Effects of Animal Pollination on Pollen Dispersal, Selfing, and Effective Population Size of Tropical Trees: A Simulation Study[1]

Bernd Degen[2]

INRA, Campus Agronomique, BP 709, 97387–Kourou cedex, France D.O.M. Guyane; Tel: +(0) 594-329290; Fax: +(0) 594-326914; E-mail: degen_b@kourou.cirad.fr

and

David W. Roubik

Smithsonian Tropical Research Institute, Apartado 2072 Balboa, Ancon, Panama; mailing address: Unit 0948, APO AA 34002-0948, U.S.A.; Tel: 011-507-212-8000; Fax: 011-507-212-8148; E-mail: roubikd@tivoli.si.edu

ABSTRACT

Animals, especially insects, are principal pollen vectors of tropical trees and have behavior patterns that affect gene dispersal. Here, we explore complex pollination systems using a new simulation model Eco-Gene and considering, among other factors, flowering synchrony, spatial distribution of trees, degree of selfing, population densities, pollinator flight distances, pollen deposition, and pollinator response to floral display size. Sensitivity analyses using two contrasting tree data sets (*Jacaranda copaia* and *Dipteryx odorata*) determined the importance of each parameter on three response variables: the proportion of seeds from self-pollination, effective population size, and pollen dispersal. Spatial considerations and attractiveness of floral displays were prominent features determining the population genetic result of pollinators, and some biological implications of the results are discussed.

RESUMEN

Animales, insectos en particular, son los vectores principales del polen de los arboles tropicales y como consecuencia su comportamiento afecta dispersión genética. Aquí se examina sistemas de la polinización en su totalidad, aplicando un nuevo programa de simulacro Eco-Gene, que se toma en cuenta, entre otros factores, sincronicidad de floración, distribución de arboles, grado de auto-fecundación, densidad poblacional, distancia de vuelo, polen deposición, y respuesta comportamiental de polenizadores al tamaño del anuncio floral. Sensitivity análisis con datos contrastantes de dos arboles (*Jacaranda copaia* y *Dipteryx odorata*) evaluó la importancia de cada parámetro y su resultado respeto a: la proporción de semillas producidas por autofecundación, tamaño poblacional efectivo, y distancia de dispersión del polen. Las cualidades espaciales de poblaciones, y la atractividad del anuncio floral determinaban fuertemente las consecuencias de polinizacion, y se considera implicaciones biológicas y genéticas de los resultados.

NEARLY ALL TROPICAL TREE SPECIES ARE POLLINATED BY ANIMALS. In wet lowland forest at La Selva, Costa Rica, only 3.6 percent of the trees are ostensibly wind-pollinated, whereas more than 50 percent of canopy species and greater than 36 percent of sub-canopy trees are pollinated by bees (Bawa *et al.* 1985). In a similar forest, bees pollinate up to 80 percent of understory plants (Rincón *et al.* 1999). In addition to bees, the study by Bawa *et al.* (1985) tallied 3 percent of tree species pollinated by bats, 4.3 percent by hummingbirds, 7.3 percent by beetles, 16 percent by moths, 4.3 percent by wasps, and 16 percent by small diverse insects. Whereas bees evidently comprise the standard pollinators in this Neotropical forest, many other animals with different characteristics of flight range and pollen dispersal capacity contribute substantially to fertilization and seed production among tropical trees worldwide.

Because animals are employed by trees as pollen vectors, behavioral flexibility disposes pollinators to manipulation by plant characteristics (Harder & Barrett 1996). The resulting mating pattern generally reflects both the behavior of the pollinator to move among neighboring flowers (reviewed by Levin & Kerster 1974, Roubik 1989) and residence of the flower's pollen on a pollinator during sequential visits to flowers (pollen carryover; Harder & Barrett 1996). Pollinator behavior is also strongly influenced by the population flowering phenol-

ogy (Frankie *et al.* 1990). The overall interaction determines (1) the proportion of cross-pollination, self-pollination, and biparental inbreeding; (2) the number and spatial origin of different pollen donors that are effective contributors to progeny (effective population size and gene flow by pollen dispersal); and (3) effectiveness of transmission of adult genetic diversity to progeny (the seed cohort). Thus, pollinators fundamentally determine maintenance and enrichment of genetic diversity in the plant population (Hamrick *et al.* 1992).

Unfortunately, few details have been elucidated on interactions among pollinator behavior, pollen carryover, and flowering phenology, or their net effect on pollen dispersal and tree mating system. A modeling approach is needed to help understand and integrate such diverse factors. In pioneering efforts toward synthetic modeling approaches, Bateman (1947) and Harder and Wilson (1998) studied pollen dispersal. In their models, a pollinator serves as both a pollen sink and a pollen source. With every flower visit, pollen is received on the body and some is also deposited on the visited flower. Pollen embarking on a pollinator's body decreases geometrically in abundance as flower visits occur. Other modeling approaches have postulated an optimal foraging strategy of pollinating bees according to a cost–benefit function (Waddington & Holden 1979). Further, Collevatti *et al.* (1997) used log linear models to describe the departure rules of pollinators from flowers of the tropical shrub *Triumfetta semitriloba*. Both models and observations showed that departure rules could be predicted from body size and energetic requirements, the pollen load size, resource availability, and the distribution and density of resource patches. Complementary models also considered plant–pollinator interactions. Bronstein *et al.* (1990) examined consequences of flowering asynchrony for reproductive success and long-term pollinator population maintenance within monoecious fig populations. In addition, Momose *et al.* (1998) modeled dynamics of aggressive generalist pollinators that replace nonaggressive specialists, as a function of floral display size.

The objective of this paper is to use simulations as a means of studying reasonably complex pollination systems. For this purpose, we developed a new version of the tree population–simulation model Eco-Gene (Degen *et al.* 1996), adding a new module for animal pollination. Our individual-based, spatially explicit model simulates pollen dispersal between trees (pollen donors) and pollen sinks (pollen receptors), representing a missing link. Specifically, our approach aims at deriving full-scale and community-level pollination models. The new module integrates several new factors into pollination simulation models. With these in place, a more realistic estimate is sought for population-level pollen dispersal, selfing, and outcrossing, and the effective population size N_e of tropical trees. Using sensitivity analysis, we tested the importance of the chosen factors, their interactions, and their biological relevance.

MATERIALS AND METHODS

MODEL.—The animal pollination model is integrated as a new module in the ecological–genetic simulation model "Eco-Gene." Eco-Gene was developed to evaluate effects of disturbance and human influence on the genetics of tree populations. It simulates the temporal and spatial dynamics of allele and genotype frequencies, tree growth, and demographic processes. Modules representing subsystems or component systems can be added to Eco-Gene. Overlapping or separate generations can be specified and a variety of mating systems, including different sexual systems (co-sexual to dioecious trees), temporal variation in flowering phenology, and individual variation in flowering intensities, can be implemented. The simulated genetic structures are of particular interest because they allow statistical "sensitivity studies" of the importance of single factors within a complex, integrated system. The model and its application are discussed further by Degen *et al.* (1996), Degen *et al.* (1997), Degen and Scholz (1998), and Degen *et al.* (2002).

ANIMAL POLLINATION MODULE.—To simulate pollen movement via pollinators, we defined a set of simple behavioral rules. Pollination as a whole is controlled by nine parameters. Our simulation generates foraging flights that lead to pollination and seeds in a population of individual trees. A flowchart for the module is given in Figure 1.

Among the traits affecting pollen dispersal (overviews in Roubik 1989, Harder & Barrett 1996, Richards 1997), we emphasize those relevant in tropical forests: (1) foraging range of the pollinators, (2) spatial distribution and nesting density of pollinators, (3) the extent that pollen remains on the pollinator's body over successive flower visits (pollen carryover) and after returning to the nest, (4) search rules, foraging constancy, departure rules from flower patches, (5) pollination self-incompatibility, (6) flowering phenology, (7) variation in inflorescence display size, (8) general response of pol-
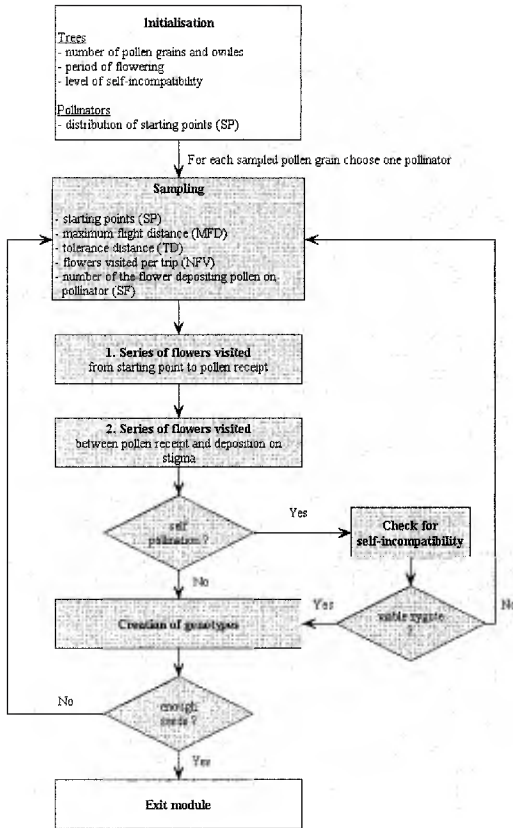
FIGURE 1. A flowchart of the animal pollination module in the simulation model Eco–Gene.

linators to display size, and (9) the spatial distribution and density of flowering plants.

INITIALIZATION.—The model receives input data on the *x*- and *y*-coordinates, diameters, and genotypes of each reproductive tree. The model also can generate artificial data sets or expand samples if inventories are unavailable or incomplete.

FLOWERING PHENOLOGY AND INTENSITY.—The model defines trees as reproductively active according to a minimum diameter (MD), set at 20 cm in all our simulations. Trees 20 cm or greater are candidates for flowering. Another parameter, percent trees flowering (PTF), determines how many candidates are flowering in a given period, fixed here at 80 percent. The program selects trees randomly among the candidates until the number indicated by PTF is reached. Flowering intensity (FI) of each tree is defined as inflorescence number. The program samples the relative flowering intensity for

each tree from a normal distribution ($\mu = 100$, $\sigma = 30$). These values are normalized afterwards with the maximum value so that each tree is assigned a relative flowering intensity varying between 0 and 1. For hermaphroditic trees, the male and female flowering intensity and flowering period are assumed to be identical. Again, the model samples a starting date for flower production from two normal distributions: one for each flowering tree (SDF, $\mu = 0$, $\sigma = 4$) and one for duration of flowering (DF, $\mu = 10$, $\sigma = 2$). Only trees that have an overlap in flowering can mate. The model assumes constant flowering intensities for a tree during the entire flowering period (SDF + DF). Different factors control the self-incompatibility of a tree (SI) to avoid selfing. The program samples, for each tree, a level of self-incompatibility (SI) from an equal distribution with an area between 0.8 and 1. Randomly distributed "starting points of pollinators" (SP) initiate a simulation run. Such points represent, for example, the location of bee or bird nests, or bat roosts. Pollinators begin and finish their flights at such locations—as central-place foragers. Pollination events occur on the foraging trip, but pollen also might remain on the pollinator and reach a stigma on a subsequent foraging trip (similar to secondary pollen dispersal; Hatjina *et al.* 1999). The density of starting points per hectare (DSP) is a parameter of the model (Table 1).

POLLINATION.—The task of the pollination module is to determine the parents of each seed. After initialization, the program simulates foraging flights that lead to pollination (pollen deposition or dispersal to stigmatic surfaces, but not necessarily fertilization) until a predefined number of seeds has been produced. Seed number is selected so that a reliable estimate of output variables is possible. The pollen donor (male tree) is the tree on which the pollinator receives pollen and the seed tree (maternal tree) is the tree on which the pollen grain has been deposited on a stigma. A pollen grain that creates (together with the ovule) a zygote is called a "successful" pollen grain. For hermaphroditic or monoecious tree species, the paternal and maternal tree may 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 on two series of foraging flights; a first series from the starting point (nest, hive) to the tree of pollen receipt and a second series from the tree of pollen receipt to the tree on which the pollen is deposited on a stigma. Only trees that have the same flowering period as the first tree vis-

TABLE 1.   *Parameters and their ranges used to generate data for sensitivity analyses. Two 1000-sample series of parameter configurations were used in simulations, each a random value between "Min" and "Max." The first series used parameters 1 through 9 and the second included all parameters but P5, which showed no significant impact according to sensitivity analysis of the first series.*

No.	Parameter	Description	Min	Max
1	MFD	Maximum flight distance (m)	300	1200
2	NFV	Number of flowers visited per trip	5	50
3	TD	Tolerance distance (m)	10	150
4	PTC	Probability of tree change	0	0.2
5	DFP	Deposition fraction pollen	0	0.5
6	ATE_F	Attractor effect finding	0	1
7	ATE_R	Attractor effect remaining	0	1
8	DSP	Starting points per hectare	0.1	30
9	DFN	Deposition fraction nest	0.7	1
10	SF_SD	Standard deviation for start of flowering (d)	0	10
11	FE_SD	Standard deviation of fertility	0	800

ited 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 (Fig. 1). Because of the phenological component indicated by the need for overlapping flowering between individuals, samples represent the entire flowering period.

First series of pollinator movement (from the nest to the flower of pollen receipt).—For each successful pollination deposition of a pollen grain on a stigma, the program randomly selects a starting point (SP) for the pollinator. In our model, all visited trees must be located within the radius of the maximum flight distance (MFD) around the starting point (SP). From this starting point, the pollinator may move up to a maximum flight distance (MFD). During flight, the pollinator may visit several trees and more than one flower on each tree. The maximum flight distance, or foraging range, is defined by pollinator size and physiology, or known behavior (Table 1). Before the pollinator starts a foraging flight, the program determines the number of flowers visited per trip (NFV). This value is sampled from a normal distribution with a mean NFV_M and a standard deviation NFV_SD (Table 1). The model assumes that the pollinator can receive a successful pollen grain with equal probabilities at any flower during a trip. Hence, a value is randomly designated for the number of the flower (SF) depositing pollen on the pollinator's body ($1 \leq SF \leq NFV$). The next step of the program is to simulate all the flights from the starting point (SP) up to this flower (SF). Thereby, a parameter (PTC) controls the probability that the pollinator changes its foraging tree between two sequential flowers (Table 1). The movement of the

pollinator from the starting point to the first tree and the selection of the following trees is controlled in our model by (a) the physical distance between the current positions of the pollinator and candidate trees, (b) the attraction values for trees (attractor effect for finding a tree, ATE_F), and (c) the flowering synchrony of the trees. Our hypothesis is that the pollinator minimizes flight distances and prefers trees with more flowers (Fig. 2). In our model, the relative flowering intensity influences both an attractor effect for remaining (ATE_R) on a plant and the attractor effect for flying to a particular candidate plant (ATE_F). These parameters have weights that can vary between 0.0 and 1.0 (Table 1). If the pollinator moves from the starting point to the first tree or from one tree to another, the tree selected has the smallest effective distance (ED) from the actual pollinator location. The effective distance (ED) is a function of physical distance, weighted by tree attractiveness with an additional stochastic component (TD) reflecting unpredictability of the pollinator decision: $ED = PD - (PD \times RFI \times ATE\_F) + RND \times TD \leq MFD$, where ED: effective distance; PD: physical distance; RFI: relative flowering intensity; ATE_F: attractor effect for finding; RND: random number between 0 and 1; TD: tolerance distance; and MFD: maximum flight distance.

Figure 2 depicts decisions of a pollinator in the module. The circles in the figure represent trees. The central circle shows the actual position of the pollinator. The pollinator cannot move more than the maximum flight distance (MFD) of 1000 m in this example. Gray circles are the trees A, B, C, and D that are flowering on the same day as the central tree. The diameters of the circles are proportional to the flowering intensities. The black
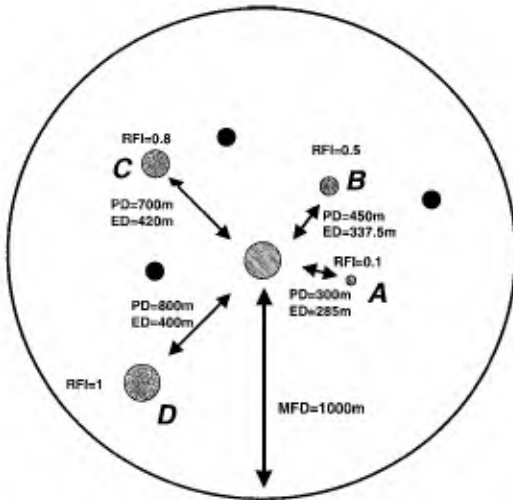
FIGURE 2. Modeled departure rules for a pollinator. The circles in the figure represent trees. The central circle shows the actual position of the pollinator. The decision as to which tree the pollinator will move to next depends on the maximum flight distance (MFD), synchronization in flowering, physical distance (PD), relative flowering intensity (RFI), stochastic uncertainty (TD), and a relative attractor effect (ATE_F), giving a weight to the flowering intensity. The decision is based on the shortest effective distances (ED), which is a function of PD, RTI, and ATE_F (see description in the text).

circles represent trees that do not flower at all or not at the same time. Hence, they are not candidates for pollinator visitation. Without any weight given to flowering intensity, the pollinator would select tree A with the shortest physical distance (PD) as its next destination. But this decision changes if we consider a certain attractor effect (ATE_F), as a function of flowering intensity. The relative flowering intensity (RTI) is a value between 0 and 1. These are the real values normalized with the maximum flowering intensity found in the population. Let us assume a weight of 0.5 (ATE_F). We can then calculate the effective distances (ED) for the trees A, B, C, and D (Fig. 2). Assuming a stochastic uncertainty of TD = 50 m, the pollinator may move to tree A or B.

Using information on the relative flowering intensity (RFI) and a second attractor effect for remaining on a tree (ATE_R), the program calculates the relative probability of moving (shifting) between trees while visiting two sequential flowers (R_PTC = PTC − (PTC × RFI × ATE_R). A random number between 0 and 1 is generated. If the number is lower than R_PTC, the program searches for the next tree visited by the pollinator.

Again, the next tree is selected according to the effective distance (ED) of all candidate trees from the last tree visited. Necessary conditions for trees to be a candidate are an overlap in flowering and the physical distance to the starting point SP must not exceed the maximum flight distance (MFD). The tree presenting the last flower of this series is the pollen donor (male tree).

SECOND SERIES OF POLLINATOR MOVEMENT (FROM THE POLLEN DONOR TO THE MATERNAL TREE).—A second series is simulated of all flowers visited, starting with pollen receipt by the pollinator and ending with pollination (stigmatic receipt of pollen). The program calculates the number of flowers visited up to pollination (NFP). This is determined by the deposition fraction (DFP) controlling pollen carryover (Table 1). While visiting a flower, the pollinator removes R pollen grains, of which a fraction π remains on its body as it moves to the next flower. Simultaneously, the floral stigma receives a fixed proportion DFP (deposition fraction) of pollen already carried, so that the fraction $1 - p$ "carries over." If the deposition fraction is low, many flowers may be visited before pollen is deposited. Using information on relative flowering intensity (RFI) and the attractor effect (ATE_R), the program calculates the relative probability of moving between trees while visiting two sequential flowers (R_PTC = PTC − (PTC × RFI × ATE_R). The pollinator returns to the starting point in the case that the total number of flowers visited exceeds the maximum flowers visited per trip. Pollination events occur on the foraging trip, but pollen also may remain on the pollinator and reach a stigma on a subsequent foraging trip. Thus, we introduced a second path of pollen carryover in our model termed ramified pollination (Roubik 2002). This pollen carryover is controlled by the deposition fraction of pollen in the nest (DFN; Table 1). In this case, a random number between 0 and 1 is generated. If the number is lower than the deposition fraction of pollen in the nest (DFN), the program restarts with another pollinator and starting point ("sampling" in Fig. 1); if higher, the program continues with the selected pollinator. The tree presenting the last flower of this series is the mother tree (stigma and seed source). After pollination, another module process is implemented. In self-pollination, a random number between 0 and 1 is generated and no seed will be produced if the number is lower than the level of self-incompatibility of the mother tree (SI). The genotype of the seed is generated using segregated haplotypes of

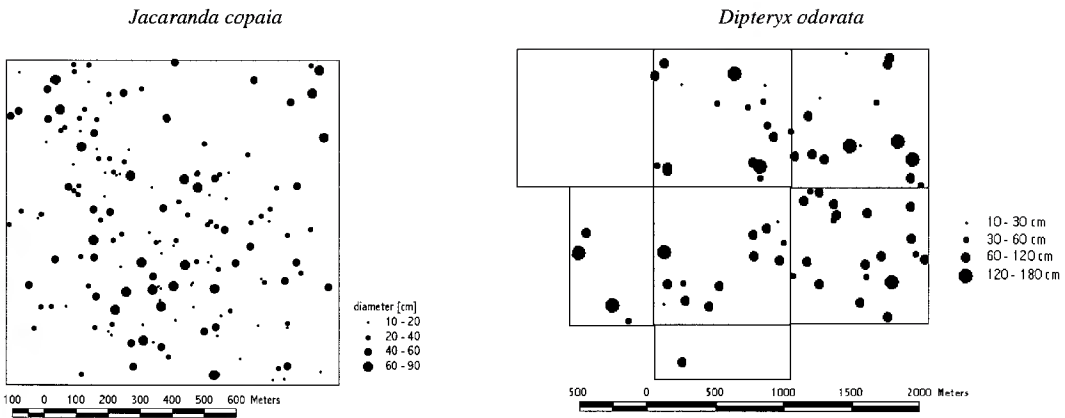*Jacaranda copaia*   *Dipteryx odorata*

FIGURE 3.   Spatial distribution of the *Jacaranda copaia* and *Dipteryx odorata* trees in experimental plots in Tapajós (see text).

pollen donor tree and pollen recipient tree. The program goes back to the beginning of step "sampling" (Fig. 1) and repeats the procedure until all seeds are produced.

TREE POPULATIONS.—Eco-Gene requires input data on tree spatial positions, stem diameters, and genotypes. To test the impact of tree density and spatial structure on animal pollination, we used two data sets based on forest inventory (stem diameter and tree position) for *Jacaranda copaia* Aublet (Bignoniaceae) from a 100 ha experimental plot and *Dipteryx odorata* Wild. (Fabaceae) from 500 ha plots in the Tapajós National Forest south of Santarém (Pará, Brazil). The field data were collected by the Dendrogene project, a research effort jointly supported by the Brazilian government (EMBRA-PA) and the British government (Department for International Development). The inventory was made by Maflops, a timber company with a logging concession for this site, under the supervision of IBAMA. All trees with a minimum diameter at breast height of 10 cm were measured and mapped for *Jacaranda* and all trees with a minimum diameter of 20 cm for *Dipteryx* (Fig. 3). The density of reproductive trees with a diameter 20 cm or greater is more than ten times higher in the plots of *Jacaranda* (N/ha = 1.8) than of *Dipteryx* (N/ha = 0.16).

Jacaranda copaia is a light-demanding pioneer tree species, germinating and growing in gaps within the forest and eventually recruiting into the canopy. It is a common component of both primary and secondary forests throughout Central and South America. Each flowering tree produces a large, showy display of lavender flowers above the crown. The hermaphroditic, zygomorphic flowers are pollinated by medium to large-sized bees (Maués 2001). Seeds are wind-dispersed. Genetic studies have shown nearly complete self-incompatibility (James *et al.* 1998). Flowering is synchronized and occurs in Pará (Brazil) during the dry season from July to September (Maués 2001).

Dipteryx odorata is a fast-growing climax species. The species is distributed from Central America to northern South America. It is hermaphroditic and pollinated by the same guild of medium to large traplining bees as *J. copaia* (Maués 2001). Its seeds are dispersed by bats and rodents. Flowering is largely asynchronous and occurs in Pará (Brazil) during the dry season from June to December (Maués 2001).

SIMULATION OUTPUTS.—The response parameters of pollination were calculated for 200 seeds generated in each simulation run. In the sensitivity analysis, we tested the impact of the model parameters on the following three output variables of the simulations. (1) The effective population size N_e (Gregorius 1991) is calculated as: $1 \leq N_e = 1/\Sigma w_i^2 \leq N$, where w_i = relative contribution of successful haplotypes of tree i (pollen, ovules) to the sampled seeds and N = absolute number of adult trees. Thus, N_e as defined is analogous to diversity measures and estimates the individual tree contribution of male and female haplotypes in seed production. N_e is a useful measure of genetic diversity and genetic differentiation. With decreasing N_e, the level of genetic diversity decreases and the genetic differentiation between an adult population and seed

cohort increases (Degen & Scholz 1996, Degen *et al.* 1996). (2) The second output variable is the proportion of selfed seeds S, among the 200 seeds produced, resulting from self-pollination. (3) The third variable is the arithmetic mean of pollen dispersal distance (mPD); for each seed, the spatial distance between pollen donor tree and seed tree has been measured.

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. Table 1 represents a list of input parameters in our model and the test interval. We made two series of sensitivity analysis with each tree data set. A first series included only parameters of the pollination module (P1–P9). In a second series, we added flowering phenology (P10) and variation in flowering intensity (P11). The comparison between the results of the first and second series should give us some ideas about the interaction of flowering phenology and variation of individual fertilities with the parameters of pollinator behavior and pollen carryover. Each series included 1000 random samples of parameter values within the interval. As output variables, we computed mean pollen dispersal (mPD), the proportion of selfs (S), and the effective population size (N_e) for each sample. Because we could not exclude the possibility of nonlinear 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 nonlinear but monotonic (Iman & Conover 1979). Finally, the sensitivity of the response parameters to the variation in input parameters was tested with a stepwise multiple regression analysis using rank transformed values (Nathan *et al.* 2001).

RESULTS

Sensitivity analysis: First series.—Selfing. The first series of 1000 random samples for parameter configurations gave a mean value for selfing of 0.129 (SD = 0.072) for *Jacaranda* and a mean of 0.157 (SD = 0.077) for *Dipteryx* (Table 2). Results of the stepwise multiple rank regression showed that the first series of tested parameters for the animal pollination module explained 57 percent of the variation in selfing (S) using the tree data set for *Jacaranda* and 44 percent for *Dipteryx*. For both data sets, the probability of tree change (PTC) had

the highest impact on selfing (R^2 = 47%, R^2 = 30%). As expected, a higher probability of tree change led to a lower proportion of selfing (negative correlation coefficient β). All other significant parameters together explained only 10 percent more of the variation in *Jacaranda* and 14 percent more in *Dipteryx*. Among these, the next two important parameters were the attractor effect to remain on a tree (ATE_R) and the deposition fraction in the nest (DFN).

In the case of *Jacaranda*, additional stochastic effects in the selection of trees by the pollinator (tolerance distance, TD) reduced the amount of selfing, but the same parameter had no significant impact for *Dipteryx*. The attractor effect in finding a tree (ATE_F) had a small but significant positive effect on selfing for *Jacaranda*. With *Dipteryx*, this effect was absent, but a significant negative effect existed for the maximum flight distances (MFD) of the pollinators.

Effective population size N_e. The 1000 random samples of parameter configurations gave a mean N_e of 47.2 (SD = 14.7) for *Jacaranda* and a mean of 20.9 (SD = 3.2) for *Dipteryx* (Table 2). The stepwise multiple rank regression explained 63 percent of the variation in N_e for *Jacaranda* but only 8.3 percent for *Dipteryx*. In both cases, the attractor effect for finding a tree (ATE_F) had the strongest effect. Moreover, this was the only parameter with a significant effect for *Dipteryx*. With increasing attractor effect (ATE_R), the effective population size decreased. For *Jacaranda*, four other parameters (TD, MFD, NFV, and DSP) had significant effects, but those parameters improved predictions less than 1 percent.

Mean pollen distance (mPD). A mean pollen dispersal of 147.9 m (SD = 42 m) was generated for *Jacaranda*. For *Dipteryx*, the mean value was twice as large (335.6 m; SD = 72.5 m). For *Jacaranda* six, and for *Dipteryx* five, of nine tested parameters produced significant effects on pollen dispersal in the multiple regression analysis. They explained 64 percent of the variation for *Jacaranda* and 57 percent for *Dipteryx*. The parameter rank differed for the two tree data sets. For the dense tree population of *Jacaranda*, the attractor effect for finding a tree (ATE_F) was the most important parameter, but for *Dipteryx*, the maximum flight distance (MFD) was most important. In addition, both cases showed that increasing the number of flowers visited per foraging trip (NFV) had a significant negative effect on pollen dispersal distances. The effects of the other parameters agreed with our intuitive expectations: higher deposition frac-

TABLE 2. *Results of the first sensitivity analysis—stepwise multiple regression of proportion of selfing (S), effective population size N_e, and mean pollen dispersal distance (mPD) against the main input parameters of the animal pollination module (Table 1) using two tree data sets, Jacaranda and Dipteryx. R^2 = the fraction of the variance accounted for by the model, adjusted for the number of independent variables; β = standardized regression coefficient.*

	Selfing (S)							
	Data set *Jacaranda* $S = 0.129 \pm 0.072$				Data set *Dipteryx* $S = 0.157 \pm 0.077$			
Step	Parameter	R^2	β	$P > t$	Parameter	R^2	β	$P > t$
1	PTC	0.471	−0.683	0.000	PTC	0.303	−0.545	0.000
2	ATE_R	0.514	0.216	0.000	DFN	0.364	0.249	0.000
3	DFN	0.553	0.201	0.000	ATE_R	0.419	0.230	0.000
4	TD	0.562	−0.099	0.000	NFV	0.442	0.159	0.000
5	NFV	0.568	0.079	0.000	MFD	0.446	−0.067	0.005
6	ATE_F	0.571	0.055	0.008				

	Effective population size (N_e)							
	Data set *Jacaranda* $N_e = 47.2 \pm 14.7$				Data set *Dipteryx* $N_e = 20.9 \pm 3.2$			
Step	Parameter	R^2	β	$P > t$	Parameter	R^2	β	$P > t$
1	ATE_F	0.632	−0.795	0.000	ATE_F	0.083	−0.289	0.000
2	TD	0.635	0.050	0.009				
3	MFD	0.637	−0.051	0.007				
4	NFV	0.638	−0.042	0.028				
5	DSP	0.639	0.039	0.039				

	Mean pollen distance (mPD)							
	Data set *Jacaranda* $mPD = 147.9 \pm 42.0$				Data set *Dipteryx* $mPD = 335.6 \pm 72.5$			
Step	Parameter	R^2	β	$P > t$	Parameter	R^2	β	$P > t$
1	ATE_F	0.409	0.656	0.000	MFD	0.468	0.681	0.000
2	NFV	0.513	−0.330	0.000	NFV	0.532	−0.258	0.000
3	DFN	0.566	−0.220	0.000	DFN	0.560	−0.166	0.000
4	MFD	0.603	0.204	0.000	ATE_F	0.573	0.121	0.000
5	TD	0.640	0.193	0.000	PTC	0.579	0.081	0.000
6	PTC	0.643	0.056	0.002				

tions in the nest (DFN) reduced the pollen dispersal distances. The probability for tree shifts (PTC) increased total pollen dispersal distance in both cases, and a higher tolerance distance (TD) increased pollen travel distances for *Jacaranda*.

Surprisingly, the deposition fraction of pollen on flowers (DFP) controlling pollen carryover had no significant effect for the three response parameters. For each response parameter, the proportion of explained variation was higher in *Jacaranda* compared to *Dipteryx*. We repeated the entire first series to check if the 1000 samples were sufficient. We obtained nearly the same values and the same ranking of sensitive parameters. Hence, we concluded that the 1000 samples were adequate.

SENSITIVITY ANALYSIS: SECOND SERIES.—Flowering phenology. Significant parameters of the first series

were combined with phenology—a standard deviation for the initiation of flowering (SF_SD) and another parameter controlling variation in flowering intensity of trees, the standard deviation of fertility (FE_SD). Results are given in Table 3. Variation of the parameter deposition fraction of pollen (DFP) was excluded from further analysis because no significant impact was found in the first series. We fixed this value at 0.05 in all simulations.

Selfing. The results of the stepwise rank correlation were similar between the first and second series. The proportion of explained variation was not improved compared to the first series. For both data sets, the probability of tree change (PTC) was the most important parameter, followed by the attractor effect to remain on a tree (ATE_R), the deposition fraction of pollen in the nest (DFN), and the number of flowers visited per foraging trip

TABLE 3. *Results of the second sensitivity analysis—stepwise multiple regression of proportion of selfing (S), reproductive effective population size (N_e), and mean pollen dispersal distance (mPD) against the main input parameters of the animal pollination module + parameters for variation in flowering phenology and tree fertilities (Table 1) using two tree data sets,* Jacaranda *and* Dipteryx. R^2 = *the fraction of the variance accounted for by the model, adjusted for the number of independent variables;* β = *standardized regression coefficient.*

		Selfing (S)						
	Data set *Jacaranda* $S = 0.131 \pm 0.069$				Data set *Dipteryx* $S = 0.157 \pm 0.078$			
Step	Parameter	R^2	β	$P > t$	Parameter	R^2	β	$P > t$
1	PTC	0.453	−0.670	0.000	PTC	0.260	−0.501	0.000
2	ATE_R	0.508	0.230	0.000	ATE_R	0.320	0.251	0.000
3	DFN	0.552	0.213	0.000	DFN	0.352	0.185	0.000
4	NFV	0.561	0.094	0.000	NFV	0.372	0.142	0.000
5	SF_SD	0.565	0.073	0.000	SF_SD	0.380	0.088	0.000
6	TD	0.568	−0.054	0.001				

		Effective population size (N_e)						
	Data set *Jacaranda* $N_e = 42.4 \pm 13.6$				Data set *Dipteryx* $N_e = 18.4 \pm 3.7$			
Step	Parameter	R^2	β	$P > t$	Parameter	R^2	β	$P > t$
1	ATE_F	0.508	−0.703	0.000	FE_SD	0.191	−0.445	0.000
2	FE_SD	0.644	−0.367	0.000	ATE_F	0.244	−0.232	0.000
3	NFV	0.648	−0.065	0.000	SF_SD	0.290	−0.220	0.000
4	MFD	0.651	−0.059	0.002	NFV	0.297	−0.085	0.001
5	SF_SD	0.654	−0.050	0.008	TD	0.302	0.073	0.006

		Mean pollen distance (mPD)						
	Data set *Jacaranda* mPD $= 162.5 \pm 50.2$				Data set *Dipteryx* mPD $= 352.9 \pm 93.8$			
Step	Parameter	R^2	β	$P > t$	Parameter	R^2	β	$P > t$
1	SF_SD	0.312	0.569	0.000	MFD	0.370	0.624	0.000
2	ATE_F	0.574	0.506	0.000	SF_SD	0.531	0.408	0.000
3	NFV	0.625	−0.235	0.000	NFV	0.566	−0.188	0.000
4	MFD	0.664	0.195	0.000	DFN	0.587	−0.142	0.000
5	TD	0.684	0.167	0.000	ATE_F	0.607	0.142	0.000
6	DFN	0.708	−0.145	0.000	FE_SD	0.611	0.065	0.001
7	FE_SD	0.726	0.135	0.000	PTC	0.613	0.046	0.021

(NFV). For the two new parameters tested, variation in flowering phenology (SF_SD) had a significant positive effect on selfing for both trees.

Effective population size (N_e). For both trees, explained variation was higher in the second series (*Jacaranda*: $R^2 = 65$ vs. 63%; *Dipteryx*: $R^2 = 30$ vs. 8.3%). This improvement was caused by the introduction of variation in flowering intensities (FE_SD), which had a significant negative effect on N_e. This parameter was, together with the attractor effect of finding a flower (ATE_F), relatively important and explained 14 percent of the variation for *Jacaranda* and 19 percent for *Dipteryx*.

Mean pollen dispersal distance (mPD). Pollen dispersal distance could also be more fully explained by the second series (*Jacaranda*: $R^2 = 72$ vs. 64%; *Dipteryx*: $R^2 = 61$ vs. 57%). For *Jacaran-*

da, variation in flowering phenology (SF_SD) ranked first and was second in importance for *Dipteryx*. A higher variation in flowering phenology made pollinators fly greater distances. Likewise, variation in flowering intensity (FE_SD) had a significantly positive but weak effect on pollen dispersal distances.

Generally, the means and standard deviations of the three response variables—selfing (S), effective population size (N_e), and mean pollen dispersal distance (mPD)—were similar to values observed in the first series.

DISCUSSION

LIMITS OF THE MODEL.—Our model included a parameter set that fits a certain pollinator profile, and

TABLE 4.   *Flowering phenology of five tropical tree species in the Tapajós National Forest (N. V. Martins Leao, EMBRAPA Belém, pers. comm.)—shortest individual flowering interval (Min FI), longest individual flowering interval (Max FI), total flowering interval of all studied trees (Total FI), and proportion of flowering trees (F %).*

Species	Year	Min FI (d)	Max FI (d)	Total FI (d)	F %
Caryocar glabrum	1985–1986	29	85	86	60
Bertholletia excelsa	1986–1987	15	122	127	100
Goupia glabra	1985	34	61	166	70
Manilkara huberi	1988	41	111	141	100
Vochysia maxima	1985–1986	14	58	155	40

thus does not portray the full range of complexity in plant–pollinator systems. In accordance with their general importance as pollinators, we paid special attention to social and solitary bees, but by no means exhausted the possibilities of modeling even for this particular group. Some aspects of ecology or behavior that are specific to other kinds of pollinators were not considered (*e.g.*, hummingbird territoriality or the large role of wind dispersal for tiny pollinating thrips or fig wasps). For trees with pollinators that show aggressive territoriality, the size of the defended territory defines the area in which pollination can occur. Hence, there is an obvious effect of pollinator behavior on gene flow and selfing or outcrossing rate (Feinsinger 1978, Franceschinelli & Bawa 2000). The contribution of each pollinator species produces the overall effect on gene flow, which must therefore vary stochastically with relative species abundance.

We used the same range of parameters for both *J. copaia* and *D. odorata*. Our main interest was to test the interaction of the tree population traits with model parameters; however, the biological differences between the two tree species may also require different parameter configurations. Whereas assemblages of pollinating bees are quite similar, the flowering phenology of *Dipteryx* is relatively much less synchronized (Maués 2001).

James *et al.* (1998) observed (using genetic markers) that in *J. copaia*, the net selfing rates were 0.018 and 0.057, indicating nearly complete outcrossing. Our simulations estimated that *Jacaranda* produced self-pollinated seeds in a proportion of 0.12. Such differences between empirically observed selfing and simulation results can be explained by an underestimate of self-incompatibility and inbreeding depression in the model. In the model, the probability that a self-pollinated ovule reached maturity was defined by a single parameter called "self-incompatibility." But in nature, incompatibility mechanisms and inbreeding depression reduce net self-pollination and the proportion of selfed seeds at several stages (Husband & Schemske

1996). Some allelic self-incompatibility systems prevent germination of pollen tubes from self-pollination. At later stages, inbreeding depression leads to postembryonic mortality. Evidently, among predominantly outcrossing species the former mechanism dominates, and species favoring self-fertilization display lower inbreeding depression (Husband & Schemske 1996).

The simulated effective population sizes N_e of 42 for *Jacaranda* and 18 for *Dipteryx* may appear small compared to other published values. For example, Eguiarte *et al.* (1993) found that the palm *Astrocaryum mexicanum* had an N_e between 23 and 100. Although there are no comparable data for the two trees that we studied, a conservative estimated effective population size is the direct result of small absolute population size used as input data for our simulations ($N = 180$ for *Jacaranda* and $N = 90$ for *Dipteryx*). Further, no gene flow from outside the populations was considered. Hence, the estimated N_e must be less than the real value. Nonetheless, relative values for the two trees were useful for our analysis of parameter sensitivity in the animal pollination model. A second reason for a difference results from the formula used to calculate N_e. Our estimate was based on the relative fitness of reproductive trees. In the literature, N_e is often calculated based on variance of gene flow and genetic differentiation among subpopulations (Eguiarte *et al.* 1993).

BIOLOGICAL EVIDENCE FOR THE TESTED PARAMETER RANGE.—The flowering pattern of tropical tree species, such as the number of flowering events per year and the percentage of flowering trees, is highly variable among tree species and may vary among years (Newstrom *et al.* 1994). In the model, we fixed a percentage of flowering trees at 80 percent and assumed annual flowering. Table 4 contains data on flowering phenology of five tree species studied in Tapajós National Forest (N. V. Martins Leao, EMBRAPA Belém, pers. comm.). The percentage of trees flowering varied in this study be-

tween 40 and 100 percent. The programmed value of 80 percent is probably an overestimate for *D. odorata*, which is known to flower intensely every five years (M. Kanashiro, pers. comm.).

The minimum diameter of flowering trees has been observed for several tree species. Such values seem relatively constant over years and depend mostly on tree species. Unfortunately, we have no values for the two tree species used in this study, but observations for other species provide an indication. Caron *et al.* (1998) observed that in *Dicorynia guianensis* the minimum diameter of flowering trees was 22 cm in French Guiana. Aldrich *et al.* (1998) reported 8.5 cm for *Symphonia globulifera*, while *Vouacapoua americana* and *Simaruba amara* flowered at 25 cm (Vargas & Portocarrero 1992, Forget 1994). Stacy *et al.* (1996) reported a minimum diameter of 30 cm for flowering *Calophyllum longifolium*, *Spondias mombin*, and *Turpinia occidentalis* in Panama. Hence, the minimum diameter of 20 cm in our simulations seems reasonable.

Studies describing maximum pollinating distances (MFD) of bees have included African honeybees in which experimental studies in Congo forest demonstrated common foraging distances up to 1.6 km (Roubik 1999), while other forest studies have shown foraging radii of 8 km (Roubik 1989). Release–recapture studies with the tropical stingless bees (Meliponini) showed flight distances of 2.2 km (Roubik 1989). Dick (2001) measured (by paternity analysis) maximum flight distances of 3.2 km for *Dinizia excelsia* in Manaus, also visited chiefly by the exotic honeybees. Maués (2001), in the experimental site Moju (Pará, Brazil), identified the main pollinators for *J. copaia* as the bees *Epicharis*, *Centris*, *Bombus transversalis*, and *Euglossa* and for *D. odorata*, many of the same medium to large species of *Bombus*, *Eulaema nigrita*, *Epicharis*, and *Xylocopa frontalis*. These are certainly capable of foraging up to 1200 m from the nest (Roubik 1989)—the maximum distance of pollinator movement used in our simulation, which although probably conservative, corresponded to the size of the tree inventory areas.

Pollinators visit a certain number of flowers (NFV) before returning home, in a sequence determined by behavior. Solitary bees and most large-bodied pollinators potentially move between several individual trees in a foraging sequence. In contrast, social bees or small pollinators will generally go to only one tree and then return to the nest (Nagamitsu & Inoue 1997). Heinrich (1979) computed a range of 5 to 200 flowers visited by *Bombus*. Such

pollinators, however, may make sequential foraging trips to different trees or leave viable pollen in the nest (Hatjina *et al.* 1999, Roubik 2002). This pollen can be transported out of the nest on subsequent foraging trips, even on bees that did not bring it in the nest. On Barro Colorado Island in Panama, Roubik (2002) studied viability of pollen on stingless bees (*Trigona fulviventris*) leaving the nest. Less than 10 percent of the pollen grains had lost their viability. The pollen diversity on exiting bees increased gradually through the day, indicating pollen transfer among bees in the colony (termed "secondary pollen dispersal"). Results have shown that even aggressive, highly eusocial bees rapidly change their individual foraging sites (Roubik 2002). Both the tendency to trapline and to change foraging routes and effect ramified pollination are controlled in the model with the parameters probability of tree change (PTC) and deposition fraction nest (DFN).

The parameter describing deposition fraction of pollen (DFP) controls pollen carryover between flowers in a visitation sequence. Published data show deposition fractions of *ca* 0.2 for bumblebees (Waddington 1981) and 0.1 for pollinators of *Erythronium grandiflorum* Pursh (Harder & Wilson 1998). In other simulation studies of pollen carryover, deposition fractions ranging from 0.01 to 0.2 were used, while pollen carryover between foraging trips was not considered (Harder & Wilson 1998).

Flowering intensities play an important role in attraction of pollinating bees (Waddington & Holden 1979, Waddington 1980, Harder & Barrett 1996, Nagamitsu & Inoue 1997). It is known that large inflorescences often attract more pollinators than small inflorescences because the proximity of many flowers reduces pollinator flight costs (Harder & Barrett 1996). In our model, the relative flowering intensity influences both the attractor effect for remaining on a plant (ATE_R) and the attractor effect for flying to a particular subsequent plant (ATE_F). These parameters vary between 0.0 and 1.0 and have standard values of 0.5. Whereas there is strong evidence for the presence and importance of an attractor effect, the way to model the phenomenon is at a preliminary stage.

The parameter for starting points per hectare (DSP) describes the density of bee colonies or any home base for other types of pollinators. A study in moist lowland forest in Panama yielded an estimated density of 6.0 nests/ha for a total of 14 different stingless bees (Meliponini; Roubik 1993), but the nest densities of other bees (most species

are solitary; Rincón *et al.* 1999) are unknown. Surveys on bee nests in the Neotropics (Hubbell & Johnson 1977, Johnson & Hubbell 1984) and in Southeast Asian forests (Roubik 1993, Nagamitsu & Inoue 1997) estimated 2–6 such colonies/ha. These studies were made on non-*Apis* bees that form large perennial colonies. Estimates on the density of honeybee colonies are lower (1 colony/ 100 ha [Seeley 1985]; 2 colonies/100 ha in Amazonia [Roubik & Stierlin, pers. obs.]).

Cruz Alencar (1998) reported normal duration of flowering in the Reserva Florestal Ducke at Manaus of three months for *J. copaia* and of four months for *D. odorata*, while Maués (2001) showed that in Pará, Brazil, flowering by *D. odorata* lasted three months longer and was less synchronized than that of *J. copaia*. In our model, this was mimicked with differences in the beginning of individual tree flowering of up to two months and varied duration of flowering (SF_SD and DF). The overall flowering period of the modeled population covered maximum periods of 2.5 months. The minimum duration of individual flowering periods varies between 15 and 41 days among other trees with available data in the study area (Table 4) and the longest individual flowering periods are in a range from 58 to 122 days. The total flowering interval for all studied trees of each species varies between 86 and 166 days. As a measure of temporal differentiation in flowering, we can use the relation of the shortest individual flowering interval compared to the total flowering interval of a population. Values closer to 0 indicate strong differentiation in flowering and values closer to 1 indicate strong synchronization. The experimental data gave estimates between 0.09 and 0.33 and the smallest value possible in the simulation was 0.13. Hence, the simulated individual differentiation in flowering phenology has values found in nature.

Compared to observations in the literature, our modeled variation in fertility (FE_SD) seems to be moderate. For example, Otero-Arnaiz & Oyama (2001) studied the pollination ecology and reproductive phenology of a dioecious palm, *Chamaedorea alternans* in Veracruz, Mexico during 1995–1996. Individual plants showed large variation in the number of inflorescences produced. Five female and eight male plants (out of 25 and 37 plants, respectively) produced 45 percent of all inflorescences in the population studied. These five females also produced *ca* 75 percent of all fruits. Another study (Bila *et al.* 1999) showed that among teak (*Tectona grandis*) planted in Mozambique, the 20 percent most fertile trees produced 55 percent of the gametes.

SENSITIVITY OF PARAMETERS.—The impacts of some parameters on selfing fit intuitive expectations. Greater likelihood for tree change (PTC) and higher stochastic selection (tolerance distance, TD) reduced the proportion of selfing (S) and stronger attractor effects to remain on the tree (ATE_R), and along with stronger temporal differentiation in flowering (SF_SD), increased the proportion of selfing. The attractor effects (ATE_R) caused the pollinator to stay longer and visit more flowers on the same tree. Hence, the probability of depositing pollen grains on flowers of the same tree increased. Evidence for the negative effect of large trees on genetic parameters was reported by Aldrich and Hamrick (1998) for the bird-pollinated tropical tree *Symphonia globulifera*. They found a positive correlation between the rank of plant size and the rank of selfing rate. This was interpreted as the result of an attractor effect of such "super adults" on pollinating hummingbirds, which our simulation confirms. The work of Aldrich and Hamrick (1998) was carried out in a highly disturbed landscape. Hence, there is the risk that the results may not be consistent with those in undisturbed forests.

The observed impact of higher pollen deposition fraction in the nest (DFN) to selfing underlines the potential importance of ramified pollen transfer (Roubik 2002). If the deposition fraction of pollen in the nest is high, ramified dispersal diminishes and inbreeding can increase. No experiments or simulations have tested the hypothesis for secondary pollen dispersal, or mixing of pollen within the next prior to subsequent dispersal, on exiting foragers. It is less obvious why a higher number of flowers visited per trip (NFV) led to increased selfing. This may be linked to the deposition of pollen in the nest (DFN). If the pollinator visits many flowers during a trip, then primary pollen dispersal may become more important.

The effective population size was strongly reduced by the modeled attractor effect of finding a tree (ATE_F) and the variation in flowering intensity (FE_SD). Hence, a few strongly flowering trees may attract a high proportion of pollinators and thus are "overrepresented" in the pool of successful haplotypes (pollen and ovules), which must decrease N_e. Harder and Barrett (1996) made controlled experiments to test the preference (attractiveness of the plants) of bees towards plants with large inflorescences. Their results suggested that flower number *per se* does not affect a bee's pref-

erence for particular inflorescences; instead, the attractive advantages of producing more flowers arise in competitive situations involving variation in daily inflorescence size. This shows the same trend as in the simulations, namely that the attractor effect is greater when combined with variation in flower number.

The variation in individual flowering periods (SF_SD) had a strong positive effect on pollen dispersal. If there are fewer trees with overlapping flowering periods, pollinators fly greater distances, and thus foraging plasticity buffers some results of lower tree density. Foraging plasticity has also been observed in the context of forest exploitation and fragmentation. Under conditions of lower tree density, pollinators fly farther (Aldrich & Hamrick 1998, Dick 2001, White & Boshier 2001). In our model, maximum flight distance of the pollinators was an important parameter for pollen dispersal only if the density of trees was relatively low, indicated by the different importance of maximum flight distance (MFD) for *Jacaranda* and *Dipteryx*.

Another surprising result was that the deposition fraction of pollen (DFP) controlling the carryover of pollen between successive flights had no significant impact on any response parameter. The far more discrete distribution and high inflorescence abundance within trees, as foraging patches, seem to prevent direct comparisons to small plants growing close together, considered in the study by Harder and Barrett (1996). They showed in simulations that the number of plants contributing pollen to each stigma was negatively correlated with the deposition fraction (DFP) and that the number of successful self-pollinations was positively correlated with the deposition fraction. The large amount of pollen acquired from an individual tree, before outcrossing occurs, likely leads to intense selfing and, indeed, in our model would generate an unviable zygote and thus return the simulation to the population sampling stage to generate a viable seed (Fig. 1). A tally of pollen wastage and stigmatic occupancy by incompatible pollen are further variables to be modeled, as is heterogeneity in the pool of available pollinators. Our general results indicate that the discrete spatial characteristics of populations have a major influence in any

realistic simulation of reproductive biology and outcrossing capacity in tropical trees.

DIFFERENCES BETWEEN THE TWO TREE DATA SETS.— The main differences between *J. copaia* and *D. odorata* were the higher tree density of *Jacaranda* (N/ha = 1.8 vs. N/ha = 0.16), the lower number of trees in the sampled population for *Dipteryx* (N = 73 vs. N = 180), and the greater area covered by the trees of *Dipteryx* (500 ha vs. 100 ha). Using the same parameter ranges, the mean proportion of selfing was similar for both data sets (S = 0.12 for *Jacaranda* and S = 0.15 for *Dipteryx*), but the mean effective population size (N_e) was more than twice as large in *Jacaranda* (N_e = 47) compared to *Dipteryx* (N_e = 20). A major result of the sensitivity analysis was that the explained variation was lower for all output parameters in *Dipteryx*. We interpret that result as consistent with the lower number of reproductive trees and the stronger impact of stochastic elements. Variation in individual flowering intensities and flowering phenology produced the high impact of parameters (FE_SD) and (SF_SD) on the effective population size (N_e) and pollen dispersal distance (mPD) in the second series of sensitivity analysis (Table 3).

The flexibility of pollinators facing lower tree densities was manifested by the much greater mean pollen distance of *Dipteryx* (352 m) compared to *Jacaranda* (162 m). The ability of animal pollinators to respond to reduced tree densities with longer pollination flights has been confirmed by paternity analysis for several tropical tree species (Dick 2001, White *et al.* 2002). A profitable tactic for sensitivity study thus combines behavioral data with spatial characteristics of tree populations.

ACKNOWLEDGMENTS

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SPECIAL SECTION