

# 4

## Dispersal Ecology of Neotropical *Piper* Shrubs and Treelets

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### 4.1. INTRODUCTION

Along with the Melastomataceae, Rubiaceae, and Solanaceae, shrubs and treelets of the Piperaceae (primarily *Piper*) are numerically dominant members of the understories of many Neotropical forests. This dominance occurs both in number of species and number of individuals. Gentry and Emmons (1987) reported that *Piper* species richness ranged from 0.3 to 6.5 species per 500-m transect along a rainfall/soil fertility gradient in Central and South America compared with ranges of 0.7–5.8 and 1.0–8.4 in the Melastomataceae and Rubiaceae, respectively. Data summarized in Gentry (1990) indicate that *Piper* species richness in certain well-studied moist or wet tropical forests ranges from 18 (Barro Colorado Island, Panama) to 60 or more species (La Selva, Costa Rica). Tropical dry forests have much lower diversity (e.g., five species at Parque Nacional Santa Rosa, Costa Rica; Fleming 1985). Forests around Manaus, Brazil, also contain few *Piper* species (Prance 1990). Overall, the pantropical genus *Piper* has been especially successful evolutionarily in the lowland Neotropics, which contains over twice as many species as the Asian tropics (700 vs. 300 species; Jaramillo and Manos 2001).

To what extent has *Piper* reproductive biology, especially its dispersal ecology, contributed to its ecological and evolutionary success? Most Neotropical pipers produce tiny self-incompatible, hermaphroditic flowers arrayed in spike-like inflorescences that are pollinated by generalized bees and flies (see Chapter 3). *Piper* pollination biology does not appear to involve specialized coevolutionary relationships with a restricted subset of insect pollinators. Successfully pollinated flowers develop into small, single-seeded fruits in infructescences (which will hereafter be called “fruits”). Number of seeds (fruits) per infructescence in a series of Costa Rican pipers ranged from just over 100 to about 3,000; seed mass ranged from 0.14 to 6.23 mg (Fleming 1985, Greig 1993a). In contrast to the pollination situation, a small number of frugivorous phyllostomid bats are the most important dispersers of *Piper* seeds. These bats appear to be specialized consumers and dispersers

**TABLE 4.1**  
**Characteristics of Bats of the Phyllostomid Subfamily Carolliinae**

Species	Mass (g)	Distribution
<i>Carollia brevicauda</i>	20.1	Southern Mexico to eastern Brazil
<i>C. castanea</i>	14.7	Honduras to western Brazil
<i>C. perspicillata</i>	19.5	Southern Mexico to Paraguay
<i>C. subrufa</i>	16.2	Southern Mexico to western Costa Rica
<i>Rhinophylla alethina</i>	—	Colombia and Ecuador
<i>R. fischeriae</i>	—	Colombia to central Brazil
<i>R. pumilio</i>	8.3	Colombia to eastern Brazil

*Note:* Data comes from Fleming (1991), Koopman (1993), and Simmons and Voss (1998). Central American forms of *C. brevicauda* are now recognized as *C. Sowell*: (Baker *et al.* 2002).

of these fruits. In this chapter, I review the dispersal ecology of Neotropical pipers in an attempt to answer the above question. I also speculate about the importance of *Piper*'s dispersal ecology for its speciation and evolutionary radiation.

#### 4.2. THE *Piper* BATS

Bats of the family Phyllostomidae (New World leaf-nosed bats) are ubiquitous and species-rich in Neotropical lowlands. Depending on location, from 31 to 49 species of phyllostomid bats have been captured in Neotropical rain forests (Simmons and Voss 1998). Of these, 12 to 25 are frugivores classified into two sister clades—the Carolliinae and Stenodermatinae (Wetterer *et al.* 2000). These clades neatly reflect an ecological separation between understory (Carolliinae) and canopy (Stenodermatinae) fruit eaters. Because of their feeding specialization, carolliinine bats can be considered to be “*Piper* bats.”

Subfamily Carolliinae contains two genera (*Carollia* and *Rhinophylla*) containing at least four and three species, respectively (Table 4.1). Species of *Carollia* are larger in body size and are much more widely distributed in the Neotropics than those of *Rhinophylla*, which occur only in South America. One or two species of *Carollia* occur in tropical dry or moist forests; up to three species co-occur in tropical wet forests (Fleming 1991). Species of *Carollia* appear to be much more specialized on a diet of *Piper* than are species of *Rhinophylla* and are probably more important dispersers of *Piper* seeds. *Piper* is a year-round dietary staple in species of *Carollia* (Fig. 4.1). In Central America, these bats eat fruits of 5–12 species per season, and percent *Piper* in *Carollia* diets is negatively correlated with a species' body size (Fleming 1991). In lowland Peruvian rain forests, Gorchov *et al.* (1995) reported that three species of *Carollia* eat seven species of *Piper* whereas two species of *Rhinophylla* eat no pipers. In French Guiana, *Piper* is a minor item in the diet of *Rhinophylla pumilio* (Charles-Dominique 1993, Charles-Dominique and Cockle 2001). Other common items in the diets of *Carollia* bats include fruits of *Solanum* (Solanaceae) and *Vismia* (Hypericaceae), two early successional shrub taxa that often co-occur with pipers.

In addition to major dietary differences, these two genera differ in their roosting behavior and degree of gregariousness. *Carollia* bats live in small to moderately large colonies (a few 100s to a few 1,000s) in caves, hollow trees, and man-made structures



FIGURE 4.1. *Carollia perspicillata* approaching a fruit of *Piper tuberculatum*, Guanacaste Province, Costa Rica. Photo reprinted with permission, courtesy of Merlin D. Tuttle/Bat Conservation International.

(e.g., wells, road culverts). In contrast, *Rhinophylla* bats live solitarily or in small groups (6) in “tents” formed from clipped palm or *Philodendron* leaves in the forest understory (Charles-Dominique 1993, Simmons and Voss 1998). Rather than creating their own tents, these bats appear to take over abandoned tents created by stenodermatine bats. At localities where both genera occur, *Carollia* bats are often at least an order of magnitude more common than *Rhinophylla* bats (Gorchov *et al.* 1995, Simmons and Voss 1998).

The foraging and fruit-harvesting behavior of *Carollia perspicillata* has been studied extensively and is known in great detail (Fleming *et al.* 1977, Heithaus and Fleming 1978, Fleming and Heithaus 1986, Bonaccorso and Gush 1987, Fleming 1988, Charles-Dominique 1991, Bizerril and Raw 1998, Thies *et al.* 1998, Thies and Kalko, unpublished manuscript). These bats are relatively sedentary and many forage within a kilometer of their day roosts. Their foraging ranges are larger during dry seasons, when fruit levels are low, than during wet seasons. Most individuals remain away from their day roost all night (e.g., from 1900 to 0500 h) and harvest fruits in one to three feeding areas often separated by a few hundred meters. Within their feeding areas, which usually overlap among individuals, bats harvest single fruits and take them to feeding roosts located 20–100 m from a fruiting plant to eat. An exception to this is the large (9.4 g) fruits of *P. arboreum*, which are harvested piecemeal by *C. perspicillata* (Bizerril and Raw 1998). Fruits are eaten quickly (in less than 3 min), and bats harvest a new fruit every 15–30 min. In one night, a bat will consume just over 100% of its body mass in fruit pulp and seeds (e.g., 40–50 *Piper* fruits). Passage time

of fruit pulp and seeds is rapid (about 5 min, early in the evening when bats are most active, and 20–30 min, later in the night).

*Carollia* bats use a combination of echolocation and olfaction to locate ripe *Piper* fruits. They use echolocation to avoid obstacles in the cluttered understory of tropical forests and olfaction to discriminate between ripe and unripe fruit. Their final approach to ripe fruits is guided by echolocation information. They usually grab ripe fruits by the distal tip in flight and carry them back to their feeding roosts to eat. Fruit relocation experiments with *P. amalago* and *P. pseudofulgineum* in western Costa Rica indicate that *Carollia* bats are acutely aware of ripe *Piper* fruits in their environment. Regardless of whether they are located in expected (i.e., in *Piper* patches) or unexpected locations (e.g., in flyways hundreds of meters away from the nearest *Piper* patch), ripe fruits have nearly a 100% chance of being located and removed from experimental “shrubs.” Observations on fruit removal rates from actual *Piper* plants confirm that first-night removal probabilities of ripe fruits are very high (typically 90%). Detailed analysis of the temporal pattern of fruit harvesting during a night indicates that members of *C. perspicillata* usually feed on *Piper* fruit early in the evening before switching to other kinds of fruit.

Social status is known to have a strong effect on the foraging behavior of *C. perspicillata* and presumably other species of *Carollia*. As described by Williams (1986) and Fleming (1988), this species has a harem-polygynous mating system in which a small number of adult males (<20%) are harem (or territorial) males that guard groups of up to about 20 adult females (“harems”) in the day roost. All subadult and most adult males are “bachelors” that reside in a different part of the day roost away from the harems. Harem males defend their groups of females or harem sites from the intrusions of bachelor males all day and night. All females and most bachelor males leave the day roost to forage all night. Harem males, in contrast, often use the day roost as their feeding roost and only leave the roost to obtain a fruit. As a result, harem males are less likely to be effective seed dispersers than females or bachelor males; most of the seeds they ingest end up either in or very close to the day roost.

Charles-Dominique (1993) used radio telemetry to document the feeding rhythms of different social and reproductive classes of *C. perspicillata* in French Guiana. He found that the rhythms of harem males and females in late pregnancy and lactation differed quantitatively from those of bachelor males and females that are not in late pregnancy (Fig. 4.2). Harem males were more active, and late pregnant/lactating females were less active, than other bats. Despite their high levels of foraging activity, harem males centered this activity around their day roosts and foraged less widely than bachelor males and females.

Radio tracking observations of *Rhinophylla pumilio* in French Guiana and Ecuador indicate that, like *Carollia*, it is a sedentary bat (Rinehart 2002). Foraging areas or home ranges of these bats averaged 10–15 ha, and bats used tents as their feeding roosts. Small groups, sometimes containing a single adult male and several adult females (i.e., a harem), roost together and frequently move between several tents in their home range (Simmons and Voss 1998, Rinehart 2002). Rinehart (2002) has suggested that since adult male ranges do not overlap, they are likely to be territories.

Two other common phyllostomid bats, *Glossophaga soricina* (Glossophaginae) and *Sturnira lilium* (Stenodermatinae), sometimes eat *Piper* fruit, but neither species can be considered to be a *Piper* specialist (Heithaus *et al.* 1975, Charles-Dominique 1986, Fleming 1988). *G. soricina* is an omnivorous species whose diet includes nectar and pollen

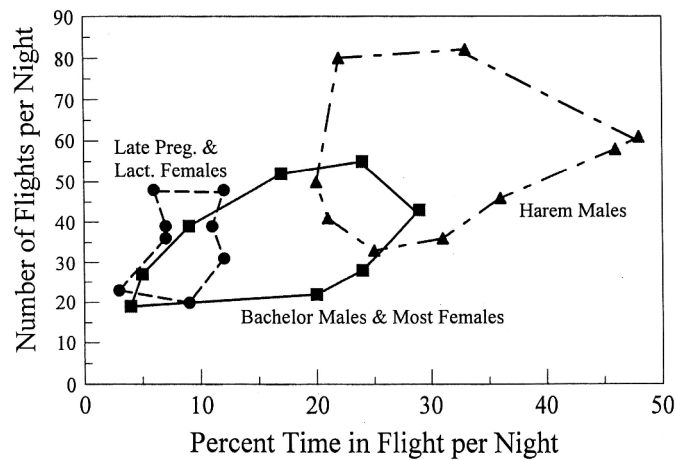


FIGURE 4.2. Foraging activity levels in three groups of adult *Carollia perspicillata* in French Guyana. Reproductively active females undergo the least, and harem males the most, flight activity each night. Data are from Charles-Dominique (1991).

(its principal specialization), fruit, and insects. *S. lilium* is an understory bat that specializes on fruits of *Solanum* (Solanaceae). At mid-montane elevations, however, *Piper* fruits become common dietary items in *S. lilium* and *S. ludovici* (Dinerstein 1986).

In summary, species of *Carollia* focus their feeding behavior on ripe *Piper* fruits whenever they are available and are the main dispersers of *Piper* seeds in the lowland Neotropics. They do this by systematically harvesting ripe fruits in one to several feeding areas each night. Most of the seeds of *Piper* (and other taxa) that they ingest are defecated relatively close to fruiting plants. Quantitative estimates of seed dispersal distances and the likelihood that defecated seeds will give rise to new seedlings will be discussed in the next section.

#### 4.3. *Piper* FRUITING PHENOLOGY AND DISPERSAL ECOLOGY

##### 4.3.1. *Fruiting Phenology*

*Piper* fruiting phenology has been studied in detail in tropical dry forest (Fleming 1985), tropical moist forest (Thies and Kalko, unpublished manuscript), and tropical wet forest (only one species, Marquis 1988). Opler *et al.* (1980) documented general flowering and fruiting patterns of pipers and other shrubs and treelets in tropical wet and dry forests in Costa Rica. Their data (Fig. 4.3) indicate that in wet forest, peak flowering occurs in April and peak fruiting occurs in June. In dry forest, there are no conspicuous flowering or fruiting peaks. In both habitats, flowering and fruiting occurs year round in the *Piper* flora. Year-round availability of *Piper* fruits in the understory of Neotropical forests has undoubtedly been a major factor in the evolution of dietary specialization in *Carollia* bats (Fleming 1986).

Studies of species-specific fruiting patterns tend to reveal staggered fruiting peaks and significant differences between the fruiting patterns of early successional (or large gap)

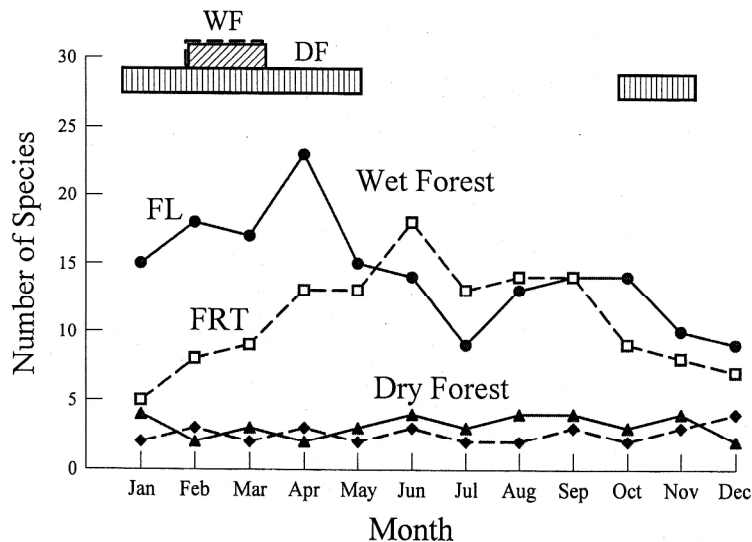


FIGURE 4.3. Flowering (FL, solid lines) and fruiting (FRT, dashed lines) phenology of *Pipers* in two Costa Rican habitats. Upper rectangles indicate the dry season in the two habitats. Data are from Opler *et al.* (1980).

species and late successional or forest species. Staggered fruiting peaks have been documented in five tropical dry forest pipers in Costa Rica (Fleming 1985), four subtropical humid forest pipers in southern Brazil (Marhino-Filho 1991), and eight tropical moist forest pipers in Panama (Thies and Kalko, unpublished manuscript). On the basis of seed size (small: 0.29–0.35 mg), number of seeds per fruit (over 1,000), and habitat distributions (i.e., in heavily disturbed sites), two of the five pipers in Costa Rican dry forest are early successional species. These species fruit in different seasons (wet season in *P. pseudofulgineum*; dry season in *P. marginatum*) (Fig. 4.4). The other three species produce fewer (100–200) and larger (0.86–1.36 mg) seeds per fruit and occur in less-disturbed, later successional habitats (dry forest, *P. amalago*; moist ravines, *P. jacquemontianum*; and riparian sites, *P. tuberculatum*). These species have fruiting peaks that differ by 1–3 months from each other; two species have two fruiting episodes per year (Fig. 4.4).

Thies and Kalko (unpublished manuscript) studied the phenology of 12 pipers in Panama, including eight forest species (*P. aequale*, *P. arboretum*, *P. carrilloanum*, *P. cordulatum*, *P. culebranum*, *P. dariense*, *P. grande*, and *P. perlasense*) and four gap species (*P. dilatatum*, *P. hispidum*, *P. marginatum*, and *P. reticulatum*), and reported that the phenological patterns of these two groups differed significantly. The forest species tended to have relatively short (1–4 months), staggered fruiting seasons in which they produced very few ripe fruits per night (means of 0.2–0.4 per plant). In contrast, gap species had longer fruiting seasons (8–11 months) with multiple peaks; fruiting periods overlapped broadly; and plants produced more fruit per night than forest species (means of 0.4–8.5 per plant). *Piper arieianum*, a common Costa Rican wet forest species, has a long fruit maturation time of 6–8 months (cf. about 2 months in dry forest *P. amalago*) and a relatively long fruiting season (3–4 months) in which very low numbers of fruits ripen per night (Marquis 1988).

As a result of different fruiting strategies, gap and forest pipers attract different groups of seed dispersers. Larger fruit crops and more ripe fruits per plant per night serve

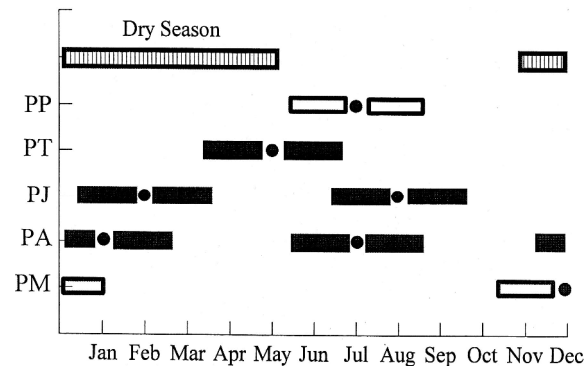


FIGURE 4.4. Fruiting phenology of five species of *Piper* in Costa Rican tropical dry forest. Data indicate peak fruiting times (circles) and extent of fruiting seasons (bars). Open bars are early successional species; closed bars are late successional species. Species are *P. amalago* (PA), *P. jacquemontianum* (PJ), *P. marginatum* (PM), *P. pseudofulgineum* (PP), and *P. tuberculatum* (PT). Data are from Fleming (1985).

to attract second growth birds as well as bats to early successional pipers. Several species of understory tanagers (Thraupinae), but not the equally common manakins (Pipridae), occasionally consume the fruit of early successional pipers (e.g., *P. auritum*, *P. hispidum*, and *P. sancti-felis* at La Selva, Costa Rica) (O'Donnell 1989, Palmeirim *et al.* 1989, Loiselle 1990). Tanagers feed by mandibulating or “mashing” fruits (Denslow and Moermond 1985, Levey 1987) and hence can more easily strip chunks of ripe fruit pulp and seeds from *Piper* infructescences than can manakins, which feed by swallowing or “gulping” entire fruits. In contrast, slow-fruiting forest pipers appear to attract only bats as fruit consumers and hence have more specialized dispersal systems than early successional species.

#### 4.3.2. Patterns of Seed Dispersal

What kinds of dispersal patterns arise from seeds that are ingested by either birds or bats? How far, on average, do *Piper* seeds move from fruiting plants before being defecated into the environment? I will first describe the general results of seed rain studies before describing more detailed quantitative estimates of seed dispersal distances. Before doing this, however, I wish to point out that researchers simultaneously studying seed dispersal patterns produced by tropical birds (mainly tanagers in the case of *Piper*) and bats have concluded that these two groups produce fundamentally different patterns of seed rain. Birds are much more likely to defecate seeds from perches (e.g., in plants where they are currently feeding or elsewhere) than while they are flying (Charles-Dominique 1986, Thomas *et al.* 1988, Gorchov *et al.* 1995). Bats, on the other hand, defecate many seeds in flight in addition to the ones they defecate from perches in their feeding roosts. As a consequence, bats are more likely to deposit seeds in a greater variety of sites than birds. Also, because understory bats appear to have a greater tendency to fly through open habitats (e.g., gaps or abandoned fields) than understory birds, they are more likely to deposit seeds in early successional sites.

Patterns of seed rain of small-seeded, vertebrate-dispersed plants around and away from fruiting plants have been documented in Mexico, Costa Rica, French Guiana, and Peru

(Fleming and Heithaus 1981, Charles-Dominique 1986, Fleming 1988, Gorchov *et al.* 1993, Medellin and Gaona 1999, Galindo-Gonzalez *et al.* 2000). These studies indicate that *Piper* seed rain has both a temporal and a spatial component. In terms of time of seed deposition, *Piper* seeds are much more likely to be deposited in seed traps (or on vegetation and leaf litter and/or soil) at night than during the day, as expected if bats are the major dispersers of these seeds. In terms of the spatial patterns of seed deposition, *Piper* seeds are deposited in a wide variety of sites, including closed forest, forest gaps, abandoned fields or pastures, and under isolated fruiting trees in open pastures. In a year-long study of seed rain in two forest habitats at Santa Rosa National Park, Costa Rica, Fleming (1988) reported that *Piper* seeds were much less common than those of several species of *Ficus* (Moraceae), *Cecropia peltata* (Cecropiaceae), and *Muntingia calabura* (Eleocarpaceae). At this same site, Fleming and Heithaus (1981) reported that seeds of *P. amalago* and *P. pseudofuligineum* occurred in transects around only three of 10 fruiting trees compared with 10 of 10 trees for *C. peltata* and *M. calabura* and 7 of 10 trees for *Ficus* spp. These results suggest that despite being bat-dispersed, *Piper* seed mobility is somewhat lower than that of the other two species, whose seeds are eaten by a greater number of species (Fleming *et al.* 1985, Fleming and Williams 1990). Dispersal by birds, bats, and monkeys may provide wider dispersal (at least within forests) than dispersal by bats alone.

Galindo-Gonzalez *et al.* (2000) captured bats and measured seed rain under isolated fruiting trees in pastures in Veracruz, Mexico. They reported that fecal samples from two species of *Carollia* and *S. liliun* contained six species of *Piper*, including three early successional species (*P. auritum*, *P. hispidum*, and *P. yzabalanum*) and three early/late successional species (*P. aequale*, *P. amalago*, and *P. sanctum*). Seed rain in traps placed under these trees also contained these species. Seed traps placed in a cornfield, an abandoned field, and a cacao plantation near a tropical wet forest in Chiapas, Mexico, received seeds from three early successional *Piper* species (*P. auritum*, *P. hispidum*, and *P. nitidum*).

Quantitative estimates of *Piper* seed dispersal distances are available from tropical dry forest in western Costa Rica (Fleming 1981, 1988). These estimates come from radio tracking studies of *C. perspicillata* plus studies of its seed retention times. Results of these studies indicate that about 67% of the seeds of *P. amalago* and *P. pseudofuligineum* ingested by *C. perspicillata* are defecated in its current feeding area (i.e., <100 m from parent plants). Many of these seeds are deposited under feeding roosts. Nonetheless, some seeds (probably  $\leq 5\%$ ) move relatively long distances (i.e.,  $\geq 1$  km) when bats change feeding areas. Relatively long-distance moves occur more frequently during the dry season, when fruit densities are low and very patchy, than during the wet season. The overall deposition curves (*vide* Janzen 1970) of *Piper* seeds are thus likely to be highly leptokurtic but with a long tail (Fig. 4.5).

#### 4.3.3. *Fates of Seeds*

What are the fates of *Piper* seeds once they have been defecated by birds or bats? Are they at risk from seed predators? What are their germination requirements and do they accumulate in the soil to form seed banks? *Piper* seeds, though small, are likely to suffer from postdispersal predators such as ants and rodents, at least when they occur in Petri dishes on the ground. Perry and Fleming (1980) and Fleming (1988) reported that most seeds (  $\sim 75\%$



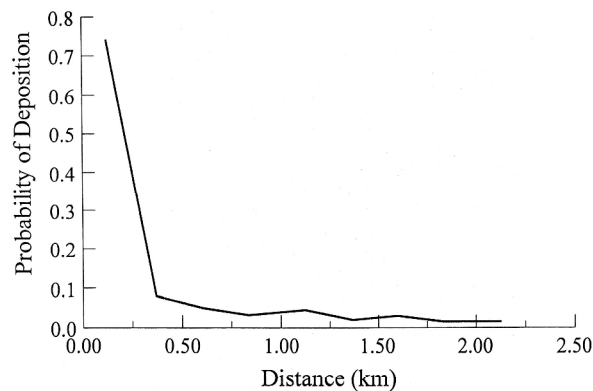


FIGURE 4.5. A generalized seed dispersal curve produced by *Carollia perspicillata* in Costa Rican tropical dry forest. The graph indicates the probability that a seed will be dispersed a given distance from the parent plant. Data are from Fleming (1988).

in most trials) of *P. amalago* were removed from dishes in 4 days of exposure in a variety of habitats at Parque Nacional Santa Rosa, Costa Rica. Ants (particularly *Pheidole* spp.) removed over twice as many seeds as two species of rodents. Despite potentially heavy predation by ants and rodents, seeds of *P. amalago* at this site occur in substantial densities (e.g., 64 seeds/m<sup>2</sup> in light gaps and 133 seeds/m<sup>2</sup> in the forest understory) in the soil. Seeds of *P. amalago* are relatively large, and it would be nice to know if the smaller seeds of early successional *Pipers* (e.g., *P. pseudofulgineum* at Santa Rosa) are at similar risk of postdispersal predation. In a study of predispersal seed predation in five species of *Piper* at La Selva, Costa Rica, Greig (1993a) found that early successional species experienced lower predation by hemipterans and weevils than late successional species. Does a similar situation hold for postdispersal predation?

In addition to predation, interspecific competition can affect the fate of *Piper* seeds. It is common to find two or more kinds of seeds in fecal samples from *Carollia* bats. During the wet season in tropical dry forests, for example, the following species can co-occur in fecal samples of *C. perspicillata*: *P. amalago*, *P. pseudofulgineum*, *P. Jacquemontianum*, *Muntingia calabura*, *Cecropia peltata*, and *Chlorophora tinctoria* (Fleming 1988). Similarly, Loiselle (1990) reported finding mixed species loads of *Piper* and other species in fecal samples from tanagers in Costa Rican wet forest. Whenever seeds are defecated in intra- or interspecific clumps, they are likely to compete for resources during seedling establishment (Howe 1989). Apparently only Loiselle (1990), however, has systematically studied this competition. She found that both growth and survival were affected when she grew different combinations of two species that co-occurred in fecal samples from tanagers in the lab. When *P. auritum* was paired with *P. sancti-felicitis*, for example, the former species had higher growth and survival rates than the latter. More studies of this kind are clearly needed.

Germination probabilities of *Piper* seeds are independent of bat (and bird?) gut passage but are highly dependent on deposition microhabitats. *Piper* seeds typically have very high germination percentages (80–100%) whether or not they are ingested and excreted by bats (Fleming 1988, Bizerril and Raw 1998, Galindo-Gonzalez *et al.* 2000). But unless

these seeds are deposited in light gaps, or become exposed to high levels of sunlight from soil or forest disturbance, their germination probabilities are low (e.g.,  $\leq 15\%$  in forest understory compared with 30% in light gaps in *P. amalago*; Fleming 1981). Because *Carollia* feeding roosts tend to be located under dark bowers of vegetation, these sites are especially poor places for germination of *Piper* seeds (5% germination). Greig (1993b) found a striking difference in the abundance of seedlings of early and late successional pipers at La Selva, Costa Rica. Whereas seedlings of the former species were common in treefall gaps, seedlings of the latter species were rare in the forest understory. From these and other observations and experiments, she concluded that shade-tolerant pipers (e.g., *P. arieanum*, *P. gargaranum*, and *P. melanocladum*) are much more likely to recruit new individuals (ramets) via vegetative reproduction than via seed dispersal. Shade-intolerant species (e.g., *P. aduncum*, *P. culebranum*, and *P. sancti-felicis*), in contrast, are more likely to recruit by seed dispersal than by vegetative reproduction.

The germination characteristics of seeds produced by Mexican tropical wet forest pipers occupying different habitats have been carefully studied by Orozco-Segovia and Vazquez-Yanes (1989). Germination rates of fresh seeds and length of dormancy and photoblastic responses of seeds in the soil differed among four species. Seeds of a large gap species, *P. umbellatum*, can remain dormant for long periods in the soil and have a long-lived photoblastic response to high light conditions. In contrast, seeds of *P. auritum*, another large gap species, and *P. hispidum*, which occurs in a variety of gap and forest habitats, exhibit short soil dormancy and a short-lived photoblastic response. Both of these species probably require continuous "broadcast" dispersal by bats and birds to recruit in light gaps. Finally, seeds of a shade-tolerant forest species, *P. aequale*, exhibit long soil dormancy and a long-lived photoblastic response that allows this species to "dribble" its seeds out and wait in the soil for new gaps to form.

In summary, *Piper* seeds experience both pre- and postdispersal predation, and Greig (1993a) has suggested this predation can sometimes be severe enough to limit seedling recruitment. These seeds do not need to pass through bats to have high germination rates, but they do need exposure to high light levels for maximum germination. It is likely, therefore, that when pipers recruit by seed, they do so in forest gaps of various sizes. Shade-tolerant species can probably recruit by seed in smaller gaps than shade-intolerant species, but vegetative recruitment is also important in the former species. Seed dispersal by bats and birds appears to be most important for early successional or large gap species.

#### 4.3.4. *Postdispersal Distribution Patterns*

Regardless of their dispersal method, species of *Piper* occur in relatively high densities in many Neotropical habitats. In this section, I describe the distribution patterns of pipers in a Costa Rican tropical wet forest at La Selva Biological Station whose *Piper* flora contains nearly 60 species (Laska 1997). I do this to address two questions: (1) How does *Piper* species diversity and density vary in space and time, and (2) are forest gaps colonized by short- or long-distance dispersal? These data were collected in a series of forty-nine 1,000-m<sup>2</sup> belt transects placed in three major habitats: primary forest on old alluvial or weathered basaltic soils (10 locations, 30 transects), secondary forest derived from abandoned pastures on old alluvial or weathered basaltic soils (3 locations, 10 transects),

**TABLE 4.2**  
**Summary of the La Selva Forest Transect Study for the Entire Data Set (A) and the Matched Primary and Secondary Sites (B)**

Parameter	Habitat		
	Primary Forest ( <i>N</i> = 30)	Plantations ( <i>N</i> = 9)	Secondary Forest ( <i>N</i> = 10)
Total <i>Piper</i> species	8.6 ± 0.3	9.0 ± 0.8	14.0 ± 0.8
Total <i>Piper</i> individuals	59.6 ± 4.3	134.2 ± 28.8	163.2 ± 22.6

Parameter	Site and Habitat			
	East Boundary		West Boundary	
	Primary ( <i>N</i> = 3)	Secondary ( <i>N</i> = 3)	Primary ( <i>N</i> = 3)	Secondary ( <i>N</i> = 3)
Total <i>Piper</i> species	8.7 ± 0.9	15.7 ± 1.5	9.0 ± 0.6	14.7 ± 1.3
Total <i>Piper</i> individuals	82.0 ± 2.6	212.0 ± 51.6	60.7 ± 6.5	170.7 ± 11.3

Note: Area of each transect was 1,000 m<sup>2</sup>. Data include mean ± 1 SE. *N* = number of transects.

and tree plantations adjacent to primary forest on recent alluvial soil (4 locations, 9 transects) [for La Selva soil maps and data, see Vitousek and Denslow (1987) and Sollins *et al.* (1994)]. Two sites, one along the east boundary line of the original La Selva tract and another along the west boundary line, were specifically chosen to compare adjacent primary and secondary forests while controlling for soil type (also see Laska 1997). In each transect, I identified and counted the number of adult-sized individuals. Identifications were based on an unpublished key devised by Michael Grayum and Barry Hammel. Robert Marquis provided Latin binomials for several species bearing only descriptive names in the Grayum-Hammel key.

To document the species composition of pipers in gaps, my field crew and I surveyed 37 gaps of various sizes and ages in a primary forest. For each gap, we recorded its greatest length and width, gap type (i.e., tree snap, tree fall, or branch fall), and relative age (e.g., “young” still full of plant debris and sometimes foliage; “old” = debris and foliage gone and 4–6 m tall saplings present). In each gap we identified and counted pipers of all sizes. To compare pipers in gaps with those in intact forest, we censused pipers in one or two 300-m<sup>2</sup> belt transects in forest adjacent to 20 gaps.

Results of our transect censuses are summarized in Table 4.2. We encountered a total of 39 species of *Piper* in the 49 transects (Table 4.3). Six of these were vines and the others were shrubs or small trees. The mean number of *Piper* species per transect differed significantly among habitats in the following order: second growth plantations > primary forest (Kruskal-Wallis ANOVA,  $\chi^2 = 18.33$ , *P* = 0.0001). Species richness was 63% higher, on average, in second growth transects than in primary forest transects. Comparisons between primary and secondary transects at the two paired sites indicated that species richness was 72% higher in secondary forest. Total density of *Piper* plants per transect paralleled trends in species richness (Table 4.2). *Piper* density in the second growth transects was nearly 3 times higher than in the primary forest transects. Five species (*P. arieianum*,

NEOTROPICAL *Piper* SHRUBS AND TREELETS

**TABLE 4.3**  
**Summary of *Piper* Density (Number of Adults per 1,000 m<sup>2</sup>) and Distribution Data from the La Selva Transect and Gap Study**

Species	Frequency of Occurrence		Density	
	Transects (N = 49)	Gaps (N = 37)	Transects (Mean SD)	Gaps (Mean ± SD)
<i>aduncum</i>	0.04	0	1.5	—
<i>aequale</i>	0.04	0.05	10	39.2
<i>arboreum</i>	0.04	0	5.5	—
<i>arieanum</i>	0.9	0.86	30 42.0	49.9 ± 101.0
<i>auritum</i>	0.1	0.11	16.8 11.0	23.6 ± 28.8
<i>biolleyi</i>	0.12	0.14	3.2 3.4	13.7 ± 13.5
<i>biseriatum</i>	0.29	0.16	2.7 2.1	15.5 ± 13.2
<i>carilloanum</i>	0.04	0	9.5	—
<i>cenocladum</i>	0.78	0.73	7.3 5.9	23.2 ± 19.6
<i>colonense</i>	0.29	0.16	22.6 29.6	85.3 ± 176.6
<i>concepcionis</i>	0.14	0.08	1.6 0.7	10.9 ± 9.1
<i>decurrens</i>	0.06	0.03	1.3 ± 0.5	26.7
<i>dolicotrichum</i>	0.57	0.59	4.6 3.7	15.9 ± 16.4
<i>friedrichsthallii</i>	0.06	0	4.3 ± 2.6	—
“forest biggie”	0.33	0.27	3.3 3.2	12.5 ± 7.4
<i>gargaranum</i>	0.12	0.16	1.8 1.5	5.5 ± 2.0
<i>glabrescens</i>	0.12	0.08	1.7 1.1	25.9 ± 24.5
<i>holdridgeianum</i>	0.63	0.76	18.2 18.7	87.9 ± 117.6
“HSF1”	0.16	0.11	3.5 4.2	7.6 ± 3.8
“HSF2”	0	0.02	—	4
“HSF4”	0.02	0.03	6	0.4
<i>imperiale</i>	0.14	0.11	2.1 1.6	8.6 ± 4.4
“lemon-lime”	0.08	0	1.8 ± 1.3	—
<i>melanocladum</i>	0.51	0.43	3.2 2.6	7.7 ± 4.5
<i>multiplinervum</i>	0.31	0.51	7.1 7.8	13.0 ± 15.9
<i>nudifolium</i>	0.04	0	10	—
<i>phytolaccaefolium</i>	0.1	0	57.2 ± 89.3	—
“Phillipe’s pubescent”	0.12	0.08	2.8 1.2	2.5 ± 0.9
<i>riparens</i>	0.06	0.14	1	8.7 ± 9.1
<i>reticulatum</i>	0.18	0.05	5.9 ± 4.2	2.6
<i>peracuminatum</i>	0.1	0	4.2 ± 3.9	—
<i>pseudobumbratum</i>	0.39	0.22	5.1 5.2	9.2 ± 4.8
<i>sancti-felicitis</i>	0.47	0.27	17.6 19.5	13.7 ± 7.5
<i>silvivagum</i>	0.06	0	1.3 ± 0.5	—
“stachyum”	0.29	0.14	1.5 0.5	4.9 ± 1.5
“swamp glabrous”	0.06	0	1.3 ± 0.5	—
<i>tonduzii</i>	0.73	0.76	3.5 2.8	19.0 ± 14.4
<i>urostachyum</i>	0.86	0.73	7.0 13.3	25.7 ± 22.5
<i>virgulatorum</i>	0.14	0	11.4 ± 8.9	—

*P. cenocladum*, *P. holdridgeianum*, *P. gargaranum*, and *P. urostachyum*) occurred in 60% of the transects and can be considered to be “common”; 28 species (76%) occurred in <20% of the transects and can be considered to be “uncommon” or “rare” (Table 4.3).

I used information in Hartshorn (1983) and from David Clark (personal communication) to determine the approximate time since last clearing of the second growth and plantation sites we surveyed. These times ranged from 10 to 30 years. Over this time span, *Piper* diversity increased from 7 to 8 species per transect at 10 years to a peak of 16–18

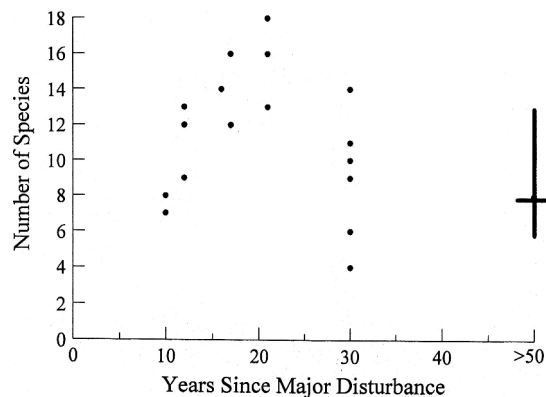


FIGURE 4.6. Number of *Piper* species in 1,000-m<sup>2</sup> belt transects in a variety of successional habitats in tropical wet forest at La Selva, Costa Rica. Each point represents one transect. Data for primary forest (>>50 years old) indicate median and range of values.

species at 15–20 years before falling to a median value of 9 species at 30 years (Fig. 4.6). Median species richness in intact primary forest was 8 species per transect. Although we did not survey cleared sites less than 10 years old, my casual observations in the systematically cleared “successional strips” (Hartshorn 1983) and in other recently cleared land around La Selva indicated that only a few species (e.g., *P. auritum*, *P. biseriatum*, *P. aduncum*, and *P. sancti-felicis*) occur in new, large clearings. Thus, *Piper* diversity increased with time since clearing, reached a peak at about 20 years postclearing, and declined as forest succession continued.

We encountered a total of 27 species of *Piper* in the 37 gaps. Each of these species occurred in one or more of our 49 transects (Table 4.3). There was a strong positive correlation between the frequency of occurrence of the 27 species in gaps and their frequency in transects (arcsine-transformed data, Pearson’s  $r = 0.94$ ,  $F_{1,25} = 206.8$ ,  $P < 0.0001$ ). The number of *Piper* species per gap was positively correlated with gap area (Pearson’s  $r = 0.57$ ,  $F_{2,35} = 16.48$ ,  $P = 0.0003$ ) but did not differ between “young” and “old” gaps (Mann–Whitney  $U$  test,  $P > 0.32$ ). On the basis of Sørensen’s (1948) similarity index, which is based on presence–absence data, similarity between the gaps and adjacent intact forest was high and averaged 0.61 ± 0.03 (SE) (out of a maximum value of 1.0) in the 20 gap–transect comparisons.

From these results, I reach the following conclusions. First, the rich *Piper* flora of this lowland wet forest contains a few (ca. five) common and broadly distributed species and many uncommon species, a pattern that characterizes most biotic communities. Second, *Piper* species richness and density varies substantially among habitats where the second growth forest has higher point diversities (i.e., the number of species co-occurring in a small area) than in other habitats. Third, *Piper* diversity has a temporal or successional component. It is initially low on newly cleared land and increases as forest succession proceeds. Point diversity peaks in relatively young forests and is low in mature forests. Fourth, colonization of gaps in primary forests appears to involve local, rather than long-distance (i.e., from distant disturbances or second growth), dispersal. Composition of the *Piper* flora in the

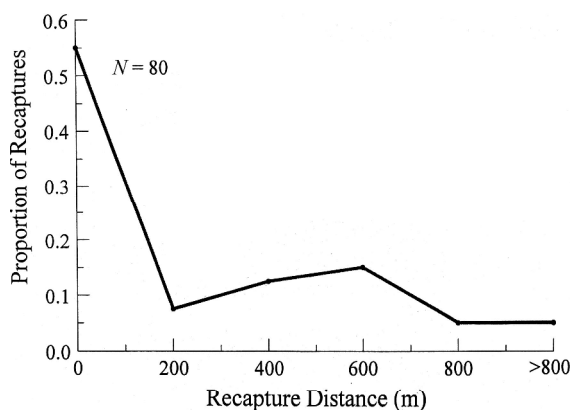


FIGURE 4.7. Distribution of recapture distances for three species of *Carollia* (data combined) in tropical wet forest at La Selva Biological Station, Costa Rica.

gaps we censused largely reflected composition of the flora in adjacent intact forests. The relative importance of fresh seed rain versus germination from the soil seed bank (or from plant fragments; Greig 1993b) in colonization of primary forest gaps needs further study. Finally, disturbance and habitat heterogeneity clearly play important roles in maintaining high local diversity in this *Piper* flora.

How do the *Piper* bats respond to this mosaic of *Piper* diversity and density? During our La Selva transect and gap study, we also captured phyllostomid bats in mist nets set at ground level in a variety of habitats (Fleming 1991). Bats were marked with ball-chain necklaces bearing a numbered aluminum bird band before being released (Fleming 1988). In a 2-month period (late May–late July), we recorded 819 captures and recaptures of three species of *Carollia* (252 *C. brevicauda*, 300 *C. castanea*, and 267 *C. perspicillata*). Proportion of fecal samples that contained *Piper* seeds ranged from 0.54 (in *C. perspicillata*) to 0.87 (in *C. castanea*). Reflecting the higher density of pipers in second growth forest, capture rates of *Carollia* in that habitat were 3.4 times higher than in the primary forest (second growth: 1.79 ± 0.43 SE captures per net-hour; primary forest: 0.53 ± 0.09 captures per net-hour). The smallest species (*C. castanea*) was most common in the second growth forest, and the largest species (*C. perspicillata*) was most common in the primary forest, a pattern that occurs elsewhere in these bats (Fleming 1991).

The distribution of recapture distances of these bats provides some insight into their movement patterns and the potential distances they can disperse *Piper* seeds. Fifty-five percent of the 80 *Carollia* recaptures occurred at the site where the bat was originally captured, but two individuals were recaptured 1.7 km from their original capture sites. In general, the distribution of recapture distances was leptokurtic and with a long tail (Fig. 4.7), a pattern also seen in my estimate of *Piper* seed dispersal distances in tropical dry forests (Fig. 4.5). These netting results suggest that the *Carollia* bats at La Selva are relatively sedentary but that they move among habitats and produce a mix of seed dispersal distances. For example, the recapture data show that the proportion of bats recaptured in a different habitat from the one in which they were first captured was 0.25 and 0.41 for bats first captured in the secondary and the primary forest, respectively. Thus, although most of the

seeds they ingest are likely to be dispersed short distances (< 100 m) from parent plants, some seeds can be dispersed substantial distances (1 km or more) and into different habitats from where they were produced.

#### 4.4. COEVOLUTIONARY ASPECTS OF BAT–*Piper* INTERACTIONS

Compared with plant–pollinator mutualisms, most fruit–frugivore interactions are relatively unspecialized (Wheelwright and Orians 1982, Janzen 1983). The relationship between *Carollia* bats and Neotropical *Piper* plants, however, appears to be quite specialized. In this system, specialization seems to be higher on the plant side than on the frugivore side. Except for a few common large gap species (e.g., *P. aduncum* and *P. auritum*), Neotropical pipers appear to be nearly exclusively dispersed by *Carollia* bats (at least on the mainland). *Carollia* dependence on *Piper* varies predictably among species, with the smaller *C. castanea* being a stronger *Piper* specialist than the larger *C. perspicillata* (Fleming 1991).

Incidentally, although Old World frugivorous bats of the family Pteropodidae rarely eat the fruits of native pipers (Mickleburgh *et al.* 1992), certain species (e.g., *Cynopterus brachyotis*, *Syconycteris australis*) avidly eat and disperse the seeds of New World early successional species such as *P. aduncum* (Winkelmann *et al.* 2000). New World pipers can clearly attract bats to their infructescences, presumably using both visual and olfactory cues. Old World pipers appear to be dispersed primarily by birds (Snow 1981).

Conditions promoting a high degree of specialization in mutualisms are generally thought to involve reliability and effectiveness (e.g., McKey 1975, Howe 1984, Fleming and Sosa 1994, Waser *et al.* 1996). On the plant side, reliability usually refers to spatio-temporal predictability in resource availability, and effectiveness refers to providing a suitable nutritional reward. On the animal side, reliability refers to predictability of visitation or resource use, and effectiveness refers to treatment of pollen or seeds in a nonharmful fashion. In fruit–frugivore systems, effectiveness ultimately involves deposition of seeds in suitable recruitment sites.

On each of these counts, the *Piper*–*Carollia* dispersal system seems to meet conditions favoring specialization. As mentioned earlier, *Piper* flowering and fruiting phenology provides year-round resources for pollinators and frugivores in many Neotropical forests. Although the nutritional characteristics of *Piper* fruit are relatively unstudied, Herbst (1985) found that fruits of *P. amalago* are rich enough in protein, often a limiting resource in fruit pulp, to support wet season pregnancies and lactation in *C. perspicillata*. Dinerstein (1986) reported that protein levels in fruits of eight species of *Piper* plus *Potomorphe peltata* (now *Piper peltata*) averaged 7.2% (dry weight) and were higher than most bat fruits in a Costa Rican cloud forest. *Carollia* bats are avid consumers of *Piper* fruits, and nearly all fruits are removed and eaten as soon as they ripen (cf. certain species of *Ficus* trees that suffer enormous fruit wastage; Kalko *et al.* 1996). Although the probability of any given *Piper* seed being deposited in a site that is suitable for immediate germination is vanishingly small, the sheer numbers of seeds dispersed nightly across a varied landscape by roosts of several hundred *Carollia* bats is enormous (i.e., in tens of thousands) (Fleming 1988). Coupled with dormancy mechanisms and photoblastic responses, this “broadcast” dispersal is sufficient for *Piper* to quickly colonize both large and small habitat disturbances whenever they occur

(e.g., see Chapter 10 in Fleming 1988). This mutual specialization has made *Piper* plants and *Carollia* bats very common in lowland Neotropical forests.

Despite a high degree of specialization between *Piper* plants and *Carollia* bats, their spatio-temporal distributions are not congruent. In terms of geographic distributions, diversity and abundance of both taxa are highest in the lowlands of the mainland Neotropics (especially in northwestern South America and southern Central America) and decrease with increasing latitude and altitude (e.g., Fleming 1986). Except for Grenada, *Carollia* bats are restricted to the mainland of Mexico and Central and South America, whereas pipers occur widely in the Greater and Lesser Antilles. *Sturnira lilium* is more broadly distributed in the Caribbean than *Carollia* bats and occurs as far north as Dominica in the Lesser Antilles; the endemic *S. thomasi* is known from Montserrat and Guadeloupe (Rodríguez-Duran and Kunz 2001). *Sturnira* bats presumably eat *Piper* fruits in the Lesser Antilles. In the Greater Antilles, *Erophylla bombifrons* (Phyllostomidae: Phyllostomycterinae) eats *Piper* fruit in Puerto Rico (T. Fleming, pers. obs.) and probably elsewhere in the Greater Antilles.

In terms of geological history, *Piper* and Piperaceae are much older than phyllostomid bats. Pollen of Piperaceae, for example, is known from the Eocene (Muller 1970). Current geographic distributions and morphological and molecular data indicate that Piperaceae evolved early in angiosperm history, before the breakup of Gondwana and therefore probably before the Cenozoic. In contrast, the earliest phyllostomid bat (*Notonycteris*; probably not a frugivore) dates from the Miocene (Koopman 1984). On the basis of allozyme data, Straney *et al.* (1979) suggested that the Phyllostomidae evolved in the early Oligocene [ca. 30 million years ago (mya)]. Using DNA restriction site data, Lim and Engstrom (1998) concluded that *C. castanea* is the basal member of the genus and evolved in South America, presumably 20 mya. If this is true, then pipers and *Carollia* bats have been interacting for no more than 20 million years—long after the initial radiation of pipers around the world. This temporal mismatch raises the question: Who were the dispersers of *Piper* seeds before the evolution of *Piper* bats? What animals (pollinators and dispersers) originally selected for *Piper* inflorescence and infructescence characteristics?

Given its exceptionally high species richness in the Neotropics, we can further ask: What role, if any, have *Carollia* bats played in *Piper* speciation? As discussed by Hamrick and Loveless (1986), the foraging behavior of both pollinators and seed dispersers can affect the genetically effective size ( $N_e$ ) of plant populations and the extent of gene flow between populations. Because seeds are diploid (cf. haploid pollen) and, in the absence of strong selective barriers, “foreign” seeds can establish as readily in local populations as “local” seeds, gene flow by seed dispersal can theoretically have a greater effect on genetic structure than gene flow by pollination. Long-distance seed dispersal will reduce levels of population subdivision and short-distance dispersal will have the opposite effect.

As described above, foraging by *Carollia* bats produces a mixture of seed dispersal distances, and these bats therefore serve as agents of both local and long-distance dispersal. Most of the seeds they ingest are deposited in clumps (of full or half-sibs) under night roosts located short distances from parent plants and will recruit locally, if they recruit at all. In contrast, some seeds move considerable distances (1–2 km) when bats change feeding areas and can potentially recruit in new habitats. Local recruitment of closely related seedlings, coupled with short-distance movements by insect pollinators, will produce high levels of genetic subdivision and potentially small values for  $N_e$ s (Hamrick and Loveless 1986). The occasional colonization of recently disturbed habitats by a small number of closely related



seedlings will also produce new populations with small  $N_e$ s. Thus, dispersal of seeds by *Carollia* bats has the potential to produce genetically subdivided *Piper* populations, an important first step toward speciation.

Do *Piper* populations show high or low levels of genetic subdivision? Unfortunately, only one study appears to address this question. Heywood and Fleming (1986) studied genetic diversity and population structure using allozymes in three species of *Piper* in Costa Rican tropical dry forest. They found very low levels of protein polymorphism within populations (proportion of polymorphic loci ranged from 0 in *P. pseudo-fuligineum* to 0.095 in *P. amalago* for 20–24 loci), significant levels of genetic subdivision between populations of *P. amalago* ( $F_{st} = 0.103$  at one locus, where a value of 0 indicates panmixia), and unusually high genetic distances (0.45–0.99 out of 1.0) between the three species. High genetic distances between congeners suggest that this genus is relatively old. Although more studies are needed to assess the role of pollinators and seed dispersers in determining the genetic structure of *Piper* populations, it appears that gene flow may indeed be limited in these bat-dispersed plants.

In his extensive review of Neotropical floral diversity, Gentry (1982) identified Piperaceae as a member of the Gondwanan, Andean-centered group of epiphytes, shrubs, and palmetto-like monocots that collectively accounts for nearly one-half of this diversity. Unlike Gentry's "Amazonian-centered trees and lianas," whose diversity is likely to be the result of allopatric speciation, Andean plants have undergone "explosive speciation and adaptive radiation, almost certainly most of it sympatric" (Gentry 1982). Gentry (1982) proposed that this speciation has occurred in small local populations and has involved constant recolonization of habitats separated by mountains, local rainshadows, shifting vegetation zones (in response to global climate fluctuations), and frequent landslides. Similarly, in his review of the ecological distributions of pipers and other species-rich genera in Costa Rica, Burger (1974) pointed out that many species have narrow ecological boundaries and that closely related species often co-occur in the same area but live in different habitats. Both scenarios suggest that genetic isolation occurs frequently in pipers. But the extent to which this is the result of limited pollen or seed movement remains to be seen. Genetic studies using both chloroplast and nuclear markers will help to clarify this issue.

#### 4.5. CONCLUSIONS

To judge from its high diversity and abundance, the genus *Piper* has been extremely successful in the Neotropics. Its current diversity encompasses a wide range of life forms, including subshrubs, vines, shrubs, and treelets, that occupy a variety of habitats ranging from early successional disturbances to mature forests. Many species appear to reproduce most often by sexual means, and seed dispersal is accomplished using a small clade of fruit-eating bats of the genus *Carollia* (Phyllostomidae, Caroliinae). Reliable, year-round availability of relatively nutritious fruit has enabled *Carollia* bats to specialize on *Piper* for most of their diet in many places in the lowland Neotropics. These common and relatively sedentary bats nightly disperse tens of thousands of *Piper* seeds into a variety of habitats. Although most seeds are deposited close to parent plants, some can move 1–2 km into new habitats. This mixture of short- and long-distance dispersal is likely to create genetically subdivided populations of pipers. Genetic subdivision, in turn, can set the stage for

speciation, especially in areas of high habitat diversity such as the foothills of the Andes in northern South America and southern Central America. It is likely that *Piper*'s relatively specialized dispersal ecology has played an important role in its evolutionary success.

#### 4.6. ACKNOWLEDGMENTS

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