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RESEARCH ARTICLE

Relationships between demography and gene flow and their importance for the conservation of tree populations in tropical forests under selective felling regimes

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Abstract Determining how tropical tree populations subject to selective felling (logging) pressure may be conserved is a crucial issue for forest management and studying this issue requires a comprehensive understanding of the relationships between population demography and gene flow. We used a simulation model, SELVA, to study (1) the relative impact of demographic factors (juvenile mortality, felling regime) and genetic factors (selfing, number and location of fathers, mating success) on long-term genetic diversity; and (2) the impact of different felling regimes on population size versus genetic diversity. Impact was measured by means of model sensitivity analyses. Juvenile mortality had the highest impact on the number of alleles and genotypes, and on the genetic distance between the original and final populations. Selfing had the greatest impact on observed heterozygote frequency and fixation index. Other factors and interactions had only minor effects. Overall, felling had a greater impact on population size than on genetic diversity. Interestingly, populations under relatively low felling pressure even had a somewhat lower fixation index than undisturbed populations (no felling). We conclude that demographic processes such as juvenile mortality should be modelled thoroughly to obtain reliable long-term predictions of genetic diversity. Mortality in selfed and outcrossed progenies should be modelled explicitly by taking inbreeding depression into account. The modelling of selfing based on population rate appeared to be oversimplifying and should account for inter-tree variation. Forest management should pay particular attention to the regeneration capacities of felled species.

Keywords Genetic diversity · Gene flow · Population dynamics · Simulation model · Conservation · Forest management

Introduction

It is widespread practice in tropical forests that contain a great diversity of tree species to fell selectively a limited number of commercial species, e.g. as occurs in the Brazilian Amazon (Asner et al. 2005) and in French Guiana. Major concerns about the impact of selective felling include the problem that a reduction in tree population size may cause loss of alleles (genetic drift) and detrimental changes to the reproductive system (Jennings et al. 2001;

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Finkeldey and Ziehe 2004). The usually low tree population densities in tropical forests, compared to temperate forests, may make the reproductive system of tropical tree species particularly vulnerable to density reduction through felling (Finkeldey and Ziehe 2004). Moreover, the preferential cutting of trees with economically interesting traits may result in detrimental genetic changes concerning these traits as it may favor reproduction of the remaining, poorer-quality trees (Jennings et al. 2001; Finkeldey and Ziehe 2004). However, such dysgenic selection is probably negligible in terms of conservation and long-term sustainable forest production next to other more significant genetic and non-genetic factors (Cornelius et al. 2005).

Given these concerns, it is crucial to determine how forest managers may conserve the size, structure and genetic diversity of felled species populations in the long term over several consecutive felling cycles. Studying this issue requires a comprehensive understanding of the demographic and genetic factors that influence time-course changes in tropical tree populations, and integration of these factors into predictive models.

Recent research has detected some striking factors. The reproductive system of many tropical tree populations is characterised by long-distance pollen flow and high out-crossing associated with occasional selfing, and these provide for demographic persistence and the maintenance of heterozygosity at low population densities (Ward et al. 2005). Selective felling interferes with the reproductive system by removing the largest trees in a population, and which often have the highest male mating success (Latouche-Hallé et al. 2004; Lourmas et al. 2007) and seed set. After felling, population recovery and the conservation of genetic diversity seem to be closely related to the presence and survival of juvenile trees (de Lacerda et al. 2008; Sebbenn et al. 2008; Silva et al. 2008; Wernsdörfer et al. 2008). For instance, rare alleles removed from a population through the felling of large adult trees can be present in juvenile trees, and may thus be reintroduced into the reproductive population by a few surviving juveniles (Silva et al. 2008; de Lacerda et al. 2008). Therefore, our first question addressed the quantitative relationships between these factors: (Q1) what are the relative impacts, including interactions, of juvenile mortality, felling regime, selfing, number and location of fathers, and mating success on the genetic diversity in tropical tree populations in the long term?

Selective felling may affect demography and genetic diversity to different extents. Several empirical studies (Gillies et al. 1999; Cloutier et al. 2007; Lourmas et al. 2007; André et al. 2008; de Lacerda et al. 2008; Silva et al. 2008) and simulation studies (Degen et al. 2006; Sebbenn et al. 2008) suggest that sensitivities to felling differ between species in terms of population recovery and the conservation of genetic diversity. But for a given species, sustainable felling regimes must at least take account of its regeneration capacities such that a target population size is maintained in the long term. Based on a literature review and theoretical considerations, Jennings et al. (2001) argue that felling regimes that allow for adequate natural regeneration to be present before felling, and for each felled adult tree to be replaced, will also ensure that felling impacts on genetic diversity are small (except for the most light-demanding climax species). Recent developments in predictive models that integrate tropical forest dynamics and gene flow have meant that the assumption made by Jennings et al. (2001) can now be analysed for several consecutive felling cycles (Degen and Roubik 2004; Phillips et al. 2004; Dreyfus et al. 2005; Degen et al. 2006). This is important if guidelines for sustainable forest management are to be drawn up: the presence of regeneration may be assessed in the field, but meaningful measurements of genetic variation are impractical for forest managers (Jennings et al. 2001). Thus, our second question was: (Q2) what is the long-term impact of different felling regimes on the size versus the genetic diversity of tropical tree populations?

To our knowledge, few simulation studies addressing the long-term impact of selective felling in tropical forests have included both forest dynamics and gene flow (Degen et al. 2006; Sebbenn et al. 2008). Several tree species were studied using ECO-GENE (Degen et al. 2006; Sebbenn et al. 2008), a model developed to focus on the simulation of genetic structures (Degen et al. 1996). However, predicted genetic diversity seems to be substantially influenced by demography, growth and felling regime (Degen et al. 2006). Our predictive model, SELVA, was developed to focus on detailed demographic and growth processes, including in particular on regeneration and juvenile stages (Gourlet-Fleury et al. 2005). For purposes of this study we specifically enhanced the gene flow sub-model in SELVA (Dreyfus et al. 2005). The model was calibrated for *Dicorynia guianensis* Amshoff (Caesalpiniaceae), a well-studied species for which detailed demography, growth and gene flow data could be obtained from an experimental research site in the tropical rainforest of French Guiana (Gourlet-Fleury et al. 2004a). *D. guianensis* occurs in French Guiana, Guyana, Surinam and northeast Brazil and is of interest both for conservation management and as a model species: (1) it is the most important timber species in French Guiana, accounting for about 30% of total wood production; (2) the ecological profile of *D. guianensis* is typical of canopy tree species that theoretically allow for some resilience under selective felling (regeneration stages are shade tolerant and young trees need moderate openings to reach the canopy). Thus, the species is an appropriate model to study relationships between demography and gene flow under selective felling, and the results may also apply for other species with similar ecological profiles.

Our aim was to study questions Q1 and Q2 by capitalising on the detailed demographic description given by SELVA combined with the enhanced gene flow sub-model.

Materials and methods

Study area and species

SELVA simulations were based on data from a 36.36-ha study area, the so-called Southern Block of the Paracou field station (5°18′N, 52°53′W) near Sinnamary in French Guiana. The climate is equatorial with two main seasons: a dry season from mid-August to mid-November, and a rainy season that is often interrupted by a short drier period between March and April. Records from 1979 to 2001 give a mean annual rainfall of 3,041 mm with a minimum in September and a maximum in May. Mean annual temperature is 26°C with an annual range of 1–1.5°C. The forest type is lowland "terra firme" Caesalpiniaceae rain forest (Gourlet-Fleury et al. 2004b). In the study area, all adult trees (diameter at breast height, dbh $\geq$10 cm) of all species have been mapped and measured periodically for growth, recruitment and mortality since 1984. Specific data on *D. guianensis* regeneration including seed production and dispersal, mortality and growth up to 10 cm dbh, and gene flow, were recorded between 1999 and 2002 (Latouche-Hallé et al. 2002, 2003, 2004; Gourlet-Fleury et al. 2005; Jésel 2005).

D. guianensis is a large canopy species endemic to the Guiana shield. It is spatially distributed in clusters of about 50 m radius (Dessard et al. 2004). About 9 adult trees per ha occurred in the study area in 1999. Adults become reproductive when reaching about 25 cm dbh (Caron et al. 1998). Flowers are bisexual and the floral syndrome suggests pollination by insects, in all likelihood by large bees. The population flowers every 2 or 3 years. Observations at the Paracou site indicate that nearly all trees flower synchronously, from early January to early February (Caron et al. 2004).

Seeds are wind-dispersed in indehiscent flat pods. Most seeds fall within a 30-m distance from the mother tree (Loubry 1993). Seeds can germinate, and seedlings establish, in the shade. The species needs moderate openings to reach the canopy.

The mating behaviour of *D. guianensis* is a combination of occasional selfing and long-distance pollen flow (Latouche-Hallé et al. 2004). Based on microsatellite analyses conducted in the study area, Latouche-Hallé et al. (2004) estimate population outcrossing rate (=1 − selfing rate) to be 89%, pollen dispersal to be weakly related to inter-tree distance, and pollen flow from outside the study area to account for 62% of crossings. Using allozymes, Caron et al. (1998) showed that allelic frequencies were very similar in the reproductive tree population and in pollen clouds by comparing different spatial scales (25, 300, 500 ha) and two different years. Male mating success is higher for larger trees (Latouche-Hallé et al. 2004).

Model description

Forest dynamics

SELVA is an individual-based spatially explicit forest dynamics model that can be used to simulate the life-cycle of *D. guianensis* (Fig. 1) in interaction with the life-cycles of any other species in the forest. SELVA is described in terms of its construction, functioning and evaluation by Gourlet-Fleury (1997), Gourlet-Fleury and Houllier (2000), Gourlet-Fleury et al. (2005) and Wernsdörfer et al. (2008). SELVA is implemented in the generic software platform CAPSIS 4.0 (de Coligny 2007).

D. guianensis trees <1 cm dbh were simulated as cohorts on 10 × 10 m cells. Trees $\geq$1 cm dbh were simulated as individuals with Cartesian coordinates (x, y). For all other species, trees $\geq$10 cm dbh were simulated as individuals with Cartesian coordinates. Competition between a focal tree and its neighbours within a 30-m radius was described by competition indices. The simulation time step was 3 years.

The life-cycle of *D. guianensis* begins with seed production and dispersal by trees $\geq$25 cm dbh. Reproduction occurs once in a time step, which is in accordance with the species' flowering rhythm. The number of seeds produced increases with crown size, which itself is related to dbh by allometry. Seeds die due to fungal rotting and insect predation (random mortality) and predation by granivorous mammals (mortality related to distance from the mother tree). Overlapping with the seed shadows of neighbouring trees creates local crowding where germinated seeds suffer mortality that increases with density. Surviving germinated seeds grow, passing through stages as seedlings (<0.5 cm dbh), saplings (0.5–1 cm dbh) and pre-recruited juveniles (1 cm dbh), with mortality occurring at each stage. Juvenile growth up to the adult stage (dbh increment from 1 to10 cm dbh) is related to the dbh at the beginning of a time step, including stochastic variation. Slower growing juveniles or those located in locally denser stand areas suffer increased standing mortality. For adult trees (dbh $\geq$10 cm), average growth is related to dbh at the beginning of a time step and is modified by competition, including stochastic variation. Slower growth or larger dbh results in increased standing adult mortality.

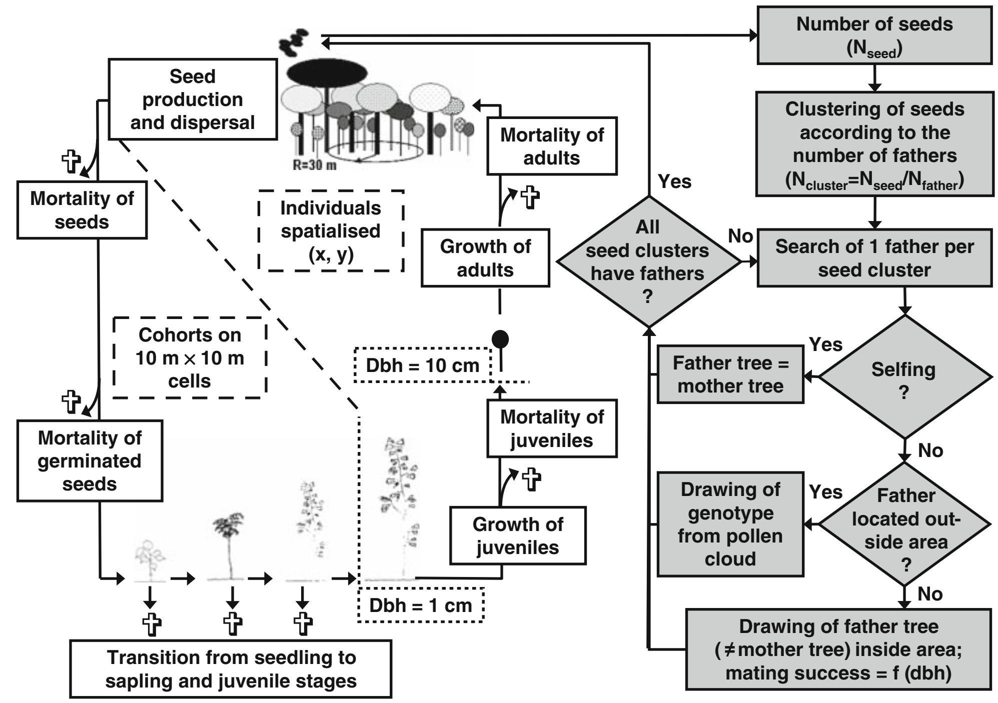

Fig. 1 Flow chart of the *D. guianensis* life-cycle implemented in SELVA, including forest dynamics (white boxes) and gene flow (grey boxes). Forest dynamics include processes from seed production and dispersal to the growth and mortality of juvenile trees (≥1 cm diameter at breast height, dbh) and adult trees (≥10 cm dbh). Trees <1 cm dbh are simulated as cohorts on 10 m × 10 m cells, trees ≥1 cm dbh as individuals with Cartesian coordinates (*x*, *y*). Gene flow includes the occurrence of selfing, the number and location of fathers, and mating success

The life-cycles of any other species include the processes of adult recruitment related to local stand density; adult growth related to dbh at the beginning of a time step and modified by competition, including stochastic variation; and adult mortality related to dbh increment.

Tree-fall deaths in adults of both *D. guianensis* and any other species rely on the same processes: a tree can fall alone (primary tree-fall), it can be broken or uprooted by the fall of a neighbouring tree (secondary tree-fall), or it can fall over at the margin of a newly created gap (complex tree-fall).

Gene flow

Based on the results of previous analyses (Dreyfus et al. 2005), we enhanced SELVA's general gene-flow sub-model and calibrated it for *D. guianensis* (Fig. 1 and Appendix 1). This was used to simulate offspring (seed) genotypes based on the recombination of maternal and paternal genotypes. Seed maternal genotype corresponds to the mother tree genotype. Seed paternal genotype is simulated based on pollen flow investigations using six microsatellite loci (Latouche-Hallé et al. 2004). For seeds produced by a given mother tree at a given point in time, the enhanced sub-model accounted for the occurrence of selfing, the number and location of fathers, and mating success. Selfing was a random event. Out of a given number of fathers, each father transferred its genes to an equal fraction of the seeds. Fathers could be located both inside and outside the study area (random event). Fathers inside the area were individually simulated trees described by their genotype and traits such as dbh (≥25 cm). Larger trees had a greater chance of mating success as a reflection of higher pollen production. The genotypes of fathers outside the area were drawn at random from an allele frequency distribution (pollen cloud) assumed to represent pollen from the outside population. We constructed the sub-model to represent the main known factors governing the gene flow of *D. guianensis*. Although rather simple, the sub-model could be used to study the long-term impact of felling on certain basic genetic characteristics of the species.

In SELVA, forest dynamics can affect gene flow in that the production of both pollen and seeds is related to the survival and dbh of reproductive trees. In contrast, a tree's genotype has no affect on its survival, growth or seed production since no appropriate empirical data were available concerning the effect of genes on the demography and growth of *D. guianensis*, as would be necessary to calibrate our model. Hence, as a working hypothesis, our genetic markers were assumed to be neutral.

Scenario analysis

Impact measurement

A global sensitivity analysis method was used to assess the relative impact of SELVA demographic and genetic input factors on a given output variable (question Q1) (Saltelli et al. 2004; Wernsdörfer et al. 2008). Default settings for different input factors were varied within a certain range and the resulting impact on the output variable was assessed by means of sensitivity measures that gave the relative impact of one, two or three input factors on an output variable, i.e. first, second or third order effects (Appendix 2). The higher the value of a sensitivity measure, the higher the impact. For a deterministic model, the sum of the sensitivity measures for all orders (e.g. first, second and third order effects in the case of three input factors) is equal to one. However, in our study the sum was less than one since SELVA is a stochastic model and we analysed up to five input factors but did not calculate effects of fourth and higher orders, assuming that they were very low. We performed an additional local sensitivity analysis for those input factors shown to be particularly interesting, i.e. we plotted the output variable over time for the different input factor settings, while the other input factors were held in their default settings.

Input factors

We analysed what in principle are the most important SELVA demographic and genetic input factors addressed in questions Q1 and Q2: juvenile mortality, felling regime, selfing, location of fathers and mating success (Table 1). In a preliminary analysis of the relationships between genetic input factors and output variables, selfing and the location of fathers had relatively high impacts (sensitivity measure first order effects of up to 0.86 and 0.56, respectively). Mating success had a relatively low impact in the preliminary analysis (maxima of 0.08 and 0.11 for first and higher order effects, respectively). We nevertheless chose to analyse this factor as it was related to dbh and could thus interact with the felling regime (described below). We chose not to analyse the number of fathers input factor, i.e. to fix it at its default value ($N_{\mathrm{father}} = 15$ deduced from Latouche-Hallé et al. 2004); since the number of fathers had a relatively low impact in the preliminary analysis (maxima of 0.09 for first order effects and 0.18 for higher order effects).

We varied the different input factors with the starting point being the default parameter settings (Table 1). With regard to juvenile mortality, parameter settings implementing higher and lower mortalities than the default setting were estimated using 10% confidence intervals of the default setting (Wernsdörfer et al. 2008). The felling regime currently planned in French Guiana fixes the minimum diameter cutting limit at 60 cm and the length of felling cycles at 60 years. Thus, we chose 42-year and 84-year felling cycles as realistic representations of high and low felling pressure, respectively. All *D. guianensis* trees ≥60 cm dbh were harvested at a felling event. By default, no felling took place, i.e. the *D. guianensis* population evolved without disturbance. High and low selfing probabilities were determined as the bounds of the 10% confidence interval of the default selfing probability

Table 1 Parameter settings of the studied demographic input factors (juvenile mortality and felling regime) and genetic input factors (selfing, location of fathers and mating success)

Input factor		Parameter setting		
		Default	High	Low
Juvenile mortality[a]		Default mortality	High mortality	Low mortality
Felling regime (harvest of all *D. guianensis* trees ≥ 60 cm dbh[b] in cycles of different length)		No felling	42-years cycles	84-years cycles
Selfing[c] (probability P_{selfing})		0.11	0.2	0.02
Location of fathers[d] (probability of a father being located outside the study area, P_{outside})		0.62	1	0
			Default	Alternative
Mating success[e]	dbh = 25–34.5 cm, weight =		1	–
	dbh = 34.5–46 cm, weight =		1 384	–
	dbh > 46 cm, weight =		17 992	–

[a] Equation and parameter values are given by Wernsdörfer et al. (2008)

[b] Diameter at breast height

[c,d,e] Parameter values were deduced from Latouche-Hallé et al. (2004)

(Latouche-Hallé et al. 2004). By default, fathers could be located both outside and inside the study area. We analysed the two extreme situations of all fathers being located either outside or inside the study area. Mating success had two settings: either it was weighted by dbh class (default) or was independent of tree traits.

Output variables

We chose the output variables in such a manner to assess possible changes in certain basic demographic and genetic characteristics of the *D. guianensis* population (Table 2).

Simulations

When starting SELVA simulations based on inventory data gathered in 1999 the number of *D. guianensis* trees $\geq$10 cm dbh over time firstly oscillated then stabilised after several hundreds of years (Gourlet-Fleury et al. 2005). Thus, we started all simulation runs after the stabilisation period, 999 years after 1999, in the same simulated forest stand. The genetic characteristics of the simulated stand were very consistent with the inventory data and the stand was thus considered as acceptable (Table 3). The starting year after stabilisation was set to year 0.

When calculating the sensitivity measures, we simulated all possible combinations of the five input factors: four input factors with three settings each and one input factor with two settings (Table 1), resulting in 162 combinations. Each combination was simulated 20 times to account for SELVA stochasticity, resulting in a total of 3,240 simulation runs. Simulation time in each run was 336 years. We calculated the sensitivity measures for years 81, 165, 249 and 333, i.e. just before felling (84-year cycles) and just before every second felling (42-year cycles) when post-felling population recovery reached its maximum.

Table 2 Definitions of the demographic output variable (*N10*) and of the genetic output variables (A, A_E, H_O, F_{IS}, *DG* and *NG*)

Output variable	Definition
N10	Number of *D. guianensis* trees $\geq$ 10 cm dbh[a] per ha
A	Average number of alleles per locus
A_E	Effective number of alleles
H_O	Observed heterozygote frequencies
F_{IS}	Fixation index (Weir and Cockerham 1984)
DG	Genetic distance to the initial population in year 0 (Nei 1972)
NG	Number of different genotypes

[a] Diameter at breast height

Table 3 Genetic characteristics of the *D. guianensis* population based on inventory data (Latouche-Hallé et al. 2003) and for the simulated stand from which simulation runs started (trees $\geq$20 cm diameter at breast height)

Variable[a]	Inventory ($N^b = 172$)	Simulated stand ($N = 149$)
A	7.33	6.67
A_E	3.23	3.28
A_E/A	0.44	0.49
H_O	6.2×10^{-1}	6.4×10^{-1}
F_{IS}	1.2×10^{-2}	-1.7×10^{-2}

[a] Definitions: Table 2

[b] Sample size

Results

Impact of demographic and genetic input factors on genetic output variables

Of all the input factors, juvenile mortality and selfing clearly had the greatest impact on the genetic output variables (first order effects; Fig. 2). In general, second and third order interaction effects were very low and did not exceed 0.07 (data not shown).

Juvenile mortality had the greatest impact of all input factors on A and A_E, and this impact increased from year 81 to 333 (Fig. 2). The impact of juvenile mortality was clearly greater on A than on A_E. Time-course of A (local sensitivity analysis) showed a clear and continuous decrease with elevated juvenile mortality (Fig. 3). When juvenile mortality was low, A was slightly higher than for default juvenile mortality but did not show any clear trend over time for either setting.

Selfing had the greatest impact on H_O and F_{IS}, with impact being similar in magnitude on both output variables (Fig. 2). Impact increased from year 81 to 249, and stabilised (or slightly decreased) in year 333. When selfing was set high or at the default settling H_O firstly decreased then stabilised towards the end of the simulation period, at which point H_O was lower for high than for default selfing (Fig. 3). H_O did scarcely vary over time when selfing was low.

Juvenile mortality had the greatest impact of all input factors on *DG* (Table 2), and this impact increased from year 81 to 333 (Fig. 2). Time-course of *DG* was slightly different between low and default juvenile mortalities (Fig. 3). At both settings *DG* increased slightly up to about half way through the simulation period (year 168) then stabilised. When juvenile mortality was set high, *DG* increased almost continuously over time, without stabilising.

Also, juvenile mortality had the greatest impact of all input factors on *NG* (Table 2) (Fig. 2). In each of years 81, 165, 249 and 333, the sums of the sensitivity measures for juvenile mortality and felling regime were close to one.

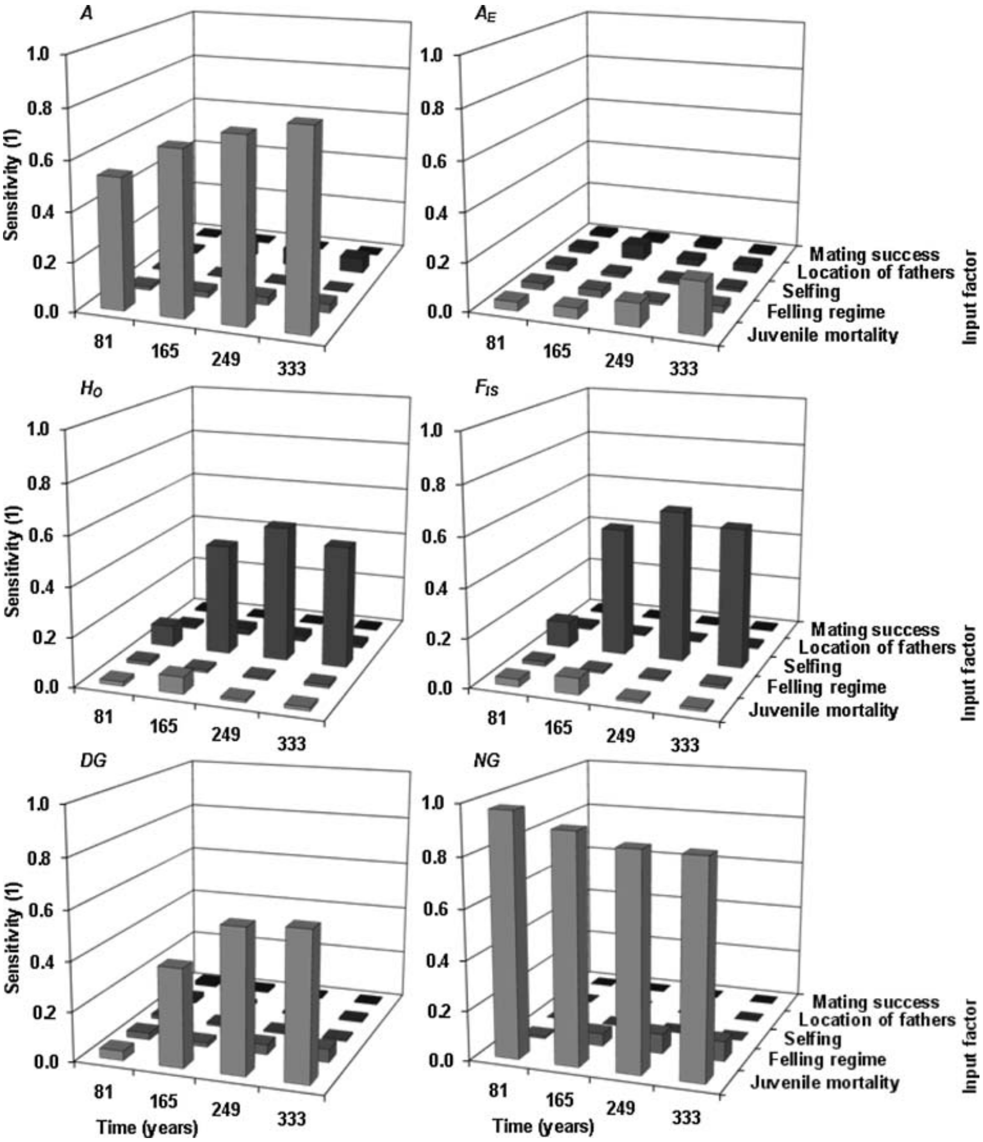

Fig. 2 Sensitivity of the genetic output variables A, A_E, H_O, F_{IS}, DG and NG (Table 2) to the input factors juvenile mortality, felling regime, selfing, location of fathers and mating success. Sensitivity measures are given for years 81, 165, 249 and 333, i.e. just before felling (84-year cycles) and just before every second felling (42-year cycles; Table 1). Second and third order interaction effects were low (maximum of 0.07); they are thus not plotted. (1) stands for no unit

This indicates that nearly all *NG* sensitivity was due to the demographic input factors. High juvenile mortality led to a clear decrease in *NG* over time, with values flattening out at very low levels towards the end of the simulation period (Fig. 3). When juvenile mortality was set low, *NG* increased almost continuously, and with default juvenile mortality *NG* was almost stable over time.

Impact of felling on demographic and genetic output variables

After a simulated 333 years, felling was seen to have the greatest impact on the demographic output variable *N10* (Table 2), which changed compared to no felling by -54% and -29% for 42- and 84-year felling cycles, respectively (Table 4). Mean values for *N10* were significantly different between 42-year felling cycles and no felling, and between 84-year felling cycles and no felling. The results obtained for genetic output variable *NG* were very similar, i.e. almost all trees had different genotypes: for instance with no felling, $N10 = 10.6$ and $NG = 383$, i.e. 10.5 different genotypes per ha. Also, genetic output variable *DG* was substantially different, by 42%, between 42-year cycles and no felling. However, mean values for *DG* at the two settings were not significantly different. The difference in *A* between 42-year felling cycles and no felling amounted to -8%, with mean values for *A* at the two settings being significantly different. Only minor differences were seen for A_E and H_O.

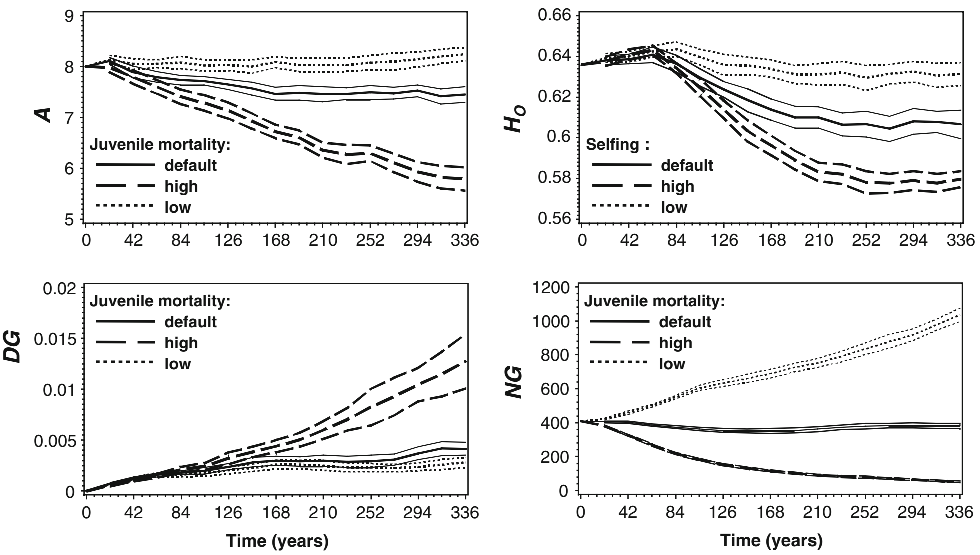

Fig. 3 Time-course of genetic output variables A, H_O, DG and NG (Table 2): A, DG and NG as functions of the different settings for juvenile mortality (Table 1); H_O as a function of the different settings for selfing. For each output variable and setting are plotted the time-course of the mean and its upper and lower 95% confidence limits. Values for means and confidence limits are based on 20 repetitions outputted every 21 years. Interpolation between values is linear

Table 4 Demographic and genetic characteristics of the *D. guianensis* population after 333 years of simulation under different felling regimes (trees ≥10 cm diameter at breast height)

Felling regime	Statistic[a]	Output variable[b]						
		N10	*A*	A_E	H_O	F_{IS}	*DG*	*NG*
No felling	Mean[c]	10.6	7.4	3.44	6.08×10^{-1}	5.0×10^{-2}	4.2×10^{-3}	383
	CI[d]	[10.2, 11.0]	[7.3, 7.6]	[3.39, 3.49]	[6.01, 6.15]	[4.2, 5.8]	[3.5, 4.9]	[369, 397]
42-years cycles	Mean	4.9*	6.8*	3.37	6.04×10^{-1}	5.4×10^{-2}	6.0×10^{-3}	178*
	CI	[4.7, 5.2]	[6.6, 7.0]	[3.33, 3.40]	[5.98, 6.10]	[4.6, 6.2]	[4.7, 7.2]	[168, 188]
	Δ[e] (%)	−53.6	−8.2	−2.1	−0.6	7.1	41.9	−53.4
84-years cycles	Mean	7.6*	7.3	3.41	6.12×10^{-1}	4.4×10^{-2}	4.5×10^{-3}	274*
	CI	[7.2, 8.0]	[7.1, 7.5]	[3.38, 3.45]	[6.06, 6.18]	[3.5, 5.2]	[3.6, 5.4]	[260, 288]
	Δ (%)	−28.5	−1.8	−0.8	0.7	−13.4	7.9	−28.4

[a] Results are based on 20 repetitions of each felling regime setting. All other input factors had the default parameter settings (Table 1). Results of the setting 42-years cycles are given after seven felling cycles just before the eighth felling, results of 84-years cycles after three felling cycles just before the fourth felling

[b] Definitions: Table 2

[c] Means for 42- or 84-years cycles marked with an asterisk (*) are significantly different from the mean for no felling at the 5% level

[d] 95% confidence interval for the mean; for H_O, F_{IS} and DG, power-of-ten factors are the same as for the respective mean

[e] Percentage change, i.e. difference between the means for felling under 42-years cycles and no felling, normalised by the mean for no felling and multiplied by 100; correspondingly for felling under 84-years cycles

Both for demographic and genetic output variables, the absolute values of their percentage changes under felling, compared to no felling, were in most cases higher for 42-year felling cycles than for 84-year felling cycles (Table 4). The only exception to this was for F_{IS}, with differences of 7% and |-13%| for 42- and 84-year cycles, respectively.

Discussion

Question Q1

Our first question addressed the relative impacts and interactions of juvenile mortality, felling regime, selfing, location of fathers and mating success on long-term genetic diversity. The results were used both to evaluate the plausibility of model predictions and identify important relationships between demographic and genetic factors that influence time-course changes in tropical tree populations under felling pressure. Hereafter, we compare the results we obtained using SELVA with those obtained by Degen et al. (2006) using ECO-GENE for the same species (*D. guianensis*). Comparing model predictions is particularly interesting for although the two models describe similar processes, they use different levels of detail. Whereas ECO-GENE describes gene flow in detail, it treats demographic processes such as mortality in a rather simple manner (Degen and Roubik 2004; Degen et al. 2006). In contrast, SELVA describes demography and growth in detail but gene flow in a simple manner (Gourlet-Fleury et al. 2005; Appendix 1).

Interaction effects were minor in our simulations and only juvenile mortality and selfing, i.e. two of the five input factors, had relatively high impacts (first order effects; Fig. 2). Also, they impacted on different output variables. Accordingly, we found little interaction between juvenile mortality and selfing, or between juvenile mortality, selfing and the other input factors, and this for all output variables. To our knowledge, interaction effects between demographic and genetic factors have scarcely been quantified in previous simulation studies evaluating long-term changes in tropical forests.

Time-course changes in genetic diversity were closely related to the demographic process of juvenile mortalities (Fig. 2). When juvenile mortality is high, low and default, the number of trees decreases, increases and remains about stable over time, respectively (Wernsdörfer et al. 2008). As expected, the decrease in the number of trees led to loss of alleles and genotypes, and to an increase in genetic distance (*A*, *NG* and *DG* for high juvenile mortality; Fig. 3). Rare alleles were likely the first to be lost, considering that the number of alleles was more sensitive to juvenile mortality than the effective number of alleles (A and A_E in Fig. 2). In contrast to the number of genotypes, the number of alleles did not increase continuously with a rise in the number of trees (*NG* and *A* for low juvenile mortality; Fig. 3), but stabilised on a slightly higher level than for a constant number of trees (*A* for default juvenile mortality; Fig. 3). This was plausible since the number of alleles in the simulated tree population was limited by the total number of different alleles occurring in the gene pool inside and outside the study area, i.e. in the simulated tree population and pollen cloud, respectively. However, a larger number of trees was associated with a higher number of different allele combinations (*NG*), and the potential number of combinations was very elevated (6 loci, each with 5–15 alleles). Thus, almost every tree had a different genotype.

In ECO-GENE, like in SELVA, genetic distance and number of genotypes are most sensitive to demographic factors. But in ECO-GENE these variables are also sensitive to growth and cutting diameter (Degen et al. 2006) that were not addressed by our first question. Moreover, the effective number of alleles in both models seems to be rather insensitive to changes in the input factors (A_E in Fig. 2 and Degen et al. 2006). In contrast, the number of alleles is rather insensitive in ECO-GENE (Degen et al. 2006), while in SELVA it was greatly affected by juvenile mortality. This may be due to model differences in the description of demography, as suggested similarly by Degen et al. (2006) concerning population recovery: under the same felling regime, predicted recovery is lower in SELVA than in ECO-GENE.

The genetic diversity of the simulated tree population was scarcely affected by changes in the potential father population (mating success; Fig. 2) which included either mainly large trees (>46 cm dbh) or all reproductive trees (≥25 cm dbh; default or alternative setting of mating success in Table 1, respectively). In line with the low impact of mating success, removal of the largest trees (≥60 cm dbh) through felling hardly affected genetic diversity (Fig. 2). This was likely due to sufficient pollen flow from the smaller trees (25–60 cm dbh) inside the study area, and from outside. In contrast, removal of juvenile trees (1–10 cm dbh) through high juvenile mortality did have an impact on genetic diversity (Fig. 3). One likely reason for this is that juvenile mortality reduced the total number of trees becoming reproductive at 25 cm dbh and transferring their genes to the next generation. This is consistent with the assumption by Jennings et al. (2001), that the presence of adequate regeneration (here sufficient juvenile survival) before felling will ensure little felling impact on genetic diversity.

Surprisingly, the origin of pollen (from inside or outside the study area, from a far distance) had little impact on genetic diversity (location of fathers; Fig. 2). Considering the population inside the ~40-ha study area, Latouche-Hallé et al. (2004) estimated that the father population occupied an area of 560 ha. Despite the lack of any significant difference observed previously with allozymes between pollen clouds from 25 and 500 ha areas (Caron et al. 1998), and because allozymes are far less variable than microsatellite markers, we expected pollen originating from a large area to show greater genetic variation than that originating from a much more restricted area, such as our study area. Therefore, we expected the location of fathers to have an impact on genetic diversity. Degen et al. (2006) reported that more distant and also more random pollen dispersal affects the fixation index in ECO-GENE. The pollen cloud used in our simulations (Appendix 1) probably did not entirely represent the genetic variation in pollen from outside the study area. Thus, genotyping additional trees outside the study area, and including these findings into the model, would likely have enhanced the realism of model predictions. Moreover, future analyses may asses the realism of using a pollen cloud to model pollen flow from outside the study area. This may be done by comparing simulations using a pollen cloud with simulations based on a larger study area.

As expected, changes in selfing affected heterozygote frequency and the fixation index (H_O and F_{IS}; Fig. 2). Increased selfing resulted in a lower heterozygote frequency, and vice versa (H_O; Fig. 3). However, at the default selfing, heterozygote frequency firstly decreased then stabilised whereas we had expected it to remain roughly stable over time. There may be two reasons for this.

First, the default selfing probability of 0.11 (Table 1) was likely too high and not representative of the behaviour of individual *D. guianensis* trees. On the one hand, this value was consistent with population outcrossing rates (=1 − selfing rate) of 0.89 and 0.85, estimated in the study area (∼40 ha) using microsatellites (Latouche-Hallé et al. 2004) and in a larger area (∼500 ha) of the Paracou field station using allozymes (Caron et al. 1998), respectively. On the other hand, single-tree outcrossing rates may vary considerably between *D. guianensis* trees (Caron et al. 1998; Latouche-Hallé et al. 2004) and for many other tropical tree species (Ward et al. 2005). Quantifying this variation through further data acquisition and analysis would have a good chance of enhancing the realism of model predictions. Among other things, this variation may be related to tree traits attracting pollinators: using ECOGENE, Degen and Roubik (2004) reported that selfing in *Jacaranda copaia* and *Dipteryx odorata* was affected by the probability that a pollinator changes its foraging tree and the attractor effect that it remains on the tree. In addition, bi-parental inbreeding may be significant on a spatial scale like that used for our study area, and may result in a decrease in observed heterozygote frequency. However, the occurrence of bi-parental inbreeding was limited because considerable pollen flow occurred from outside the study area. As some scenarios gave an observed heterozygote frequency that was roughly stable over time, the impact of bi-parental inbreeding was probably limited (low selfing; Fig. 3).

Second, observed outcrossing rates may be affected by inbreeding depression (Ward et al. 2005). Inbred progenies may be completely lost prior to maturity (Scofield and Schultz 2006), resulting in an apparently outcrossed adult population (Hufford and Hamrick 2003). However, inbreeding depression is only implicitly taken into account in SELVA which plausibly renders mortality at different regeneration and juvenile stages of selfed and outcrossed progenies in total. However, selfed and outcrossed progenies in SELVA have the same mortality probabilities, while in reality the mortality probability for selfed progeny may well be higher. Thus, SELVA may give an unrealistically high proportion of selfed progenies reaching maturity, and the observed heterozygote frequency of the adult population then decreases (Fig. 3). Also, in reality, the survival of selfed progeny may depend on environmental conditions. Under unfavourable conditions such as high intra-specific competition, selfed progenies probably die completely and only the more vigorous outcrossed progeny survives. But under favourable conditions such as extremely low intra-specific competition, selfed progenies may survive and colonise new areas. Latouche-Hallé et al. (2004) suggest that tolerance to selfing is a reproductive strategy under low density conditions in tropical forests. However, little empirical knowledge has been gained concerning the relationships between selfing, inbreeding depression, low seed set and population viability (Oostermeijer et al. 2003; Ward et al. 2005), and no empirical data were available to calibrate an inbreeding depression sub-model for *D. guianensis*. The potential role of selfing as a reproductive strategy (Latouche-Hallé et al. 2004) and the high sensitivity of genetic output variables to selfing and juvenile mortality (Fig. 2) underline the importance of acquiring such data.

In this respect, the performance of the molecular genetic markers (microsatellites) used in our study may have reached its limits. For instance, confronting heterozygote frequency, as measured using molecular markers, with fitness is debatable (Reed and Frankham 2001). Fitness-related traits, such as seed set, are associated with quantitative genetic variation and subjected to selection. In contrast, molecular genetic markers are commonly assumed to be insensitive (neutral) to natural selection. There is evidence that the correlation between molecular and quantitative measures of genetic variation may be weak (Pfrender et al. 2000; Reed and Frankham 2001). Neuenschwander et al. (2008) illustrated with their simulation program, quantiNemo, that differentiation at neutral markers (F_{ST}) may differ from differentiation at a quantitative trait (Q_{ST}) determined by quantitative trait loci, under the impact of selection and migration. However, the acquisition of genetic variation data for quantitative traits is technically difficult due to the possibly large number of loci and environmental effects involved in their expression (Pfrender et al. 2000). Most of the gene markers currently available for forest trees are selectively (almost) neutral (Finkeldey and Ziehe 2004), which among other things is due to easier data acquisition of molecular markers than for genetic variation of quantitative traits. Reed and Frankham (2001) concluded from their meta-analysis that molecular markers mainly reflect effects of genetic drift, but do not accurately reflect adaptive evolutionary processes. It therefore follows that our results on changes in heterozygote frequency should be interpreted with caution in regard to their effects on fitness.

Despite constraints imposed on gene flow modelling due, as discussed above, to the limited amount of data available, we feel confident that SELVA can be used to answer question Q2. To ensure a sound interpretation of its predictions on genetic diversity, we undertook to assess both the limitations and the performance of the enhanced gene flow sub-model: the sensitivity analysis both identified the most uncertain input factors (juvenile mortality, selfing) and demonstrated plausible responses to changes in input factors. Concerning predictions on demography, Wernsdörfer et al. (2008) have already identified uncertain input factors (primarily juvenile mortality) and demonstrated plausible SELVA responses.

Question Q2

Our second question addressed the impact of different felling regimes on the size versus the genetic diversity of tropical tree populations.

Overall, felling had a greater impact on population size than on genetic diversity. Note that we do not discuss the results obtained for the number of genotypes as the per-hectare values for this variable were very similar to population size (*NG* and *N10*). The statistical analysis indicated significant differences between felling and no felling only for population size and number of alleles (*N10* and *A*; Table 4). Moreover, in absolute terms, the percentage changes between felling and no felling were clearly more elevated for population size than for any of the genetic output variables (except *NG*; Table 4). Similarly, in an intensive felling scenario where the *D. guianensis* population did not completely recover (45 cm cutting diameter with 10% of remaining trees above that diameter, 30-year felling cycles, 215-year simulation time), Degen et al. (2006) reported that no strong changes occurred in genetic output variables. Note that in our simulations, even for the low felling pressure scenario (84-year cycles), population size (*N10*) was predicted to decrease over time. This somewhat surprising result may indicate that our model overestimates juvenile mortality; we suspect that the enhanced light level after felling should increase the survival of juveniles, whereas so far this relationship is hardly taken into account in SELVA.

Of the different genetic output variables, the most marked changes taking place under the impact of long-term felling have been reported in the number of alleles, genetic distance and number of genotypes in populations of several tropical tree species (Degen et al. 2006; Sebbenn et al. 2008). This is in accordance with our results even though changes in genetic distance were not statistically significant. Also, changes in the fixation index were not statistically significant, but may indicate interesting relationships between demography and gene flow, as discussed hereafter.

Theory suggests that increased inbreeding is one of the main potentially deleterious consequences of habitat degradation, through fragmentation or disturbance such as selective felling (Lowe et al. 2005). Interestingly, according to our simulations, low felling pressure may even reduce inbreeding in comparison with no felling (fixation index, F_{IS}, for 84-year cycles; Table 4). Positive values for the fixation index indicate an excess of homozygotes compared to the Hardy–Weinberg equilibrium which may be a result of inbreeding. The fixation index was positive at the end of all scenarios (Table 4), likely due to an unrealistically high selfing probability or the disregarding of inbreeding depression (as discussed above). The fact that the fixation index was more elevated under high felling pressure (42-year cycles) than under no felling may be explained by the decrease in population size due to felling (F_{IS} and *N10*; Table 4), and the related higher chance of inbreeding. However, the population size also decreased under low felling pressure, while the fixation index was lower than under no felling. This may be explained by differences in the effective father population. Under no felling, mainly large trees had mating success (dbh >46 cm; Table 1). Under felling (42- or 84-year cycles) the largest trees (dbh $\geq$60 cm) were periodically removed, so that probably more of the smaller reproductive trees (dbh $\geq$25 cm) also had mating success. Smaller trees are usually more frequent than larger trees (reverse-J-shaped dbh distribution; Gourlet-Fleury et al. 2005). Hence, removal of the largest trees may have led to a greater number of different fathers, and thus to lower inbreeding. This was likely the case under low felling pressure, where a relatively large population size was maintained over several felling cycles. In contrast, high felling pressure likely reduced population size to such an extent that inbreeding increased. However, the extent of this inbreeding was buffered through pollen flow from outside the study area.

Concerning the management of tropical forests, the results of our felling scenarios so far support the theoretical consideration by Jennings et al. (2001) that the risk of losing genetic diversity is low if there are sufficient juveniles to replace each felled adult tree, i.e. if the felled species population can recover completely. Even for incomplete recovery, we found that felling had relatively little impact on genetic diversity. These overall relationships may vary for different species which may have different sensitivities to felling (Degen et al. 2006; Sebbenn et al. 2008). Finally, van Gardingen et al. (2006) argue that the structure of a managed "natural" forest will differ from that of the original primary forest in terms of species composition, size distribution and probably demographic variables. Our results suggest that differences may also occur in genetic composition, but to a lesser extent than for demography. Acceptable extents of change may be a compromise between ecologic, economic and social functions targeted for a particular forest area.

Conclusions

- SELVA's enhanced gene-flow sub-model provided plausible responses to changes in demographic and genetic input factors. The precision and relevance of model predictions could be improved by providing further data on and knowledge of inter-tree variations in selfing, and on the genetic composition of the *D. guianensis* population outside the study area.

- Particularly, demographic processes such as juvenile mortality should be modelled thoroughly in order to yield reliable long-term predictions of genetic diversity in tropical forests subjected to selective felling. Mortality in selfed progeny due to inbreeding depression, and in outcrossed progeny, should be modelled explicitly. Meaningful results could then be obtained using a simple gene-flow sub-model.
- As an answer to question Q1, we found that juvenile mortality and selfing had the greatest impact on long-term genetic diversity. Although it was possible to interpret this and the relatively low impact of felling regime and mating success, the impact of the location of fathers should be further analysed based on additional data.
- As an answer to question Q2, both selective felling regimes analysed had a greater impact on population size than on genetic diversity. We suggest that for *D. guianensis,* and possibly for other tropical tree species with similar ecological profiles, the risk of seeing population sizes decrease due to insufficient regeneration is likely to be higher than the risk of losing genetic diversity. Management guidelines should therefore pay special attention to the regeneration capacities of felled species.
- As a perspective, SELVA with its detailed sub-models of demography at the regeneration and juvenile stages, and its gene-flow sub-model, may be calibrated for different tropical tree species, providing for a study of the relationships between demography and gene flow under selective felling for model species of different ecological profiles.

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Appendix 1: Gene flow sub-model

The description of the *D. guianensis* gene flow sub-model refers to the grey boxes in the flow chart (Fig. 1).

Number and clustering of seeds

The number of seeds, N_{seed}, produced by a given mother tree at a given point in time was governed by forest dynamics. All seeds possessed the maternal genotype of the mother tree. To attribute the genotypes of several fathers, the seeds were subdivided into clusters with the number of clusters corresponding to the number of fathers, N_{father} (=15 by default). The number of seeds per cluster, N_{cluster}, was equal between clusters: $N_{\mathrm{cluster}} = N_{\mathrm{seed}}/N_{\mathrm{father}}$.

Search for fathers

One father was determined for each seed cluster by subsequently checking the occurrence of selfing and, if applicable, the location of the father.

Selfing

Selfing was a random event occurring with the probability P_{selfing} (Table 1). In the event of selfing, the paternal genotype was the same as the maternal genotype. In the event of outcrossing (i.e. no selfing), the next step was to determine the location of the father.

Location of fathers

Fathers could be located both outside and inside the study area. The random event of a father being located outside the area occurred with the probability P_{outside} (Table 1). If this event occurred, a paternal genotype was drawn at random from an allele frequency distribution, called a pollen cloud. The pollen cloud included allele frequencies for six loci, where the number of alleles per locus ranged between 5 and 15. Allele frequencies were based on 246 seeds collected inside the study area (Latouche-Hallé et al. 2004; samples from outside the area were not available), hypothesising that the observed seed genotypes represented the male allele frequencies occurring outside the area. In the event of the father being located inside the area, which occurred with the probability $1 - P_{\mathrm{outside}}$, a father tree was drawn at random from among the population of potential father trees inside the area. This population included all trees ≥25 cm dbh apart from the mother tree, as selfing had already been checked in the previous step.

Mating success

For the random drawing of a father tree inside the area, the default setting accounted for an effect of dbh on mating success (Latouche-Hallé et al. 2004; Table 1). Potential father trees were classified by dbh and a weight was attributed to each tree according to its dbh class. Larger trees had higher mating success. As an alternative setting, a father was drawn independently of its traits. For both settings, father trees were drawn with replacement.

Miscellaneous

If the setting was such that fathers could be located both outside and inside the study area (i.e. $P_{\text{outside}} \neq 0$ and $P_{\text{outside}} \neq 1$), then P_{outside} was adjusted to account for changes in the population of potential father trees occurring inside the area. Such changes could occur in the course of a simulation run due to mortality or felling, for instance. We assumed that P_{outside} increased if the potential amount of pollen arriving from inside the area decreased, and vice versa. We also assumed an ideal *D. guianensis* population outside the area, which was undisturbed or managed in a manner such that pollen production was unaffected; the pollen cloud was constant at all times in a simulation run. We used two methods to calculate the change in P_{outside}, depending on the mating success setting.

If mating success was independent of tree traits, P_{outside} was adjusted to the number of potential father trees occurring inside the area at a given point in time during a simulation run, N_{pot}. Let $N_{\text{pot\_mean}}$ be the mean number of potential father trees occurring inside the area during a simulation run. Then, a fictitious number of potential father trees occurring outside the area can be calculated as $N_{\text{fict}} = N_{\text{pot\_mean}} \times P_{\text{outside}}/(1 - P_{\text{outside}})$. We assumed N_{fict} to be constant at all time points during a simulation run. Based on this, at a given point in time, the probability of a father being located outside the area was calculated as $P'_{\text{outside}} = N_{\text{fict}}/(N_{\text{fict}} + N_{\text{pot}})$. To illustrate this, we plotted P'_{outside} in relation to N_{pot} for $P_{\text{outside}} = 0.62$ and $N_{\text{pot\_mean}} = 117$ (Fig. 4). Note that P'_{outside} clearly increased as values of N_{pot} decreased. In contrast, a considerable pollen flow from outside the area was maintained even if N_{pot} reached very high (unrealistic) values, e.g. $P'_{\text{outside}} > 0.3$ for $N_{\text{pot}} = 400$.

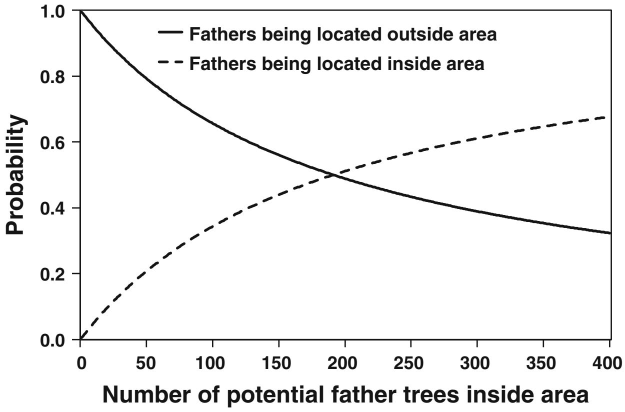

Fig. 4 Probability of fathers being located outside the study area (P'_{outside}), and inside the area ($1 - P'_{\text{outside}}$), as a function of the number of potential father trees occurring inside the area at a given point in time during a simulation run (N_{pot}). The mean number of potential father trees occurring inside the area during a simulation run was $N_{\text{pot\_mean}} = 117$. By default, $P_{\text{outside}} = 0.62$

If mating success was weighted by dbh class, a similar method was applied. But instead of adjusting P_{outside} to N_{pot}, P_{outside} was adjusted to the sum of the weights of the potential father trees occurring inside the area at a given point in time during a simulation run, $\sum_{\text{pot}}$. Let $\sum_{\text{pot\_mean}}$ be the sum of the weights of the average population of potential father trees occurring inside the area during a simulation run, and let $\sum_{\text{fict}} = \sum_{\text{pot\_mean}} \times P_{\text{outside}}/(1 - P_{\text{outside}})$ be the fictitious sum of the weights of potential fathers occurring outside the area, then $P''_{\text{outside}} = \sum_{\text{fict}}/(\sum_{\text{fict}} + \sum_{\text{pot}})$.

In the case of $P_{\text{outside}} = 0$, father trees were always drawn from inside the area. Thus, for numerical reasons, we had to consider the special case where only one mother tree but no potential father tree was left inside the area (e.g. due to high mortality). In this special case, the father tree corresponded to the mother tree (selfing).

Appendix 2: Sensitivity measures

The sensitivity of an output variable Y to one input factor X_{i} (first order effect) is measured as the ratio between the output variance V_{i}, due to X_{i}, and the total output variance $V(Y)$ (Saltelli et al. 2004; Wernsdörfer et al. 2008):

$$S_{\text{i}} = \frac{V_i}{V(Y)}. \tag{1}$$

Similarly, the sensitivity of Y to two input factors X_{i}, X_{j} (second order effect) and three input factors X_{i}, X_{j}, X_{m} (third order effect) is measured as

$$S_{\text{ij}} = \frac{V_{\text{ij}}}{V(Y)} \tag{2}$$

and

$$S_{\text{ijm}} = \frac{V_{\text{ijm}}}{V(Y)}, \tag{3}$$

where V_{ij} and V_{ijm} are the output variances due to X_{i}, X_{j} and X_{i}, X_{j}, X_{m}, respectively. The variances V_{i}, V_{ij} and V_{ijm} are calculated as

$$V_{\text{i}} = V[E(Y|X_{\text{i}})], \tag{4}$$

$$V_{\text{ij}} = V[E(Y|X_{\text{i}}, X_{\text{j}})] - V_{\text{i}} - V_{\text{j}} \tag{5}$$

and

$$V_{\text{ijm}} = V[E(Y|X_{\text{i}}, X_{\text{j}}, X_{\text{m}})] - V_{\text{ij}} - V_{\text{im}} - V_{\text{jm}} - V_{\text{i}} - V_{\text{j}} - V_{\text{m}}, \tag{6}$$

where the expectation E is approximated as a mean.

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