsuko et al., 2004). It is an example of the evolutionary adaptation of species living in perturbed and fragmented ecosystems (Paciorek et al., 2000; Bond and Midgley, 2003; Bubb et al., 2004), observed also among other species of semi-deciduous (Mwavu and Witkowski, 2008) and dry forests (Vieira et al., 2006). Unfortunately, no demographic studies are available to demonstrate the contribution of resprouting to the growth rates among tree populations.

Should illegal logging continue, special emphasis would have to be placed in caring for seedling and samplings, the main contributors to  $\lambda$  (Table 2). Another important aspect to focus on is the early fecundity (seeds) of individuals belonging to samplings, which presented the highest variation in the LTRE analysis. These size classes must be given priority when devising production management or conservation practices. Similar results have been obtained with other *Magnolia* species. For example, in the case of *Magnolia mexicana*, the individuals that contributed the most to  $\lambda$  were those with <5 cm dbh (Baltazar-García et al., unpublished), whereas with *M. dealbata* it was individuals with >10 cm dbh (Sánchez-Velásquez and Pineda-López, 2010).

Disturbance (defined by the presence of stumps) has impacted the population growth rate of *M. schiedeana* in 3.67%, a greater result than the one found for *M. dealbata* populations (0.039%) disturbed by livestock (Sánchez-Velásquez and Pineda-López, 2010).

However, as the disturbed population has very high growth rate values (never below one), it may be concluded that the impact of disturbance does not endanger the population.

Finally, the size structure presented by both populations suggests the existence of regeneration pulses. Independently of a moderate disturbance, the growth rate in both was well above one, and not significantly different. All stumps of *M. schiedeana* individuals have the ability to produce new sprouts. However, this attribute in moderate disturbance contributes little to the high growth rates. Our results suggest that *M. schiedeana* populations are resistant to disturbance, and their population growth rates are little affected by it (3.67%). It is still unknown how regeneration and stasis would respond to larger disturbances, such as deforestation or clearing of large patches.

#### Conflict of interest

The authors declare no conflict of interest.

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Compliance with ethical standards

#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.flora.2017.07.005>.

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