

## Effects of Forest Fragmentation on Pollinator Activity and Consequences for Plant Reproductive Success and Mating Patterns in Bat-pollinated Bombacaceous Trees<sup>1</sup>

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### ABSTRACT

Forest fragmentation and the resulting spatial isolation of tree species can modify the activity of pollinators and may have important implications for the reproductive success and mating systems of the plants they pollinate. The objectives of this study were to (1) evaluate the effect of forest fragmentation on pollinator activity in bat-pollinated bombacaceous trees and (2) determine the effects of forest fragmentation on reproductive success and mating systems of bombacaceous trees. We studied these parameters in three bombacaceous tree species in tropical seasonal forest of Chamela, Jalisco, Mexico, and Osa and Guanacaste, Costa Rica. For *Ceiba aesculifolia*, more visits were observed in fragments by both *Glossophaga soricina* and *Leptonycteris curasoae*. For *Ceiba grandiflora*, *Musonycteris harrisoni* visited flowers exclusively in forest and *G. soricina* visited more flowers in forest than in fragments; no difference was shown by *L. curasoae*. For *Ceiba pentandra* in Chamela, no differences were found in visitation by *G. soricina* between forest and fragments; *L. curasoae* visited significantly more flowers in forest. *Ceiba pentandra* received more visits by *Phyllostomus discolor* than *G. soricina* in Guanacaste, whereas no bat visitors were observed in Osa. Total mean flower production was greater in fragments than forest for *C. aesculifolia*, whereas no difference was observed for *C. grandiflora*. Fruit set was greater in forest than in fragments for *C. grandiflora*, whereas no difference was observed for *C. aesculifolia*. Outcrossing rates were high for *C. aesculifolia* and *C. grandiflora* in Chamela, and for *C. pentandra* in Guanacaste, independent of tree habitat, while *C. pentandra* in Osa showed a mixed-mating system. The effects of forest fragmentation on bat pollinators, plant reproductive success, and mating patterns varied depending upon the bombacaceous species. This variability was associated with the effects that forest fragmentation may have on differences in flowering patterns, bat foraging behavior, and plant self-incompatibility systems.

### RESUMEN

La fragmentación de bosques y el aislamiento espacial, producto de este fenómeno, pueden modificar la actividad de los polinizadores y pueden tener implicaciones importantes sobre el éxito reproductivo y los sistemas de apareamiento de las plantas que polinizan. Los objetivos de este estudio consisten en: (1) evaluar los efectos de la fragmentación de bosque sobre la actividad de los polinizadores de árboles de Bombacaceae, y (2) determinar los efectos de la fragmentación sobre el éxito reproductivo y el sistema de apareamiento de árboles de Bombacaceae. Evaluamos estos parámetros en 3 especies de árboles de esta familia en bosques estacionales en Jalisco, México y Guanacaste y Osa, Costa Rica. Las flores de *Ceiba aesculifolia* fueron más visitadas en fragmentos por *Glossophaga soricina* y *Leptonycteris curasoae*. En *Ceiba grandiflora*, *Musonycteris harrisoni* visitó flores exclusivamente en el bosque y *G. soricina* visitó más flores en el bosque que en los fragmentos mientras que no hubo diferencias para *L. curasoae*. En Chamela, no hubo diferencias en la tasa de visitas de flores entre bosque y fragmentos para *G. soricina* en *Ceiba pentandra* mientras que *L. curasoae* visitó más flores en el bosque. En Guanacaste, *C. pentandra* recibió más visitas de *Phyllostomus discolor* que de *G. soricina* mientras que no hubo visitas por murciélagos en Osa. La producción total promedio de flores fue mayor en los fragmentos que en el bosque para *C. aesculifolia* mientras que no hubo diferencias para *C. grandiflora*. La probabilidad de que una flor produzca fruto fue mayor en el bosque que en los fragmentos para *C. grandiflora* pero no hubo diferencias en *C. aesculifolia*. La tasa de exocruzamiento fue alta para *C. aesculifolia* y *C. grandiflora* en Chamela, y para *C. pentandra* en Guanacaste, mientras que *C. pentandra* en Osa mostró un sistema de apareamiento mixto. Los efectos de la fragmentación de bosques sobre la polinización por murciélagos, la reproducción de plantas y sus patrones de apareamiento varían dependiendo de la especie de Bombacaceae. Esta variabilidad está asociada a los efectos que la fragmentación de bosques puede tener sobre diferencias en los patrones de floración, el comportamiento de forrajeo de los polinizadores, y los sistemas de incompatibilidad de las plantas.

*Key words:* Bombacaceae; Chamela–Cuixmala Biosphere Reserve; fragmentation; Guanacaste; outcrossing rates; nectarivorous bats; plant reproductive success; tropical dry forest.

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DEFORESTATION IN TROPICAL AREAS, PARTICULARLY IN DRY FORESTS, produces more spatially isolated forest fragments every day, in spite of efforts to create protected areas to buffer this problem (Sanchez-Azofeifa *et al.* 2003, Quesada & Stoner 2004). Forest fragmentation and the resulting spatial isolation of tree species can modify the activity of pollinators by reducing the density of potential food resources and increasing the distance between those resources (Sih & Baltus 1987). The reduction of floral resources results in longer travel distances between resting and feeding areas and often results in pollinators crossing disturbed areas that are dominated by agriculture (Kearns *et al.* 1998). When the distance between plants is greater than the home range of the pollinators, their density will decrease in the disturbed areas and this will result in fewer pollinator visits (Kearns *et al.* 1998). Specialist pollinators that are less flexible in exploiting food resources are the most susceptible to local extinction (Estrada *et al.* 1993, Cosson *et al.* 1999, Stoner *et al.* 2002).

The effects of fragmentation on pollinator diversity and foraging behavior may have important implications for both the reproductive success and mating systems of the plants they pollinate. Because resources in fragmented landscapes may be less abundant and the distance between resources greater, many pollinators invest more time foraging within the same plant or flower, increasing the level of selfing (Mustajärvi *et al.* 2001, Cascante *et al.* 2002, Fuchs *et al.* 2003) or reducing seed set in self-incompatible species (Lamont *et al.* 1993, Aizen & Feinsinger 1994, Costin *et al.* 2001, Steffan-Dewenter *et al.* 2001, Cascante *et al.* 2002, Quesada *et al.* 2003). For example, in the tropical dry forest insect-pollinated tree *Samanea saman*, Cascante *et al.* (2002) showed that seeds produced by different fruits within trees were more likely to be related in isolated trees than trees from continuous populations. Nevertheless, studies on tropical trees have shown that some generalist pollinators are not negatively affected by forest fragmentation and increase pollen movement in open areas (Dick 2001, White *et al.* 2002).

Specialist pollinators are expected to be more susceptible to forest fragmentation because they use flowers from a limited number of plant species that usually occur at low densities, particularly in the tropics. Only a few studies have evaluated the consequences of forest fragmentation on the relationship between specialist pollinators and the reproduction of plants (Law & Lean 1999, Parra-Tabla *et al.* 2000, Murren 2002, Stoner *et al.* 2002, Que-

sada *et al.* 2003). For example, Law and Lean (1999) evaluated the role of bat pollinators within fragmented landscapes in rain forest of north Queensland, Australia, comparing the effectiveness of the common blossom bat (*Synconycteris australis*) with the effectiveness of birds for pollinating the tree *Syzygium cormiflorum* in a fragmented landscape. They found that bats carried six times more pollen than birds, but were less frequent visitors to the flowers. They also observed that bats fed for shorter periods within one tree and moved much larger distances between trees than birds. They concluded that bats carry much higher quality pollen than birds in fragmented landscapes; nevertheless, they did not compare the effectiveness of bats as pollinators in fragmented and continuous forests.

A few studies have evaluated the effects of forest fragmentation on both plant reproduction and genetic structure or mating systems of the populations (Aldrich *et al.* 1998, Dayanandan *et al.* 1999, Dick 2001, Cascante *et al.* 2002, White *et al.* 2002, Fuchs *et al.* 2003); however, no studies have simultaneously evaluated pollinator behavior, plant reproductive success, and genetic structure or mating systems in tropical trees. In general, there is a lack of information that directly evaluates the effects of pollinator activity on the reproductive success of plants in fragmented environments. In particular, almost no information exists about bat pollinators (Law & Lean 1999, Stoner *et al.* 2002, Quesada *et al.* 2003). Our study is the first to directly analyze the activity of bat pollinators in relation to reproductive success and mating system of tropical tree species in spatially isolated forest fragments. The objectives of our study were to (1) evaluate the effect of forest fragmentation on pollinator activity at bat-pollinated bombacaceous trees and (2) determine the effects of forest fragmentation on reproductive success and mating systems of bombacaceous trees.

## METHODS

**STUDY SITES AND SPECIES.**—This study was conducted in three seasonal tropical forests on the Pacific coast of Mesoamerica. The first site was located in tropical dry forest on the central Pacific coast of Mexico within and surrounding the Chamela-Cuixmala Biosphere Reserve (ca 19°30'N, 105°03'W) with an area of 13,200 ha. The second site also consisted of tropical dry forest and was located in the northern Pacific coast of Costa Rica in the province of Guanacaste (10°45'N, 85°30'W) within and surrounding Guanacaste National Park

with an extension of 50,000 ha. The third site was located in seasonal tropical wet forest in the Osa Peninsula in the southern Pacific coast of Costa Rica (88°26'N, 83°83'W) within and surrounding Corcovado National Park with an extension of 50,200 ha. Trees were evaluated in two habitat conditions. A tree was considered in a fragmented habitat if it was surrounded by agricultural fields or pastures and had less than five reproductive conspecifics per hectare, usually distributed in small clumps. *Ceiba pentandra* was only found as isolated individuals. Trees in fragmented habitats were separated from each other by at least 5 km and were at least 10 km from the continuous forest. Trees in forest were found within undisturbed continuous forest in protected areas. We used reproductive trees of similar size (*i.e.*, diameter at breast height) for each species in both tree habitats.

We studied three species from the family Bombacaceae in Jalisco, Mexico (*Ceiba aesculifolia*, *C. grandiflora*, and *C. pentandra*) and one species in Guanacaste and Osa, Costa Rica (*C. pentandra*). All species studied are predominantly self-incompatible, hermaphroditic, and possess chiropterophilic flowers that are principally visited by bats and sphingid moths (Heithaus *et al.* 1975; Haber & Frankie 1989; Quesada *et al.* 2001, 2003; Stoner 2002; Fuchs *et al.* 2003; Stoner *et al.* 2003). Data were collected for one year for each species between 1999 and 2003.

ACTIVITY OF POLLINATOR VISITS.—The activity of nocturnal visitors was recorded during the dry season with a Sony digital camcorder (Handycam DCR-TRV18) using the technique of Quesada *et al.* (2003). Videotaping of flowers (inflorescences in *C. pentandra*) began at sunset right before anthesis and continued for 4.5 hours, which corresponded to peak foraging times of most phyllostomid bats (Fenton & Kunz 1977). For inflorescences found higher than 15 m, we used an infrared flash (Sony HVL-IRH2) and a 2x teleconverter (Sony VCL-HG2030X) to improve visibility. The average number of visits for each bat species per hour was calculated for each flower or inflorescence filmed. Bat species were identified based on size differences and snout morphology (Stoner *et al.* 2003). We filmed 26 flowers from 15 trees located in fragmented habitats and 25 flowers from 9 trees in forest for *C. aesculifolia*. For *C. grandiflora*, we filmed 25 flowers from 17 trees in fragmented habitats and 39 flowers from 18 trees in forest. For *C. pentandra* in Chamela, we filmed 10 inflorescences from 5 trees in fragmented habitats and 9 inflores-

cences from 6 trees in forest. For *C. pentandra* in Guanacaste, we filmed 193 inflorescences from 5 trees in fragmented habitats and none in forest (because none could be located) and in Osa, we filmed 100 inflorescences from 5 trees in fragmented habitats and 93 inflorescences from 3 trees in forest.

To determine if the number of bat visits depended upon habitat condition, for each tree species the average number of visits per hour per flower of each bat species each night was used as the dependent variable. Because the scale and distribution of this variable did not follow a normal distribution, we used a generalized linear model using a gamma distribution for the dependent variable and the logarithmic function as a link function using the GENMOD procedure from SAS (SAS 2000, Stokes *et al.* 2000). The model used tree habitat as the categorical independent variable. We used a likelihood ratio test to determine if tree habitat significantly affected the average number of visits per hour per inflorescence per night. This statistic had a chi-square distribution and the degrees of freedom were calculated as the difference in the number of parameters between models (McCullagh & Nelder 1989, Stokes *et al.* 2000).

ESTIMATION OF REPRODUCTIVE SUCCESS.—Reproductive success was evaluated as fruit set, which was estimated as the proportion of the total number of fruits over the total number of flowers produced by each individual tree during one flowering season. Flower and fruit production were estimated using the same methodology described by Fuchs *et al.* (2003). We counted the number of flowers produced by each individual every 15 days and estimated the total flower production of each tree as the area under the distribution obtained by the number of flowers versus time. We estimated the production of fruits for each individual tree by counting the total number of fruits produced every 15 days during the fruiting period. The total number of fruits produced by each individual was estimated as the maximum number of fruits produced at the end of the fruiting period. This was a good estimate of total fruit production because all species have dry fruit capsules that remain attached to the mother tree for several months. Flowers and fruits were counted on 20 trees located in disturbed sites and 9 trees in continuous forest for *C. aesculifolia* and on 17 trees located in disturbed sites and 18 trees in continuous forest for *C. grandiflora*. We used an analysis of variance (GLM; SAS 2000) to analyze the effect of habitat condition on total flower production and fruit set. The model

TABLE 1. Average number of bat visits  $\pm$  SE per flower (inflorescence for *Ceiba pentandra*) per hour per night for different bat species in fragmented habitats and forest by tree species in Chamela. The number of flowers or inflorescences filmed for each species in each forest condition is given in parentheses. Each flower or inflorescence was filmed for 4.5 hours after anthesis. Results are from a generalized linear model analysis to determine if tree habitat significantly affected the average number of visits per hour per inflorescence per night (\* $P < 0.05$ ).

	<i>Glossophaga soricina</i>		<i>Leptonycteris curasoae</i>		<i>Musonycteris harrisoni</i>	
	Fragment	Forest	Fragment	Forest	Fragment	Forest
<i>Ceiba aesculifolia</i>	3.9 $\pm$ 1.9 (26)*	1.6 $\pm$ 1.2 (25)	12.9 $\pm$ 3.3 (26)*	1.9 $\pm$ 0.8 (25)	0	0
<i>C. grandiflora</i>	1.3 $\pm$ 0.3 (25)	3.33 $\pm$ 0.5 (39)*	2.4 $\pm$ 0.6 (25)	2.0 $\pm$ 0.4 (39)	0	0.5 $\pm$ 0.2 (39)*
<i>C. pentandra</i>	0.9 $\pm$ 0.3 (9)	1.5 $\pm$ 0.7 (7)	2.6 $\pm$ 0.9 (9)	11.5 $\pm$ 2.8 (7)*	0	0

we used considered tree habitat (*i.e.*, forest or fragment) as the main effect. To achieve normality, we transformed the data by using the square root of the arcsine for fruit set and the natural logarithm for total flower production.

GENETIC ANALYSIS.—Approximately 10 fruits per tree and 4–10 seeds per fruit were analyzed for the genetic analysis. Mating patterns in the progeny of the tress were determined by analyzing the variation in isozymes (*C. aesculifolia* and *C. grandiflora*) or microsatellite markers (*C. pentandra* in Costa Rica) developed by Brondani *et al.* (2003). We studied variation in six isozymes (AAT1, AAT2, EST, GPI, ICD, and SKDH) and six microsatellites (CP1, CP12, CP13, CP15, CP19, and CP22). The methods of isozymes followed Fuchs *et al.* (2003) and the methods for PCR were the same used by Brondani *et al.* (2003). We estimated multilocus outcrossing rate (*tm*) for each tree species by tree habitat using the models proposed by Ritland (1989) and the MLTR computer program (Ritland 2002).

## RESULTS

EFFECT OF FOREST FRAGMENTATION ON BAT POLLINATOR ACTIVITY.—The effect of forest fragmentation on the average number of bat visits per hour was variable in Chamela depending on the bat species and the tree species (Table 1). Significantly more visits were observed in fragments by both *Glossophaga soricina* ( $\chi^2 = 3.7$ ,  $P = 0.05$ ) and *Leptonycteris curasoae* ( $\chi^2 = 22$ ,  $P < 0.005$ ) for *C. aesculifolia*. For *C. grandiflora*, *Musonycteris harrisoni* visited flowers exclusively in forest and *G. soricina* visited flowers significantly more in forest than in fragments ( $\chi^2 = 11.7$ ,  $P = 0.0006$ ), while *L. curasoae* showed no difference ( $\chi^2 = 0.31$ ;  $P = 0.57$ ).

No differences were found in visitation by *G. soricina* between forest and fragments for *C. pentandra* in Chamela, whereas *L. curasoae* visited significantly more flowers in forest ( $\chi^2 = 10.8$ ,  $P = 0.0009$ ). No bat visits were observed in forests or fragments in the seasonal tropical wet forest of Osa. No comparisons could be made between forest and fragments for *C. pentandra* in the tropical dry forest of Guanacaste because they are only found in disturbed areas of this region. The inflorescences filmed in Guanacaste received an average of 2.5  $\pm$  0.5 visits/inflorescence/hour/night by *Phyllostomus discolor* and 0.25  $\pm$  0.16 by *G. soricina*.

CONSEQUENCES FOR REPRODUCTIVE SUCCESS.—Total mean flower production was significantly greater in fragments than in the forest for *C. aesculifolia* ( $F_{1, 26} = 5.63$ ,  $P = 0.025$ ), while no differences were observed for *C. grandiflora* ( $F_{1, 33} = 0.42$ ,  $P = 0.52$ ; Table 2). Fruit set was significantly greater in forest than in fragments for *C. grandiflora* ( $F_{1, 33} = 5.12$ ,  $P = 0.03$ ), while no differences were observed for *C. aesculifolia* ( $F_{1, 28} = 0.15$ ,  $P = 0.45$ ; Table 2).

CONSEQUENCES FOR MATING PATTERNS.—Outcrossing rates were high for *C. aesculifolia* and *C. grandiflora* in both fragmented and forest areas, indicating that these species are predominantly outcrossing (Table 3). Similarly, outcrossing rates for *C. pentandra* populations in fragments at Guanacaste were high but a change to a mixed-mating system was observed in fragments for the Osa population.

## DISCUSSION

The effects of forest fragmentation on bat pollinators, plant reproductive success, and mating pat-

TABLE 2. Least-square means (LSMeans) for total number of flowers and fruit set  $\pm$  SE in two species of bombacaceous trees in fragmented habitats and forest. Fruit set was calculated as the percent of total fruit production over total flower production for each individual tree. Results are from an analysis of variance to evaluate the effect of habitat condition on total flower production and fruit set (\*  $P < 0.05$ ).

	Fragment			Forest		
	N	Flowers	Fruit set	N	Flowers	Fruit set
<i>Ceiba aesculifolia</i>	20	1130 $\pm$ 245*	3.7 $\pm$ 1.14	9	320 $\pm$ 300*	5.5 $\pm$ 1.7
<i>C. grandiflora</i>	17	515 $\pm$ 147	3.5 $\pm$ 1.24*	18	352 $\pm$ 143	6.9 $\pm$ 1.21*

terns varied depending upon the bombacaceous species. The variable response of bat pollinators to forest fragmentation was likely a consequence of the flowering pattern of each tree species and the availability of other chiropterophilic resources, as well as the foraging patterns of the bats. For *C. aesculifolia*, both *G. soricina* and *L. curasoe* visited flowers in fragments significantly more than in forest. This may have been due to the fact that *C. aesculifolia* produces between 20 and 100 flowers per night and blooms from May to June when few other chiropterophilic flowers are available (Stoner *et al.* 2003) and because isolated trees in fragments produce twice as many flowers than trees in the forest (Table 2). In contrast, for *C. grandiflora*, which produces only a few flowers (1–3) a night over an extended period (Lobo *et al.* 2003), the small-bodied species of *M. harrisoni* and *G. soricina* visited flowers found in fragments significantly less than forest, while the larger, more mobile *L. curasoe* showed no difference. Although *G. soricina* may be found in fragmented areas (Lemke 1985), the cost of foraging in trees with very few flowers does not outweigh the benefit, especially when other resources are available within their relatively small home range (Heithaus *et al.* 1975). Finally, the short-term (*ca* 1 mo) massive flowering species *C. pentandra* received significantly more visits from

*L. curasoe* in forest than fragments while *G. soricina* showed no differences in the tropical dry forest of Guanacaste. This result was likely due to the proximity of the *C. pentandra* individuals in forest to the primary perch of *L. curasoe* in the region (Stoner *et al.* 2003) and the superabundance of resource at this massive flowering species. Although *L. curasoe* has the ability to forage over long distances to obtain resources when they are scarce, if long movements are not necessary, they forage as close to their home perch as possible (Horner *et al.* 1998). *Glossophaga soricina* does not forage over long distances, but abundant resources provided from *C. pentandra* would make this an attractive resource in forests as well as fragments (Heithaus *et al.* 1975). The notable lack of bat visits to *C. pentandra* in Osa was likely related to the availability of other chiropterophilic resources in this wet forest.

Our results indicate that fruit set was significantly less in fragments for *C. grandiflora*; a similar trend was observed for *C. aesculifolia*, although this difference was not significant. Trees in fragments produced more flowers than trees in forest, but fruit production was lower in fragments. Because most of these species are self-incompatible, it is likely that pollinators in isolated trees facilitate mostly geitonogamous crosses; this promotes self-

TABLE 3. Outcrossing rates  $\pm$  SE in four species of bombacaceous trees in forest fragments and continuous forest by tree species, habitats (TDF = Tropical Dry Forest and TWF = Tropical Wet Forest), and site. ND refers to no data.

	Fragment		Forest	
	N	Outcrossing rate	N	Outcrossing rate
TDF, Chamela				
<i>Ceiba aesculifolia</i>	31	0.969 $\pm$ 0.060	36	0.962 $\pm$ 0.048
<i>C. grandiflora</i>	18	0.913 $\pm$ 0.067	12	0.896 $\pm$ 0.140
TDF, Guanacaste				
<i>C. pentandra</i>	8	0.885 $\pm$ 0.041		ND
TWF, Osa				
<i>C. pentandra</i>	7	0.400 $\pm$ 0.059		ND

ing within individuals, which results in lower fruit set. Pollination with compatible pollen is hindered in fragmented habitats, thereby limiting the ability of individuals to achieve high levels of fruit set. Similar results have been reported for *Paquiria quinata* in Guanacaste, where fruit set is less in fragmented habitats than continuous forest (Fuchs *et al.* 2003). Although bats are visiting flowers in fragmented habitats, and in the case of *C. aesculifolia*, the visitation rate was actually higher than in forest, they may not be moving pollen between fragments as well as in forests, given the spatial isolation of many trees in fragments. Other researchers have found a similar relationship between fruit set and/or seed production and forest fragmentation (Aizen & Feinsinger 1994, Ghazoul *et al.* 1998, Gigord *et al.* 1999, Cunningham 2000, Parra-Tabla *et al.* 2000, Ghazoul & McLeish 2001), but a few studies have found no differences in seed production (Dick 2001, Murren 2002).

Our study also showed that the mating system was not affected by isolation due to forest fragmentation. *Ceiba aesculifolia* and *C. grandiflora* maintained a predominantly self-incompatible system. *Ceiba pentandra* showed a flexible mating system depending upon the forest type (*i.e.*, tropical wet forest or tropical dry forest). Studies on the mating systems and incompatibility mechanisms of the family Bombacaceae suggest that population estimates of outcrossing rates can be influenced by density or spatial isolation (Murawski & Hamrick 1992, Gribel *et al.* 1999, Quesada *et al.* 2001, Fuchs *et al.* 2003). Our study also suggests that the absence of pollinators may change the mating patterns in trees, as observed for *C. pentandra*. Similarly, populations of *P. quinata* located in continuous forest are mainly self-incompatible but trees in isolation tend to be partially self-compatible (Quesada *et al.* 2001, Fuchs *et al.* 2003). Self-incompatibility has been reported for several species of the family Bombacaceae and apparently the incompatibility reaction occurs at the base of the flower style or at the ovary, but self-fertilization is not completely discarded (Baum 1995, Gribel *et al.* 1999, Quesada *et al.* 2001, Gribel & Gibbs 2002). In other species, pleiotropic effects of modifying genes (Levin 1996, Ivey *et al.* 1999, Good-Avila & Stephenson 2003), polyploidy or gene duplication (de Nettancourt 2001), or temporal plasticity in the expression of self-incompatibility (Richardson *et al.* 1990, Vogler *et al.* 1998) can change a strict self-incompatible system to a mixed

mating system in natural populations, as may be occurring in *P. quinata*. Even though the fragmented population of *C. pentandra* in Guanacaste was predominantly outcrossing, the population in Osa and other studies indicate that this species is capable of expressing a mixed-mating system (Murawski & Hamrick 1992, Gribel *et al.* 1999). *Ceiba pentandra* in Osa had a mixed-mating system, possibly associated with the absence of pollinators at this site. A similar flexible breeding system has been observed in dipterocarp trees after forest fragmentation or logging modified the original continuous population (Murawski *et al.* 1994, Lee 2000). In sum, the patterns of visitation of pollinators may modify the mating system of trees from outcrossing to selfing with a possible reduction in the genetic diversity of the remnant populations for certain species.

The experimental design used in our study established a comparison between bat pollinators and plant reproductive success and between continuous forest and nearby fragmented populations. It is likely that the main refuge and resources for some of the bat species come from the continuous forest and that the elimination of this forest would negatively reduce the bat pollinators that we observed in the fragments. Even for long-distance pollinators (*e.g.*, *L. curasoeae*) that can travel up to 100 km a night in search for flowers (Horner *et al.* 1998), this highly gregarious species is found principally roosting in caves within undisturbed areas, which makes it vulnerable to human disturbance (Stoner *et al.* 2003). To evaluate the importance of continuous forest for maintaining bat pollinators, future studies should analyze the movement of bat pollinators and gene flow patterns of the plants they pollinate in corridors and forest fragments at variable distances from continuous forests.

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