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# Mating system and genetic diversity of progenies before and after logging: a case study of *Bagassa guianensis* (Moraceae), a low-density dioecious tree of the Amazonian forest

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**Abstract** The logging of large trees in tropical forests causes a decrease in the density of reproductive individuals, which likely affects the pattern of pollen dispersal and the mating system of the remaining trees in the population. Here, we investigate the impact of logging on mating system and genetic diversity of the low-density, thrip-pollinated, dioecious tree *Bagassa guianensis* within a 500-ha plot at Tapajós National Forest, Pará State, Brazil. Mating system parameters of the logged population were estimated using mixed-mating model. Six microsatellite loci were used to genotype 232 seeds from

ten remnant female trees over three seasons (2006, 2007, and 2008). The data were compared with the mating system of the unlogged population of *B. guianensis* (18 female trees, 488 seeds) in the same plot. The overall number of alleles found in the open-pollinated progenies decreased after logging ( $K=71$  before logging and  $K=57$  after logging, considering the three after logging seasons pooled), as well as the average number of alleles per locus ( $A = 11.8$  and  $9.5$ , respectively). Similarly, the number of private alleles, which is defined in the context of this study as the number of alleles observed in the population exclusively before or after logging, also decreased after logging (15 and 1, respectively). However, the average number of alleles per locus and the observed and expected heterozygosities were not significantly higher before logging than after logging. Logging also did not affect the inbreeding of progenies in the population. Somewhat unexpectedly, the effective number of pollen donors was consistently higher after ( $N_{ep} = 14.5$  in 2006, 8.1 in 2007, and 6.3 in 2008) than before logging ( $N_{ep} = 3.4$ ), suggesting that the loss of alleles in the population was compensated by the higher heterogeneity in the pollen pool after the removal of the largest trees by logging. Potential causes explaining the patterns found here include the maintenance of large patches of forest around the logged plot and the species' ability to perform long-distance pollination by airborne thrips. Maintenance of landscape integrity as logged and unlogged forests around the exploited areas is recommended to enhance pollen migration and to avoid long-term losses in genetic diversity.

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## Introduction

One of the human activities that may pose risks to forest biodiversity is logging (Asner et al. 2005; Laurance et al. 2012; Schulze et al. 2008). In the Brazilian Amazonia, legal logging activities are based on the principles of Reduced Impact Logging (RIL), which allows the harvesting up to 90 % of the trees above the minimum cutting diameter (50 cm diameter at breast height (dbh) in cutting cycles of 30 years (Ministério do Meio Ambiente 2006). Although causing limited damage to the forest structure, selective logging has a direct impact on the demography of exploited species, mainly reducing the density (Johns et al. 1996; Holmes et al. 2002) as well as modifying the pollen movement and other reproductive functions among the remaining individuals (Ghazoul and McLeish 2001). Logging may also induce changes in patterns of genetic diversity (André et al. 2008; Carneiro et al. 2011; Lacerda et al. 2013, 2008b; Sebbenn et al. 2008; Silva et al. 2008) and mating systems of harvested species (Carneiro et al. 2011).

Several studies have suggested that the reduction of adult tree density might lead to an increase of selfing in tropical trees (Bawa et al. 1985; Lowe et al. 2005; Murawski and Hamrick 1991, 1992; Ward et al. 2005) and detrimental changes in patterns of genetic diversity such as the loss of alleles (André et al. 2008; Lacerda et al. 2008b). However, other studies have shown that some species of tropical trees maintain progenies with high levels of genetic diversity even after their adult populations have been reduced by logging activities (Cloutier et al. 2007; Lemes et al. 2007; Vinson 2009).

Naturally, most tropical tree species occur at low densities (<1 tree/ha) in their natural populations, and this may be compensated by the high levels of genetic diversity maintained within their populations (Ward et al. 2005). The maintenance of genetic diversity within populations may be attributed to the foraging behavior of specialized pollinators, which promote pollen dispersal over long distances and high levels of outcrossing in most tropical trees (Ahmed et al. 2009; Lowe et al. 2005; Ratnam and Boyle 2000; Ward et al. 2005).

The matter of forest management sustainability requires basic biological information of the exploited species for evaluation. Ecological factors (size class distribution, regeneration, growth, mortality, and critical density limits) and genetic patterns should be understood when one aims to preserve reproductive patterns and avoid reproductive isolation (Kanashiro et al. 2002; Schulze et al. 2008). Forest management practices should minimize the potential costs and consequences of an ecological imbalance caused by logging activities, such as reduction on the ecosystem resilience and loss of genetic diversity (Schaberg et al. 2008).

To elucidate the long-term processes that affect the genetic diversity and demography of a logged population,

modeling analyses have been performed (Degen et al. 1996, 2006; Gourlet-Fleury et al. 2005; Lacerda et al. 2013; Sebbenn et al. 2008; Vinson 2009) considering different logging scenarios with varying minimum cutting diameters (MCD), harvest intensities above the MCD, and cutting cycle lengths for commercial species with different population densities and reproductive systems. These analyses have shown that the impact of these activities is associated with the intensity of exploitation and the genetic background of the logged species.

Other studies have shown that regeneration and recruitment rates are insufficient to recover gaps or other disturbed areas and that even using RIL after a third cutting cycle, the wood yield will not be sustainable for populations of most commercial Amazonian tree species without implementation of silvicultural techniques based on ecological knowledge (Grogan et al. 2008; Schulze et al. 2008; Putz et al. 2012). On the other hand, an examination of generations of descended trees before and after logging may help to elucidate the putative detrimental genetic effects caused by logging and better understanding of its direct applications for conservation of forest genetic resources.

In this study, we investigated the impacts of logging on the mating system and genetic diversity of progeny arrays of a *Bagassa guianensis* population based on the analysis of variation at six microsatellite loci. Our main goal was to understand how the reduction in the density of conspecific individuals influences the allelic richness, variance effective size, and the effective number of pollen donors in a new seed generation produced after logging.

## Material and methods

### The studied species

*B. guianensis* Aubl. (Moraceae) is an endemic Amazonian tree species, and its geographic distribution ranges from the Amazon Basin to the Guyana and Suriname forests (Berg 2001). It is a long-lived pioneer species (Alencar and Araújo 1980), and populations occur naturally at very low densities, approximately 0.2 individuals/ha (Silva et al. 1985). Their sexual system is dioecious, with populations consisting of both male and female trees (Vega 1976; Berg 2001). *B. guianensis* timber exhibits high durability as well as resistance to fungi, rot, and marine organisms, and its texture produces an excellent finish. Thus, the timber is used to manufacture high-quality furniture, decorative veneer, ships, and tools. It is also regarded as promising for cellulose production (Tomazello et al. 1983). *B. guianensis* exhibits anemophilous pollination with the participation of tiny insects (thrips, order

*Thysanoptera*) moving through the wind (Silva 2005; Maués 2006). At the Tapajos National Forest, Para, Brazil, trees are randomly distributed by sex, and the sex ratio is 1:1 (Silva 2005). Flowering occurs annually, but individual trees may exhibit supra-annual flowering, with female trees having a shorter blooming period (2–4 weeks) compared to male trees (1–2 months) and the fruiting period occurring during the wet season which lasts for 6 months (Silva 2005). The infructescence contains hundreds of seeds that are dispersed by a variety of vertebrate animals that consume them in the canopy (e.g., parrots and monkeys) or on the ground (e.g., turtles, deer, and tapirs) (Fragoso and Huffman 2000; Juliot 1996; Moskovits and Bjorndal 1990; Roosmalen 1985; Silva 2005).

#### Intensive studies plot

The study area comprises 500 ha of upland forest belonging to the Tapajos National Forest located at Para State, Brazil. This area is an Intensive Studies Plot used by the Dendrogene Project (Genetic Conservation within Managed Forests in Amazonia, Embrapa Eastern Amazon/DFID) located at 83 km of the Santarém-Cuiabá highway (BR-163) in Belterra municipality PA (3°2' S, 54°56' W, 175 m above sea level). This area was associated with the Wood for Sustainable Industrial Production (ITTO PD 68/89) project of the Tapajós National Forest, which was sponsored by the Brazilian Institute of Environment and Natural Renewable Resources (IBAMA). This area was logged under RIL prescriptions in the second semester of 2003. The logging operation harvested 43 *B. guianensis* trees, which represented 61 % of trees with dbh > 60 cm within the plot. The density of the reproductive population decreased from 0.142 to 0.056 trees/ha after logging, with 15 females and 15 males (density of 0.03 trees/ha) remaining within the plot (Fig. 1).

#### Sampling

All *B. guianensis* reproductive trees found in the plot were mapped, sampled, and genotyped. Open-pollinated seeds were collected in the plot prior to logging in 2003 (18 trees) and after logging in 2006, 2007, and 2008 (ten trees). Seeds were germinated in a substrate composed of clay, sand, and vermiculite (1:1:1) at a greenhouse of the Laboratory of Plant Biology, Federal University of Para, Campus of Bragança. Seeds from each open-pollinated progeny array were sown in separate pots in the nursery, and leaf samples were collected 10–20 days after germination for further genetic analysis. Among the 15 females remaining after logging, ten had their fruits sampled in at least one reproductive event. Due to supra-annual reproduction of many individuals, not all trees produced fruits every year. Thus, seeds were collected

from only two to eight trees during the years after logging, and the number of seeds collected during these years was lower than in 2003 (62 seeds in 2006, 80 seeds in 2007, and 89 seeds in 2008).

#### Microsatellite analysis

Total genomic DNA was extracted from silica-dried young leaves from seedlings and from the cambium tissue of maternal trees using a Tissue Lyser Machine (Qiagen) and 2 % CTAB protocol (Doyle and Doyle 1990). Six primer pairs (Bg14, Bg16, Bg28, Bg32, Bg35, and Bg39) previously developed for *B. guianensis* (Vinson et al. 2010) were fluorescently labeled (6-FAM, NED, and HEX) and used to amplify the microsatellite loci. PCR reactions contained genomic DNA (4 ng), 1X PCR reaction buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.5 mM MgCl<sub>2</sub>), primers (0.23 μM of each primer described above), bovine serum albumin (New England Biolabs) (0.25 mg/ml), dNTPs (0.25 mM), and Taq DNA polymerase (Invitrogen, Life Technologies) (1.3 U) in a final volume of 13 μl. The amplifications were carried out in a Biocycler thermocycler (Model MJ25+) as follows: 94 ° C for 1 min, 30 cycles of 94 ° C for 1 min, locus-specific annealing temperature (50–54 ° C) for 1 min, and 72 ° C extension for 1 min. After 30 cycles, a final stage of extension of 30 min at 72 ° C was added. Genotyping was performed in an ABI 3130XL sequencer (Life Technologies Inc.), and GeneMapper version 4.1 software was used to estimate the allele sizes (Life Technologies Inc.).

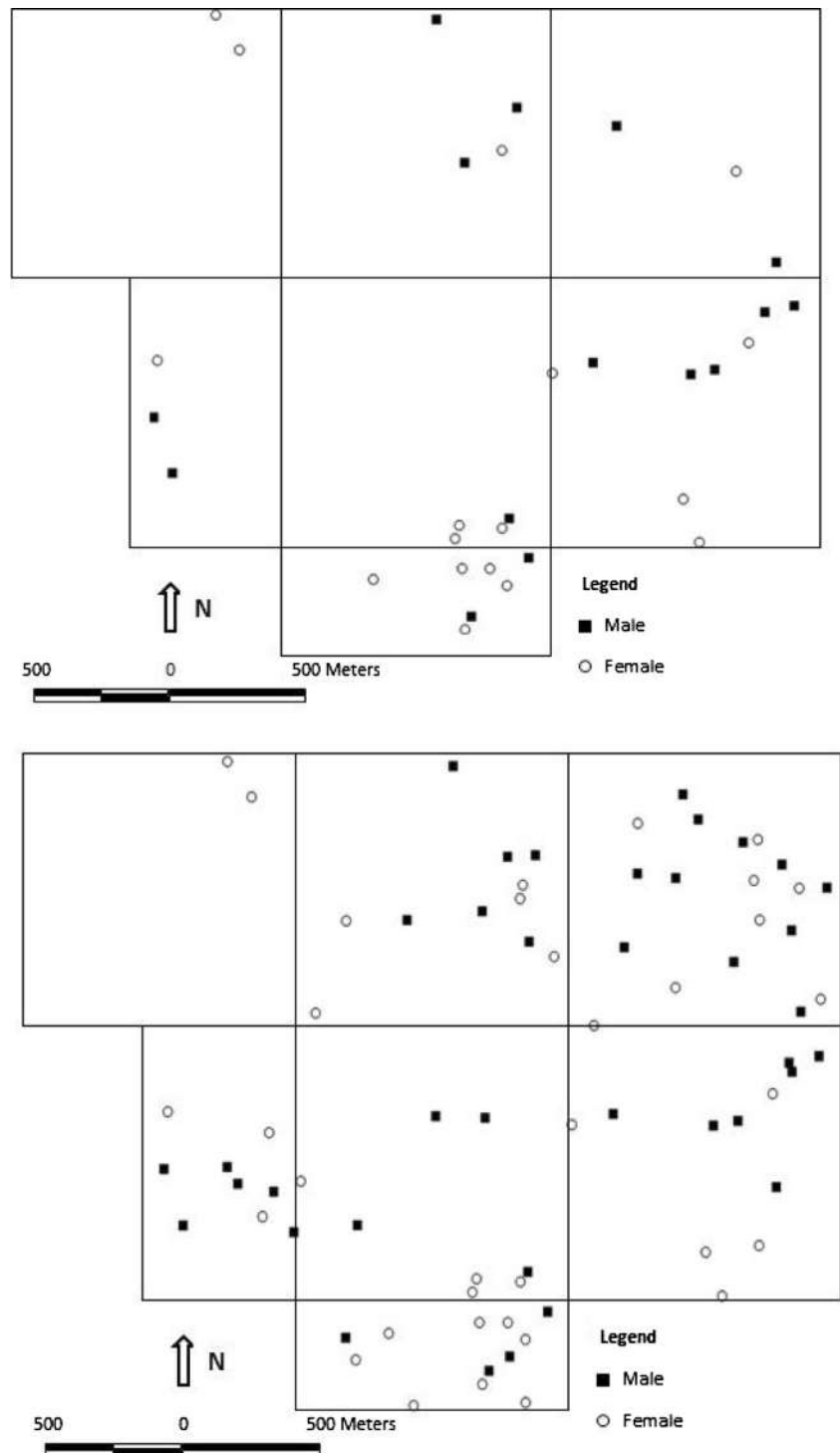
#### Calibration data

Since pre-logging data on genetic diversity and mating system were based on genotyping performed in an ABI 377 sequencer, it was necessary to verify the reproducibility and to calibrate the data set acquired in the different platforms. For that, we compared genotyping of six mother trees, which were carried out in both sequencers (ABI 377 and ABI 3130 XL) for the six SSR loci. There was a consistent difference of two base pairs for all loci in the fragment sizes obtained in the ABI 3130 XL sequencer. Hence, all data sets obtained in the ABI 3130 XL were adjusted by systematically adding 2 bp for all alleles obtained at the six loci. For all analysis, data obtained from seeds that were genotyped to less than four loci were excluded since such samples could affect the estimates.

#### Analysis of genetic diversity

Genetic diversity was analyzed for the progenies collected before (2003) and after (2006, 2007, and 2008) logging using FSTAT software (Goudet 2002). Because the sample sizes of the three reproductive events after logging were small (62, 80, and 89 seeds, respectively) compared to the sample size in

**Fig. 1** Spatial distribution of male and female trees of *B. guianensis* in the studied plot located at Tapajós National Forest, Pará state, North Brazil. **a** before logging and **b** after logging



2003 (488 seeds), we pooled the post-logging seed collections (231 seeds) to carry out some comparative analysis of genetic diversity of progenies before and after logging. The following genetic estimates were performed: number of alleles per locus ( $K$ ), average number of alleles per locus ( $A$ ), allelic richness ( $R$ ) estimated using rarefaction (El Moussadik and Petit 1996), observed heterozygosity ( $H_o$ ), and expected heterozygosity

under Hardy–Weinberg equilibrium ( $H_e$ ). In the context of this study, the number of private alleles was defined as the number of alleles observed exclusively in the population before or after logging. To infer inbreeding in the samples, we estimated the fixation index,  $F=1-(H_o/H_e)$  (Nei et al. 1975). The statistical significance of  $F$  was estimated by 600 random permutations of alleles among individuals using a Bonferroni



correction ( $\alpha=0.05$ ). To investigate if the genetic parameters  $A$ ,  $R$ ,  $H_o$ ,  $H_e$  and  $F$  were significantly different between years,  $t$  test (Sokal and Rohlf 1995) was used.

### Mating system analysis

The mating system analysis was carried out using the mixed-mating model (Ritland and Jain 1981) and the correlated mating model (Ritland 1989) implemented in the Multilocus MLTR 3.4 software (Ritland 2002). We analyzed the following parameters: multilocus outcrossing rate ( $t_m$ ), single-locus outcrossing rate ( $t_s$ ), rate of effective mating between relatives ( $1-t_s$ ), and multilocus paternity correlation ( $r_{p(m)}$ ). We performed a population-level analysis using the Newton–Raphson numerical method. The 95 % confidence interval of the parameters was calculated from 1,000 bootstraps using 2.5 and 95 % quartiles and individual within progenies as sample unity. The effective number of pollen donors was calculated as  $\hat{N}_{ep} = 1/\hat{r}_{p(m)}$  (Ritland 1989). To characterize the genetic structure within progenies, the average coancestry coefficient was estimated following Sousa et al. (2005):  $\hat{\Theta} = 0.125(1 + \hat{F})(1 + \hat{r}_{pm})$ . Additionally, the average variance effective size was estimated using the Cockerham (1969) estimator:  $\hat{N}_e = 0.5/\{\hat{\Theta}[(n-1)/n] + [(1 + \hat{F}_o)/2n]\}$ , where  $n$  is the number of seeds within progenies (assumed as 1,000 to minimize sampling errors) and  $F_o$  is the inbreeding in the progenies. The mating system parameters were estimated using two open pollinated progeny arrays from 2006 (62 seeds), five from 2007 (80 seeds), eight from 2008 (89 seeds), and 18 from 2003 (488 seeds). Because the sample sizes of the reproductive events post-logging were small in comparison with the pre-logging collection, we aggregated the former as a single post-logging population for some of the analyses. Seeds collected from the same seed tree in more than one reproductive event were also grouped. After aggregation, the post-logging population consisted of ten progeny arrays and 231 seeds.

## Results

### Genetic diversity and fixation index

The total number of alleles over the six loci was higher in the reproductive event before ( $K=71$ ) than in the three reproductive events after logging ( $K=46$ , 47, and 42 respectively; pooled  $K=57$ ) (Table 1). Fifteen alleles were private before and only one was kept as private after logging. Despite the loss of alleles after logging, the allelic richness ( $R_{42}$ ) and

observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosities were not significantly higher before compared to after logging. The average fixation index was significantly higher than zero before logging.

### Mating system

The multilocus outcrossing rate ( $t_m$ ) was significantly lower than 1.0 before logging and in the 2007 reproductive event as well (Table 2). The single-locus outcrossing rate ( $t_s$ ) was significantly lower from the unity, and the rate of mating among relatives ( $1-t_s$ ) was significantly higher than zero before and after logging. This suggests some level of mating among relatives, even after logging. The multilocus correlated paternity ( $r_{p(m)}$ ) was significantly different from zero before and after logging, except in 2006 and 2007 reproductive events, denoting that open-pollinated offspring have a mixture of half- and full-sibs. However, based on 95 % confidence interval, the correlated paternity and coancestry within progenies were significantly lower after logging. Thus, the effective number of pollen donors ( $N_{ep}$ ) and variance effective size within progenies ( $N_e$ ) was significantly higher after than before logging.

## Discussion

### Genetic diversity

The results indicate that some genetic variation was lost in the progenies due to selective logging since the total number of alleles and the number of private alleles were substantially lower after logging. Some caution is necessary in this conclusion, however, since the higher number of alleles found before logging may be a reflection of the larger sample size before logging (488 seeds) than after logging (231 seeds). No significant difference was detected in the average number of alleles per locus before and after logging when the estimation took into account the unequal population sizes among reproductive events through the use of rarefaction ( $\hat{R}_{42} = 7.90$  and 7.20 alleles per locus, before and after logging, respectively).

The analysis showed no significant differences in the heterozygosity of the progenies before and after logging. It is not an unexpected result since population bottlenecks of short duration normally have little effect on the heterozygosity, although it can reduce severely the number of rare alleles in the population. The loss of rare alleles, which are especially susceptible to bottlenecks, has a usually minor effect on heterozygosity (Nei et al. 1975).

**Table 1** Genetic diversity parameters estimated of *B. guianensis* offspring in different reproductive events before and after logging in Tapajós National Forest, PA, Brazil

Reproductive event	$N$	$K$	$\hat{A}$ (SD)	$\hat{R}_{42}$ (SD)	$\hat{H}_e$ (SD)	$\hat{H}_o$ (SD)	$\hat{F}$ (SD)
Before logging: 2003	488	71	11.83 (1.83)	7.91 (1.69)	0.693 (0.071)	0.626 (0.063)	0.097 (0.110) *
After logging: 2006	62	46	7.67 (1.37)	7.39 (1.35)	0.726 (0.040)	0.782 (0.111)	-0.078 (0.152)
After logging: 2007	80	47	7.83 (2.79)	6.82 (2.07)	0.652 (0.103)	0.639 (0.118)	0.019 (0.214)
After logging: 2008	89	42	7.00 (1.41)	6.38 (1.39)	0.658 (0.062)	0.641 (0.115)	0.028 (0.104)
After logging, pooled	231	57	9.50 (2.35)	7.20 (1.49)	0.690 (0.060)	0.676 (0.099)	0.020 (0.134)

Using unpaired  $t$  test, the mean values of all parameters are not significantly different between before logging and after logging pooled ( $A$ :  $t$  test=1.92,  $P=0.0839$ ;  $df=10$ ;  $R_{42}$ :  $t$  test=0.66,  $P=0.5220$ ,  $df=10$ ;  $H_e$ :  $t$  test=0.08,  $P=0.9348$ ,  $df=10$ ;  $H_o$ :  $t$  test=1.04,  $P=0.3204$ ,  $df=10$ ;  $\hat{F}$ :  $t$  test=1.05,  $P=0.3197$ )

$N$  sample size,  $K$  overall number of alleles,  $A$  average number of alleles per locus,  $R_{42}$  allelic richness to 42 diploid individuals,  $H_e$  expected heterozygosity,  $H_o$  observed heterozygosity,  $F$  fixation index

\* $P < 0.05$

### Mating system

Dioecism is an evolutionary adaptation that contributes to enhance heterozygosity since it prevents self-fertilization and favors the participation of many paternal parents in the mating process (Bawa and Opler 1975; Boshier 2000). According to Barret and Thompson (1982), the breeding success of dioecious species involves important factors such as the frequency of sexual forms in the population, the spatial distribution of individuals, and the abundance and behavior of pollinators. High estimates of multilocus outcrossing rates are expected in a dioecious species such as *B. guianensis*, both before and after logging. Mating among relatives, however, is a possible source of inbreeding (biparental inbreeding) in dioecious species. In our mating system analysis of *B. guianensis*, we found 17.2 % of among-relatives mating before logging and 3.4 to 12.5 % after logging. This type of mating occurs when

populations exhibit a spatial genetic structure, as observed for this population of *B. guianensis* by Silva et al. (2008) before logging (Table 1). Although mating among relatives remained after logging, it is likely that logging has partially ruptured the previous spatial genetic structure in this population of *B. guianensis*, as reported previously on other forest species (Carneiro et al. 2009; 2011; Lacerda et al. 2008b, 2013; Vinson 2009), which may explain why the fixation index did not detect inbreeding after logging. The mating among relatives of *B. guianensis* detected before and after logging was similar to that observed in hermaphroditic neotropical tree species from the same plot (Azevedo et al. 2007; Carneiro et al. 2011, 2007; Lacerda et al. 2008b).

Although quite variable, the effective number of pollen donors in all three post-logging reproductive events ( $N_{ep}$  ranging from 6.3 to 14.5) was significantly higher than the number observed prior to logging ( $N_{ep} = 3.4$ ). This result may be a

**Table 2** Mating system parameters estimated before and after logging for *B. guianensis* Tapajós National Forest, PA, Brazil

Parameter	Before logging: 2002	After logging: 2006	After logging: 2007	After logging: 2008	After logging, pooled
Progeny array (progenies)	18 (488)	2 (62)	5 (80)	8 (89)	10 (231)
Multilocus outcrossing rate: $t_m$	0.974 (0.953–0.984)	1.000 (1.000–1.000)	0.905 (0.836–0.968)	0.994 (0.935–1.000)	0.953 (0.882–1.000)
Single locus outcrossing rate: $t_s$	0.829 (0.779–0.896)	0.967 (0.962–0.989)	0.878 (0.788–0.955)	0.875 (0.809–0.930)	0.865 (0.778–0.999)
Effective mating among relatives: $1-t_s$	0.171 (0.104–0.221)	0.033 (0.011–0.38)	0.122 (0.045–0.212)	0.125 (0.070–0.191)	0.135 (0.001–0.222)
Multilocus paternity correlation: $r_{p(m)}$	0.293 (0.200–0.341)	0.069 (0.000–0.082)	0.124 (0.000–0.173)	0.160 (0.042–0.237)	0.151 (0.036–0.184)
Effective number of pollen donors: $N_{ep}$	3.4 (2.9–5.0)	14.5 (12.2– $\infty$ )	8.1 (5.8– $\infty$ )	6.3 (4.2–23.8)	6.6 (5.4–27.8)
Coancestry within progenies: $\theta$	0.162 (0.150–0.168)	0.134 (0.125–0.135)	0.141 (0.125–0.147)	0.145 (0.130–0.155)	0.144 (0.130–0.148)
Variance effective size: $N_e$	3.09 (2.98–3.33)	3.73 (3.69–3.99)	3.55 (3.40–3.99)	3.44 (3.23–3.83)	3.47 (3.37–3.85)

Value inside parentheses is the 5 % confidence interval; number of progeny array (progenies). The number of seed trees ( $m$ ) for collected seeds was estimated in order to retain the reference population effective size of 150 individuals

reflection of the removal of the largest male trees from the population by logging. These trees probably had a disproportional contribution to the pollen pool, and their removal may increase the number of male trees siring individual mother trees after logging. The higher effective number of pollen donors after than before logging also explains the higher values found to the coancestry coefficient ( $\Theta$ ) and lower variance effective size ( $N_e$ ) compared to before logging. The values found here for  $\Theta$  and  $N_e$  after logging were close to those found in progenies formed predominantly by half-sibs ( $\Theta = 0.125$ ,  $N_e = 4$ ).

#### Management and conservation of *B. guianensis*

The present work and other recent studies using variable and informative microsatellite loci provide evidences that mating system parameters of some tropical trees may be somewhat resilient to density reduction of adult trees, such as that caused by logging (Carneiro et al. 2011; Lacerda et al. 2008a), once the forest matrix is preserved. The maintenance of landscape integrity, including stands of logged and unlogged forests around the exploited areas, is therefore strongly recommended to enhance pollen migration and avoid long-term losses in genetic diversity.

In this study, we found that logging may have some genetic detrimental effect on the *B. guianensis* population especially due to the loss of less frequent alleles. The loss of rare alleles had however little effect in the heterozygosity. Potential causal mechanisms to this pattern may include a more evenly distributed contribution of pollen donors to the pollen pool after the removal of the larger trees, the migration of pollen from undisturbed forests around the plot, and the effects of dioecism. Further information on the pattern of pollen dispersal before and after logging will be covered elsewhere.

High levels of heterozygosity alone are not a guarantee that population will be resilient to successive cutting cycles. The loss of rare alleles may affect the population capacity to long-term response to selection. Furthermore, long-term sustainable production of timber in managed forests also depends on other variables such as the seed output of the remnant trees and the regeneration of the species in the logged forest.

The sustainability of forest management, under the current legal logging regime in Amazonian, based on a 30-year cutting cycle and the removal of a high proportion (up to 90 %) of adult trees, should rely mainly on population dynamics parameters such as recruitment and growth rate. Simulation studies for several Amazonian trees, including *B. guianensis*, have shown that the current cutting cycle and the intensity of timber harvest applied by the logging industries are unsustainable and can drive populations toward demographic collapse (Sebbenn et al. 2008; Gardingen et al. 2006; Lacerda et al. 2013).

Even with the long-lived pioneer features of *B. guianensis*, the rescue of genetic variation based on regeneration is an uncertain question. Heliophytes trees regenerate from the seed bank in natural gaps. If the species regeneration is high, seed banks could act as reservoirs of storage alleles and can replenish the genetic losses caused by the removal of adults from the population. However, *B. guianensis* in the same plot presents low levels of regeneration due to high mortality rate 6 years after logging (Schwartz et al. 2012). This reinforces the need for investigations in silvicultural techniques to increase recruitment, growth rates, and survival of commercial timber species in logged areas.

In the Amazon region, legal logging activities based on sound scientific data should counteract the widespread tendency to convert forests, logged or unlogged, into cattle ranching pastures or extensive monocultures such as soybean. These are currently the main threats to the conservation of the Amazonian forest resources and the environmental services provided by them.

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**Data archiving statement** Microsatellite genotypes of all individuals analyzed are available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.58mg2>. Primer sequences of the six microsatellite primer pairs (Bg14, Bg16, Bg28, Bg32, Bg35, and Bg39) used in this study were previously developed for *B. guianensis* by Vinson et al. (2010) and have been deposited at GenBank: accession numbers GU969286.1, GU969287.1, GU969291.1, GU969292.1, GU969295.1, and GU969296.1 respectively.

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