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PLANT ANIMAL INTERACTIONS

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Effects of habitat disruption on the activity of nectarivorous bats (Chiroptera: Phyllostomidae) in a dry tropical forest: implications for the reproductive success of the neotropical tree *Ceiba grandiflora*

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Abstract In the tropical dry forest of the central Pacific coast of Mexico the pollination and reproductive success of the bombacaceous tree *Ceiba grandiflora* was negatively affected by habitat disruption. Two of the three bat species that function as effective pollinators for this species (*Glossophaga soricina* and *Musonycteris harrisoni*) visited flowers found in trees in disturbed habitats significantly less than trees found in undisturbed habitats. A similar pattern was observed for the effective bat pollinator, *Leptonycteris curasoae*; however the difference was not significant. The three nectarivorous bats that functioned as effective pollinators of *C. grandiflora* also visited flowers to exclusively feed on pollen by biting or pulling off an anther (see Fig. S1 of Electronic Supplementary Material). The number of pollen grains deposited on stigmas from flowers in undisturbed areas was significantly greater than from flowers in disturbed habitats. The greater visitation rate and the greater number of pollen grains deposited on flowers from trees in undisturbed forest resulted in a significantly greater fruit set for trees in these areas. Our study demonstrates the negative effect that habitat disruption has on bat pollinators in tropical dry forest ecosystems and documents the negative consequences for the plants they pollinate.

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Keywords Habitat fragmentation · Pollination decline · Phyllostomid bats · Plant reproductive success · Plant–animal interactions

Introduction

Habitat disruption and forest fragmentation are likely to affect plant–animal interactions at pollination and seed dispersal stages (Feinsinger 1987; Bawa 1990; Aizen and Feinsinger 1994; Ghazoul et al. 1998; Cunningham 2000a; Cascante et al. 2002). Moreover, forest fragmentation may reduce the population size of plants which often results in the loss of genetic variation and fixation of deleterious alleles due to high levels of genetic drift and inbreeding depression (Charlesworth and Charlesworth 1987; Ellstrand and Elam 1993; Young et al. 1996; Nason et al. 1997).

Animals that move genetic material (pollen or seeds) between fragments can help reduce the negative effects of forest fragmentation (Young et al. 1996). The abundance and movement of animal vectors and density of reproductive trees is expected to affect the quantity and quality of pollen flow and seed dispersal (Nason et al. 1997). This, in turn, is likely to affect the genetic structure and mating patterns of plants in fragmented landscapes, especially in the case of outcrossing species. Therefore, gene flow between fragments promoted by pollinators will reduce the rate of fixation of alleles obtained from genetic drift (Charlesworth and Charlesworth 1987; Ellstrand 1992; Ellstrand and Ellam 1993).

Bats are especially important pollinators because of their ability to carry pollen over short or long distances resulting in outcrossing between unrelated trees and promoting gene flow in a fragmented landscape (Heithaus et al. 1975; Bawa 1990; Flemming and Sosa 1994). In addition, bats are key pollinators of several economically important species in the neotropics including many species from the families Agavaceae, Bombacaceae and Cactaceae (Nobel and Quero 1986; Casas et al. 1999; Quesada et al. 2001). Several studies that have evaluated the effect of forest fragmentation on the diversity and abundance of bats have concluded that habitat disruption negatively affects bat communities (Brosset et al. 1996; Cosson et al. 1999; Medellín et al. 2000; Schulze et al. 2000; Estrada and Coates-Estrada 2002). However, none of these studies have focused specifically on nectarivorous bats or documented the consequences that the disruption of these pollinators may have on the reproduction of plants.

Many of the studies examining the effect of forest fragmentation on pollinators and reproductive success of plants have worked with herbaceous plants and most of them have been conducted in grasslands, woodlands and shrublands in temperate or subtropical zones (Sih and Baltus 1987; Spears 1987; Jennersten 1988; Aizen and Feinsinger 1994; Ghazoul et al. 1998; Steffan-Dewenter and Tscharntke 1999; Cunningham 2000a, 2000b; Somanathan and Borges 2000; Steffan-Dewenter et al. 2001; Donaldson et al. 2002; Murren 2002). Moreover, the great majority of studies looked at insect-pollinated plants. Studies in the tropics that have evaluated the effect of forest fragmentation on pollinator activity have used genetic estimates of gene flow to infer pollinator behavior. These studies suggest an apparent increase in distance of pollen movement by animal vectors between fragmented habitats. However, the genetic diversity of the progeny of trees in fragments tends to decrease as a result of a reduction in the number of pollen donors (Aldrich and Hamrick 1998; Dayanandan et al. 1999; Sork et al. 1999; Dick 2001; Cascante et al. 2002; White et al. 2002; Fuchs et al. 2003). Therefore, more studies need to directly relate the behavior and movement of pollinators with plant reproductive success and gene flow of tropical trees.

Our study was designed to document the effect of forest disruption on pollinator visitation and plant reproductive success of the bat-pollinated tropical dry forest tree *Ceiba grandiflora*. Our objectives include to: (1) determine the effects of forest disruption on the diversity and abundance of effective pollinators, (2) compare pollinator activity in disturbed areas with undisturbed forest, (3) compare the amount of pollen deposited on flowers found in disturbed and undisturbed forest, and (4) compare the reproductive success of *C. grandiflora* in disturbed and undisturbed forest.

Materials and methods

Study area and study species

The study was conducted between February 2001 and April 2002 in the central Pacific coast of Mexico within and surrounding the Chamela-Cuixmala Biosphere Reserve (ca. 19'30'N, 105°03'W). This reserve is located approximately between Puerto Vallarta, Jalisco and Manzanillo, Colima and has an extension of 13,200 ha. The predominant vegetation type in this region is tropical dry forest with an average annual rainfall of 750 mm and a marked dry season from November until June (Bullock 1995).

Ceiba grandiflora Rose (Bombacaceae) is a neotropical tree (8–12 m high) endemic to the tropical dry forest of the states of Jalisco and Colima in central western Mexico. This is a deciduous species which begins flowering at the end of the rainy season in December and continues flowering until May or June (Lobo et al. 2003). The flowers are hermaphroditic with five filaments and a single central style. Anthesis occurs at dusk and the flowers last for only one night. Fruits are dehiscent and seeds are wind dispersed (Rose 1895). Each ovary contains 120 (SD 6) ovules. The breeding system of this species is predominately outcrossing, although selfing is possible to some degree (i.e. 3%; Palacios-Guevarra 2002).

Selection of trees

Trees were evaluated in two habitat conditions in our study. A tree was considered in a disturbed habitat if it was surrounded by agricultural fields or pastures, and had less than three reproductive conspecifics per hectare. Trees in disturbed sites were located along Highway 200 between the towns of Careyes and Puerto Vallarta and were separated by a minimum of 5 km. Trees from undisturbed habitat consisted of groups of ten or more reproductive individuals per hectare surrounded by undisturbed mature forest and were located within the Chamela-Cuixmala Biosphere Reserve. Four undisturbed populations separated by at least 8 km were sampled in different watersheds within the reserve.

Diversity, abundance and visitation rates

The diversity, abundance, and activity of the night visitors were recorded using a Sony Digital Handycam DCR-PC 100 camcorder adapted to a Dark Invader Owl Super Gen 2 pocketscope with a laser illuminator (MSE, St. Charles, Mo.). The camera was placed sufficiently close to the flower to allow clear vision of the anthers and stigma. Videotaping began at sunset right before anthesis and continued for 4.5 h, which corresponds to peak foraging times of most phyllostomid bats (Fenton and Kunz 1977). The following data were collected for each pollinator visit: (1) species; (2) duration of visit; (3) if contact was made with the stigma or anthers; and (4) if pollen or nectar was fed upon. If the snout of the bat was inserted into the flower corolla we assumed the bat was feeding on nectar. If the anther was bitten or pulled off, we assumed the bat was feeding on pollen. The three bat species observed visiting *C. grandiflora* flowers were distinguished based on their relative size and body proportions in comparison to the length of the flower petals and reproductive parts. *Leptonycteris curasoae* weighs 20–30 g with a forearm measuring 46–57 mm and *Glossophaga soricna* weighs 8–11 g with a forearm measuring 36–38 mm (Nowak 1994). Although *Musonycteris harrisoni* is similar in weight to *G. soricina* (12–13 g) the forearm is larger (41–43 mm; Nowak 1994). Flowers were filmed for 1–3 nights a week alternating habitat condition (i.e. disturbed and undisturbed) from February to May 2001 and February to April 2002. In 64 nights of video recording (351 h), 35 flowers from 15 trees (1–3 flowers/tree) were filmed in disturbed habitat (158 h) and 43 flowers (1–3 flowers/tree) from 24 trees were filmed in undisturbed habitat (194 h). To estimate potential pollen resources within the area, each night the number of open flowers on the focal tree and conspecifics within a 500 m^2 radius were counted.

To compare time spent per flower for each bat species we conducted an analysis of covariance (GLM, SAS 2001) with time per visit as the response variable, species as the independent variable, and the total number of flowers within a 500 m^2 radius as a covariate. To determine if the number of bat visits depended upon habitat condition, the total number of visits of each bat species each night was used as the dependent variable. Because the scale and distribution of this variable does not follow a normal distribution, we used a generalized linear model using a Poisson distribution for the dependent variable and the logarithmic function as a link function using the GENMOD procedure from SAS (Stokes et al. 2000). A scaling parameter was calculated to improve the fit of the residuals to the Poisson distribution because the data were over-dispersed (McCullagh and Nelder 1989). The model used tree condition as the categorical independent variable. The number of visits of other bat species, and the number of open flowers in conspecific trees within a 500 m^2 radius were used as covariates. We used a type III likelihood ratio to determine if habitat condition significantly affected the number of visits per flower per night. In the GENMOD procedure from SAS (Stokes et al. 2000), Type III statistics are calculated for each principal effect as the difference of two log likelihood models with and without the effect. This statistic has a chi-square distribution and the degrees of freedom are calculated as the difference in the number of parameters between models (McCullagh and Nelder 1989; Stokes et al. 2000).

Natural pollination and reproductive success

To determine the effect of forest disruption on natural pollination, we collected 39 styles from flowers from 13 trees in undisturbed sites and 49 styles from 16 trees in disturbed sites. Styles were only collected from flowers that initiated fruit development. Styles were preserved in formalin and alcohol (FAA) and then fixed and stained using Martin's (1959) aniline blue technique. Pollen grains on the stigmatic surface were counted with epifluorescent microscopy. Similar to the previous statistical analysis, we conducted a generalized linear model using a Poisson distribution adjusted for over-dispersion (Stokes et al. 2000) to assess whether the number of pollen grains deposited on the stigma varied between habitat condition (i.e. disturbed and undisturbed). The model uses tree condition as the independent variable and the number of pollen grains as the response variable.

To evaluate reproductive success of *C. grandiflora*, we estimated fruit set by documenting flower and fruit production from 17 trees in disturbed and 18 trees in undisturbed habitat. We counted the number of flowers and fruits produced by each tree every 7 days. We estimated the total flower production of each individual as the area under the distribution obtained by the number of flowers produced versus time (Fuchs et al. 2003). The total number of fruits produced by each tree was the maximum fruit produced during the fruiting season. Fruit set was calculated for each tree as the number of fruits produced/ number of flowers. A binary logistic regression was used to analyze the effect of habitat condition on fruit set (Stokes et al. 2000). The model uses tree condition as the independent variable and the logit of fruit set as the response variable.

Results

A total of 1,059 visits in undisturbed habitat were observed and 419 visits in disturbed habitat. Although six flower visitors were observed in undisturbed sites (three species of bats, the marsupial *Marmosa canescens*, and two species of moths), bats made up more than 96.7% of all visits. In disturbed habitat, only two species of bats were observed, accounting for 97.6% of all visits, and one species of moth. *Glossophaga soricina* was the most common bat observed visiting *C. grandiflora* flowers, accounting for 51% of the observed bat visits, followed by *Leptonycteris curasoae* accounting for 43%, and *Musonycteris harrisoni* accounting for 6% (*n*=1,434 total bat visits).

These three nectarivorous bats were the only effective pollinators because they were the only visitors that made direct contact with the reproductive parts of the flower. Nevertheless, during some visits the bats bit or broke off the anther in a form of "pollinivory" (Table 1; Fig. S1 of electronic supplementary material). In spite of the fact that *G. soricina* spent significantly more time per flower visit than the other two species ($F_{2,95}$=3.0, $P<0.05$), it did not come in contact with the reproductive parts as often as the other two species (Table 1). The number of open flowers within a 500 m^2 radius did not affect the time spent per visit ($F_{2,95}$=1.12, P=0.29)

There were significantly more visits by *G. soricina* in undisturbed than in disturbed habitat (regression coefficient =1.18, χ^2 =18.7, *df*=1, $P<0.001$; Fig. 1), and the number of visits were negatively affected by the number of visits of *L. curasoae* (regression coefficient =–0.04, χ^2=7.5, *df*=1, $P<0.01$). In contrast, although *L. curasoae* was observed visiting flowers more frequently in undisturbed than disturbed habitats, this difference was not statistically significant (regression coefficient=0.31, χ^2=0.9, *df*=1, P=0.31. The number of visits by *L. curasoae* was negatively affected by the number of visits by *G. soricina* (regression coefficient =–0.045, χ^2=6.8, *df*=1, $P<0.01$). Similar to *G. soricina*, there were significantly more visits by *M. harrisoni* in undisturbed than in

Table 1 Details of floral visitation on *Ceiba grandiflora* in the region of the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico. The frequency that nectar or pollen was fed upon, the frequency of contact with reproductive parts, and the time spent per flower visit for each of the three bat species (*n*=number of floral visits)

Species	Feeding on nectar[a] (%)	Feeding on pollen[b] (%)	Contact with anthers (%)	Contact with stigma (%)	Time (s/flower)[c]
Glossophaga soricina (*n*=728)	92	8	79	45	0.54±0.02
Leptonycteris curasoae (*n*=614)	93	7	98	83	0.45±0.03
Musonycteris harrisoni (*n*=92)	99	1	98	82	0.49±0.07

[a] If the snout of the bat was inserted into the flower corolla we assumed the bat was feeding on nectar

[b] If the anther was bitten or pulled off, we assumed the bat was feeding on pollen

[c] Values are means±SE

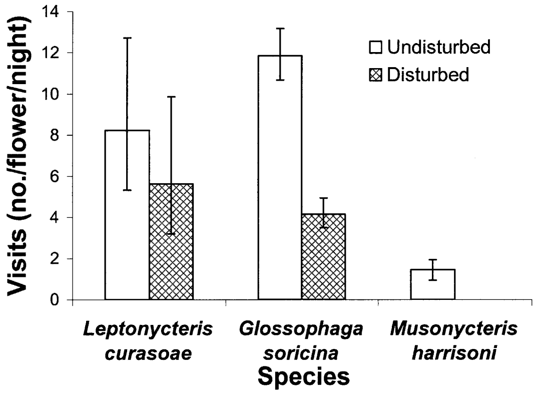

Fig. 1 Average number of bat visits per *Ceiba grandiflora* flower per night (LS means ±95% confidence interval) in disturbed and undisturbed habitat in the region of the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico

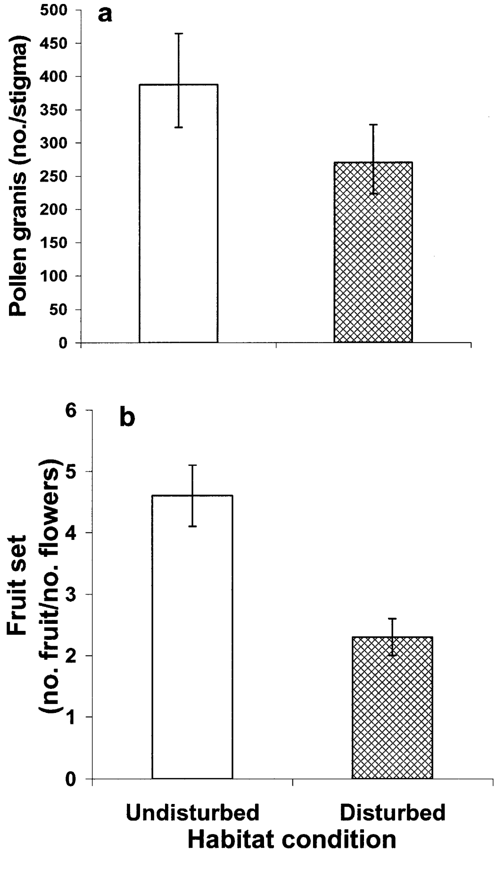

Fig. 2 **a** Average number of pollen grains deposited onto stigmas (LS means ±95% confidence interval) and **b** average fruit set (LS means ±95% confidence interval) for *Ceiba grandiflora* trees found in disturbed and undisturbed habitats in the region of the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico

disturbed habitats (regression coefficient =27.5, χ^2=8.8, *df*=1, *P*<0.01; Fig. 1); however the number of visits were not affected by either of the other bats.

Significantly more pollen grains were deposited on stigmas from flowers found in undisturbed than those found within disturbed habitat (χ^2=7.3, *df*=1, *P*<0.007; Fig. 2). Furthermore, fruit set was significantly greater in trees found in undisturbed habitat than in disturbed habitat (χ^2=59.9, *df*=1, *P*<0.0001; Fig. 2).

Discussion

Our study shows that three nectarivorous bats were the only effective pollinators of *C. grandiflora*. Other nocturnal visitors did not touch the stigma or anthers, and thus cannot be effective pollinators for this species. Several studies have identified other flower visitors as potential pollinators of some bombacaeous trees (Baker et al. 1971; Ayensu 1974; Toledo 1977; Baker 1983; Gribel et al. 1999), nevertheless, our study demonstrates that detailed observations are necessary to better document pollinator behavior and their role in pollination. Moreover, the time spent per visit is not necessarily an indicator of the frequency of contact with reproductive parts, as *G. soricina* spent significantly more time per visit but had less contact with anthers and stigmas than the shorter visits of *L. curasoae* or *M. harrisoni.*

Flowers of *C. grandiflora* found in undisturbed habitat received significantly more pollinator visits than flowers found in trees in disturbed habitat. This observation agrees with some previous studies that have shown that many pollinators are negatively affected by forest fragmentation and that abundance and visitation rates are lower in disturbed areas (Powell and Powell 1987; Aizen and Feinsinger 1994; Cunningham 2000a; Dick 2001; Ghazoul et al. 2001; Steffan-Dewenter et al. 2001; Murren 2002).

The smaller nectarivores, *G. soricina* and *M. harrisoni* were both negatively affected by forest disruption. *Musonycteris harrisoni* was exclusively observed in undisturbed habitat. Although *G. soricina* was observed in disturbed habitat, it was significantly more common in undisturbed areas. The larger nectarivore, *L. curasoae* was found in a similar frequency in disturbed and undisturbed habitats. Even though *L. curasoae* may be the most important effective pollinator (i.e. based on contact with reproductive parts), the reduction in visits by the other two bat species in disturbed habitat appears to have negative consequences on fruit set.

One possible explanation for the foraging differences observed between these bat species is related to the size of home ranges utilized and their capacity to fly, both of which are related to their body sizes. Evidence from the literature indicates that *L. curasoae* is a latitudinal migrant that may cover more than 2,000 km during migration (Cockrum 1991) and may fly as much as 100 km in a single night (Horner et al. 1998). In contrast, *G. soricina* does not migrate (Fleming et al. 1993) and has been reported to use a relatively small home range (2–4 ha, Heithaus et al. 1975; Lemke 1984). Unfortunately, there is no information about home range size or migratory patterns of the endangered endemic bat *M. harrisoni*. Our previous results suggest that this species is restricted to undisturbed habitat and is found at very low population densities in the study area (Stoner et al. 2002).

Another factor that facilitates the use of *C. grandiflora* flowers in disturbed areas by *L. curasoae* is the fact that this species is a specialist nectarivore and these flowers provide an important resource during the dry season when other bat-pollinated flowers are scarce (Stoner et al. 2003). Each flower produces an average of 600 μl nectar per night (Palacios-Guevara 2002), thus, isolated trees may provide valuable sources of food for large-bodied nectar specialists moving between trees in disturbed areas. In contrast, *G. soricina* is a generalist that consumes many other items in the diet besides nectar and pollen and thus allows it to obtain resources within a smaller area. Similar to *L. curasoae*, *M. harrisoni* is a specialist nectarivore, however, its smaller body size likely results in a smaller home range accounting for its absence in disturbed habitat.

In spite of the fact that these three nectarivorous bats are the only effective pollinators of *C. grandiflora*, they also visit the flowers to exclusively feed on pollen. All three species were observed arriving at the flower and biting or pulling off an anther (Table 1; see Fig. S1 of Electronic Supplementary Material). This form of "pollinivory" by bats has not previously been described for any species of plant and it has been assumed that pollen ingestion in nectarivorous bats results from grooming pollen from their face and body (Nowak 1994). Given the importance of pollen in the diet of specialized nectarivores (Howell 1974; Law 1992; Herrera and Martínez del Río 1998), especially to obtain protein, this phenomenon may be common in nectarivorous bats, but previously undescribed. In particular, bombacaceous species are likely an important source of pollen for nectarivorous bats because of the relatively higher percentage of protein compared to other plant families (Roulston et al. 2000).

Our study indicates that habitat disruption negatively affects reproduction in *C. grandiflora*. Significantly fewer pollen grains were deposited on the stigmas of flowers that produced fruits in disturbed than those in undisturbed habitats. Moreover, the probability that a flower produces a fruit was significantly lower in disturbed than undisturbed habitats. These results are similar to those reported by Cunningham (2000a) who found that habitat fragmentation can lead to decline in pollination with subsequent decrease in fruit set in *Acacia brachybotrya* and *Eremophila glabra* in the woodlands of New South Wales, Australia.

One explanation for lower reproductive success in disturbed habitat may be related to the greater number of pollinator visits in undisturbed areas. The pollen deposited resulted from animal-vector dispersion, since the separation and distance between anthers and the stigma rarely allows for self-deposition. Therefore, the greater number of pollen grains deposited on stigmas in undisturbed areas is a result of the greater number of pollinator visits. The flowers of trees in undisturbed areas received an average of 100 pollen grains per flower more than trees in disturbed areas (Fig. 2). Even though flowers within both habitats received sufficient pollen grains to fertilize all the ovules in the ovary, a greater pollen load size on the stigmas of flowers of undisturbed sites may have resulted in an increase in fruit set. Several studies have demonstrated that the size of the pollen load per pistil is important in determining the probability of fruit abortion and maturation under natural pollination conditions (Sutherland and Delph 1984; Stephenson et al. 1995; Quesada et al. 2001).

Another explanation for lower reproductive success in disturbed habitat may be related to the pattern of pollinator visitation (i.e. the number of trees visited) in disturbed and undisturbed habitats. It has been shown in one hummingbird pollinated plant that pollinators are less abundant in isolated plants, but once the pollinators locate isolated patches they receive more visits (Schulke and Waser 2001). A similar pattern was observed for the bee pollinated tree *Shorea siamensis*, in which bees spent more time foraging in the canopies of isolated trees (Ghazoul and McLeish 2001). Finally, Fuchs et al. (2003) showed that in *Paquira quinata*, another bombacaceous tree principally pollinated by *G. soricina*, trees within disturbed habitat have a tendency to produce single sired fruits whereas in undisturbed habitat multiple paternity is more common. This suggests that *G. soricina* forages in several different conspecific trees within forests, whereas, in disturbed habitat they concentrate on fewer trees. Since *C. grandiflora* is principally an outcrossing species, visits to flowers in disturbed areas are more likely within isolated individuals that could result in apparently sufficient pollen to produce a fruit, but would result in geitonogamous crosses that are less likely to set fruit. Finally, an alternative explanation for lower reproductive success is that trees in disturbed areas are more resource limited (e.g. areas with soil erosion and decreased water availability) than trees in the forest, and reproductive success might be influenced by environmental factors other than the amount of pollen transferred by pollinators (Stephenson 1992).

Although fruit set is affected by many genetic and environmental factors, our study suggests that reduced pollinator visitation and the consequent reduction in pollen grains deposited on flowers found in disturbed areas may reduce fruit set of *C. grandiflora* by as much as 50%. Moreover, our study demonstrates how forest disruption may differentially affect sympatric pollinator species that are closely related and use the same resource. The endemic dry forest bat *M. harrisonni* and *G. soricina* appear to be vulnerable to habitat disruption. Conservation strategies that involve forest management plans or ecological restoration should consider the changes that habitat disruption may have on the behavior of pollinators and the consequences on the reproductive success and population structure of plants.

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