

Chapter 11

Human Impacts on Pollination, Reproduction, and Breeding Systems in Tropical Forest Plants

MAURICIO QUESADA, FERNANDO ROSAS,
RAMIRO AGUILAR, LORENA ASHWORTH,
VÍCTOR M. ROSAS-GUERRERO, ROBERTO SAYAGO,
JORGE A. LOBO, YVONNE HERRERÍAS-DIEGO,
AND GUMERSINDO SÁNCHEZ-MONTOYA

Over the last two decades several studies have shown that plant species of contrasting life-forms ranging from small herbs to large trees may experience a decline in reproductive success following habitat fragmentation and population disruption (Bawa 1990; Aizen and Feinsinger 1994; Aguilar et al. 2006). Such outcome has been shown for many plants throughout the tropics, particularly trees, where human activities have resulted in elevated rates of habitat fragmentation and degradation (Ghazoul and Shaanker 2004; Quesada and Stoner 2004; Quesada et al. 2004). Because almost 90 percent of angiosperms (i.e., flowering plants) depend on animals for effective pollination and sexual reproduction (Buchmann and Nabhan 1996), it is of central concern to understand the capacity of pollinators for transferring pollen among individuals and its consequences on plant reproduction in newly created anthropogenic landscapes.

While evolutionary dependence of plants on animal mutualists for sexual reproduction has improved pollen transfer to stigmas, it has also prompted increased plant susceptibility to fragmentation and other forms of anthropogenic disturbance that characterize today's landscapes (e.g., Aizen et al. 2002; Ashworth et al. 2004). Changes in abundance, composition, and/or foraging behavior of pollinators as a consequence of habitat disturbance will have an effect on the amount and/or quality (autogamous

vs. xenogamous) of pollen deposited on stigmas, thus affecting reproduction and the genetic structure of plants (Wilcock and Neiland 2002).

Much research has been conducted with regard to the effects of habitat loss and fragmentation on pollination, plant reproduction, and genetic diversity of plant populations over the past 20 years. Nevertheless, there has been certain research bias in the selected natural systems evaluated, where species from tropical forests represent only 16 percent of the entire studied species around the world (Aguilar et al. 2006; Aguilar et al. 2008). Moreover, no specific analysis of this subset of species has yet been conducted. This comparative underrepresentation of tropical plant species in fragmentation studies highlights the need to focus more thoroughly on population studies from these threatened and fragile habitats.

Some expected outcomes of habitat fragmentation include local extinction of plant and animal populations, the alteration of species richness and abundance, and changes in the trophic structure of communities. These negative effects of habitat fragmentation can be expressed at the landscape and population levels. At the landscape scale, fragmentation involves the transformation of a large area of habitat into several patches of smaller size, isolated from each other by surrounding anthropogenic habitats different from the original. Such loss and breaking apart of the habitat alters negatively the connectivity, functioning, and biodiversity within the matrix of the fragmented habitat (Fahrig 2003). At the population level, habitat fragmentation may reduce the effective population size and the magnitude and direction of gene flow, which in turn would produce negative changes in the population and genetic structure of plant species (Young et al. 1996; Aguilar et al. 2008). The reduction of both gene flow and effective population size by habitat fragmentation may cause inbreeding, genetic drift, and a consequent decline of genetic variation. Therefore, the loss of genetic diversity may limit the ability of local populations to respond selectively to varying local conditions, compromising their persistence and increasing their risk of extinction due to inbreeding depression.

Habitat fragmentation may not only lead to a reduction in population size and genetic variation but also disrupt key interactions of the plants with their pollinators and seed dispersers. The interaction between plants and pollinators can be disrupted by habitat loss, reduction of pollinator abundance, changes in floral resource availability and distribution, or competitive exclusion from floral resources by inefficient or exotic pollinators. Most of the plant-pollinator interactions may depend on the relative abundance of floral resources; thus, changes in plant abundances caused by forest disturbance may lead to modification in the composition, functioning,

and maintenance of plant-pollinator webs (Aizen and Feinsinger 2003; Lopezaraiza et al. 2007). We should expect small isolated or fragmented plant populations to be less attractive to pollinators than large populations. As a result of this, rates of pollinator visitation and seed production may often be lower in small than in large populations of plants pollinated by animals.

The negative consequences of habitat fragmentation for plant populations could be exacerbated by the complex interactions of reproductive (sex expression) and mating systems (selfing vs. outcrossing or mixed strategies) in combination with population size and pollination and seed dispersal systems. Previous studies of seasonally dry tropical forests (SDTFs) indicate that the reproduction of plants is dependent on the presence of natural pollinators (Frankie et al. 1974; Bullock 1985). Therefore, changes in the abundance and activity patterns of pollinators induced by habitat fragmentation are expected to reduce gene flow between isolated plant populations. The negative effects of forest fragmentation on the viability of populations could be particularly noticeable in tropical tree species that possess self-incompatibility systems and depend on pollinators for sexual reproduction (Bawa 1974, 1990; Aguilar et al. 2006). Disturbances that impact animal vectors of pollen transfer may therefore affect the reproductive output of tropical trees. Pollination of tropical plants is mainly conducted by animal vectors such as bees, butterflies, flies, birds, and bats, and the natural populations of these animals inhabit and depend on the existence of forests.

The objectives of this chapter are to (1) evaluate the effects of forest fragmentation on plant-pollinator interactions, plant phenology, reproductive dynamics, and genetic parameters of tropical plants; (2) describe and compare plant life-history traits, pollination systems, and plant reproductive traits between tropical forests; and (3) predict vulnerability patterns to forest fragmentation based on ecological and reproductive traits of plants.

Habitat Fragmentation Effects on Pollinator and Reproductive Dynamics and Genetic Parameters

We conducted a quantitative synthesis of the published literature on the effects of habitat fragmentation on plant reproductive dynamics and population genetic parameters of tropical plant species. To accomplish this, we gathered data from two published databases (Aguilar et al. 2006; Aguilar et al. 2008).

To assess the effects of habitat fragmentation on the pollination process

and on the sexual reproduction of tropical plant species, we used an extract of the database compiled by Aguilar et al. (2006). This meta-analysis used published data from the literature within the period of 1987–2006 to evaluate the effects of habitat fragmentation on pollination and reproduction of plant species from different habitats throughout the world (see Aguilar et al. 2006). This analysis included articles that evaluated directly or indirectly, explicitly or implicitly, the effects of habitat fragmentation on the reproductive dynamics of animal-pollinated plants. As response variables, we used pollinator visit frequency, pollen loads on stigmas, or pollen tubes in styles for assessing the effects on pollination. We used fruit or seed production to assess the effects on plant reproductive success as provided by the published studies.

To assess the effects of habitat fragmentation on population genetic parameters of tropical plant species, we used part of the data obtained by Aguilar et al. (2008) through a literature search in the Science Citation Index and Biological Abstracts databases using a combination of “fragment*” and “genet*” and “plant” as keywords within the period of 1989–2007. This quantitative review evaluated the effects of habitat fragmentation on the genetic variability and inbreeding parameters of plant populations in fragmented habitats around the world. As measures of genetic variability, we considered both expected heterozygosity and allelic richness and analyzed them separately. Inbreeding was measured through Wright’s fixation index (f_{IS}).

With these reproductive and genetic variables provided by the published studies that evaluated the effects of fragmentation, we calculated the effect size using Hedges’s d . This effect size is calculated using the mean values, sample sizes, and standard deviations of each parameter (from text, tables, or graphs) and represents a standardized measure of the magnitude and direction of fragmentation effects for each of the species included in the analysis (cf. Gurevitch and Hedges 2001). Positive values of the effect size (d) imply positive effects of habitat fragmentation on a given parameter, whereas negative d values imply negative effects of fragmentation on these parameters. The only exception is the inbreeding coefficient parameter, which has an opposite interpretation: positive d values imply higher inbreeding in fragmented conditions, whereas negative d values mean lower inbreeding in fragmented habitats.

Within both databases (for reproductive and genetic parameters), we selected exclusively the results for tropical plant species and ran separated meta-analyses with these species using the MetaWin 2.0 statistical program (Rosenberg et al. 2000). Confidence intervals of effect sizes were calculated using bootstrap resampling procedures as described in Adams et al.

(1997). An effect of habitat fragmentation was considered significant if the 95 percent bias-corrected bootstrap confidence intervals (CI) of the effect size (d) did not overlap zero (Rosenberg et al. 2000). Data were analyzed using random-effect models, which assume that differences among studies are due to both sampling error and random variation, which is usually the rule in ecological data (Gurevitch and Hedges 2001).

Habitat Fragmentation Effects on Pollinator and Reproductive Dynamics

The literature search conducted by Aguilar et al. (2006) gathered 54 published studies that evaluated the effects of fragmentation on pollination and/or plant reproduction in 89 unique plant species from different regions of the world. Within this sample, there were 17 species from tropical forests, most of them (70 percent) trees, which represent 19 percent of the total sample of species included in this quantitative review. We ran two separate meta-analyses: one assessing fragmentation effects on pollination on 11 data points from 10 unique species and another one assessing effects on sexual reproduction on 17 data points from 16 unique species (table 11-1). In both analyses we included a replicate of *Ceiba grandiflora* data, as this species was studied twice in two different regions (Quesada et al. 2003; Quesada et al. 2004).

The overall effect size of habitat fragmentation on the pollination process of tropical plants was negative, of a large magnitude ($d = -0.923$), and significantly different from zero, according to the 95 percent bias-corrected bootstrap confidence limits (fig. 11-1A). Similarly, the overall effect size of habitat fragmentation on the sexual reproduction of tropical plants was also negative, of a large magnitude ($d = -0.971$), and significantly different from zero (i.e., confidence limits do not overlap zero; fig. 11-1A). These response patterns are in agreement with the overall general effect size found in Aguilar et al. (2006), but with larger magnitude of effect sizes for tropical species.

One of the best examples showing these patterns was in the SDTF species *Samanea saman* (Cascante et al. 2002). This study demonstrated that fragmentation of SDTF changed pollination patterns, which in turn reduced the genetic variability of the progeny and seedling vigor of this tree species (Cascante et al. 2002). The study also showed higher genetic similarity in the progeny of isolated trees, both within and between fruits. Seeds produced by different fruits within isolated trees were more likely to

TABLE II-1. Tropical plant species in the meta-analyses evaluating the effects of fragmentation on pollination, reproduction, heterozygosity, allelic richness, and/or inbreeding coefficient

Species	Family	Life-form	Parameter evaluated					Geographic region	Source
			P	RS	He	AR	IC		
<i>Anacardium excelsum</i>	Anacardiaceae	Tree	X	X				Central America	Ghazoul and McLeish 2001
<i>Brongniartia vazquezii</i>	Fabaceae	Shrub			X	X	X	North America	González-Astorga and Núñez-Farfán 2001
<i>Carapa guianensis</i>	Meliaceae	Tree			X	X	X	Central America	Dayanandan et al. 1999
<i>Caryocar brasiliense</i>	Caryocaraceae	Tree			X	X	X	South America	Collevatti et al. 2001
<i>Catasetum viridiflavum</i>	Orchidaceae	Epiphyte	X	X	X	X		Central America	Murren 2002, 2003
<i>Ceiba aesculifolia</i>	Bombacaceae	Tree	X	X	X		X	Central America	Quesada et al. 2004
<i>Ceiba grandiflora</i>	Bombacaceae	Tree	X	X				Central America	Quesada et al. 2003, Quesada et al. 2004
<i>Ceiba pentandra</i>	Bombacaceae	Tree	X					Central America	Quesada et al. 2004
<i>Dieffenbachia seguine</i>	Araceae	Perennial herb			X	X	X	North America	Cuartas-Hernández and Núñez-Farfán 2006
<i>Dinizia excelsa</i>	Fabaceae	Tree		X		X		South America	Dick 2001
<i>Dombeya acutangula</i>	Sterculiaceae	Tree		X				Asia	Gigord et al. 1999
<i>Dyospiros montana</i>	Ebenaceae	Tree	X	X				Asia	Somanathan and Borges 2000
<i>Elaeocarpus williamsianus</i>	Elaeocarpaceae	Tree		X				Oceania	Rossetto et al. 2004

TABLE II-1. (continued)

Species	Family	Life-form	Parameter evaluated					Geographic region	Source
			P	RS	He	AR	IC		
<i>Enterolobium cyclocarpum</i>	Fabaceae	Tree	X	X				Central America	Rocha and Aguilar 2001
<i>Heliconia acuminata</i>	Heliconiaceae	Perennial herb			X			South America	Bruna and Kress 2002
<i>Oncidium ascendens</i>	Orchidaceae	Epiphyte			X			Central America	Parra-Tabla et al. 2000
<i>Pachira quinata</i>	Bombacaceae	Tree		X	X			Central America	Fuchs et al. 2003
<i>Pentadethra macroloba</i>	Fabaceae	Tree			X	X		Central America	Hall, Chase et al. 1994
<i>Pithecellobium elegans</i>	Fabaceae	Tree			X	X	X	Central America	Hall et al. 1996
<i>Psychotria tenuinervis</i>	Rubiaceae	Shrub	X	X				South America	Ramos and Santos 2006
<i>Samanea saman</i>	Mimosaceae	Tree	X	X				Central America	Cascante et al. 2002
<i>Shorea siamensis</i>	Dipterocarpaceae	Tree	X	X				Asia	Ghazoul et al. 1998
<i>Spondias mombin</i>	Anacardiaceae	Tree		X				Central America	Nason and Hamrick 1997
<i>Swietenia humilis</i>	Meliaceae	Tree			X	X	X	Central America	G.M. White et al. 1999
<i>Swietenia macrophylla</i>	Meliaceae	Tree			X	X	X	Central America	Novick et al. 2003
<i>Symphonia globurifera</i>	Clusiaceae	Tree			X	X	X	Central America	Aldrich et al. 1998

For each species we show the botanical family, the parameter evaluated by the authors, geographic region where the study was conducted, and the source publication. For parameters, P = pollination, RS = reproductive success, He = heterozygosity, AR = allelic richness, IC = inbreeding coefficient.

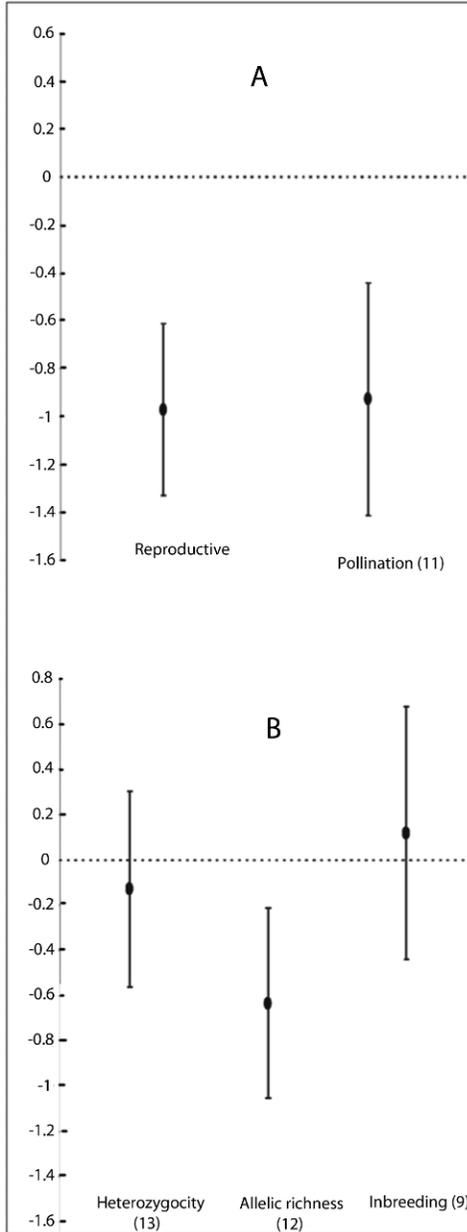


FIGURE 11-1. Overall effect of habitat fragmentation on pollination and reproduction (A) and on genetic parameters (B) of tropical plant species. Weighted-mean effect sizes and 95 percent bias-corrected confidence intervals are shown. Sample sizes are given in parentheses. Dotted line shows Hedges's $d = 0$.

be related than seeds from trees in continuous populations. Seeds produced by trees from continuous populations were more likely to germinate and to produce greater leaf area and biomass as seedlings than progeny from isolated trees. However, isolated trees showed high reproductive capacity in spite of their habitat condition. Few other studies recognize the importance of quantifying fragmentation effects on pollinator activity and its consequences for the reproductive success and genetic variation of tropical trees (Quesada et al. 2003; Quesada et al. 2004; Cuartas-Hernández and Núñez-Farfán 2006).

Habitat Fragmentation Effects on Population Genetic Parameters

Our previous literature survey (Aguilar et al. 2008) measured the effects of habitat fragmentation on the genetic variability of 102 unique plant species from many different regions around the world. From this list, 13 species (nearly 13 percent) belonged to tropical forests, and most of them (77 percent) were trees (table 11-1). We ran three separate meta-analyses evaluating the fragmentation effects on three genetic parameters: heterozygosity (13 data points from 12 unique species), allelic richness (12 data points from 11 unique species), and inbreeding coefficient (9 data points from 9 unique species). In each of the first two meta-analyses, we included a replicate of *Carapa guianensis* data, as two different authors studied this species in different regions (Hall, Orrell et al. 1994; Dayanandan et al. 1999).

The overall effect size of habitat fragmentation on expected heterozygosity of tropical plants was negative and of a small magnitude ($d = -0.129$). However, this value was not significantly different from zero, given that the 95 percent bias-corrected bootstrap confidence limits overlap zero (fig. 11-1B). Thus, fragmentation is not having a significant effect on the expected heterozygosity of this sample of tropical plants. The overall effect size of fragmentation on allelic richness was also negative but of a larger magnitude ($d = -0.634$) and significantly different from zero (fig. 11-1B), which implies fragmentation is decreasing allelic richness in these tropical plant species. This result indicates that forest fragmentation at a regional scale decreases the genetic diversity of remnant populations. For example, in *Carapa guianensis*, allelic richness of the cohort in forest fragments was lower than of the cohort in undisturbed habitats. This difference could be caused by changes in local mating patterns of this species.

Finally, the overall effect size of fragmentation on inbreeding coefficient was positive (meaning increased inbreeding in fragmented habitats com-

pared with continuous forests), of a small magnitude ($d = +0.117$), but not significantly different from zero, as confidence intervals overlap zero (fig. 11-1B). This result indicates fragmentation is not significantly affecting the inbreeding coefficient of these fragmented tropical plant populations.

Habitat Fragmentation Effects on Phenological Patterns

In this section we review the literature and analyze the possible consequences of forest fragmentation on the phenology of tropical plants.

Few studies have indicated that forest fragmentation affects climate or several environmental factors in forest remnants (Laurance, Lovejoy et al. 2002). Remnant forest fragments tend to show increased average temperatures, higher rates of evapotranspiration, and higher exposure to winds, which result in decreased soil moisture compared with continuous forests (Wright 1996; Kapos et al. 1997; Laurance, Albernaz et al. 2002). Several of these environmental factors, such as changes in water content stored by plants (Reich and Borchert 1984; but see Wright and Cornejo 1990; Wright 1991), seasonal variations in rainfall (Opler et al. 1976), changes in temperature (Ashton et al. 1988; Williams-Linera 1997), photoperiod (Leopold 1951; Tallak and Muller 1981), irradiance (Wright and van Schaik 1994), and sporadic climatic events (Sakai et al. 1999), have been shown to trigger phenological events in tropical plants. However, very few studies have analyzed the effects of forest fragmentation on plant phenology.

Many studies in the tropics have found that leaf abscission is highly synchronized with dry conditions that are related to soil water content and tree water status (Reich and Borchert 1984; Borchert 1994b). In tropical wet forests, most tree species are evergreen with a relatively continuous pattern of leaf production, but the amount of leaf fall is correlated with the intensity of a dry season. In SDTF, the dry deciduous community of plants drops its leaves at the beginning of the dry season. Leaf flushing appears to be different between habitats (Reich 1995). In wet forests, leaves tend to be produced during the driest period (Frankie et al. 1974), but foliar development is apparently controlled more by internal than by environmental factors (Reich 1995). In contrast, dry forests flush predominantly at the beginning of the wet season, but there is also a small peak during the beginning of the dry season in riparian habitat plant communities (Frankie et al. 1974). In dry forests, primordial leaf buds and leaf expansion take place before the initiation of the rainy season. There is also intra- and interspecific variation in leaf production's response to soil water content and stored stem

water availability in dry tropical species (Borchert 1994). Leaf production of trees of the same species varies according to habitat soil water availability. Different species of trees vary in their stem water storage capacity, and this in turn is related to the timing of leaf production. Given the understanding of the environmental factors that affect leaf phenology in tropical plants, we predict that SDTF will be more sensitive to environmental changes caused by forest fragmentation. A greater increase in temperature and evapotranspiration and a decrease in soil moisture in forest fragments are likely to reduce leaf life span, possibly affecting carbon uptake of trees more in dry forests than in wet forests.

Certain plant-herbivore interactions are affected by the timing of leaf flushing because many herbivores depend on leaves to complete part of their life cycle (Janzen 1970; Marquis 1988; Aide 1993). This is particularly important in SDTF. Changes in the timing of leaf flushing and leaf life span provoked by habitat fragmentation's effects on environmental factors may negatively affect herbivore population dynamics. Environmental changes caused by habitat fragmentation are also likely to trigger changes in the phenology of flowering and fruiting. Synchronization of flowering seems to be partially controlled by physical abiotic factors; in wet forests a flowering peak usually occurs at the beginning of the wet and dry seasons, whereas in dry forests most plant species flower during the dry season. Little is known about the physiological processes that control flower and fruit production in tropical plants (Chapotin et al. 2003). Apparently, a certain threshold level of drought is required to trigger flowering in some tropical plant species (Alvim 1960; Wright et al. 1999). One of the few studies that have evaluated this phenomenon found that the frequency of flowering was similar in populations of the tree *Ceiba aesculifolia* in disturbed and undisturbed conditions, but flowering initiation date and flowering peak occurred between 2 and 3 weeks earlier in disturbed populations than in undisturbed habitats during 3 consecutive years (Herrerías-Diego et al. 2006). Tree populations in disturbed areas may be experiencing drier soil conditions and greater temperatures that trigger their flowering period earlier than the flowering of trees in undisturbed populations.

Changes in flowering phenology caused by habitat loss will also disrupt the pollination patterns of many long-distance pollinators and trap-liners such as some large bees, hawkmoths, nectarivorous bats, and hummingbirds that follow the flowering sequential phenology of plant communities (Stiles 1977; Fleming et al. 1993; Haber and Stevenson 2004; Lobo et al. 2003; Quesada et al. 2003; Quesada et al. 2004).

Variation in the synchrony of flowering also has been proposed as

an important factor that affects the reproduction, genetic structure, and mating patterns of tropical plant populations in disturbed habitats (Stephenson 1982; Murawski and Hamrick 1992; Chase et al. 1996; Nason and Hamrick 1997; Fuchs et al. 2003). For example, Fuchs et al. (2003) found for the SDTF tree *Paquira quinata* that trees in fragmented habitats consistently presented either early or late flowering peaks. This resulted in higher selfing rates within trees through geitonogamy and the production of single-sired fruits. In contrast, trees in undisturbed natural forests had higher outcrossing rates and multiple paternity of fruits.

Several biotic factors, such as pollinator attraction and competition for pollinators, have been proposed as important evolutionary forces responsible for phenological patterns in tropical plants (Janzen 1967; Stiles 1975; Appanah 1985; Zimmerman et al. 1989; Sakai et al. 1999; Lobo et al. 2003). Changes in flowering phenological patterns caused by forest fragmentation are likely to affect the behavior and visitation rate of pollinators. If the flowering pattern of plant species that share pollinators of the same guild is displaced over time (Frankie et al. 1974; Stiles 1975; Lobo et al. 2003), competition for the same pollinators will occur, resulting in negative consequences for the reproductive success of the plants and the ability of the pollinators to obtain resources over time. For example, in a SDTF in Mexico, trees of the family Bombacaceae provided the main resource to nectarivorous bats during 8 months of the year (Lobo et al. 2003; Stoner et al. 2003). The sequential use of bombacaceous species by these bats was coupled with the flowering phenology of the tree species. Changes in flowering phenology caused by habitat fragmentation changed the pollination patterns of bats and negatively affected the reproductive output and mating patterns of some of these trees species (Quesada et al. 2004).

Fruiting phenology may also be altered by environmental changes associated with habitat disturbance, but this has remained unexplored. Timing of fruit and seed production is key to understand dispersal, regeneration, and establishment of natural populations in disturbed habitats. Most species of tropical trees fruit after they flower; thus, delays in the flowering patterns will directly affect fruiting and seed dispersal patterns. In SDTF, most tree species are wind dispersed and depend on high temperature and low relative humidity for abscission and dispersal (Greene et al. 2008). Changes of such environmental conditions in disturbed habitats will change fruit maturation and seed dispersal patterns. Displacement in time of fruiting phenology of tropical tree species that provide keystone resources could have negative consequences on populations of birds and mammals that disperse their seeds and, ultimately, negative effects on re-

recruitment of the species they disperse (Howe 1984). Seed dispersal by animals is negatively affected by deforestation and results in lower recruitment in forest fragments (Cordeiro and Howe 2001).

Comparison of Plant Life History and Reproductive Traits and Pollination Systems between Forests

To predict the possible vulnerability of tropical plants to forest fragmentation, we first compiled basic information on plant life-history traits of species from several SDTFs from different published and unpublished databases. Specifically, we gathered information on life-form, sexual expression, compatibility systems, and pollination and seed dispersal vectors of SDTF plant species from Brazil (Caatinga: Machado and Lopes 2004; Machado et al. 2006; Cerrado: Oliveira and Gibbs 2000), Venezuela (Colinas de Bello Monte: Jaimes and Ramírez 1999), Mexico (Chamela: Bullock 1985; Lott 2002; our own database), and Costa Rica (Guanacaste: Bawa 1974; Bawa and Opler 1975; our own database). Also, we obtained the same information for plant species from different regions of tropical rain forest, such as Brazil (Atlantic forest: Silva et al. 1997), Costa Rica (La Selva: Janzen 1983; Bawa et al. 1985; Chazdon et al. 2003), Mexico (Los Tuxtlas: Ibarra-Manríquez and Oyama 1992), Panama (Barro Colorado: Croat 1979), and Venezuela (montane tropical forest: Sobrevila and Arroyo 1982). We made a complete list of plant species from each type of forest and carefully checked it to avoid repetition of species taxonomic identities. With this information we were able to determine the incidence of the different plant life-history traits in each type of forest and also to compare the frequency distribution of these traits between SDTF and tropical rain forest plant species.

Patterns of Plant Life-History Traits, Pollination Systems, and Plant Reproductive Traits

The available published and unpublished databases allowed us to obtain information on a total of 1364 unique plant species from SDTFs and 668 unique plant species from tropical rain forests (TRFs). We were able to assign at least one of the five life-history traits (namely, life-form, sexual expression, compatibility system, and pollen and seed dispersal vectors)

to each one of these species. Our analysis contains the largest and most comprehensive database of tropical plant reproductive traits compiled to this date.

Herbs represented nearly 33 percent of life-forms, while shrubs and trees characterized 24 percent and 23 percent of sampled species from SDTF, respectively. Vines made up 18 percent of the species, and nearly 4 percent were epiphytes. The sexual expression of plants was obtained for 1310 species of SDTF and 443 species of TRF. Hermaphroditism was by far the most represented type of sexual expression throughout all life-forms: about 70 percent of the species were hermaphrodite (fig. 11-2). Monoecious and dioecious species were less frequent, and both were similarly represented within this sample of species (about 15 percent of the species; fig. 11-2). The incidence of monoecy was comparable (between 3 and 5 percent) in herbs, shrubs, trees, and vines. Dioecy was mainly represented in trees and shrubs (5 percent and 2.5 percent, respectively) and less represented in vines, epiphytes, and herbs (1.7 percent, 0.8 percent, and 0.6 percent, respectively).

The overall percentages of occurrence of sexual expressions were very similar between SDTF and TRF, and there was a significantly higher pro-

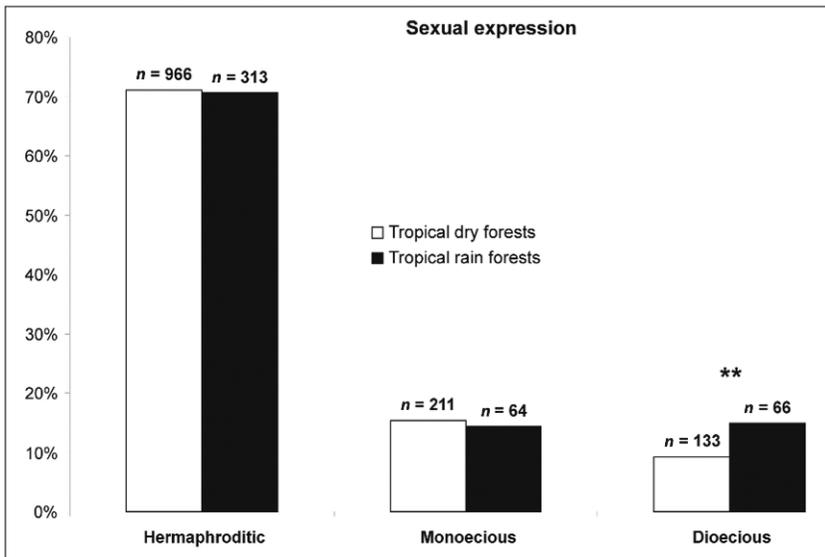


FIGURE 11-2. Frequency distribution patterns of sexual expression in plant species from tropical dry and tropical rain forests. Numbers of species are displayed on the tops of the bars. ** $P < 0.05$ for chi-square test.

portion of dioecious species in TRF compared with SDTF (chi-square = 5.86; $p = 0.015$; fig. 11-2). Furthermore, in a comparison of the distribution patterns of sexual expression using the proportions previously calculated by several authors (synthesized in table 2 in Machado et al. 2006) from four SDTFs and five TRFs from different countries, the results were comparable to ours. On average, hermaphrodite species represent 75 percent and 70 percent of the species from these SDTFs and TRFs, respectively. Monoecious species are on average 10 percent and 11 percent of the species, while dioecious species represent 14 percent and 20 percent of the species from SDTFs and TRFs, respectively. In this case, however, the larger proportion of dioecious species in TRFs was not significantly different from the proportion found in SDTFs (Mann-Whitney $U = 6.12$; $p = 0.327$).

Information on compatibility systems was obtained for 171 SDTF species and 104 TRF species. A great majority of the sampled species from SDTF, nearly 75 percent, was self-incompatible. Most of the long-lived, woody species such as trees (85.7 percent), shrubs (64.5 percent), and vines (70.6 percent) were self-incompatible, as were 50 percent of the herbaceous species from SDTF. The distribution pattern of compatibility systems between the two types of forests was similar. Although there was a higher proportion of self-incompatible species in SDTF and of self-compatible species in TRF, these differences were not statistically significant (chi-square = 0.77, $p = 0.380$ and chi-square = 2.23, $p = 0.135$, respectively). The higher proportion of self-compatible species in TRF is mostly due to the higher incidence (72 percent) of self-compatibility among the herbaceous species of the sample. Furthermore, we evaluated the incidence of obligate outcrossing species by adding the proportion of self-incompatible and dioecious species in each type of forest. Overall there was a higher proportion of obligate outcross species in SDTF compared with TRF, and this difference was statistically significant (chi-square = 6.93, $p = 0.01$).

We gathered information on the type of pollination vector for 585 SDTF species and 516 TRF species. We grouped the pollinator vectors in three main categories: wind, insect, and vertebrate. Clearly, insect-pollinated species are the vast majority of species in both tropical forests. In SDTF, insects are the pollination vectors of more than 83 percent of the species, vertebrates pollinate almost 12 percent of the species, and wind is responsible for the pollination of nearly 3.5 percent of the species. These proportions remain similar among species sharing the same life-form, with the few wind-pollinated species being herbs and shrubs. Regarding the pollination vector and the sexual expression of plants, we found that almost 95 percent of the vertebrate pollinators interact with hermaphrodite plants,

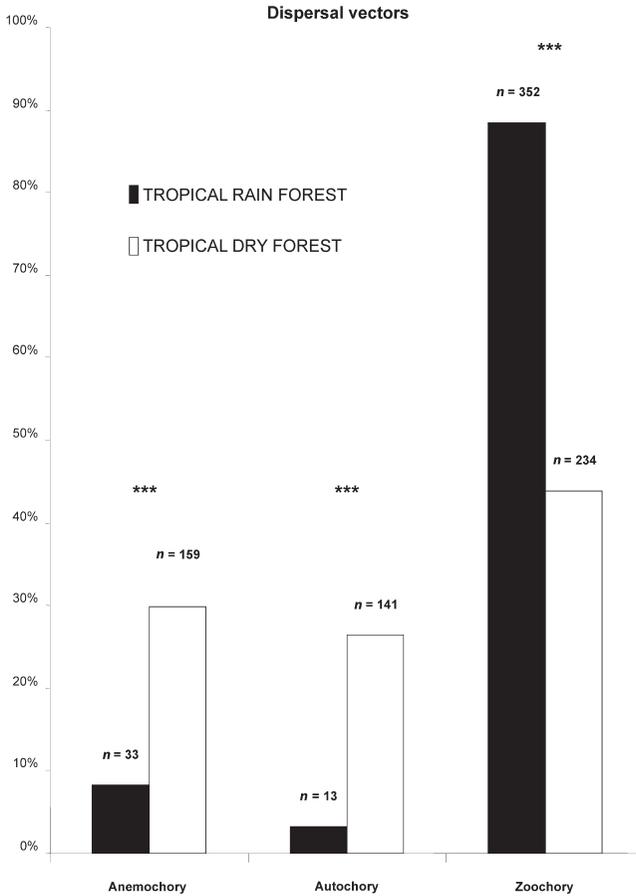


FIGURE 11-3. Frequency distribution patterns of seed dispersal vectors in plant species from tropical dry and tropical rain forests. Numbers of species are displayed on the top of the bars. *** $P < 0.01$ for chi-square test.

whereas 80 percent of the wind-pollinated species were monoecious plants. Insects are the pollinators of almost all (98 percent) dioecious species. The overall distribution of pollinator vectors between both SDTF and TRF is quite comparable. A rather different pattern, however, was observed in TRF species when pollinator vectors, life-form, and sexual expression were combined. Unlike SDTF species, most wind-pollinated species in TRF (nearly 70 percent) were dioecious trees.

It is important to notice that most of the information on pollination systems, from our databases as well as many others from the literature, is

based mainly on indirect observation of floral visitors. Nevertheless, floral visitors do not necessarily always function as legitimate pollinators, because not all floral visitors transport pollen from anthers to stigmas (e.g., Schemske and Horvitz 1984; Bawa et al. 1985; Armbruster et al. 1989). For example, in a study to discriminate visitors from legitimate pollinators in 22 sympatric species of *Ipomoea* that occur in a SDTF in Mexico, we found that 12 plant species appeared to be generalists when all flower visitors were included as pollinators, whereas only 8 plant species appeared to be generalists when just legitimate pollinators were assigned to each species (Rosas-Guerrero et al., in prep.). Therefore, it is likely that many studies have overestimated the frequency of legitimate pollinators by interpreting the pollination syndrome from flower morphology or by observations of flower visitors.

Finally, we characterized the seed dispersal vector for 534 SDTF species and 398 TRF species. To do this, we summarized the dispersal vectors in three main categories: anemochory, autochory, and zoochory. For species of SDTF, there was a higher proportion of animal-dispersed seeds (zoochory), followed by quite similar proportions of anemochorous and autochorous plants (fig. 11-3). In fact, these two nonanimal dispersal types make up over 56 percent of the total sample of species in SDTF. The three dispersal types were compared among the different life-forms and sexual expressions, and the following patterns were observed: anemochory was present in more than 90 percent of epiphytes, whereas zoochory was more frequent in trees and shrubs (60.4 percent and 54.2 percent, respectively), and autochory was more common in herbs (52.3 percent). Nearly 70 percent of hermaphrodite plants were either anemochorous (41 percent) or zoochorous (38 percent), whereas 94 percent of monoecious plants were autochorous (47 percent) or zoochorous (47 percent), and almost 60 percent of dioecious species were zoochorous.

We found very different distribution patterns when comparing types of dispersal vectors between species from SDTF and TRF (fig. 11-3). Anemochory and autochory were significantly more frequent in SDTF than in TRF (chi-square = 43.8, $p < 0.001$ and chi-square = 65.9, $p < 0.001$, respectively; fig. 11-3). Zoochory, on the contrary, was significantly more represented in TRF compared with SDTF (chi-square = 43.4, $p < 0.001$; fig. 11-3). In species of TRF, zoochory is the main dispersal type for all the different life-forms (frequency range of 79 percent and 100 percent of occurrence), and sexual expressions (frequency range of 83 percent and 100 percent of occurrence). Anemochorous and autochorous species in TRF were mostly present in hermaphrodite trees.

Vulnerability of Plants to Anthropogenic Disturbance in SDTFs: Conclusions

The literature review analyzed in this chapter has shown that forest fragmentation affects important life-history components of tropical plants, particularly biotic pollination, plant phenology, plant reproductive success, and genetic diversity. A meta-analysis showed that tropical plant populations in fragmented forests show a decrease in pollination, decrease in reproductive output, and loss of genetic diversity. Given these results, we should expect a reduction in plant populations with greater probability of local extinction because of demographic, environmental, and genetic stochasticity (Young et al. 1996; Aguilar et al. 2008).

Mutualisms between Plants and Pollinators

A quantitative analysis shows that most tropical plants are animal pollinated, with a high incidence of outcrossing, mediated by either self-incompatibility systems or dioecy. Flowering plants of tropical ecosystems are highly dependent on animals to move their pollen to receptive compatible plants of the same species to accomplish sexual reproduction. Such dependence of tropical plants on mutualistic relationships with pollinators for reproduction is the result of a long history of evolutionary changes. Hence, disruption of such long-term plant-pollinator interactions will make tropical plants particularly vulnerable to forest fragmentation, more so than temperate systems that are mainly wind pollinated.

Our results showed that pollination and plant reproductive success are negatively affected by fragmentation (fig. 11-1). There were negative effects of fragmentation on pollination, interpreted as pollination visitation frequency, deposition of pollen on stigmas, and number of pollen tubes in styles. Because native small insects and native bees are the main pollinators of the species considered in the meta-analysis, we predict that this guild of insect pollinators will be the most susceptible to forest fragmentation. At the community level we expect their abundance and species richness to be reduced in remnant fragments, compared with continuous forest. We expect a reduction of the pollinators' population sizes due to reduced availability of flower resources and nesting sites. Moreover, small native insects and native bees will be more susceptible to fragmentation because they have a limited ability to fly between remnant fragments. Such restriction on

pollinator movement may translate into a reduction of plant fitness due to pollen limitation, biparental inbreeding, and geitonogamy.

Unlike native insect pollinators, exotic pollinators such as feral honey bees (*Apis mellifera*) are able to dominate flower visitor assemblages on fragmented habitats (Aizen and Feinsinger 1994). Thus, there is a potential that native pollinators will be replaced by exotic ones following forest fragmentation. The success of these exotic bees has been related to their social and generalized pollinator behavior; thus, it is expected that these bees will prefer common plants with massive synchronous flowering rather than plants that flower asynchronously or in lower density. Therefore vulnerability of specialized pollination systems will increase because of disappearance of legitimate pollinators. Furthermore, the foraging behavior of *Apis mellifera*, typically characterized by long visitation time to many flowers of the same individual before movement to another plant, increases the deposition of geitonogamous pollen. While this may represent a short-term rescue effect in self-compatible species in fragmented habitats (Dick 2001; Aguilar et al. 2006), it increases the chances of reproductive failure among outcrossing, self-incompatible plants, which, as shown here, represent the majority of species in tropical systems.

A general prediction is that large-bodied pollinators such as birds, bats, large bees, and hawkmoths can fly long distances and are less likely than smaller pollinators to be affected by the increased distance between flower resources in remnant fragments (Ghazoul and Shaanker 2004). However, Quesada et al. (2004) showed that the effects of forest fragmentation on bat pollination in SDTF are plant-pollinator specific. Based on the evidence presented in this study, we predict that highly specialized pollination systems involving large pollinators of self-incompatible plants with prolonged flowering patterns will be especially susceptible to forest fragmentation (e.g., the *Ceiba grandiflora*-bat pollination system).

Sexual Expression and Mating Systems

The extent of the effect of fragmentation on biotic pollination and its translation into seed production is closely related to the degree of dependence of plants on cross-pollination. The breeding system is a relevant trait of plants, determining both the dependence of plants' reproductive success on the availability of pollinators and the extent of reproductive vulnerability of plants to forest fragmentation. It is expected that automatic self-pollination through reproductive assurance will be the most

successful reproductive mechanism for survival in fragmented habitats, but it may suffer problems associated with inbreeding in the long term. Conversely, obligate hermaphroditic outcrossing and dioecious plants will show complete dependence, not only on pollinators, but also on the presence of other reproductive individuals of the same species for mating and seed production. Our results showed that 76 percent of the species are self-incompatible or dioecious. These obligate outcrossing species will be particularly vulnerable to the disruption of pollination mutualisms caused by forest fragmentation, particularly dioecious species that are essentially pollinated by small insects with restricted flying movement. In addition, because our analysis showed a higher proportion of obligate outcrossing species in SDTF than in TRF, we may predict more susceptibility of SDTF to forest fragmentation.

The presence of mixed mating systems has been suggested for few tropical tree species (Bullock 1995). Such variation in breeding systems has been associated with changes in pollinators between different habitats or along altitudinal gradients (Murawski and Hamrick 1992; Lobo et al. 2005). For example, Lobo et al. (2005) showed that differences in pollinators between two habitats were correlated with the breeding system and the levels of relatedness of the progeny produced in *Ceiba pentandra* in Costa Rica. High levels of outcrossing were found in the SDTF where bats were the predominant pollinators, whereas a mixed mating system was found in wet seasonal forests where bats were not common pollinators. Genetic relatedness of seeds was greater in the region where bats were absent, indicating higher probability of selfing (Lobo et al. 2005). Other studies on temperate regions have shown that self-incompatibility can be flexible. These studies have proposed different genetic mechanisms to explain such flexibility; ability to switch to partial self-incompatibility has particularly been related to polyploidy or gene duplication (de Nettancourt 2001), pleiotropic effects of modifying genes (Levin 1996; Good-Avila and Stephenson 2002, 2003), or temporal plasticity of self-incompatibility proteins (Richardson et al. 1990; Vogler et al. 1998). These mechanisms can be present in tropical plants, but this field remains completely unexplored.

Changes in mating systems have also been associated with forest fragmentation and habitat disturbance. For example, in the SDTF tree *Pachira quinata*, populations from continuous forest presented high levels of outcrossing rates, whereas populations from fragments experienced a mixed mating system (Quesada et al. 2001; Fuchs et al. 2003). Disturbance and habitat fragmentation may change mating patterns and gene flow of natural

populations of tropical plants, with possible consequences for the genetic diversity of these systems.

In an ongoing study in the SDTF of Mexico, we found changes in the composition of plant communities under different successional stages. The number of plant families declined almost linearly, from 35 families in mature forest to 28, 10, and 7 families in sites that were 8 to 12 years old, 3 to 5 years old, and grassland, respectively. The number of tree species showed an evident reduction in grassland and early successional stages, and this is also related to a significant reduction of monoecious and dioecious reproductive systems (fig. 11-4).

Hermaphroditic and monoecious systems are maintained in all the successional stages, whereas dioecy disappears in grassland. Therefore, it is expected that mature and intermediate successional stages are more susceptible to habitat fragmentation.

Finally, obligate outcrossing species will be particularly vulnerable to the disruption of pollination mutualisms caused by forest fragmentation, particularly dioecious species that are essentially pollinated by small insects with restricted flying movement. We predict more susceptibility of SDTF to forest fragmentation because of a higher proportion of obligate outcrossing species in SDTF than TRF.

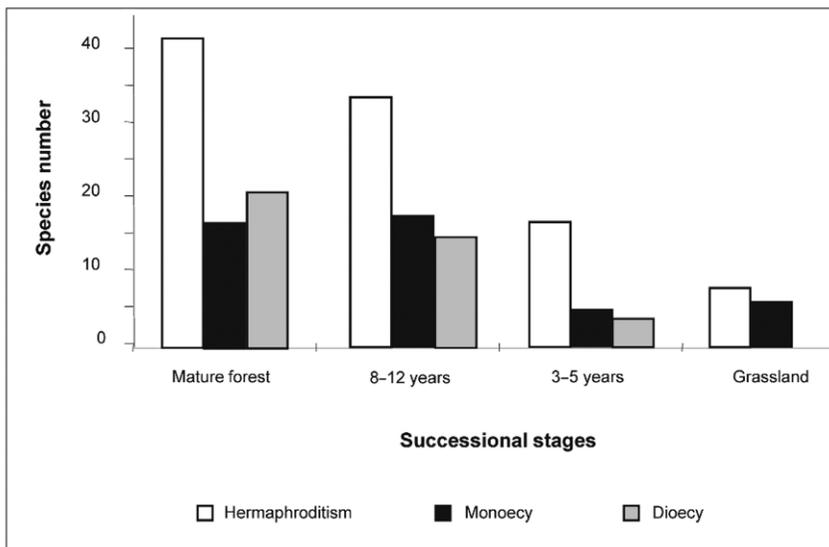


FIGURE 11-4. Frequency of plant reproductive systems in different successional stages of a SDTF of Mexico.

Conclusions

In this review we were able to show general patterns of the effects of forest fragmentation on plant-pollinator interactions, plant phenology, reproductive dynamics, and genetic parameters of tropical plants. However, it is clear that our conclusions are limited to fewer than 30 species of plants that are biased by trees. Other life-forms with contrasting pollination systems, sexual expression, and breeding systems need to be studied in this context. Particular attention is needed in the case of insect pollinators and their interactions with dioecious plants.

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