Impact of selective logging on genetic composition and demographic structure of four tropical tree species

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ABSTRACT

Over-exploitation and fragmentation are serious problems for tropical forests. Most sustainable forest management practices avoid clear-cuts and apply selective logging systems focused on a few commercial species. We applied a simulation model to estimate the impact of such selective logging scenarios on the genetic diversity and demography of four tropical tree species from French Guiana. The simulations used data on genetic and demographic composition, growth, phenology and pollen and seed dispersal obtained for Dicorynia guianensis, Sextonia rubra, Symphonia globulifera and Vouacapoua americana at the experimental site in Paracou. Whereas Symphonia globulifera serves as a model for a species with low logging pressure, the other three species represent the most exploited tree species in French Guiana. In simulations with moderate logging, typical for French Guiana, with large cutting diameter (>60 cm diameter) and long cutting cycles (65 years), the two species V. americana and Sextonia rubra were not able to recover their initial stock at the end of the rotation period, with a large decrease in the number of individuals and in basal area. Under a more intensive logging system (cutting diameter >45 cm diameter, cutting cycles of 30 years) that is common practice in the Brazilian Amazon, only Symphonia globulifera showed no negative impact. Generally, the differences between the genetic parameters in the control scenarios without logging and the logging scenarios were surprisingly small. The main reasons for this were the overlapping of generations and the effective dispersal ability of gene vectors in all species, which guarantee relative homogeneity of the genetic structure in different age classes. Nevertheless, decreasing the population size by logging reduced the number of genotypes and caused higher genetic distances between the original population and the population at the end of the logging cycles. Sensitivity analysis showed that genetic changes in the logging scenarios were principally determined by the growth, densities and cutting diameter of each species, and only to a very small extent by the reproductive system including factors such as pollen and seed dispersal and flowering phenology.

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1. Introduction

As a result of forest conversion to agriculture and other land uses, tropical forests have been disappearing on a global scale in the last 20 years. An estimated area of 4.9–5.8 million ha has been deforested every year in the period 1990–2000 (Mayaux et al., 2005). In addition, various less intensive land uses are altering the composition of tree communities in tropical forests. Selective logging is common in most tropical forests, indeed, the Brazilian Amazon, which covers 285 million ha, experienced an annual harvest of more than 50 million m³ of timber in 2000 (Asner et al., 2005). Such harvest intensities are unlikely to be sustainable over the long-term. In French Guiana the actual pressure on the primary forest is very low, but this could change in the near future with the increase of the Guianese population, and with the decline of forest resources in other tropical regions (Degen et al., 2003).

In comparison to other organisms, trees have a relative high level of genetic variation (Hamrick and Godt, 1990; Nybom, 2004). Trees have high levels of genetic variation because they need it to guarantee high adaptability to diverse environments. This is particularly important for sessile organisms with long life spans. Due to its importance for adaptation and adaptability, genetic diversity of tree populations has a significant function in ecosystem stability (Gregorius, 1991). Thus, information on the impact of forest management systems on the structure and dynamics of genetic variation is important in efforts to conserve forest genetic resources. Conservation of genetic diversity is a key element of many initiatives and guidelines for sustainable management of tropical forests (Namkoong et al., 1996).

The result of logging and land use practices is either a forest with a reduced density of reproducing trees, or a fragmented forest, with local patches of degraded woodlands separated by non-forested habitat. Recent studies have focused on trying to understand the impact of such changes in the forest on genetic variation in tree populations. Reduction of population sizes after logging may lead to genetic erosion, especially the loss of rare alleles (Ellstrand and Elam, 1993a;b; White et al., 2002). In addition, changes in adult densities in the logged forest may alter pollen movement and other reproductive functions among residual individuals (Loveless and Hamrick, 1984; Rossetto et al., 2004a,b). This could reduce cross-pollination and gene flow by impeding pollinator movement between trees (Goverde et al., 2002). On the other hand, evidence from some studies suggests that while pollinator species composition may be altered, pollinators may be able to alter their behaviours to adapt to reduced density and continue to provide effective gene flow (Aldrich and Hamrick, 1998; Chase et al., 1996; Dick, 2001). However, logging also reduces mean tree sizes in the residual population, and as remaining trees become increasingly reproductively isolated, more frequent inbreeding and lower seed production are likely to occur (Cascante et al., 2002; Ghazoul et al., 1998; Stacy et al., 1996). Thus, the impacts of disturbance and fragmentation on the genetic structure of tree populations may vary, depending on the ecological details of each tree species. Other authors have predicted a generally small impact of selective logging on the genetic diversity of tropical trees (Jennings et al., 2001). They argued that strongly light-demanding species with a commercial value are because of their lower number of different age classes the most likely to suffer loss of genetic variation from logging, whereas most tropical species have a sufficient number of individuals below cutting diameters and thus are not endangered.

In this study, we used the simulation model Eco-Gene (Degen et al., 1996; Degen and Roubik, 2004) to examine the genetic consequences associated with logging. The objectives of our study were to use the simulation model for (a) a comparative analysis of the impact of selective logging on the genetic diversity of different timber species in French Guiana, and (b) to identify, by use of sensitivity analysis, those parameters that have a significant impact on genetic and demographic dynamics of logged tropical forests. The results will help to deduce critical thresholds and practical recommendations for conservation of genetic diversity in managed tropical forests.

The model was parameterised using data on genetics, demography, growth, phenology, and pollen and seed dispersal of four well-studied timber species from French Guiana: Dicorynia guianensis (Dg), Sextonia rubra (Sr), Symphonia globulifera (Sg) and Vouacapoua americana (Va). The four species include the three most important timber species in French Guiana (Dg, Va, Sr) and Sg as a model for a species with low logging pressure.

2. Materials and methods

2.1. Study area

The data used for simulations were collected at the “Paracou” experimental site located in French Guiana near Sinnamary (5°18’N, 52°53’W). The forest of Paracou is classified as lowland moist forest on ferrallitic soil. Between 1979 and 2001 the mean annual rainfall in this area was 3041 mm, with peaks in April–June and December (Gourlet-Fleury et al., 2004c). There are two dry seasons: a long one from August to November and a shorter one in March. The experimental trial consisted of 16 plots: 15 were 6.25 ha in size and one covered an area of 25 ha. Since 1984, all trees with a diameter at breast height ≥10 cm have been measured by the Forestry Department of CIRAD. The trees have been mapped and most species have been identified. The tree species diversity is high as for most tropical forests. Between 140 and 200 different tree species are found per ha in Paracou (Blanc et al., 2003). As typical for the Guiana Shield most species belong to the families Leguminosae, Lecythidaceae, Chrysobalanaceae, Sapotaceae and Burseraceae (Steeg e et al., 2000).

Three silvicultural treatments of different intensities were applied to different plots from 1986 to 1988 but some were left as unlogged controls. During the last 10 years genetic data have been collected for the four study species (Caron et al., 1998; Degen et al., 2004, 2001; Dutech et al., 2002; Latouche-Halle et al., 2003, 2004; Veron et al., 2005).

2.2. Species

2.2.1. Dicorynia guianensis (Dg)

Dicorynia guianensis (Fabaceae) is a canopy tree endemic to the Guiana tropical moist forest (Sabatier and Prévost, 1990). It is...
Sextonia rubra (Lauraceae) is a hermaphrodite species that exhibits variation in outcrossing rates among trees (Caron et al., 1998). The species has single, white, bisexual flowers and the floral syndrome suggests pollination by large bees. The population flowers synchronously every 2 or 3 years from November to January. Flowering intensity, and consequently seed production, is extremely heterogeneous among adult trees within a stand. D. guianensis is the most harvested species in French Guiana.

2.2.2. Sextonia rubra (Sr)
Sextonia rubra (Lauraceae) is a hermaphrodite species that produces small, scented white flowers in August and September in French Guiana. Although the actual pollinators of Sr are unknown, the flower attributes suggest that pollination is mediated by small diverse insects (Bawa et al., 1985). Flowers were produced on most large individuals in the population in 2002 (Cloutier and Hardy, unpublished data). The fruits of Sr contain a single seed and are produced in January in French Guiana. It has been reported that the seed can be dispersed by birds (Sabatier, 1983). A genetic structure study of the adult trees at Paracou has not revealed any spatial structure, suggesting that the seed have the potential to be dispersed over large distances (Vekemans and Hardy, 2004). Sr is a canopy tree species that reaches at least 1.50 m dbh at Paracou and 40 m height. The estimated multilocus outcrossing rate, tm, was 0.992 indicating nearly complete outcrossing (Veron et al., 2005). Veron et al. (2005) observed mean pollen dispersal distances between 65 and 89 m and the density of reproductive trees was 2.1–2.2 trees/ha. It is the third most harvested timber tree species in French Guiana.

2.2.3. Symphonia globulifera (Sg)
This hermaphroditic species has an exceptionally large geographic distribution from Mexico to Rio de Janeiro and it is present also in tropical West Africa. The density of Symphonia globulifera is extremely variable among populations. For trees with dbh > 10 cm, densities of 122/ha (Quakal swamp forest) and 65/ha (Manicole swamp forest) have been reported in Guiana (Andel, 2003). At the other extreme the population of Sg on Barro Colorado Island (Panama) has a density of only 0.5 trees/ha (Center for Tropical Forest Sciences, 2000 forest census). There are also contrasting reports for the community of pollinators of Sg at different locations. In Costa Rica, Pasquarella (1992) observed Lepidoptera as the most important pollinators, in central French Guiana, Gill et al. (1998) identified perching birds as the principal pollinators, whereas others suggested hummingbirds as the pollinators in the Central Amazon (Bittrich and Amaral, 1996; Machuel, 2001). The species displays high outcrossing rates (t = 0.8–0.95). Estimations of pollen dispersal (Degen et al., 2004) suggest very short distribution distances for successful pollen (mean 27–53 m). In our simulation study Symphonia globulifera serves as a model for an abundant species that is only occasionally logged in French Guiana (low logging pressure).

2.2.4. Vouacapoua americana (Va)
Vouacapoua americana (Caesalpinioideae) is a hermaphroditic tree species of mature tropical rainforests with a distribution that spans the eastern part of the Guiana shield. Its local density averages around 10 individuals/ha, but there is large variation, due to spatial clustering (Forget et al., 1996). Individuals are clustered in large patches of several hectares that are mainly located on the tops and slopes of hills (Traissac, 1998). Lowlands are mainly associated with hydromorphic soils in which seedling recruitment (Forget, 1994) and probably adult growth are inhibited. Flowering occurs from February to March with important variation in flowering rate among years (Forget, 1990). The minimum observed dbh of flowering trees was 19 cm in Paracou. The floral syndrome (small, yellow and fragrant flowers) suggests that individuals are pollinated by small bees and thrips. Self-fertilization occurs at low rates. From April to June, mature pods, generally containing one large seed (mean weight around 30 g), fall under the maternal trees. A proportion of seeds is dispersed, mainly by two rodent species (Dasypus leporina and Myoprocta exilis), which bury seeds usually less than 10 m from their source, but occasionally up to 30 m (Forget, 1990). The occurrence of isolated seedlings suggests that seeds may sometimes be dispersed to greater distances. Buried seeds have higher survival rates than unburied ones. The recruitment of seedlings may occur under large trees, since Va is shade-tolerant (Forget, 1997), but seems to be strongly limited by high adult densities of conspecifics (Joly, 1996). Small canopy gaps enhance the survival and growth of seedlings. Va is the second most harvested species in French Guiana.

2.3. Model
We used the simulation model Eco-Gene to evaluate disturbance and human influence on the demography and genetics of tree populations. The model simulates the temporal and spatial dynamics of allele and genotype frequencies, tree growth, and demographic processes (Degen et al., 1996; Degen and Roubik, 2004). At the beginning of the simulation, the model gets initiated by reading the input data and by setting the parameters (Table 1). The dynamics of a tree species population was simulated over 215 and 460 years. Each simulated year included the steps “tree growth”, “logging” if appropriate, “reproduction” if appropriate, and “mortality” (Fig. 1). Each step will be explained below.

2.3.1. Data sets
The spatial position, diameter and genotype of each tree from a 100 ha stand served as input for each run (Fig. 2). This size is close to the smallest management units in many tropical countries and is large enough to be considered the area of a biological population. Despite intensive demographic and genetic studies at Paracou, we have an incomplete genetic inventory of all trees, especially of smaller trees. Thus, we generated for each species an artificial data set with a
population of 100 ha (1000 m × 1000 m). The generated data set has the demographic structure (densities in diameter classes), spatial structure of trees (aggregation index R) and the genetic structure (frequencies of alleles, fixation index) as observed in Paracou (Fig. 3). For D. guianensis the genetic structure corresponds to the observation of Latouche-Halle et al. (2004) for five nuclear microsatellites. For Sextonia rubra data of six nuclear microsatellites (Veron et al., 2005) form the basis, for Symphonia globulifera we used data on seven microsatellites studied in the population in Paracou (Degen et al., 2004; Vinson et al., 2005) and for V. americana we used data of 10 microsatellites (Dutech et al., 2000).

In most cases the genotypes are not randomly distributed in natural tree stands (Degen et al., 2001, 2004). Due to limited pollen and seed dispersal, family structures are created that might make the tree population more sensitive to the negative impacts of logging (higher risk for inbreeding). Thus, it was important that our artificially generated stands showed a spatial structure that is close to real observed spatial structure.

In order to get the generated data closer to the measured spatial genetic structures, simulations were run for 1000 years with the species specific parameters on pollen and seed dispersal. Then the data sets were saved as the final input data sets for the simulations (Fig. 2). A comparison between the spatial genetic structure in the generated data sets and the results obtained from real samples taken from Paracou show the strong spatial genetic structure for both real and generated structure of D. guianensis and V. americana, whereas Symphonia globulifera had a generally weak spatial genetic structure (Fig. 3). Observed and generated data for Sextonia rubra showed a random spatial genetic structure.

### Table 1 – Parameters in the scenarios of the four species: Dicorynia guianensis (Dg), Sextonia rubra (Sr), Symphonia globulifera (Sg) and Vouacapoua americana (Va)

<table>
<thead>
<tr>
<th>No.</th>
<th>Parameter</th>
<th>Dg</th>
<th>Sr</th>
<th>Sg</th>
<th>Va</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Growth</strong></td>
<td>Mean growth rate (cm/year)</td>
<td>0.23</td>
<td>0.16</td>
<td>0.36</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>Standard deviation growth rate (cm/year)</td>
<td>0.14</td>
<td>0.18</td>
<td>0.23</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Temporal autocorrelation growth</td>
<td>0.39</td>
<td>0.46</td>
<td>0.53</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>Maximum diameter at the 95% (cm)</td>
<td>80</td>
<td>90</td>
<td>70</td>
<td>70</td>
</tr>
<tr>
<td><strong>Demography</strong></td>
<td>Density diameter class 0–10 cm (N/ha)</td>
<td>5.30</td>
<td>5.30</td>
<td>5.30</td>
<td>5.30</td>
</tr>
<tr>
<td></td>
<td>Density diameter class 10–20 cm (N/ha)</td>
<td>2.27</td>
<td>0.75</td>
<td>3.71</td>
<td>2.69</td>
</tr>
<tr>
<td></td>
<td>Density diameter class 20–30 cm (N/ha)</td>
<td>1.09</td>
<td>0.40</td>
<td>2.75</td>
<td>2.45</td>
</tr>
<tr>
<td></td>
<td>Density diameter class 30–40 cm (N/ha)</td>
<td>0.75</td>
<td>0.24</td>
<td>0.72</td>
<td>2.24</td>
</tr>
<tr>
<td></td>
<td>Density diameter class 40–50 cm (N/ha)</td>
<td>0.80</td>
<td>0.21</td>
<td>0.35</td>
<td>1.41</td>
</tr>
<tr>
<td></td>
<td>Density diameter class 50–60 cm (N/ha)</td>
<td>0.51</td>
<td>0.13</td>
<td>0.16</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>Density diameter class 60–70 cm (N/ha)</td>
<td>0.32</td>
<td>0.19</td>
<td>0.13</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>Density diameter class 70–100 cm (N/ha)</td>
<td>0.11</td>
<td>0.35</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Phenology</strong></td>
<td>Percentage of flowering adults – minimum</td>
<td>15</td>
<td>25</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Percentage of flowering adults – maximum</td>
<td>75</td>
<td>70</td>
<td>70</td>
<td>70</td>
</tr>
<tr>
<td></td>
<td>Minimum diameter of flowering trees (cm)</td>
<td>18.3</td>
<td>30</td>
<td>18</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Flowering rhythm (Years/years)</td>
<td>2/3</td>
<td>1/1</td>
<td>1/1</td>
<td>1/1</td>
</tr>
<tr>
<td><strong>Pollination</strong></td>
<td>Self-incompatibility – minimum</td>
<td>0.95</td>
<td>0.8</td>
<td>0.8</td>
<td>0.95</td>
</tr>
<tr>
<td></td>
<td>Self-incompatibility – maximum</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td>Flight distance pollinator – maximum (m)</td>
<td>700</td>
<td>500</td>
<td>150</td>
<td>500</td>
</tr>
<tr>
<td></td>
<td>Distance of random pollination (m)</td>
<td>70</td>
<td>50</td>
<td>30</td>
<td>50</td>
</tr>
<tr>
<td><strong>Seed dispersal</strong></td>
<td>Proportion wind dispersal</td>
<td>1</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Exponent for wind dispersal</td>
<td>5</td>
<td>–</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Proportion dispersal by small birds or bats</td>
<td>0</td>
<td>1</td>
<td>0.4</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Distance random seed dispersal (m)</td>
<td>–</td>
<td>450</td>
<td>350</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Proportion of dispersal by large bats (roosts)</td>
<td>0</td>
<td>0</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Maximum flight distance to roosts (m)</td>
<td>–</td>
<td>–</td>
<td>1000</td>
<td>–</td>
</tr>
</tbody>
</table>
events than smaller trees. The estimates of these parameters were based on a few hundred observations for each species in Paracou. Thus, they should be very precise for the region of Paracou. The main differences among the four species are the high mean growth rate of $S_g$, the extreme slow growth of $V_a$ (Table 1, parameter 1 = P1), the weak temporal autocorrelation of $V_a$ (P3) and the large maximum diameter of $S_r$ (P4).

2.3.3. Logging

So-called “selective logging” is the legal logging system in French Guiana and in Brazil. Here, clear cuts are avoided and the logging is concentrated on a limited number of commercial timber species (French Guiana <10 species, Brazil <50 in each region). In Brazil the logging companies are obliged to make a pre-inventory surveys that results in a map with diameter and position of all bigger commercial trees (Kanashiro et al., 2002). Then the company proposes a forest management plan that has to be approved by the environmental agency (IBAMA) before the logging can start. In French Guiana the pre-inventories are done by the French National Forest Service (Brunaux and Demenois, 2003).

To simulate the applied logging system we included in the model the: “Rotation of treatments” (logging cycles in years), the first and last year of treatment, the minimum dbh of extracted trees (cutting diameter) and the proportion of remaining trees with a dbh greater than the cutting diameter (voluntarily left seed trees, hollow trees, etc.). Another set of parameters characterised the post-logging mortality. For each species and for three different diameter classes, specific diameter limits and mortalities were estimated from data at hand. In the simulations we assumed a post-logging mortality between 10% and 20% (Table 2). This fits with the scale of observed mortality values directly linked to logging events at Paracou (Gourlet-Fleury et al., 2004b).

2.3.4. Reproduction

The simulated reproduction includes parameters controlling the flowering phenology, differences in male and female fertilities of the trees, pollen and seed dispersal.

2.3.5. Phenology – population level

Following a framework given by Newstrom et al. (1994) we defined three types of flowering patterns: (1) the population flowers once every year; (2) the population flowers in regular cycles once every X years with a standard deviation of Y years; and (3) the population flowers in an unpredictable way with X flowering events in a period of Y years. Observations in Paracou

Fig. 1 – Flow chart of the different steps and integrated processes of the simulations.
showed that Sr, Sg and Va flower once every year (Table 1, P16), whereas Dg has a more irregular flowering with on average two flowering years among three years (Caron et al., 1998).

The proportion of plants flowering was estimated from a rectangular distribution with the minimum value of X and a maximum value of Y. Within a rectangular distribution each value between minimum and maximum has the same probability to occur. Trees need to have a certain diameter to be fertile. This is controlled by two parameters, a mean and a standard deviation describing a normal distribution for the minimum diameter of flowering trees. We observed for Dg a higher variation of percentage of flowering adults (15–75%, Table 1, P16) and for Sr a larger size of reproductive trees (P15).

2.3.6. Phenology – individual level
These parameters define for each flowering individual: (a) the beginning and duration of the female and male flowering phase; (b) whether there is an identical female and male flowering period as for hermaphroditic plants; (c) if there are correlations in timing for female and male flowering for non-hermaphroditic plants; and (d) if there is a correlation in the order of flowering among years. All these parameters define the overlap in flowering within the female and male flowering phase within each individual and among different individuals of a population. All four species are hermaphroditic. Thus, we used identical periods of male and female flowering for each tree. The variation of flowering between trees of the same population was determined by variation in starting dates and duration of flowering, both sampled from normal distributions. These parameters were assumed to be the same for all species (duration of individual flowering: mean = 10 days, SD = 2 days; starting day of flowering: mean = day 0; SD = 4). This parameter configuration leads to an overall flowering period of 50 days which can be found for many tropical tree species (Bawa et al., 2003).

2.3.7. Fertilities and seeds
We simulated seed production, taking into account the variation in male and female fertility among trees. Trees with higher female or male fertility (higher number of ovules or pollen grains produced) have a proportionally higher probability of contributing their ovules or pollen grains to the sampled seeds. Each flowering tree was assigned a relative value for its ovule and pollen production proportional to its diameter. These values were estimated from normal distributions for which the user needs to define means and standard deviations. For hermaphroditic tree species we would expect equal

Fig. 2 – Spatial genetic structure of the generated data sets for Dicorynia guianensis at locus Am29, for Sextonia rubra at locus Sr3, Symphonia globulifera at locus Sg06 and Vouacapoua americana at locus Wa14. Each circle represent a tree, the colours show the alleles, the radius of the circles is proportional to the diameter of the trees. Heterozygous trees have two circles with different colours.
female and male fertility within an individual tree. Variation in fertilities between individuals of each population was simulated based on a normal distribution with a standard deviation of 40% of the mean (Kang et al., 2003).

2.3.8. Pollen dispersal by animals

All four tree species are pollinated by animals. We simulated the number of foraging flights that lead to pollination (pollen deposition or dispersal to stigmatic surfaces, but not necessarily fertilization) until a pre-defined number of seeds have been produced (Degen and Roubik, 2004). The required number of seeds is calculated according to the number of individuals in the first diameter class. Twice as much as observed in the first diameter class were simulated. The pollen donor (male tree) is the tree where the pollinator receives pollen and the seed tree (maternal tree) is the tree where the pollen grain has been deposited on a stigma. A pollen grain that, together with the ovule, creates a zygote is called a “successful” pollen grain. For hermaphroditic or monoecious tree species the paternal and maternal tree might be the same (defined as within-plant or within-inflorescence selfing). To find the two parents of a seed, the model simulates the movement of the pollinator in two series of foraging flights; a first series from the starting point (nest and hive) to the tree of pollen receipt and a second series from the tree of pollen receipt to the tree where the pollen is deposited on a stigma. Only trees that have the same flowering period as the first tree visited can be candidates for both pollen donor and seed tree, and flights that do not result in inter-tree pollen dispersal may be eliminated according to the level of self-incompatibility. Because of the need for flowering overlap between individuals, samples represent the whole flowering period. Differences in pollination among the species were implemented by parameters controlling the level of self-incompatibility (Table 1, P17–P18).

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**Table 2 – Parameter configuration for two control scenarios without logging (C1 and C2) and two scenarios with different logging intensities (L1 and L2)**

<table>
<thead>
<tr>
<th></th>
<th>C1</th>
<th>L1</th>
<th>C2</th>
<th>L2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration (years)</td>
<td>460</td>
<td>460</td>
<td>215</td>
<td>215</td>
</tr>
<tr>
<td>Cutting diameter (cm)</td>
<td>60 (50)*</td>
<td>65</td>
<td>45</td>
<td>30</td>
</tr>
<tr>
<td>Cutting cycles (years)</td>
<td>65</td>
<td>30</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>First year of cut</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Number of cutting cycles</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Post-logging mortality 0–10 cm dbh</td>
<td>0.20</td>
<td>0.20</td>
<td>0.20</td>
<td>0.20</td>
</tr>
<tr>
<td>Post-logging mortality 10–20 cm dbh</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>Post-logging mortality 20–45 cm dbh</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td>Post-logging mortality 20–60 cm dbh</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td>Proportion of remaining trees above cutting diameter</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
</tr>
</tbody>
</table>

* The cutting diameter for Symphonia globulifera is 50 cm.

---

Fig. 3 – Spatial genetic structure measured with the Moran’s Index at nuclear microsatellites of real samples from Paracou (Dicorynia guianensis = Dg Real, Symphonia globulifera = Sg Real, Vouacapoua americana = Va Real) and spatial genetic structure in the generated data sets (Dicorynia guianensis = Dg Gen, Symphonia globulifera = Sg Gen, Vouacapoua americana = Va Gen).
and flight distances of the pollinator (P17–P20). In accordance with experimental data we set higher self-incompatibility for Dg and Va and shorter pollination distances for Sg (Degen et al., 2004; Dutech et al., 2000; Latouche-Halle et al., 2004; Veron et al., 2005).

2.3.9. Seed dispersal
The seed dispersal of Dg and Va was simulated by a negative exponential function as typical for seeds dispersed by wind and gravity (Levin and Kerster, 1974). Here, a parameter representing the exponent of the function controls the distances of seed dispersal (Table 1, P21). Due to larger seed/fruit size the dispersal is more restricted for Dg (Latouche-Halle et al., 2004). The seed dispersal of Sg was simulated by a combination of different distribution functions, with 10% of the seed dispersal following a negative exponential function. All seeds of Sr and 40% of the seeds of Sg were simulated by a random distribution with a pre-defined range around the seed trees (450 m for Sr and 350 m for Sg) for seeds distributed by small birds (Sr) and bats (Sg) that defecate seeds during flights (P23 and P24). For 50% of the seeds of Sg an aggregate distribution function to focal points representing roosts for bats up to 1000 m away from the seed trees (Bernard and Fenton, 2003) were simulated (P25 and P26).

2.3.10. Mortality
The number of trees/ha of each diameter class (N/ha = target value), and the upper and lower limit diameter in centimetres for each class were measured in unlogged plots for each species in Paracou. The population was considered to be at equilibrium in these unlogged plots for the diameter classes of each tree species. Thus, the observed diameter frequency distribution in unlogged forests was considered the absolute “target”. If there is sufficient reproduction the population will return to this diameter distribution. We calculated the probabilities of mortality from the ratio of actual densities and target density. We modified these probabilities according to the position of the tree in a diameter class, giving a higher probability of death to trees closer to the lower limit of the diameter class. The main reason for this simplicity of the model was the objective to create a model that can be applied also for cases with poor or no data on long-term time series of mortality and growth development.

The expected basal area (carrying capacity) was calculated using the target values for the densities in all diameter classes. To apply density dependent mortalities, we subdivided the population area into grid cells and applied the expected basal area to each cell. Thus, areas with a higher basal area than expected had higher mortality rates, whereas areas that did not reach the expected basal area had lower mortality rates. Whereas the diameter distribution of Dg, Sg, and Va followed approximately an geometric series, we found an clear L-shape distributions of the densities in diameter classes for Sextonia rubra (Table 1, P5–P12).

Due to a lack of field data, some of the ecological parameters were set equal across the species. Thus, the density of saplings in the diameter class 0–10 cm (P5) is set to 5.3 for all species. This is probably an underestimation for Dg and Sg but higher values severely reduced the simulation speed and had no strong influence on simulation results.

2.4. Scenarios
2.4.1. Impact of logging
For each species two control scenarios without logging (C1 and C2) and two scenarios with logging representing the moderate logging system in French Guiana (L1) and the much more intensive logging practice in the Brazilian Amazon (L2) were run (Table 2). The applied logging scenarios used in French Guiana have much longer cutting cycles and higher cutting diameters compared to those in Brazil. In both logging scenarios we applied seven cutting cycles but changed the number of simulated years. The comparison of the two control and logging scenarios allowed the effect of pure genetic drift (C1 versus C2) and the additional effect of different logging systems (L1 versus L2) to be distinguished.

The simulations were repeated 50 times in order to estimate the stochastic variation of results for the same parameter configuration.

The following parameters were calculated for each simulation as output: N = number of individuals, BA = basal area in m², A = mean number of alleles, A_e = mean effective number of alleles, Ha = mean observed heterozygosity, F = mean fixation index, Dis = genetic distance between the initial population and the population at the end of the simulations, NG = number of single locus genotypes at all loci.

2.4.2. Sensitivity analysis
Sensitivity analysis is used to assess the relationship between variation in input and variation in output (predicted) values. The parameters that have the greatest influence are termed the sensitive parameters in the model. The objectives of the sensitivity analysis were (a) to identify those parameters of the model that have the strongest impact on negative effects after logging, and (b) to identify the most sensitive genetic and demographical output parameters to monitor the impact of logging. Eco-Gene allows up to 13 different parameters to be included in a sensitivity analysis. For each parameter a range is defined and within a series of 1000 simulations random samples of parameter values within the interval are taken. So each of these 1000 simulations represents a new combination of 13 tested and randomly chosen parameters. At the end of each simulation seven output parameters were computed for the population including all trees at year 215: mean number of alleles (A), effective number of alleles (A_e), number of genotypes (NG), fixation index (F), genetic distance to origin (Dis), basal area (BA) and number individuals (N). Because we could not exclude the possibility of non-linear relationships between input parameters and response variables, all values were rank-transformed. This technique is useful when the relationship between the response and input variables is non-linear but monotonic. Finally, the sensitivity of the response parameters to the variation of input parameters was tested with a stepwise multiple regression analysis using rank-transformed values (Nathan et al., 2001).

We carried out initial sensitivity analyses and grouped those parameters that were most sensitive (Table 3). We did the final sensitivity analysis with the data sets for Dicorynia and Vouacapoua in order to check also the impact of different input data sets.
3. Results

3.1. Impact of logging

3.1.1. Moderate logging (L1)

At the end of the rotation period of 65 years *Sextonia rubra* and *V. americana* still had a reduced basal area (BA) and the total number of trees (N) was also below the control value for *V. americana* (Table 4, Fig. 4). The other two species recovered completely.

We would assume that the species are differently sensitive toward logging according to their initial level of genetic diversity. Species with higher levels of genetic diversity might lose higher proportions of this diversity. At the beginning of the simulations the genetic variation for each species (A, A<sub>e</sub>, Ha) was exactly as it was estimated in genetic inventories in Para-cou. The highest values were found for Sg and Sr whereas the values for Va and Dg were substantially smaller. Number of alleles was three times higher for Sg than for Va. These a priori differences make species with high genetic variation such as Sg more vulnerable to changes by genetic drift. At the end of the simulations the values for the genetic distance between the initial genetic composition and the genetic structure at the end were in all four scenarios of Sg higher than the other species (Table 4). All species had a slight excess of homozygotes (positive F-values) indicating the impact of inbreeding.

Generally only small differences between logging and control scenarios were observed. For all four species the genetic distance (Dis) between the genetic composition of the original population and the population at the end of the simulations was higher in the logging scenarios (L1 and L2) compared to the controls (L1 versus C1). The number of genotypes (NG)

Table 4 – Means and standard deviations of demographic and genetic parameters for the species *Dicorynia guianensis* (*Dg*), *Symphonia globulifera* (*Sg*), *Sextonia rubra* (*Sr*), and *Vouacapoua americana* (*Va*) after 460 simulated years in scenarios without logging (*C1*) and with logging (*L1*) and 215 years (*C2* and *L2*)

<table>
<thead>
<tr>
<th>No.</th>
<th>Parameter</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>DgC1</td>
<td>Cutting diameter (cm)</td>
<td>6.58 ± 0.11</td>
<td>2.32 ± 0.05</td>
</tr>
<tr>
<td>DgC2</td>
<td>Cutting diameter (cm)</td>
<td>6.66 ± 0.12</td>
<td>2.33 ± 0.04</td>
</tr>
<tr>
<td>DgL1</td>
<td>Cutting diameter (cm)</td>
<td>6.44 ± 0.12</td>
<td>2.37 ± 0.06</td>
</tr>
<tr>
<td>SgC1</td>
<td>Cutting diameter (cm)</td>
<td>12.9 ± 0.28</td>
<td>6.02 ± 0.23</td>
</tr>
<tr>
<td>SgC2</td>
<td>Cutting diameter (cm)</td>
<td>13.2 ± 0.18</td>
<td>6.14 ± 0.20</td>
</tr>
<tr>
<td>SgL1</td>
<td>Cutting diameter (cm)</td>
<td>12.8 ± 0.20</td>
<td>5.98 ± 0.27</td>
</tr>
<tr>
<td>SgL2</td>
<td>Cutting diameter (cm)</td>
<td>13.1 ± 0.17</td>
<td>6.05 ± 0.19</td>
</tr>
<tr>
<td>SrC1</td>
<td>Cutting diameter (cm)</td>
<td>7.15 ± 0.27</td>
<td>3.97 ± 0.18</td>
</tr>
<tr>
<td>SrC2</td>
<td>Cutting diameter (cm)</td>
<td>7.48 ± 0.18</td>
<td>4.01 ± 0.19</td>
</tr>
<tr>
<td>SrL1</td>
<td>Cutting diameter (cm)</td>
<td>7.17 ± 0.21</td>
<td>3.89 ± 0.27</td>
</tr>
<tr>
<td>SrL2</td>
<td>Cutting diameter (cm)</td>
<td>7.35 ± 0.21</td>
<td>4.05 ± 0.29</td>
</tr>
<tr>
<td>VaC1</td>
<td>Cutting diameter (cm)</td>
<td>6.94 ± 0.07</td>
<td>2.00 ± 0.01</td>
</tr>
<tr>
<td>VaC2</td>
<td>Cutting diameter (cm)</td>
<td>6.98 ± 0.03</td>
<td>2.00 ± 0.01</td>
</tr>
<tr>
<td>VaL1</td>
<td>Cutting diameter (cm)</td>
<td>6.87 ± 0.10</td>
<td>2.00 ± 0.02</td>
</tr>
<tr>
<td>VaL2</td>
<td>Cutting diameter (cm)</td>
<td>6.82 ± 0.11</td>
<td>2.00 ± 0.02</td>
</tr>
</tbody>
</table>
were reduced in all logging scenarios. The number of alleles \((A)\) were less except for Sextonia rubra. No clear trends were observed for the effective number of alleles \((A_e)\), heterozygosity \((H_a)\) and the fixation indices \((F)\). Surprisingly the fixation index \((F)\) for Sextonia rubra was much higher in the control scenario (0.11) compared to the logging scenario (0.058).

3.1.2. Intensive logging \((L2)\)

Dg, Sr and Va showed a significant decrease in the number of individuals and basal area at year 215 in the logging scenarios L2 (Table 4). This implies that even 30 years after the last cut (year 185) the species had not sufficiently recovered. Sg had a higher number of individuals and the same basal area at the end of the logging scenario. Thus, logging did change the diameter distribution towards smaller trees, but the total stock recuperated each time on a 30 year logging rotation.

A closer look at the temporal dynamics of the basal area (Fig. 4) showed that 30 years is a too short cutting cycle for all species except Sg. V. americana demonstrated the strongest negative impact, the basal area never recovered within 30 years and the final level of the stock decreased after each rotation period.

The genetic parameters did not differ strongly between the control \((C2)\) and the logging \((L2)\). The most striking results were the increased genetic distance \((D\text{is})\) after logging for Sextonia rubra and V. americana and the reduced number of genotypes for V. americana after logging (Table 4).

The comparison of the genetic distances between the two control \((C1 \text{ versus } C2)\) and the two logging scenarios \((L1 \text{ versus } L2)\) showed that for each species the effect of genetic drift due to the higher number of simulated years is larger than the effect of stronger logging.

3.2. Sensitivity analysis

3.2.1. Sensitivity of output parameters

At the end of the stepwise regression analysis all significant parameters of the model were put together in a function to explain the variation of a given output parameter. We computed the \(R^2\) values at this final step to see which output parameter could be explained best by the model (Table 5).

![Fig. 4 – Examples for the dynamics of the total basal area in the two control and two logging scenarios of the four species during 215 years and 460 years of simulation.](image-url)
The number of genotypes (NG) was largely determined by the number of alleles, while the genetic distance (Dis) were most sensitive whereas the number of genotypes (NG) and the genetic differentiation were rather insensitive in both cases. The highest number of significant input parameters (8 for Dg and 10 for Va) was found for the fixation index (F). The parameter “percentage of flowering adults” had the strongest positive correlation with the fixation index (F) for both data sets. Thus, higher percentages of flowering trees increased the excess of homozygotes. Besides this unexpected result, parameters controlling the pollen dispersal were on second and third rank position. As expected, longer and more random pollen dispersal reduced the fixation index (negative correlation). In lower ranked positions, mean growth rates and densities in different diameter classes were positively correlated with the fixation index.

### 3.2.2. Sensitivity of input parameters

The number of genotypes (NG) was largely determined by growth and demographic parameters as well as the cutting diameter (Table 6). For Dicorynia pollination parameters also had a minor impact. The densities in different diameter classes and the cutting diameter were positively correlated with the number of genotypes for both data sets. Mean growth rate and number of genotypes (NG) were positively correlated for Dg, but negatively correlated for Va. More limited seed dispersal and stronger attraction of the pollinators were slightly but positively correlated with higher genetic distances in the data set Dg.

The highest number of significant input parameters (8 for Dg and 10 for Va) was found for the fixation index (F). The parameter “percentage of flowering adults” had the strongest positive correlation with the fixation index (F) for both data sets. Thus, higher percentages of flowering trees increased the excess of homozygotes. Besides this unexpected result, parameters controlling the pollen dispersal were on second and third rank position. As expected, longer and more random pollen dispersal reduced the fixation index (negative correlation). In lower ranked positions, mean growth rates and densities in different diameter classes were positively correlated with the fixation index.

### Table 6 – Results of the sensitivity analysis

<table>
<thead>
<tr>
<th>Number of genotypes (NG)</th>
<th>Data set Dicorynia guianensis</th>
<th></th>
<th></th>
<th>Data set Vouacapoua americana</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Step</td>
<td>Parameter</td>
<td>β</td>
<td>R²</td>
<td>Parameter</td>
<td>β</td>
<td>R²</td>
</tr>
<tr>
<td>1</td>
<td>Density diameter class 30–40 cm</td>
<td>0.231</td>
<td>0.054</td>
<td>Density diameter class 20–30 cm</td>
<td>0.331</td>
<td>0.107</td>
</tr>
<tr>
<td>2</td>
<td>Cutting diameter</td>
<td>0.126</td>
<td>0.068</td>
<td>Cutting diameter</td>
<td>0.263</td>
<td>0.180</td>
</tr>
<tr>
<td>3</td>
<td>Mean growth rate</td>
<td>0.094</td>
<td>0.078</td>
<td>Mean growth rate</td>
<td>-0.210</td>
<td>0.225</td>
</tr>
<tr>
<td>4</td>
<td>Density diameter class 20–30 cm</td>
<td>0.091</td>
<td>0.086</td>
<td>Density diameter class 30–40 cm</td>
<td>0.192</td>
<td>0.262</td>
</tr>
<tr>
<td>5</td>
<td>Maximum flight distance pollinator</td>
<td>0.079</td>
<td>0.092</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Attractor effect for pollinator</td>
<td>0.077</td>
<td>0.098</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Genetic distance (Dis)</th>
<th>Data set Dicorynia guianensis</th>
<th></th>
<th></th>
<th>Data set Vouacapoua americana</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Step</td>
<td>Parameter</td>
<td>β</td>
<td>R²</td>
<td>Parameter</td>
<td>β</td>
<td>R²</td>
</tr>
<tr>
<td>1</td>
<td>Density diameter class 30–40 cm</td>
<td>-0.204</td>
<td>0.047</td>
<td>Mean growth rate</td>
<td>0.393</td>
<td>0.144</td>
</tr>
<tr>
<td>2</td>
<td>Cutting diameter</td>
<td>-0.169</td>
<td>0.079</td>
<td>Cutting diameter</td>
<td>-0.288</td>
<td>0.240</td>
</tr>
<tr>
<td>3</td>
<td>Temporal autocorrelation growth</td>
<td>0.139</td>
<td>0.099</td>
<td>Density diameter class 30–40 cm</td>
<td>-0.264</td>
<td>0.317</td>
</tr>
<tr>
<td>4</td>
<td>Density diameter class 20–30 cm</td>
<td>-0.113</td>
<td>0.112</td>
<td>Density diameter class 10–20 cm</td>
<td>-0.208</td>
<td>0.357</td>
</tr>
<tr>
<td>5</td>
<td>Exponent for seed dispersal</td>
<td>0.076</td>
<td>0.117</td>
<td>Density diameter class 20–30 cm</td>
<td>-0.109</td>
<td>0.369</td>
</tr>
<tr>
<td>6</td>
<td>Attractor effect for pollinator</td>
<td>-0.061</td>
<td>0.121</td>
<td>Proportion remaining trees</td>
<td>-0.055</td>
<td>0.372</td>
</tr>
</tbody>
</table>

Stepwise multiple regression of number of genotypes (NG) and genetic distance (Dis) against the main input parameters (Table 1) using the two tree data sets Dicorynia guianensis and Vouacapoua americana. R² is the fraction of the variance accounted for by the model, adjusted for the number of independent variables; β is the standardized regression coefficient (all significant).

The results on the sensitivity of output parameters were very similar for both input data sets (correlation coefficient between the R²: r = 0.938). The highest R² values were found for the demographic parameters (BA, N) and the fixation index (F). The tested parameters of the model accounted for 37.8–91.4% of the variation in the dependent variables. Among the output parameters for genetic variation and genetic differentiation the number of genotypes (NG) and the genetic distance (Dis) were most sensitive whereas the number of alleles (A) was only sensitive for Va and the effective number of alleles (Ae) was rather insensitive in both cases. Thus, we excluded the last two parameters for a more detailed analysis.

### 3.2.2. Sensitivity of input parameters

The number of genotypes (NG) was largely determined by growth and demographic parameters as well as the cutting diameter (Table 6). For Dicorynia pollination parameters also had a minor impact. The densities in different diameter classes and the cutting diameter were positively correlated with the number of genotypes for both data sets. Mean growth rate and number of genotypes (NG) were positively correlated for Dg, but negatively correlated for Va. More limited seed dispersal and stronger attraction of the pollinators were slightly but positively correlated with higher genetic distances in the data set Dg.

The highest number of significant input parameters (8 for Dg and 10 for Va) was found for the fixation index (F). The parameter “percentage of flowering adults” had the strongest positive correlation with the fixation index (F) for both data sets. Thus, higher percentages of flowering trees increased the excess of homozygotes. Besides this unexpected result, parameters controlling the pollen dispersal were on second and third rank position. As expected, longer and more random pollen dispersal reduced the fixation index (negative correlation). In lower ranked positions, mean growth rates and densities in different diameter classes were positively correlated with the fixation index.

The results of the sensitivity analysis were very similar between the two data sets for the basal area (BA). The parameter “cutting diameter” had the strongest correlation with the basal area (BA) for both data sets. In both cases the “density diameter class 30–40” was ranked second. In subsequent rankings were growth parameters, the proportion of remaining trees after logging and densities in smaller diameter classes.

### 4. Discussion

#### 4.1. Comparison with results of other models

During the last 10 years, various types of population dynamics models have been built using data from the Paracou site (Picard et al., 2004). A single-tree distance dependent model (Selva) was recently completed to explore the spatio-temporal
behaviour of D. guianensis populations on the Paracou site, and to simulate the impact of logging on the structure and demography of the species (Gourlet-Fleury et al., 2004a). Results from this Selva model were compared to those from a stochastic matrix model (StoMat software), calibrated using another data set from Paracou, and proved to be completely consistent in terms of the development of tree numbers and diameter structure (Gourlet-Fleury et al., 2005). For a logging scenario using a cutting cycle of 42 years and a cutting diameter of 60 cm dbh, both models indicated a rapid decrease of the population in terms of the number of trees >10 cm dbh (50% of the population lost within 200 years) and, for the exploitable stock (trees >60 cm dbh), a stabilisation around 60% of the initial value until 160 years, then a clear decrease. StoMat was also calibrated for Sextonia rubra (Gourlet-Fleury et al., 2004a). We used this software to simulate the dynamics of both D. guianensis and Sextonia rubra according to the strong logging scenario (L2) tested in this article (starting from the same diameter structure, and with the same damage levels): for both species, conclusions on the demographic development were more pessimistic than those produced by EcoGene. For Dg, no more than 14% of the initial tree number would be left at the end of the seven 30 years cycles, and it would be less than 2% for Sr. The discrepancies observed between Selva/StoMat and Eco-Gene come from the way demography is described. In Eco-Gene, demography is highly dependent on the diameter structure of the undisturbed population, assumed to be at equilibrium: in reality this assumption may be violated. But in contrast to many other tropical countries the human impact on the forest in French Guiana and the influence of large scale disturbances like storms and fires was very low during the last centuries. Thus, there are good reasons to consider the tree diameter distribution to be close to an equilibrium.

On the whole, the populations simulated by Eco-Gene are more resilient than is probably the case in reality. However, the sensitivity analysis highlighted the importance of growth and demography on the predictions made by Eco-Gene, compared to all the other input parameters: this motivates in favour of a greater realism in the modelling of those components and more data collection for model parameterisation and validation.

To our knowledge our study is the first to simulate the impact of silviculture practices in the tropics that aims to combine genetics, demography and growth. In temperate forest this approach has been applied for some years longer. The simulations in temperate forests concentrated on seed harvesting and natural regeneration (Degen et al., 1997) and logging and thinning (Scholz and Degen, 1999; Takahashi et al., 2000). Similar models have been applied in temperate forests for large scale, long-term simulations on the adaptation of tree populations to global change and recolonisation from glacial refugia (Austerlitz et al., 2000; Kramer, 1995).

4.2. Realism of simulated pollen and seed dispersal

Limited pollen and seed dispersal and the level of tree clustering are the main forces that create a spatial genetic structure in naturally regenerated populations. Thus, if the parameters in the model did not fit reality very well we would expect the model to be unable to reproduce the observed spatial structure of the tree species. We compared observed and simulated spatial genetic structure of the four species (Fig. 3) and found a good accordance. The ranking of the intensity of the spatial genetic structure was also correctly reproduced. Tree species that have a spatial genetic structure are more sensitive to inbreeding after logging. Inbreeding due to mating among relatives increases the mortality and leads to lower growth rates. This is of a particularly negative impact in a multi species forest with strong inter- and intraspecific competition (Durel et al., 1996; Elstrand and Elam, 1993a,b).

4.3. Different sensitivities of the species

The simulations indicated that, even for the moderate logging system applied in French Guiana (L1), V. americana and Sextonia rubra were not able to recover their initial volume at the end of the rotation period. In the stronger logging scenarios D. guianensis was also unable to recuperate the original basal area. Only the demography of Symphonia globulifera gave no indication of a negative impact of logging. Although the differences among the genetic parameters were small we saw a general tendency of increased genetic distances and a reduced number of genotypes due to logging. No clear tendencies were observed for the other genetic parameters: A, A, Ha, and F. The comparison of the genetic distances between the two control scenarios (C1 versus C2) and the two logging scenarios (L1 versus L2) showed that the impact of genetic drift as a function of time was even higher than the impact of a stronger logging. From the demographic and genetic differences of the simulations, we conclude the following ranking from sensitive to less sensitive species: V. americana > Sextonia rubra > D. guianensis > Symphonia globulifera.

Generally we saw only small differences between the genetic parameters in the control and logging scenarios. The main explanation is that all four species had sufficient recruitment and that there were only small genetic differences between the diameter classes of a species. The mating system of the species with different age classes and pronounced overlapping of generations efficiently maintained genetic diversity in the different demes of the populations. Thus, most of the genetic diversity lost by logging was still present in the recruitment.

The demographic structure of a tree species, the possibility of recruitment after logging and the genetic similarity among different demes of a population are the important points for predicting the sensitivity of a tree species to genetic erosion due to logging (Jennings et al., 2001). Higher risks for genetic diversity due to logging are expected for fast growing pioneer species with deficits in tree abundance in lower diameter classes and weak overlapping of generations (Jennings et al., 2001). Thus, for most slow growing climax tree species selective logging per se is not expected to have a strong negative impact on the genetic diversity. More critical for the genetic conservation of tree species are changes at a higher spatial scale due to forest fragmentation (Aldrich and Hamrick, 1998). The mating systems of most tropical tree species are adapted to low densities of reproductive trees (dominance of animal pollination, mechanisms to avoid selfing). The risk
of gene erosion by logging is expected to be low as long as the
neighbourhood of a logged forest has sufficient reproductive
trees. Thus for several tropical tree species effective long-di-
gistance gene flow has been reported (Apsit et al., 2001; Dick
et al., 2003; Rossetto et al., 2004a,b; White et al., 1999).
In contrast to our expectations the model predicted no
higher level of inbreeding after logging, which would have re-
sulted in higher F-values in the logging scenarios. This might
be explained by the pollinator behaviour parameters imple-
mented in the model (Degen and Roubik, 2004). The pollina-
tors were able to react to reduced tree densities by longer
flight distances (and hence their capacities for gene dispersal)
have changed (Kenta et al., 2004). Thus, a reduction of adult
densities might even increase the number of effective pollen
donors of remnant trees (Dick, 2001).

4.4. Important parameters

Among the genetic output parameters the number of alleles
(A) and the effective number of alleles (Aₑ) were rather insen-
sitive to changes of the model during the sensitivity analysis.
Most sensitive were the fixation index (F), number of geno-
types (NG) and the genetic distance (Dis). The fixation index
measures the excess or deficit of homozygotes compared to
Hardy–Weinberg proportions. Values >0 indicate an excess
which might be caused by inbreeding. Flowering phenology
and pollination distance were the most important input
parameters influencing F-values. Against expectations, a
higher percentage of flowering trees was positively correlated
with the fixation index (Table 7). This might be explained by
reinforced bi-parental inbreeding. If more trees are flowering
and if the pollinators prefer short flight distances, than the
risk of pollination among nearby trees (relatives) increases
(Degen et al., 2004).

The number of genotypes (NG) is the sum of genotypes at
all loci. Thus, it is determined by the number of alleles and
their combination. This multilocus approach of the output
parameter NG explains its higher sensitivity to impact. The
genetic distance is more sensitive than just the number of al-
leles because it considers both changes in the number of al-
leles and their relative frequencies (Gregorius, 1978).

When experimental studies on logging did not come up
with a proof for a negative impact this might have been be-
cause (a) there was really no negative impact, or (b) the genet-
ic parameters used were not sufficiently sensitive. The
contrasting responses of the genetic output parameters used
in our simulation indicate that future studies should also in-
clude multilocus measures because of their higher sensitivity.

As shown by the sensitivity analysis, the output param-
ters genetic diversity and genetic distance from the original
population were largely determined by the logging system,
demographic and growth parameters and only to a small ex-
tent to pollen and seed dispersal and phenology. Rapid
growth combined with small maximum diameters and low

---

### Table 7 – Results of the sensitivity analysis

<table>
<thead>
<tr>
<th>Step</th>
<th>Parameter</th>
<th>F 0.107 ± 0.022</th>
<th>β</th>
<th>R²</th>
<th>Parameter</th>
<th>F 0.045 ± 0.014</th>
<th>β</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Percentage of flowering adults</td>
<td>0.350</td>
<td>0.127</td>
<td></td>
<td>Percentage of flowering adults</td>
<td>0.394</td>
<td>0.151</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Distance of random pollination</td>
<td>−0.303</td>
<td>0.218</td>
<td></td>
<td>Distance of random pollination</td>
<td>−0.303</td>
<td>0.239</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Maximum flight distance pollinator</td>
<td>−0.257</td>
<td>0.281</td>
<td></td>
<td>Maximum flight distance pollinator</td>
<td>−0.281</td>
<td>0.321</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Temporal autocorrelation growth</td>
<td>0.196</td>
<td>0.317</td>
<td></td>
<td>Cutting diameter r</td>
<td>0.133</td>
<td>0.343</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Mean growth rate</td>
<td>0.190</td>
<td>0.352</td>
<td></td>
<td>Mean growth rate</td>
<td>0.115</td>
<td>0.356</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Attractor effect for pollinator</td>
<td>0.122</td>
<td>0.369</td>
<td></td>
<td>Exponent for seed dispersal</td>
<td>0.099</td>
<td>0.366</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Exponent for seed dispersal</td>
<td>0.086</td>
<td>0.376</td>
<td></td>
<td>Density diameter class 10–20 cm</td>
<td>0.091</td>
<td>0.375</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Density diameter class 30–40 cm</td>
<td>0.049</td>
<td>0.378</td>
<td></td>
<td>Density diameter class 30–40 cm</td>
<td>0.073</td>
<td>0.380</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Temporal autocorrelation growth</td>
<td></td>
<td></td>
<td></td>
<td>Attractor effect for pollinator</td>
<td>0.049</td>
<td>0.387</td>
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<tr>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Step</th>
<th>Parameter</th>
<th>BA 0.240 ± 0.065</th>
<th>β</th>
<th>R²</th>
<th>Parameter</th>
<th>BA 0.244 ± 0.066</th>
<th>β</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Cutting diameter</td>
<td>0.395</td>
<td>0.329</td>
<td></td>
<td>Cutting diameter</td>
<td>0.626</td>
<td>0.450</td>
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<tr>
<td>2</td>
<td>Density diameter class 30–40 cm</td>
<td>0.589</td>
<td>0.642</td>
<td></td>
<td>Density diameter class 30–40 cm</td>
<td>0.545</td>
<td>0.758</td>
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</tr>
<tr>
<td>3</td>
<td>Temporal autocorrelation growth</td>
<td>0.317</td>
<td>0.754</td>
<td></td>
<td>Maximum diameter</td>
<td>0.178</td>
<td>0.791</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Mean growth rate</td>
<td>0.282</td>
<td>0.836</td>
<td></td>
<td>Mean growth rate</td>
<td>0.159</td>
<td>0.820</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Maximum diameter</td>
<td>0.171</td>
<td>0.866</td>
<td></td>
<td>Temporal autocorrelation growth</td>
<td>0.116</td>
<td>0.833</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Proportion remaining trees</td>
<td>0.102</td>
<td>0.876</td>
<td></td>
<td>Proportion remaining trees</td>
<td>0.119</td>
<td>0.846</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Density diameter class 20–30 cm</td>
<td>−0.033</td>
<td>0.878</td>
<td></td>
<td>Density diameter class 10–20 cm</td>
<td>0.105</td>
<td>0.857</td>
<td></td>
</tr>
</tbody>
</table>

Stepwise multiple regression of fixation index (F) and basal area (BA) against the main input parameters (Table 1) using the two tree data sets Dicorynia guianensis and Vouacapoua americana.

R² is the fraction of the variance accounted for by the model, adjusted for the number of independent variables; β is the standardized regression coefficient (all significant).
densities in the diameter classes characterised the most sensitive tree species. This is typical for species with low population size and weak overlapping of generations. The main advantage of slow growing species is that they allow many reproductive events which stabilize genetic diversity.

4.5. Outlook

The application of the simulation model Eco-Gene with its integration of genetics and demography showed that it is possible to produce meaningful results ranking the sensitivity of tropical tree species towards logging. The model should therefore provide valuable support for conservation of genetic resources and will be a useful tool for developing recommendations of sustainable forest management practices. We were able to make a ranking for the sensitivity of species. However, there is a need to combine the modelling of the dynamics of a stand with changes in the landscape. The impact of selective logging needs to be evaluated in the context of wider forest fragmentation. As indicated by the sensitivity analysis, future model applications and data collections should place more emphasis on demographic and growth processes. Experimental approaches to monitoring the impact of logging should include highly sensitive multilocus parameters.

Our study is a first step toward elaboration species specific rules and regulations for selective logging (Kanashiro et al., 2002). Species that are more sensitive need higher cutting diameters, longer cutting cycles and a higher proportion of remaining reproductive trees.

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