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# Post-logging loss of genetic diversity in a mahogany (*Swietenia macrophylla* King, Meliaceae) population in Brazilian Amazonia

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## Abstract

Big-leaf mahogany (*Swietenia macrophylla* King, Meliaceae) is the most valuable widely traded timber species from the Neotropics. Mahogany has been severely overexploited throughout its natural range, which stretches from southern Mexico through Central and South America as far south as the Bolivian Amazon. We investigated effects of selective logging on the genetic diversity of a mahogany population in eastern Amazonia. Using eight hypervariable microsatellite loci, we estimated the number of alleles per locus ($A$), mean expected and observed heterozygosity ($H_e$, $H_o$), the number of distinct multilocus genotypes ($G_o$), and the inbreeding coefficient ($f$) for pre- and post-logging cohorts (adults and seedlings) collected over identical spatial scales. We found a significant reduction in the number of alleles, observed heterozygosity, and distinct multilocus genotype number in the post- compared to the pre-logging cohort. The loss of genetic diversity is likely to have occurred due to a reduction in the effective population size as a consequence of logging, which leads to the loss of alleles and limits mating possibilities. The results raise concerns about the conservation genetics of logged mahogany populations where a high proportion of adults are removed from the system. We suggest initiatives to promote the maintenance of genetic diversity as an integral part of the production system, allowing genetically sustainable use of this valuable timber resource.

*Keywords:* Conservation genetics; Genetic variation; Microsatellites; Tropical trees

## 1. Introduction

Timber species of the Neotropics typically occur in primary forests at densities ≤1 adult or commercial-sized tree per hectare at landscape-scales (Wright, 2002). This is true for high-value Meliaceae (*Swietenia*, *Cedrela*, and *Carapa*) as well as other coveted species such as *Tabebuia* spp., *Hymenaea courbaril*, *Dipteryx odorata*, *Cedrelinga catenaeformis*, and *Couratari* spp. (Schulze et al., 2005). As most tropical tree species require outbreeding for seed production (Alvarez-Buylla et al., 1996a; Ward et al., 2005), effective breeding populations of low-density species may be dispersed across forests covering hundreds of square kilometers (Chase et al., 1996; Kaufman et al., 1998; Nason, 2002).

Conventional or predatory logging practices in the Brazilian Amazon eliminate nearly all merchantable adult trees of high-value species during a single harvest (Uhl and Vieira, 1989; Uhl et al., 1991; Martini et al., 1994; Veríssimo et al., 1995). Current Brazilian legislation regulating the timber industry permits harvest of up to 90% of trees ≥50 cm diameter (Brazil, 2006). Martini et al. (1994) estimated that 30% of 305 widely exploited timber species in Brazilian Amazonia will suffer drastic long-term reductions in population densities due to conventional logging. Population densities face further threats from habitat degradation following logging due to forest structural disintegration and fire (Holdsworth and Uhl, 1997; Nepstad et al., 1999), and from landscape fragmentation and loss of habitat as logged forests are converted to pasture and agriculture (Uhl et al., 1993).

Logged species experience reduction in genetic diversity largely through allele removal from the exploited population (Bawa, 1993; Murawski et al., 1994). Inbreeding rates may also

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be dependent on adult density (Murawski et al., 1994) and are thus sensitive to logging practices. Current logging activities in the Amazon typically occur in forest patches within an already deeply fragmented landscape, which may contribute to an even higher loss of genetic diversity on a meta-population scale. A majority of studies assessing progeny arrays of degraded tree populations have shown negative impacts in terms of levels of inbreeding, reproductive output, and fitness, though genetic diversity appears to decline slowly over subsequent generations (Lowe et al., 2005). Despite evidence provided by these studies, forest managers rarely consider or account for possible impacts of logging on the genetic structure of tree populations.

Big-leaf mahogany (*Swietenia macrophylla* King, Meliaceae) is the most valuable widely traded Neotropical timber species. Mahogany has experienced intense population reductions across its vast natural range since Europeans first learned of its remarkable working properties (Lamb, 1966; Snook, 1996). International concerns over mahogany's conservation status were addressed in 2002 when natural populations were listed on Appendix II of the Convention on International Trade in Endangered Species of Fauna and Flora (CITES). This listing requires cooperation among producer and consumer nations to verify that exported volumes are logged according to national legal standards and without detriment to the species in its environment (Grogan and Barreto, 2005). Coupled with decisive action by the Brazilian federal government since 2001 to halt illegal trafficking in mahogany, the CITES listing has greatly decreased production from Brazil, the country with by far the historically largest natural stocks, from nearly 500,000 $m^3$ per year in the late 1980s (Grogan et al., 2002). New harvest regulations for mahogany (Brazil, 2003) seek to ameliorate logging impacts on commercial populations (Grogan et al., this volume), but no empirical data yet exists to evaluate their impact on population genetic structures. These concerns extend to other widely exploited high-value timber species in Amazonia.

Mahogany is a relatively fast-growing, light demanding emergent tree occurring in seasonally dry forests along the southern rim of Amazonia. Its wind-dispersed seeds are highly germinable but lack dormancy mechanisms, meaning no seed banks accumulate in the soil (Lamb, 1966). Seeds germinate readily in the forest understory, but seedlings require gaps for optimal growth and survival; they suffer high mortality in the forest understory, usually surviving only 1–2 years without release from canopy shade (Gullison et al., 1996; Grogan et al., 2003, 2005). Mahogany is monoecious; its flowers are pollinated by a diverse range of small generalist insects such as stingless bees, flies, butterflies, and moths (Styles, 1972; R. Gribel, *personal observation*). Reproductive trees exhibit outcrossing rates of >90% (Lemes, 2000; White et al., 2002). Inbreeding may be avoided through asynchronous anthesis of male and female flowers within tree crowns (Styles, 1972), though White and Boshier (2000) observed synchronous within-crown male and female flowering by *S. humilis* in Central America. Studies of *S. macrophylla* population genetics have shown high levels of genetic diversity and significant genetic differentiation among populations in Brazilian Amazonia (Lemes et al., 2003) and in Mesoamerica (Gillies et al., 1999; Novick et al., 2003). Mahogany's outbreeding mating system and high levels of genetic diversity indicate that effective population sizes are large, reinforcing the need to protect adult trees within extensive and widely distributed forests.

Here we quantify the effects of selective logging on genetic diversity within a single natural population of mahogany by comparing the genetic diversity and inbreeding coefficient of adult trees surviving the harvest 10 years before sampling, which we assumed to be a pre-logging sample, with the genetic diversity and inbreeding coefficient of seedlings recently germinated in the forest understory, which we assumed to be a post-logging sample. We anticipate that findings reported here will stimulate logging companies, environmental agencies and resource managers to take compensatory actions aimed at overcoming genetic losses caused by logging practices, as required by mahogany's listing on CITES Appendix II.

## 2. Methods

### 2.1. Study site

The study site is located in southeastern Pará state, Brazil, a region where mahogany historically occurred at high densities relative to the rest of its South American range (Grogan et al., 2002; Brown et al., 2003). Fieldwork was conducted in August 2003 at the 4100-ha Marajoara forest industry-owned management area (7°50′ S, 50°16′ W, 34 km northwest of Redenção), where mahogany was selectively logged from seasonally dry semi-evergreen forest during 1992–1994, or 10 years before sampling. Forests surrounding Marajoara have been cleared for ranching and agriculture. Logging intensity was relatively low at the site due to its intended status as a showcase management project. An estimated 15% of commercial-sized trees (≥45 cm diameter at the time of logging) survived the harvest, compared to ∼5% survivorship typically reported from this region (Grogan, 2001; Zimmerman et al., 2001; Brown et al., 2003). Pre- and post-logging commercial densities were 0.51 trees $ha^{-1}$ and 0.08 trees $ha^{-1}$, respectively.

### 2.2. Population sampling

To evaluate the impact of removing 85% of commercial-sized trees on mahogany's population-level genetic diversity, we sampled two generational cohorts of individuals: adults surviving the logging event 10 years prior to sampling, the pre-logging cohort; and seedlings established during 10 years since logging, the post-logging cohort. Leaf tissue was collected in August 2003 from 55 adults (≥45 cm diameter) and from 51 1- to 2-year-old seedlings that were distributed throughout an area of 1250 ha (Fig. 1). To avoid bias caused by patchy seedling establishment near adult trees, we collected only one sample from each seedling aggregation, ensuring that adults and seedlings were collected over the same spatial scale within the study area.

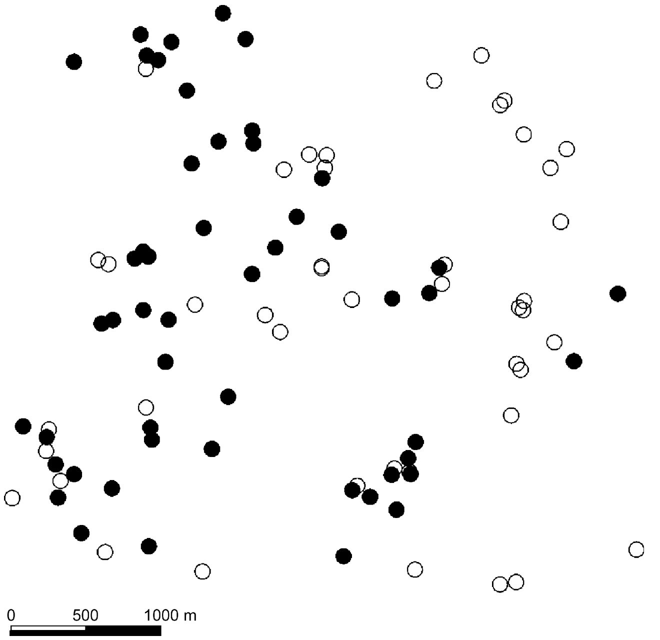

Fig. 1. Spatial distribution of adult trees (empty circles, $n = 55$) and seedlings (filled circles, $n = 51$) of *Swietenia macrophylla* sampled in 1250 ha at Marajoara, Brazilian Amazonia. Note spatial scale. Seedling aggregations may be associated with unsampled adult trees, while no seedling regeneration was found near many sampled adults.

### 2.3. Microsatellite analysis

Microsatellites are highly polymorphic DNA markers with powerful individual discriminating power (Tautz and Renz, 1984; Litt and Lutty, 1989; Condit and Hubbell, 1991; Powell et al., 1996). Microsatellites are widely used in studies of gene flow and genetic structure, allowing inferences about recent demographic events and the impacts of human activities on population genetics (Chase et al., 1996; Rafalski et al., 1996; Pearse and Crandall, 2004). In recent years, population genetics studies based on variation at microsatellite loci have been increasingly reported for tropical tree species, including mahoganies (White et al., 1999; Lemes et al., 2003; Novick et al., 2003).

Total genomic DNA was extracted from dried leaf samples following a standard CTAB protocol (Doyle and Doyle, 1987). Genetic analyses were based on PCR amplification of eight highly polymorphic loci (*sm01, sm22, sm31, sm32, sm40, sm46, sm47,*and *sm51*) previously isolated and characterized for *S. macrophylla* by Lemes et al. (2002). PCRs were performed in 25 μl for multiplex reactions or 10 μl for single reactions (one primer). Each reaction had 1.25–2.0 μM of primer, one unit of Taq DNA polymerase, 200 μM of each nucleotide (dNTP), PCR buffer 1× (10 mM Tris–HCl pH 8.3, 50 mM KCl, 1.5 mM $MgCl_2$), BSA (2.5 mg/ml), and 5.0 ng of DNA. PCR amplifications were performed as follows: (1) 94 °C for 5 min; (2) 30 cycles at 94 °C for 1 min + 56 °C for 1 min (all primers) + 72 °C for 1 min; (3) final extension at 72 °C for 45 min. Following amplification, PCR products were diluted, added to internal size standard (GeneScan 500 TAMRA, ABI), and electrophoresed in 5% denaturing polyacrylamide gel on an ABI 377XL sequencer. GeneScan and Genotyper (ABI) software were used for data collection and allele size estimation.

### 2.4. Data analysis

To estimate the levels of genetic diversity over all loci, the following measures were calculated for both life stages using GDA 1.1 software (Lewis and Zaykin, 2001): mean number of alleles ($A$), the expected ($H_e$) and observed ($H_o$) mean heterozygosities, and the inbreeding coefficient ($f$). The number of distinct multilocus genotypes observed ($G_o$) was estimated following Aldrich and Hamrick (1998). Differences between generational cohorts were tested for statistical significance for each parameter except $G_o$ by the Wilcoxon signed rank test (Sokal and Rohlf, 1995) using Systat 9.0 software (Wilkinson, 1998).

## 3. Results

The comparative analysis demonstrated a marked reduction in genetic diversity from adult to seedling cohorts of this selectively logged mahogany population. For three of four genetic parameters subject to statistical comparison, seedlings had significantly lower (or higher, in the case of inbreeding $f$) values compared to adults, indicating genetic erosion (Table 1). Mean observed heterozygosity ($H_o$) per life stage was 0.722 and 0.646 for adults and seedlings, respectively. Only expected heterozygosity ($H_e$) demonstrated non-significant difference, with seedling values nonetheless lower than adult values. The summed number of distinct multilocus genotypes observed was

Table 1
Genetic diversity ($A$, allele number; $H_e$, expected heterozygosity; $H_o$, observed heterozygosity; and $G_o$, number of distinct multilocus genotypes observed) and the inbreeding coefficient ($f$) for seedling and adult life stages of a logged population of *Swietenia macrophylla* in eastern Amazonia, Bold values indicate means per measure by life stage except for summed values for $G_o$. Significant differences in the Wilcoxon test are indicated by letters ($a > b$; $A$: $Z = 2.555$, $p = 0.011$; $H_o$: $Z = 2.240$, $p = 0.025$; and $f$: $Z = 2.380$, $p = 0.017$)

| Life stage | Locus | $A$ | $H_e$ | $H_o$ | $G_o$ | $f$ |
|---|---|---|---|---|---|---|
| Seedling ($n = 51$) | *sm01* | 12 | 0.840 | 0.813 | 8 | 0.033 |
| | *sm22* | 12 | 0.782 | 0.583 | 3 | 0.256 |
| | *sm31* | 13 | 0.893 | 0.739 | 14 | 0.174 |
| | *sm32* | 12 | 0.888 | 0.783 | 8 | 0.120 |
| | *sm40* | 8 | 0.761 | 0.680 | 1 | 0.107 |
| | *sm46* | 5 | 0.685 | 0.477 | 1 | 0.306 |
| | *sm47* | 3 | 0.407 | 0.412 | 0 | −0.012 |
| | *sm51* | 7 | 0.669 | 0.683 | 1 | −0.021 |
| | | **9.0**b | **0.741** | **0.646**b | **36** | **0.129**a |
| Adult ($n = 55$) | *sm01* | 16 | 0.875 | 0.891 | 15 | −0.018 |
| | *sm22* | 13 | 0.793 | 0.691 | 10 | 0.130 |
| | *sm31* | 16 | 0.910 | 0.833 | 16 | 0.085 |
| | *sm32* | 13 | 0.846 | 0.815 | 7 | 0.038 |
| | *sm40* | 10 | 0.752 | 0.636 | 4 | 0.155 |
| | *sm46* | 7 | 0.778 | 0.611 | 5 | 0.216 |
| | *sm47* | 5 | 0.514 | 0.556 | 3 | −0.081 |
| | *sm51* | 9 | 0.685 | 0.745 | 1 | −0.089 |
| | | **11.1**a | **0.769** | **0.722**a | **61** | **0.062**b |

much higher in adults ($G_o = 61$) than seedlings ($G_o = 36$), though these results cannot be compared statistically. The mean number of alleles declined by 20% from adult to seedling generations ($A = 11.1$ vs. 9.0, respectively; $Z = 2.555$, $p = 0.011$). Tree removal with consequent elimination of alleles from the gene pool can increase the proportion of homozygotes because the probability of the same allele encountering itself in a random mating event rises with lower allele richness. This outcome can be reinforced by inbreeding, which was detected at rates twice as high in seedlings as in adults ($f = 0.129$ vs. 0.062, respectively; $Z = 2.380$, $p = 0.017$), also indicating loss of genetic diversity from adult to seedling life stages.

## 4. Discussion

Results reported here demonstrate a significant loss of genetic diversity in post-logging seedling vs. pre-logging adult generational cohorts of a logged mahogany population in southeastern Brazilian Amazonia. Several co-acting factors may have influenced the dynamics of genetic diversity between generations at the Marajoara study site.

One possible explanation for these results is that selection favors more heterozygous individuals in post-seedling life stages (saplings, juveniles, and adults) such that older life stages exhibit higher heterozygosity than predecessor life phases. Under this scenario, inbreeding depression ultimately forces convergence towards adult heterozygosity. Early inbreeding depression has been demonstrated for pioneer species with seed dormancy allowing formation of soil seed banks (Tonsor et al., 1993; Alvarez-Buylla and Garay, 1994; Alvarez-Buylla et al., 1996b; Cabin, 1996; McCue and Holtsford, 1998). However, differential selection favoring heterozygosity would explain lower $H_o$ found for mahogany seedlings in the current study but not the loss of alleles and the great reduction in the number of unique multilocus genotypes in seedlings compared to adults.

A second possible explanation for these results is that the seedling cohort may represent progeny from only a subsample of adult trees that flowered and fruited during the years before field sampling. As there is no dormancy in mahogany seeds under natural conditions (Lamb, 1966; Morris et al., 2000), seedlings should be derived from a single or few breeding periods in contrast with the adult cohort derived from several or many distinct breeding periods (Grogan, 2001). By this reasoning, full diversity would be restored if seedlings were sampled over a longer time period. However, most studies with tropical tree species on the genetic effects of habitat degradation have not found diversity reduction at seedling or sapling stages (Lowe et al., 2005). Genetic diversity is apparently a quite resilient parameter whose degradation may require a number of generations, depending on the intensity of logging and fragmentation (but see Dayanandan et al., 1999). Our experimental design, sampling seedling aggregations over the same spatial scale as the adult population and choosing only one seedling per aggregation, was chosen to minimize sampling artifact and to maximize the seedling cohort's diversity estimate. The drastic reduction in three measures of genetic diversity therefore seems more likely to be caused by the severe reduction in the number of reproductive trees (ca. 85%) rather than by a sampling artifact. Further studies will be necessary to quantify the relative impact of reproductive skew on seedling cohort genetic diversity.

A third possible explanation concerns the reduction in the effective population size of adult mahogany trees in the study area caused by logging intensity at Marajoara. Tree populations that have suffered a recent decline in effective breeding population density are expected to show a related reduction in allele number and heterozygosity (Cornuet and Luikart, 1996; Lowe et al., 2005). Recently established mahogany seedlings at Marajoara are the result of matings between remnant trees, with the chance of outside gene flow greatly reduced due to large-scale forest fragmentation and intensive illegal logging of mahogany across this region. In fact the mahogany population at Marajoara occurs in an island of forest situated within a larger matrix of pasture, small-holder agriculture and severely degraded forests. Although some between-fragment gene flow may occur at the landscape-scale, as described by Céspedes et al. (2003) in Costa Rica and White et al. (2002) in Honduras, the isolated nature of the Marajoara forest and the relatively high number of remnant trees in this stand suggest that most of the current gene movement occurs within the population. The decrease in genetic diversity observed in the new generation of seedlings may therefore reflect both *in situ* lower adult density and disruption of landscape-scale meta-population structure, with both circumstances limiting mating possibilities.

Separating genetic consequences generated by logging from those caused by the historical fragmentation process in this region is virtually impossible. It is likely that the relatively large number of remnant trees at Marajoara (more than 400 trees >10 cm diameter in a larger area of 2100 ha) make the population resilient for short-term genetic changes caused by outside forest degradation. We therefore consider it probable that the within-population logging effect was the major factor responsible for the significant decline observed in seedling genetic diversity, noting that adverse genetic consequences of conventional or predatory logging removing up to 95% of commercial-sized trees (vs. 85% in this study) may be more severe than reported here. Recognizing that results from a single – albeit large and logistically challenging – research site are prone to error, we recommend that future studies include multi-site comparisons.

The spatial genetic structure of the mahogany population at Marajoara is weak (Lemes et al., *unpublished data*), probably because logging has disrupted genetic neighbourhoods that establish naturally within undisturbed forest. This contrasts with the quite strong spatial genetic structure found by Lowe et al. (2003) within relatively undisturbed mahogany populations in Costa Rica. The disruption of genetic structure would act to reduce inbreeding effects since pollinators may be forced to forage over longer distances in order to compensate for the decrease in adult tree density, as demonstrated by White and Boshier (2000) and White et al. (2002) for *Swietenia humilis* in Central America. It is likely, therefore, that inbreeding affected the mating system of trees in the pre-logging population more intensely than remnant trees in the post-logging population. Again, the loss of alleles in the gene pool and consequent reduction in possible genetic combinations are more likely to account for the genetic depletion currently exhibited by mahogany seedlings at Marajoara than does increased inbreeding among surviving adult trees.

Our data demonstrate that management initiatives will be necessary to halt the current loss of diversity and avoid further genetic erosion in remnant mahogany populations on this landscape. In order to guarantee a broad genetic base in germplasm collections, we propose that any new forest management project involving mahogany should implement active programs for remunerated seed collection by surrounding local communities and small-holder families, which could also participate in the inventory, mapping and selection of seed–trees with superior phenotypes as previously recommended by Lemes et al. (2003). Logging companies should be required to operate appropriate nursery infrastructure for seed germination and seedling production. Seedlings resulting from this program should be outplanted into logging gaps, abandoned skidtrails, and other disturbed areas associated with logging activities (d'Oliveira, 2000). Dissemination programs would also stimulate the inclusion of mahogany seedlings in regional agroforestry systems, increasing the potential for genetic connectivity between fragmented forests. All of these activities should be associated with initiatives to promote education and awareness at both political and popular levels about plant diversity and the need for its conservation and sustainable use. Adoption of these basic practices should additionally be a pre-condition for access to new logging licenses and for Forest Stewardship Council (FSC)-standard certification of forest management projects involving mahogany.

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