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Implications of community forest management for the conservation of the genetic diversity of big-leaf mahogany (*Swietenia macrophylla* King, Meliaceae) in the Maya Biosphere Reserve, Petén, Guatemala

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ABSTRACT

Community Forest Management in the Maya Biosphere Reserve (MBR; Petén, Guatemala) has been recognized internationally for yielding forest conservation and socioeconomic benefits. However, the effect of current timber harvesting practices on the genetic diversity of timber species populations has not previously been documented. This study assessed the effects of timber harvesting on the genetic diversity and viability of regeneration of the most commercially important timber species in the MBR: big-leaf mahogany (*Swietenia macrophylla* King). Trees and seeds were sampled for two consecutive years in two Forest Management Units of the Multiple Use Zone (MUZ) of the MBR: Cruce a la Colorada and Carmelita. We correlated genetic diversity parameters (as measured using nuclear microsatellites) with seed germination percentages and compared genetic diversity of adults and seeds in stands that had been affected by timber harvesting and those that had not. We found a significant correlation between seed germination percentages (81–83%) and observed heterozygosity (rho=0.27), confirming that genetic diversity is important to regeneration success. No significant differences were found in allelic richness (A_R), expected and observed heterozygosity (H_E and H_O), or inbreeding (F_{IS}), between adults and seeds in harvested vs. undisturbed stands; or before and after timber harvesting. We found low inbreeding levels (F_{IS}=0.040–0.094), low biparental inbreeding (0–0.01), and high outcrossing rates (0.925–0.970) in the populations of *S. macrophylla* analyzed. Our study therefore provides evidence that genetic diversity in big-leaf mahogany populations was not diminished by one cutting cycle under current practices of community forest management in the MUZ of the MBR.

1. Introduction

Covering close to 2.1 million ha, the Maya Biosphere Reserve (MBR) in Petén, Guatemala is the largest protected area in Central America. Established in 1990, it is divided into three different zones allowing for varying degrees of resource management: the Core Zone (36% of the reserve); the Multiple Use Zone (MUZ), covering 40% of the reserve, in which low-impact natural resource management activities are allowed; and the Buffer Zone (24%). In the MUZ, usufruct rights were granted by the Guatemalan government in the late 1990s and early 2000s to twelve community organizations and two private industrial firms to manage timber and non-timber forest products (Grogan et al., 2015; Millner et al., 2020). Management of these forests is overseen by the Consejo Nacional de Áreas Protegidas (CONAP; the government organization overseeing the management of Protected Areas in Guatemala), according to management regulations detailed in the "Protected Areas Management Manual". All concessioned forests must operate according to an overall management plan for the concession area, covering the full term of the concession (25 to 40 years), which is developed and implemented under the supervision of a licensed forester, or "regent". Implementation

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of the plan is further detailed in five-year plans that define the boundaries of five annual cutting areas, derived from estimations of volumes of commercial trees determined on the basis of a 3% sample inventory. In addition, each year the communities and their forester must develop a harvesting plan for the annual cutting area, based on a 100% georeferenced inventory of commercial timber trees > 30 cm in diameter. Harvests are calculated based on existing standing volumes of each species, and each plan must also describe how commercial trees will be sustained for future harvests, either through planting or natural regeneration. Particularly healthy and well-formed individuals of each commercial species must be left standing as seed trees. These plans must all be approved by CONAP and followed by the concessionaires. In addition, since 1999 CONAP has required that forest management in the MBR be certified by the independent Forest Stewardship Council (FSC; Grogan et al., 2015). FSC conducts annual audits to ensure that forest management practices have been implemented as per the plans. Several international studies have been carried out to evaluate the impacts of the community forest concessions on the forests of the MBR and on the communities, concluding that community forest management has benefited tropical forest conservation, significantly reducing deforestation and forest fires (ACOFOP PRISMA, 2017); as well as yielding socioeconomic development benefits (Rodas and Stoian, 2015; Hodgdon et al., 2015; Stoian et al., 2018; FAO, 2018; Millner et al., 2020).

The major source of income for the communities is harvesting timber. Five commercial timber species are harvested: 40 percent of the timber volume is obtained from *Lonchocarpus castilloi* (locally known as 'manchiche'), *Bucida buceras* ('pucté'), and *Calophyllum brasiliense* ('santa maria'). The bulk of the timber volume comes from two Meliaceae species, *Cedrela odorata* and big-leaf mahogany (*Swietenia macrophylla* King; Grogan et al., 2015). Mahogany accounted for 74% of the income concessions obtained from timber harvesting between 2012 and 2016 (Stoian et al., 2018). Because past logging in most of its range has led to the depletion of mahogany populations, largely because of a lack of regeneration, mahogany is listed on Appendix II of the Convention on International Trade in Endangered Species (CITES; Finegan, 2016). This means that national governments must require of those who harvest this species that it is managed in a way that is not detrimental for the long-term health of its populations. Results of a recent study on the conservation status of the five timber species harvested from these community concessions, including big-leaf mahogany, indicated that timber harvests in the MUZ have stimulated regeneration of mahogany at a rate sufficient to provide for future timber harvests that can be expected to be commercially viable (Grogan et al., 2015; Finegan, 2016). This suggests that the current management practices of these communities, under CONAP's guidelines and with FSC certification, are ecologically sustainable. These results provide the foundation for the international recognition of the communities' efforts to achieve sustainable forest management (Hodgdon et al., 2015; Finegan, 2016). However, previous studies have not addressed the maintenance of the genetic diversity of mahogany populations.

Natural regeneration of tree populations is key to maintaining forest ecosystem dynamics (Ratnam et al., 2014). Timber harvesting reduces the population size of adult individuals, which could reduce the allele frequencies in timber species populations, resulting in the loss of alleles and heterozygosity. Moreover, such a reduction in the density of reproductive individuals can increase inbreeding (Sebben et al., 2008), which in turn can have detrimental effects on seedling establishment and survival. Seeds resulting from self-pollination generally do not reach maturity: either they do not germinate or they die at an early stage, due to inbreeding depression (Duminil et al., 2009, 2016). Although genetic diversity is seldom considered in sustainable forest management, it provides the basis for tree populations to adapt to changing conditions from one generation to the next. Forest management should therefore include activities to monitor genetic variation and to ensure that processes of evolution are maintained (Namkoong et al., 2002).

Previous genetic diversity studies in the Mesoamerican populations of big-leaf mahogany, using Random Amplified Polymorphic DNAs (RAPDs; Gillies et al., 1999), showed a decrease in population diversity in harvested populations as compared to undisturbed populations across Central America ($p = 0.034$). However, these undisturbed populations were sampled in different locations with different histories. So far, no studies have assessed the impact of current management on the genetic diversity of big-leaf mahogany populations at the MBR. This study aims to fill that gap by evaluating the effect of a timber harvest on the genetic diversity, outcrossing rates, and germination capacity of big-leaf mahogany in managed stands.

2. Materials and methods

2.1. Species description

Big-leaf mahogany is a canopy-emergent tree species native to the Neotropics. It is found at low densities of one or fewer individuals per ha in wet and dry tropical forests from southern Mexico to the Amazon in Brazil (Whitmore, 1983; Mayhew and Newton, 1998). Big leaf mahogany is a monoecious, protogynous and light-demanding tree species. Individuals may reach heights of 40 m and a diameter at breast height (DBH) of over two meters. Mahogany trees have been documented to fruit as early as 12 years old (Mayhew and Newton, 1998), although individuals do not produce large quantities of seed consistently until they reach ≥ 75 cm DBH (Snook et al., 2005). Their flowers are unisexual and pollinated by small generalist insects such as butterflies and moths (Mayhew and Newton, 1998). Pollen flow distances of up to 200 m were reported in natural populations in Costa Rica (Novick et al., 2003). Flowering occurs after leaf flushing (Grogan and Loveless, 2013). In Guatemala, flowering occurs between February and March (Navarro, 1999). Fruit pods are hard capsules that mature in 10–12 months, each containing 40 or more winged seeds (Niembro, 1995; Gullison et al., 1996; Snook et al., 2005). The seeds can be dispersed by water, but most commonly by wind, falling at distances from 20 m to more than 50 m from the mother tree, depending on the direction of prevailing winds (Grogan and Galvao, 2006; Cámara-Cabrales and Kelty, 2009).

2.2. Sampling of adult trees and seeds

The big-leaf mahogany populations studied were located in two Forest Management Units in the western part of the MUZ: Asociación Forestal Cruce a la Colorada (AFICC), covering 20,469 ha; and Cooperativa Carmelita (RL), covering 53,797 ha (Fig. 1). Studies were carried out with active support in sampling, experimental set-up, and data collection on the part of community members (van Zonneveld et al., 2018a). In each Forest Management Unit, sampling was carried out in three different Annual Cutting Areas, each managed according to a *Plan Operativo Anual Forestal* (POAF). These POAFs guide timber harvesting and include a geo-referenced census or inventory of individuals of commercial trees larger than 30 cm diameter in the harvest area (Grogan et al., 2015). In each Unit, sampling was carried out in one POAF where timber harvesting had taken place several years previously (2005/06); in another POAF where timber harvesting took place in 2015, after the first sampling (2014/2015); and in a third POAF where timber harvesting was scheduled for 2017, and had not yet taken place (Table 1). This allowed us to maximize the number of trees sampled before and after harvesting, within the time and budget available. Leaf samples were used to determine the genetic diversity of adult mahogany trees, and seeds were collected to sample the next generation. It is considered that sampling at least eight seeds per tree is sufficient to reveal the mating system of a tree (auto/allofecundation rate) and the genetic diversity of the seed cohort (Ritland, 1986). Because seeds within a single fruit may result from one fecundation, we sampled individual seeds from different fruits on a single tree, and obtained sample fruits and leaves from multiple trees within each sampled POAF.

A selected group of community members of Cruce a la Colorada, and

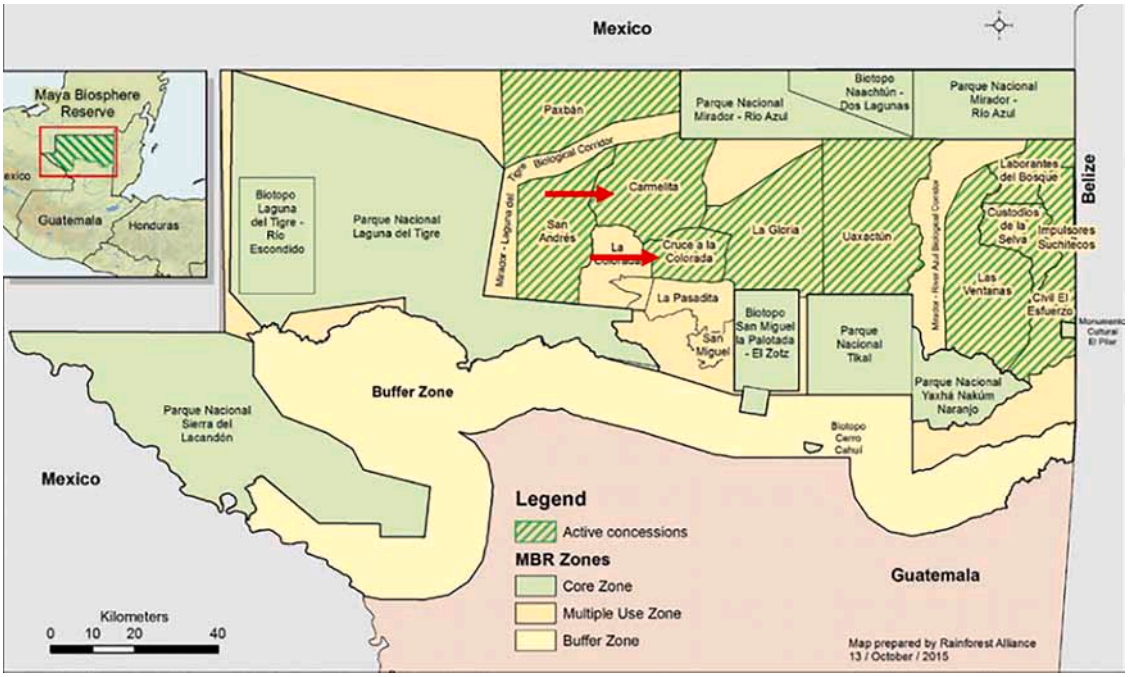

Fig. 1. Maya Biosphere Reserve in Petén, Guatemala, showing the three zones: Core, Multiple Use (MUZ) and Buffer. The MUZ includes the two Forest Management Units where the study took place: Cruce a la Colorada (AFICC) and Carmelita. These Units are indicated with a red arrow. Source: Rainforest Alliance, 2015.

Table 1
Number of adults from which seed pods were collected, number of seeds per pod, and forest status on sample areas (POAFs) at the time of collection in Cruce a la Colorada and Carmelita in 2015 and 2016.

Sampling Year	Cruce a la Colorada			Carmelita			POAFs forest status		
	Adults	Pods	Seeds per Pod (mean ± SD)	Adults	Pods	Seeds per Pod (mean ± SD)	2005/06	2014/2015*	2017
2015	71	710	66±5.1	90	320	64±7.9	Harvested	Not harvested	Not harvested
2016	66	368	62±8.3	57	359	63±7.7	Harvested	Harvested	Not harvested

* In 2015, seeds were collected before the harvest.

Carmelita received capacity building on sample collection. In each of the sampled POAFs, they collected leaves and seed pods from 28 to 35 trees > 45 cm DBH in March, when seeds were mature. Seeds and leaves were collected in 2015 and again in 2016. In 2015, approximately 10 pods were collected from each sample tree in Cruce a la Colorada; fewer in Carmelita. Where sufficient pods were available on sample trees, one seed per pod was selected for genetic analysis. Where too few seed pods were available on the sample trees, more than one seed was sampled from some pods, and both pods and leaves were collected from additional trees within each POAF (Table 1). Where possible, trees sampled in 2015 were also sampled in 2016. However, errors in some coordinates meant that not all the 2015 sample trees could be re-identified.

2.2.1. *Microsatellite analysis*

In total, we isolated genomic DNA from leaf samples of 284 trees across 2015 and 2016. From the collected seeds, we obtained 1153 DNA samples from Cruce a la Colorada and 1369 DNA samples from Carmelita (Table 1). The DNA was extracted using the Doyle and Doyle (1990) protocol at the Biology Department of Universidad del Valle de Guatemala.

The microsatellite analyses were done at the French National Research Institute for Sustainable Development (IRD) in France. Eleven nuclear microsatellites (SSR) developed by Lemes et al. (2002, 2011) were used for DNA amplification. A modification to the Micheneau et al. (2011) protocol for PCR amplification was carried out, adding linker tails to forward primers (F) and using dyed-labeled tails (FAM, VIC, PET or HEX). Amplifications were done using the QIAGEN Multiplex PCR kit, in two multiplex reactions. Mix 1 used the following microsatellites: sm08 (NED), sm28 (FAM), sm32 (NED), sm36 (PET), sm39 (VIC) and sm51 (PET). Mix 2 used the following microsatellites: sm07 (VIC), sm20 (PET), sm31 (NED), sm45 (FAM) and sm48 (NED). Each primer Mix contained 0.15 μl of the reverse primer and 0.10 μl of the F primer, plus 0.15 μl of each of the four dyed-labeled tails used. A total volume of 15 μl was used for the Multiplex PCR solution, containing 1.84 μl (mix 1) or 2.1 μl (mix 2) of the primer mix, 1 μl of sample DNA and distilled water.

The PCR amplification program was performed as follows: 95 °C for five minutes, 30 cycles at 95 °C (30 s), 48 °C (1.5 min), 72 °C (30 s), and a final elongation period of 60 °C for 30 minutes. PCR products were run on an ABI3500 XL Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). The LIZ 500 was used as reference to determine the size of the PCR fragments, using the Peak Scanner v1.0 software (Applied BioSystems).

The final dataset was composed of six of the eleven nuclear microsatellites: sm08, sm28, sm31, sm32, sm39 and sm51. The number of loci was reduced when it became clear that some were replicated (identical loci but named differently), which had not been referenced as such in Lemes et al. (2002, 2011). We found that: sm8 = sm36, sm20 = sm31, sm32 = sm45, and sm39 = sm48.

2.3. *Genetic diversity analyses*

We first determined the following genetic diversity parameters: allelic richness (A_R), genetic diversity given as expected heterozygosity (H_E), the observed heterozygosity (H_O), and the inbreeding coefficient (F_{IS}) using SPAGeDi v. 1–5 (Hardy and Vekemans, 2002). We also estimated the inbreeding coefficient unbiased by null alleles (Fnull) using

the software INEST (Chybicki and Burczyk, 2009). The influence of forest management practices on the genetic diversity of mahogany was investigated by comparing the genetic diversity parameters: (i) between adults (leaves) and offspring (seeds) for each Forest Management Unit and for each sampling year; and (ii) between samples (adults and seeds bulked together to provide a larger sample size) collected before and after harvest from POAF 2014/2015. Similarities in genetic diversity parameters between leaves and seeds, and between collecting years, were analyzed using an ANOVA test carried out in R-4.0.3. (R Core Team, 2020).

The mating system parameters multi-locus outcrossing rate (t_m), single locus outcrossing rate (t_s), and their standard deviations (SD) were analyzed using the Multi Locus Mating System Program (MLTR, Ritland, 2002). To approximate biparental inbreeding, t_m and t_s were used as t_m-t_s, since this difference is used to estimate selfing caused by biparental inbreeding (Shaw et al., 1981).

The neighborhood size and the gene dispersal distance (σ_g) were calculated using SPAGEDi v. 1–5 (Hardy and Vekemans, 2002). Assuming drift-dispersal equilibrium, these can be estimated for each population relying on patterns of Spatial Genetic Structure, as described in Hardy et al. (2006). We thus tested, respectively, for Carmelita and Cruce a la Colorada, the following effective densities: 0.31/0.25, 0.155/0.125, 0.0775/0.0625 (ind/ha). Approximate standard errors were obtained by jack-knifing over loci.

2.4. Germination tests

To assess the viability of natural regeneration of big-leaf mahogany populations in the POAFs affected by different timber-harvesting histories, seed germination tests were carried out by trained community members in the two Forest Management Units, Cruce a la Colorada and Carmelita. Seeds from 15 parent trees from each of the three sampled POAFs were used for the tests, giving a total of 45 parent trees per Unit. Seeds from the different parents were sown in aluminum trays, each one labeled with the number of the parent tree. Trays were filled with sand that had been previously sterilized for three hours over low heat. For each sample tree, 100 seeds were randomly selected from a mixture of seeds obtained from two to ten fruits from that tree (depending on the number of fruits produced). For each tree, 50 seeds were sown in each of two trays. Trays were placed on benches in outdoor nurseries with palm-leaf roofs, oriented N-S to ensure consistent sun exposure among all seed trays. The sand was moistened with water that had been sterilized through previous boiling, and trays were covered with transparent lids (van Zonneveld et al., 2018b). Trays were checked every two days to ensure the sand was kept moist. Every week the number of germinating seedlings was counted, until 50 days had passed. When the seedlings touched the plastic lids of the trays, the lids were removed. Women in the two communities cared for and counted the seeds and seedlings.

The percentages of seeds that had germinated, from each tree and each sampling Unit, were compared using an Analysis of Variance with R Software. The trees from each POAF ($N = 15$) were used as fixed factors and the Units as random factors. Germination percentages were ranked before applying F analyses following van Zonneveld et al. (2012). This is a function of the Friedman statistic, which can be treated as a normal distribution for F-tests (Conover and Iman, 1981). Because the ANOVA was carried out with ranked data, mean values and corresponding standard errors were not displayed. The Spearmaṅs Rho Correlation Coefficient was used to test the correlation between the germination percentages of sibling populations from 71 parent trees with their genetic results: observed and expected heterozygosity (H_O and H_E); allelic richness (A_R); and inbreeding coefficient (F_{IS}). This correlation coefficient was used because germination percentages did not follow normal distributions.

3. Results

3.1. Genetic diversity analyses

No statistically significant differences (one-way ANOVA, $p < 0.05$) were found for the genetic diversity parameters between adults and seeds in Cruce a la Colorada or Carmelita, for either year of sampling (Table 2). F_{IS} values were close to zero, indicating that there was not much inbreeding among the adult trees, nor in their offspring. No significant differences were found in genetic diversity parameters (A_R, H_E, H_O, F_{IS}) before and after timber harvesting in the 2014/015 POAFs of Cruce a la Colorada or Carmelita (Table 3).

3.2. Mating system

High outcrossing rates (0.93 - 0.97) and low biparental inbreeding (0 – 0.04) were found in both Cruce a la Colorada and Carmelita for the two collecting years (Table 4). Trees in Carmelita showed the same level of biparental inbreeding in both sampling years, but their outcrossing rate was lower in 2016.

3.3. Gene flow

A convergence (σ_g) was found only for Carmelita in 2015. The estimates of historical gene flow (σ_g) integrated pollen- and seed-mediated dispersal distance. The σ_g values in Carmelita varied from 1300 m for an estimated population density of 0.151 individuals per ha, to 2817 m for a density of 0.03 individuals per ha.

3.4. Germination test analyses

The mean number of seeds counted per pod for the three POAFs in Cruce a la Colorada was 66 ($N = 710$ pods) in 2015 and 61 ($N = 368$) in 2016. In Carmelita, the mean number of seeds per pod was 64 ($N = 320$) in 2015 and 63 ($N = 359$) in 2016. Mean germination percentages were 81% for Carmelita and 83% for Cruce a la Colorada. No statistically significant differences in germination percentages were found among seeds from the three POAFs, either harvested in the past (POAF 2005/06), recently harvested (POAF 2014/2015), or not yet harvested (POAF 2017). Fig. 2 shows the medians in boxplots obtained from the germination tests in each Forest Management Unit for the three POAFs.

The germination percentages of sibling populations from 71 trees were related to genetic parameters: heterozygosity, allelic richness and inbreeding coefficient of these sibling populations. A positive correlation between the germination percentage and H_O was obtained (rho = 0.27; $p = 0.001$). The correlation between the germination percentage and F_{IS} was negative (rho 0 0.21; $p = 0$ 0.01). No correlations were found between the germination percentage and A_R or H_E, as shown in Fig. 3.

4. Discussion

We analyzed parameters of genetic diversity, mating system and seed germination rates before and after logging in two community Forest Management Units in Petén, Guatemala. We compared the genetic diversity of adult trees (leaves) and their offspring (seeds) before and after logging to determine the effect of a timber harvest on the genetic diversity of mahogany in managed stands. In Cruce a la Colorada and Carmelita the comparison of parameters of genetic diversity of big-leaf mahogany revealed no differences in the genetic parameters (A_R, H_E, H_O, F_{IS}) between adults and seeds, or before and after harvesting. This suggests that the single harvest did not reduce the genetic diversity or gene flow in the sampled concessions.

Other studies have also found no differences in genetic diversity parameters between exploited and unexploited areas for a set of different tropical timber species (Rajora et al., 2000; Cloutier et al., 2007; Sebben et al., 2008; Silva et al., 2008). However, these results

Table 2
Genetic diversity parameters of adults and offspring of big-leaf mahogany (*Swietenia macrophylla* King) analyzed from leaf or seed samples, respectively, in Cruce a la Colorada and Carmelita in 2015 and 2016.*.

Forest Mgmt Unit	Sampling Year	Cohort	N*	$A_{R\ (k\ =\ x)}$	H_E	H_O	F_{IS}	F_{null}
Cruce a la Colorada	2015	Adults (leaves)	68	8.22	0.600	0.564	0.062	0
		Offspring (seeds)	710	7.75	0.570	0.542	0.049	0
	2016	Adults (leaves)	66	7.16	0.585	0.575	0.017	0.013
		Offspring (seeds)	432	7.18	0.558	0.532	0.048	0.014
Carmelita	2015	Adults (leaves)	88	7.07	0.553	0.532	0.038	0.017
		Offspring (seeds)	922	6.77	0.546	0.512	0.062	0.016
	2016	Adults (leaves)	74	7.41	0.543	0.540	0.006	0.013
		Offspring (seeds)	421	7.33	0.551	0.520	0.057	0.031

$A_{R\ (k\ =\ x)}$: Rarefied allelic richness ($k = 110$ for Cruce a la Colorada and Carmelita 2015, $k = 130$ for Cruce a la Colorada and Carmelita 2016), H_E: Expected heterozygosity, H_O: Observed heterozygosity, F_{IS}: Inbreeding coefficient (biased by null alleles), F_{null}: Inbreeding coefficient (unbiased by null alleles).

* Numbers of seeds analyzed differ from the numbers in Table 1 because in 2016 pods were collected from additional trees, and when fewer than 10 pods were found on some sample trees, additional seeds were selected from the pods available.

Table 3
Genetic diversity parameters of *Swietenia macrophylla,* leaves and seeds combined, in Cruce a la Colorada and Carmelita for POAF 2014/2015 as measured before (2015 sampling) and after (2016 sampling) harvesting.

Forest Management Unit	Sampling year	N	A_R (k = 220)	H_E	H_O	F_{IS}
Cruce a la Colorada	2015	314	6.87	0.532	0.507	0.047
	2016	144	7.06 ^{NS}	0.586 ^{NS}	0.583 ^{NS}	0.005 ^{NS}
Carmelita	2015	304	7.88	0.572	0.555	0.030
	2016	161	6.82 ^{NS}	0.573 ^{NS}	0.559 ^{NS}	0.025 ^{NS}

A_R: Allelic richness, H_E: Expected heterozygosity, H_O: Observed heterozygosity, F_{IS}: Inbreeding coefficient, *NS* indicates that the diversity statistic is not different before and after harvest, as per a one-way ANOVA procedure.

Table 4
Biparental inbreeding and outcrossing rate in both Cruce a la Colorada and Carmelita, obtained in sampling years 2015 and 2016.

Forest Management Unit	Sampling year	Biparental inbreeding	Outcrossing rate
Cruce a la Colorada	2015	0 (se 0.01)	0.970 (SD 0.017)
	2016	0.01 (se 0.01)	0.957 (SD 0.013)
Carmelita	2015	0.04 (se 0.13)	0.928 (SD 0.023)
	2016	0.04 (se 0.02)	0.925 (SD 0.032)

need to be interpreted with caution, as the impact of harvesting on genetic diversity parameters was measured after only one cutting cycle. If timber harvesting repeatedly removes trees larger than a minimum cutting diameter, the number of mahogany trees large enough to produce significant quantities of pollen and seed can be expected to decline from one cycle to the next. However, it is important to note that management guidelines for these community forests require that seed trees be retained on each annual cutting area, and that these guidelines are apparently followed (Grogan et al., 2015).

The number of alleles per locus found in our study ($A_R = 7.9$ in Cruce a la Colorada and $A_R = 7.8$ in Carmelita) was only slightly lower than those found previously in the MBR populations of Bethel ($A_R = 9$) and Tikal ($A_R = 11$), which had been considered to have been undisturbed when leaf samples were collected by Navarro (1999) and studied by Novick et al. (2003) and Degen et al. (2013). They used three of the same microsatellites (SSR) we used (sm32, sm32, sm51). Our numbers were considerably lower than those reported by Lemes et al. (2010) for Amazonian big-leaf mahogany populations ($A_R = 18$ alleles per locus), based on chloroplast microsatellites.

Our genetic diversity parameters H_O and H_E between adults and seeds, between POAFs, and before and after timber harvesting (Tables 2 and 3), differed from the species Hsp = 0.45 assessed using RAPD by Gillies et al. (1999), in that our mean values of the H_O and H_E parameters were higher even after harvesting ($H_O = 0.555$, $H_E = 0.572$). Our mean values of the H_O and H_E parameters between the Forest Management Units before ($H_O = 0.549$, $H_E = 0.568$) and after harvesting ($H_O = 0.555$, $H_E = 0.572$) were not different from those reported by Novick et al. (2003) in eight Mesoamerican populations ($H_O = 0.559$, $H_E = 0.657$), using microsatellite (SSR) markers. They were higher than those reported in two Costa Rican populations ($H_O = 0.14$ and 0.52, $H_E = 0.30$ and 0.58) by Lowe et al. (2003), using AFLPs and SSR markers; higher than same parameters ($H_O = 0.41$, $H_E = 0.71$) obtained in four populations (Campeche, Chiapas, Quintana Roo and Veracruz) from México (Alcalá et al., 2014) using SSR markers; and higher than four other big-leaf mahogany populations studied (Adults: $H_O = 0.45$, $H_E = 0.79$; saplings: $H_O = 0.34$, $H_E = 0.77$) in the Maya Zone of Quintana Roo, México (Alcalá et al., 2015), using SSR markers. Mexican populations were reported to have low levels of genetic diversity, probably as a result of timber harvesting down to a minimum diameter limit of 55 cm, considerably below the 75 cm diameter at which mahogany trees start to produce significant quantities of flowers and seed (Snook et al., 2005). Furthermore, it seems likely that timber harvesting, involving a series of successive removals of mahogany trees, has been under way in Quintana Roo for longer than it has in the Maya Biosphere Reserve. Even the community-managed forests in Quintana Roo are now well into their second cutting cycle (Snook, 2002; Snook et al., 2021). In contrast, our study in the MBR did not reveal a reduction in genetic diversity parameters after one timber harvest.

Swietenia macrophylla is a predominantly outcrossing species. Results from the mating system analysis (Table 4) indicated low inbreeding levels ($F_{IS} = 0.04 - 0.094$) and low biparental inbreeding (0.01 – 0) levels, along with high outcrossing rates (0.93 – 0.97) for both Forest Management Units. These results are good indicators that the genetic diversity has been maintained under current forest management, and that the harvesting practices have not affected the outcrossing rates. The values obtained from the estimate of historical gene flow (for Carmelita in 2015) indicated that pollen flow and seed dispersal distances (1300 m for 0.151 individuals/ha, and 2816 m for 0.031 individuals/ha) are very efficient, and significantly higher than the 200 m reported by Lowe et al. (2003) for two Costa Rican *S. macrophylla* populations. These results support the assumption that the higher the gene flow (via pollen and seeds), the more genetically diverse populations will be, and that populations may also be more similar when gene flow is high (Ratnam et al., 2014).

In the germination trials, we aimed to have a representative number of fruits from the same mother tree. We tested germination rates of the pooled seeds against expected and observed heterozygosity, inbreeding

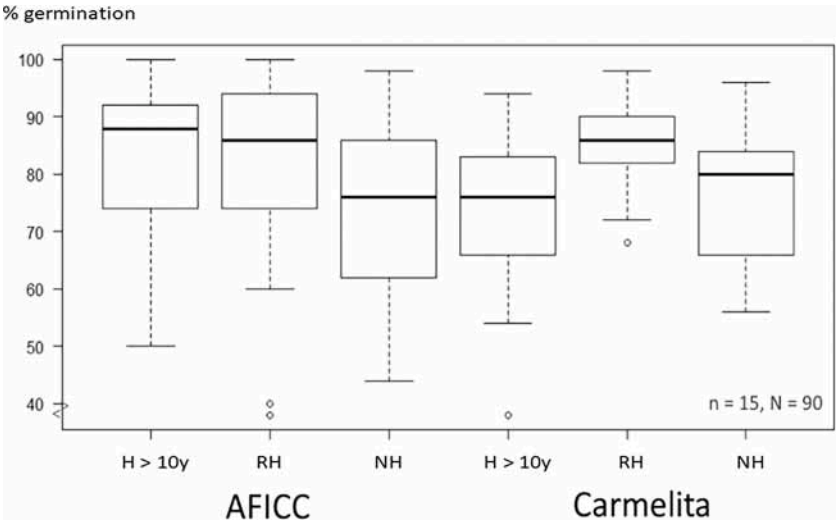

Fig. 2. Each boxplot represents one POAF out of the three surveyed and analyzed for each of the Forest Management Units (Cruce a la Colorada – AFICC and Carmelita). Each box represents the range of 95% of the germination percentages from the seeds obtained from each POAF. The line on each box represents the median germination percentage. Legend: "*H* > 10 y" = harvested more than 10 years ago; "RH"= recently harvested, "NH" = never harvested. Fifteen trees were sampled in each POAF ($n = 15$); 90 trees in total across six POAFs of two Forest Management Units ($N = 90$).

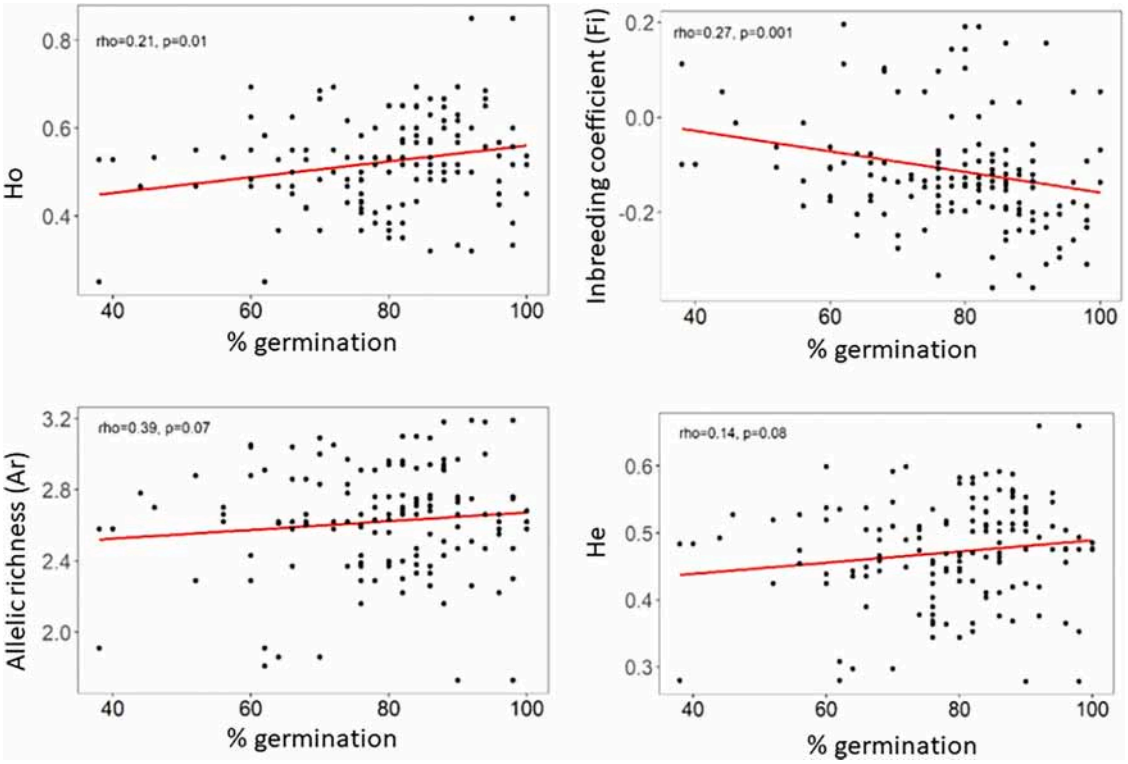

Fig. 3. Correlations between the germination percentages obtained from the seeds of 71 trees from the Forest Management Units studied (Cruce a la Colorada and Carmelita), and the genetic diversity parameters (A_R, H_O, H_E, F_{IS}) obtained for adults and seeds.

coefficient and allelic richness because these are standard parameters used to describe genetic diversity and geneflow. We recognize that by pooling the seeds from multiple fruits per tree and selecting 100, we increased the degrees of freedom and also the probability of obtaining a significant correlation coefficient.

The mean number of seeds per pod found across the two sampling years (Cruce a la Colorada = 64, Carmelita = 63.5) was up to 50% higher, or more, that the 40–50 seeds/pod reported for the neighboring Maya Forest in Quintana Roo, Mexico, on the Yucatán peninsula (Niembro, 1995; Snook et al., 2005). The positive correlations found between germination percentages of individual trees and their H_O (rho 0 0.27) suggests that trees with higher heterozygosity are more likely to produce seeds with higher germination capacity. Our average germination rates (81–83%) were similar to those reported for other germination studies done in the San Andrés Forest Management Unit in the MUZ of the MBR (85–94%), and populations in Quintana Roo, México (84%; Morris et al., 2000). Therefore, even though seed production can vary greatly among years and individuals (Snook et al., 2005), our results suggest sufficient seed, genetic diversity and germination potential to provide for both natural regeneration and enrichment planting of mahogany. Communities involved in the germination studies insisted on planting out the seedlings that had emerged in those experiments; there are other areas in the vicinity, notably those affected by fire, that could be restored through planting with mahogany. Training community members to collect seed pods for this study meant that this was carried out without the high levels of damage to seed trees

sometimes encountered as a result of seed collection by untrained collectors in Mexico (Snook et al., 2005).

5. Conclusions

Our findings suggest that levels of genetic diversity of mahogany trees in the Forest Management Units studied have been maintained under current harvesting practices defined and approved by CONAP and certified by the Forest Stewardship Council. These findings are consistent with results obtained by Grogan et al. (2015), who concluded that mahogany regeneration had become successfully established after earlier harvests in these community-managed concessions. This contributes to the evidence that community forestry in the MUZ of the MBR of Guatemala appears to be ecologically and genetically sustainable, contributing to the conservation of this valuable timber species and the viability of forestry, and thus, also to the conservation of forest biodiversity. The high numbers of seeds in each seed pod and their high levels of genetic diversity provide a foundation for considering the possibility of instituting careful collection and sale of mahogany seeds from these forests. In light of the commitments made by Guatemala and other countries in the region to restore large areas of forest, forest communities could become commercial suppliers of mahogany seed, making it another of their forest products and sources of income. Considering the correlation between germination and observed heterozygosity and the high regeneration viability in general, we propose that germination tests could be used as an important indicator for monitoring the genetic health and population viability of mahogany populations in general, and more specifically in the Forest Management Mnits in the MUZ of the Maya Biosphere Reserve.

CRediT authorship contribution statement

M. Alarcón-Méndez: Methodology, Formal analysis, Investigation, Data curation, Writing – original draft. **S. Maselli:** Investigation, Writing – review & editing, Supervision. **M. van Zonneveld:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Supervision, Validation, Writing – review & editing. **J. Loo:** Conceptualization, Methodology, Supervision, Funding acquisition. **L. Snook:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition, Project administration. **A. Oliva:** Formal analysis, Validation, Visualization. **A. Franco:** Formal analysis, Validation, Visualization, Project administration. **J. Duminil:** Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Validation, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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