

The Role of Frugivorous Bats in Tropical Forest Succession

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ABSTRACT

Discussion of successional change has traditionally focused on plants. The role of animals in producing and responding to successional change has received far less attention. Dispersal of plant propagules by animals is a fundamental part of successional change in the tropics. Here we review the role played by frugivorous bats in successional change in tropical forests. We explore the similarities and differences of this ecological service provided by New and Old World seed-dispersing bats and conclude with a discussion of their current economic and conservation implications. Our review suggests that frugivorous New World phyllostomid bats play a more important role in early plant succession than their Old World pteropodid counterparts. We propose that phyllostomid bats have shared a long evolutionary history with small-seeded early successional shrubs and treelets while pteropodid bats are principally dispersers of the seeds of later successional canopy fruits. When species of figs (*Ficus*) are involved in the early stages of primary succession (e.g. in the river meander system in Amazonia and on Krakatau, Indonesia), both groups of bats are important contributors of propagules. Because they disperse and sometimes pollinate canopy trees, pteropodid bats have a considerable impact on the economic value of Old World tropical forests; phyllostomid bats appear to make a more modest direct contribution to the economic value of New World tropical forests. Nonetheless, because they critically influence forest regeneration, phyllostomid bats make an important indirect contribution to the economic value of these forests. Overall, fruit-eating bats play important roles in forest regeneration throughout the tropics, making their conservation highly desirable.

Key words: frugivory, Phyllostomidae, Pteropodidae, seed dispersal, tropical succession.

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I. INTRODUCTION

Successional change in biological communities can be defined as the sequential change of the relative abundances of the dominant species in a community. Discussion of successional change in tropical ecosystems has often been limited to changes in plant community composition and structure despite the numerous contributions made by animals. Animals may influence successional change by affecting soil structure and turnover, litter decomposition, nutrient cycling, primary productivity, plant species composition, dispersal of mycorrhizal fungi, pollination of plants and dispersal of seeds (Majer, 1989). These functions play an important role in determining the rate at which newly exposed or disturbed land is initially colonized or recolonized as well as the patterns of subsequent succession or community change. Gaining knowledge of the processes of natural regeneration in disturbed habitats (i.e. secondary succession) and the roles that animals play in these processes is of considerable conservation concern today due to the vast area of disturbed land being created by human activity (Brown & Lugo, 1990; Bawa & Seidler, 1998; Holl & Kappelle, 1999; Neef, 2005).

Since H.C. Cowles' (1899) pioneering work, ecologists have attempted to generalize patterns of successional change with limited success (Finegan, 1984; Huston & Smith, 1987; Guariguata & Ostertag, 2001). In the textbook scenario, 'pioneer' species initially colonize a disturbed environment, altering the abiotic conditions and allowing other species to invade and outcompete them, eventually leading to one or more 'climax' communities. An alternative to this kind of 'relay floristics' model of successional change is an 'initial floristic composition' model in which most of the plants colonizing a disturbance arrive at the beginning of forest regeneration and then reach peak abundances at different times post-disturbance (Egler, 1954). These two models are clearly oversimplifications, however, because they fail to acknowledge the multitude of pathways and community interactions involved with successional change (e.g. Olson, 1958; Connell & Slayter, 1977; Ewel, 1980; Pickett, Collins & Armesto, 1987; Uhl, 1987; Mesquita *et al.*, 2001; Guariguata & Ostertag, 2001; Platt & Connell, 2003; Duncan, 2006; Chazdon *et al.*, 2007). Factors that increase the complexity of successional pathways include local site factors, landscape history, regional species pools, and plant life histories (Pickett *et al.*, 1987; Platt & Connell, 2003; Chazdon *et al.*, 2007). Our understanding of succession would benefit from a synthesis of traditional studies on changes in plant community composition along with a more informed perspective on the role of animals in mediating these processes.

Seed dispersal is a major way that animals contribute to successional change in tropical ecosystems. Soil seed banks are often severely depleted in disturbed areas, making deposition of seeds from undisturbed areas critical for succession to proceed (Duncan & Chapman, 1999; Rodrigues da Silva & Matos, 2006; Franklin & Rey, 2007; Simoes & Marques, 2007). Given that an estimated 50–

90% of tropical trees and shrubs produce fleshy fruits adapted for consumption by vertebrates (Howe & Smallwood, 1982; Howe, 1986), the role that frugivores play in delivering propagules to disturbed areas can be very important.

The prevalence of plants producing vertebrate-dispersed fruits in the tropics has prompted extensive theoretical and empirical research about the fitness benefits received by plants involved in frugivore mutualisms (reviewed in Howe & Smallwood, 1982; Levin *et al.*, 2003; Levine & Murrell, 2003), and this research has a direct bearing on processes involved in ecological succession. At least three hypotheses have been proposed to explain how the benefits of animal dispersal may outweigh the energetic costs of producing fleshy fruits (Janzen, 1970; Connell, 1971; Howe & Smallwood, 1982; Terborgh *et al.*, 2002; Howe & Miriti, 2004). (1) The escape hypothesis postulates that animal-mediated seed dispersal is advantageous because the probability of seedling recruitment increases with distance away from parent plants. This can result from density-dependent processes such as seed predation, pathogen attack, or intraspecific competition (Harms *et al.*, 2000). (2) The colonization hypothesis postulates that seed dispersal by animals increases the number of different sites into which seeds are deposited, allowing some seeds to colonize new disturbances. This hypothesis is particularly relevant for early successional plants whose establishment sites can be highly patchy in time and space (Fleming & Heithaus, 1981; Levey & Benkman, 1999; Muller-Landau *et al.*, 2002). (3) The directed dispersal hypothesis postulates that seed dispersal by animals can result in a disproportionate number of seeds arriving at a non-random subset of available sites in which seedling survival is especially high (Wenny, 2001). While these hypotheses are not mutually exclusive, their relative importance likely varies in different systems and for different plant species. For example, directed dispersal may be particularly important in physiologically harsh environments such as deserts where non-random seed deposition under 'nurse plants' can significantly increase seedling recruitment probabilities (e.g. Sosa & Fleming, 2002). The colonization hypothesis is clearly relevant to any discussion of tropical succession.

Attempts to generalize the fitness advantages of seed dispersal have been hampered by a lack of data on the quality and quantity of the services provided by various dispersal agents. Three of the main questions when investigating the role of various dispersal agents are: (i) which seeds are eaten, (ii) where are they dispersed, and (iii) do they successfully establish following dispersal (see Fleming & Sosa, 1994; Dennis & Westcott, 2006)? While knowledge of animal foraging behaviour and plant characteristics could, theoretically, lead to prediction of seed dispersal patterns (e.g. Murray, 1988; Levin *et al.*, 2003; Takahashi & Kamitani, 2004; Westcott *et al.*, 2005), difficulties arise due to the complexities involved with obtaining these types of data (Nathan & Muller-Landau, 2000; Russo, Portnoy & Augspurger, 2006). Recently, efforts have been made to incorporate information on animal behavior into seed dispersal models (Russo *et al.*, 2006) and to place animal dispersers into functional groups based on

the nature of dispersal services they provide to plants (Dennis & Westcott, 2006). These studies are relevant to successional processes because they indicate which species are likely to be responsible for short- or long-distance seed dispersal. Similarly, molecular tools are beginning to be used to increase our insights into animal-mediated seed movement between habitats (e.g. Jordano *et al.*, 2007). Overall, however, these questions remain unanswered for the majority of tropical frugivores, especially when considering the occurrence of long-distance dispersal (Nathan, 2006). For example, with the exception of several detailed studies on two species of New World fruit-eating bats (*Carollia perspicillata* – Fleming, 1988, 1991; Heithaus, Fleming & Opler, 1975; Fleming, Heithaus & Sawyer, 1977; *Artibeus jamaicensis* – Morrison, 1978; August, 1981; Handley, Wilson & Gardner, 1991; Banack, Horn & Gawlicka, 2002), little information is available about the dispersal services provided by most species of frugivorous bats.

Herein, we review the role played by frugivorous bats in tropical succession, primarily in lowland rainforests. In the New World tropics, frugivorous bats are among the most abundant seed-dispersing animals and play a crucial role in tropical succession (Medellin & Gaona, 1999). Frugivorous bats in the Old World tropics also comprise a significant proportion of vertebrate frugivores and are important seed dispersers (Corlett, 1998). We focus on bats because, unlike frugivorous birds (Snow, 1981), they represent a phylogenetically restricted and relatively homogeneous group of frugivores whose functional roles can be easily compared from a biogeographic perspective. Three questions motivate this review: (1) what is the relative importance of fruit-eating bats compared with other frugivores in tropical forest succession? (2) Do bats play an equally important role in plant succession in the Neotropics and Paleotropics? (3) What are the economic and conservation implications of the role that frugivorous bats play in tropical succession?

II. FRUGIVOROUS BATS

Fruit-eating bats have evolved independently in the New and Old World tropics. New World frugivores occur in the Phyllostomidae (American leaf-nosed bats), and Old World frugivores occur in the Pteropodidae (flying foxes and their relatives). These two families belong to different suborders of order Chiroptera (Yangochiroptera and Yngpterochiroptera, respectively) and are not closely related. According

to Teeling *et al.* (2005) and Jones, Bininda-Emonds & Gittleman (2005), Pteropodidae is the older family, having diverged from its sister group (rhinolophoid bats) approximately 56 million years ago (Myr); Phyllostomidae diverged from its sister family (Mormoopidae) approximately 39 Myr. The crown groups (i.e. extant taxa) of both families, however, are of similar age (approximately 25–28 Myr).

The two families differ significantly in their taxonomic diversity and geographic distributions (Table 1). All members of Pteropodidae are plant visitors (frugivores or nectarivores) and 36 of the 42 genera (173 of 187 species) have traditionally been considered to be frugivorous, although many of these species are well-known flower visitors (e.g. Baker & Harris, 1957, 1959; Marshall & McWilliam, 1982; Richards, 1995). By contrast, basal members of Phyllostomidae are either insect- or blood-feeders (Baker *et al.*, 2003), and only 22 of 56 genera (90 of 173 species) are primarily or exclusively frugivorous. An additional 13 genera (approximately 33 species) of phyllostomids are primarily nectar-feeders, although some of these taxa (e.g. *Glossophaga*, *Leptonycteris*) also eat fruit (Fleming, Muchhala & Ornelas, 2005). Regarding geographic distributions, only two pteropodid genera (*Pteropus* and *Rousettus*) have ranges that encompass most of the family's distribution whereas 50% of phyllostomid genera are geographically widespread (Table 1). Most genera of phyllostomids (64%) have exclusively mainland distributions, whereas about 75% of pteropodid genera occur on islands in at least part of their geographic ranges. In sum, many frugivorous phyllostomids are relatively 'cosmopolitan' (within the distribution of the family as a whole) non-island-dwellers compared to pteropodids, whose taxa are more likely to be 'provincial' island-dwellers. As a result, certain phyllostomid genera (e.g. *Carollia*, *Sturnira*, and *Artibeus*) play important roles in tropical succession throughout the mainland Neotropics, whereas no single pteropodid genus is associated with tropical succession throughout the Paleotropics. Reflecting the Asian origin of the family (Teeling *et al.*, 2005), 24 genera of pteropodids (approximately 141 species) occur exclusively in Asia whereas 10 genera (approximately 25 species) are exclusively African. Asian taxa are basal in the phylogeny of this family, and African taxa are derived (Giannini & Simmons, 2005).

Body size is an important characteristic of all organisms (e.g. Peters, 1983; Calder, 1984), and size matters for frugivorous bats for at least two reasons. First, body size is positively correlated with both average food size and range of food sizes taken by consumers. Average fruit size

Table 1. Summary of the diversity and distribution of fruit-eating phyllostomid and pteropodid bats based on Simmons (2005)

Characteristic	Phyllostomidae	Pteropodidae
Taxonomic diversity	22 genera, 90 species	36 genera, 173 species
Number of genera that are:		
i. Geographically widespread ^a	11 (50%)	2 (5.6%)
ii. Mostly mainland in distribution	14 (63.6%)	9 (25.0%)
iii. Both mainland and island in distribution	3 (13.6%)	11 (30.1%)
iv. Mostly island in distribution	5 (22.7%)	16 (44.4%)

^a Occur throughout most of the family's geographic distribution.

correlates positively with body size in phyllostomid bats (e.g. Heithaus *et al.*, 1975; Bonaccorso, 1979; Kalko, Herre & Handley, 1996; Wendeln, Runkle & Kalko, 2000). It is not clear whether this is also true for pteropodids. Uzzurum (1995) did not find a correlation between body size and fruit size in Philippine pteropodids, but Dumont (2003) reported such a correlation in a small group of Australasian pteropodids. Second, size determines the microhabitats where frugivorous bats forage. Because of their greater manoeuvrability, small bats can potentially forage both in the understorey and canopy/subcanopy of tropical forests whereas less manoeuvrable large bats (e.g. *Pteropus*, *Eidolon*, or *Acerodon*) are restricted to foraging in the canopy/subcanopy of these forests (Norberg & Rayner, 1987; Stockwell, 2001; Henry *et al.*, 2004; Hodgkinson *et al.*, 2004). In general, frugivorous canopy-feeding bats (and birds) tend to be larger than understorey frugivores (Fleming, 1988).

Body size distributions differ significantly in the two families of frugivorous bats. In the 'traditional' classification of bats (e.g. Koopman, 1993), pteropodids were classified in suborder Megachiroptera and phyllostomids were classified in suborder Microchiroptera, reflecting significant differences in their body sizes. While it is true that certain pteropodids weigh more than 1 kg (e.g. *Pteropus vampyrus*) and no frugivorous phyllostomid weighs more than about 90 g, not all pteropodids are 'mega' in size. In fact, the frequency distribution of median body sizes of pteropodid genera is bimodal with one mode occurring at a mass of less than 20 g and the other occurring between 100 and 200 g (Fig. 1). Size distribution of phyllostomid genera is unimodal with a peak at less than 20 g, which coincides with the first mode of the Pteropodidae.

To obtain a broader view of the morphospace occupied by frugivorous bats, we conducted a principal components analysis (PCA) based on generic means of four morphological measurements: (i) forearm length (a measure of overall size in bats); (ii) length of the maxillary tooththrow (i.e. upper jaw length), (iii) width across the upper molars

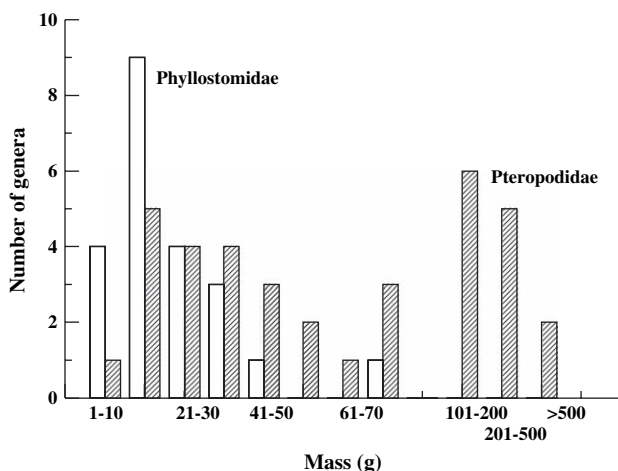


Fig. 1. Size frequency distribution of phyllostomid and pteropodid bats based on generic medians taken from Nowak (1994).

(i.e. upper jaw width), and (iv) the ratio of maxillary tooththrow length to upper molar width (i.e. relative jaw length) based on data found in Swanepoel & Genoways (1979) and Andersen (1912). We chose these morphological measurements because they are directly relevant to the feeding ecology of these bats (Dumont, 2003; Swartz, Freeman & Stockwell, 2003). Our database included species from all 22 genera of frugivorous phyllostomids and 28 of 36 genera of frugivorous pteropodids. A plot of principal components axes 1 and 2, which account for 99% of the variation in the data, indicates that the size/jaw morphospace of these two families overlaps minimally (Fig. 2). The overall morphospace of frugivorous pteropodids is much larger than that of the phyllostomids and reflects substantial variation among genera in both overall size (PC axis 1) and relative jaw length (PC axis 2). By contrast, phyllostomid morphospace reflects greater variation among genera in relative jaw length than in overall size (Fig. 2). The most highly derived frugivorous phyllostomids (tribe Stenodermatina; Baker *et al.*, 2003) have extremely short and wide jaws (Freeman, 1988). A closer examination of the pteropodid data indicates that the Asian and African clades (*sensu* Giannini & Simmons, 2005) occupy overlapping and nearly parallel regions of morphospace (Fig. 2). That is, these two radiations have filled virtually the same amount of morphospace in similar fashion. Reflecting this, the cumulative frequency distributions of median body masses of genera in the two clades do not differ significantly (Kolmogorov-Smirnov two-sample test, $P = 0.99$). In both clades, median body mass is ≤ 50 g in about 50% of the genera. By contrast, median body mass of the two "cosmopolitan" pteropodid genera (*Pteropus* and *Rousettus*) is ≥ 100 g.

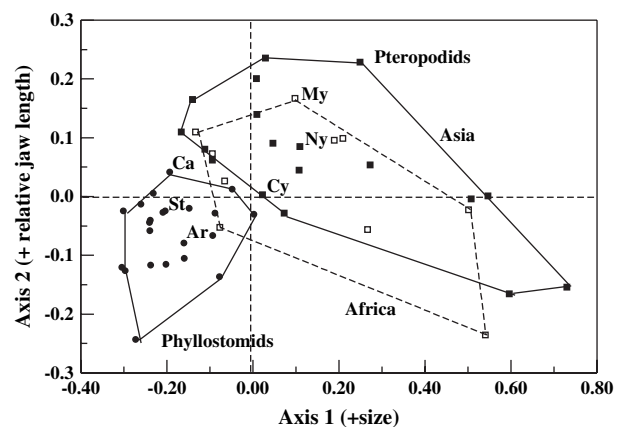


Fig. 2. Principal components (PC) ordination of 22 genera of fruit-eating phyllostomid and 28 genera of pteropodid bats based on four morphological variables. Morphological interpretation of PC axes 1 and 2 are given in the axis labels; "+" means a positive correlation between the morphological variable and the PC axis. Genera that play important roles in tropical succession are identified: Ar = *Artibeus*, Ca = *Carollia*, Cy = *Cynopterus*, My = *Myonycteris*, Ny = *Nyctimene*, St = *Sturnira*. African pteropodids are shown by open squares; Asian pteropodids by filled squares.

Most early successional plants, the botanical subjects of this review, are generally fast-growing, relatively small in stature, short-lived, and produce small fruits containing many small seeds (Grime, 1979; Swaine & Whitmore, 1988). How do these characteristics influence the foraging and food choice of frugivorous bats? Fruit and seed size alone suggest that early successional plants will interact with small bats in both bat families (Fig. 1). Among phyllostomids, genera that appear to specialize on early successional fruit include *Carollia*, *Sturnira*, and *Glossophaga* (which is primarily a nectar-feeder). Weighing 10–20 g, members of these genera belong to different subfamilies and are not closely related (Baker *et al.*, 2003). Along with bats of the genus *Artibeus*, species of these genera are the most common phyllostomid bats in many mainland forest habitats (Fleming, 1988; Handley *et al.*, 1991; Simmons & Voss, 1998). Old World ecological counterparts of these phyllostomids are not as well known but likely include members of the following genera: *Cynopterus* (Asia), *Syconycteris* (which, like *Glossophaga*, is also a nectar-feeder) and *Nyctimene* (Australasia), and *Epomops* and possibly *Myonycteris* (Africa). Bats of the genus *Nyctimene* are basal and *Cynopterus* occurs in the next most-basal node in the most recent phylogeny of the Pteropodidae (Giannini & Simmons, 2005), which suggests that these relatively small bats (≤ 60 g) have been potentially important members of early successional plant communities for tens of millions of years.

Positions of genera of early successional frugivorous phyllostomid and pteropodid bats in PCA morphospace are indicated in Fig. 2. PC axis 1 reflects overall body size and PC axis 2 reflects relative jaw length. Except for *Carollia*, which is relatively long-jawed for a frugivore, the phyllostomid genera are located in the interior of the phyllostomid polygon. Likewise, *Nyctimene*, *Cynopterus*, and *Myonycteris* are located in the interior of the pteropodid polygons. These distributions suggest that generalized, rather than extreme (specialized?), morphologies characterize frugivorous bats that play important roles in tropical succession.

In addition to differing in overall size and skull morphology, frugivorous phyllostomid and pteropodid bats also differ in the way they process fruits when they feed. These differences have potentially important implications for their roles as dispersers of early successional seeds. As reviewed by Dumont (2003), frugivorous bats can be divided into two groups based on the way they process fruits: (1) understory frugivores that eat relatively small, non-fibrous fruits are fast feeders that generally consume fruits in 1–2 min, swallow all or most of the seeds, and begin defaecating seeds in ≤ 30 min; (2) fig-eating or canopy-feeding frugivores that eat fibrous fruits are slow feeders that slowly chew a fruit and swallow its juices while pressing the pulp and seeds into a “spat” or “wad” which they spit out. Slow feeders swallow and defaecate far fewer seeds and hence are less likely to disperse seeds over large distances (e.g. while in flight) than fast feeders. Among phyllostomids, fast feeders include species of *Carollia* and *Glossophaga*, and slow feeders are represented by *Artibeus* and their relatives, including members of the understory-feeding genus *Sturnira* (Bonaccorso & Gush, 1987). Nearly all pteropodid bats eat figs to some extent and are slow feeders that produce spats; *Syconycteris*,

which does not produce spats, appears to be an exception (Dumont, 2003; Dumont & O’Neal, 2004). Even when feeding on non-fibrous banana fruit, the small African pteropodids *Micropteropus pusillus* (28 g) and *Nanonycteris veldkampii* (21 g) produce spats (Marshall & McWilliam, 1982). From a plant’s perspective, spat-producing bats are less effective seed dispersers for at least two reasons: (1) spats are often deposited under the canopies of fruiting trees (Utzurum, 1995; McConkey & Drake, 2006) and (2) seeds that end up in spats are more likely to be killed by fungal infections than those that are defaecated (Utzurum, 1995). Interestingly, a similar dichotomy in feeding methods exists in New World frugivorous birds: “gaspers” (e.g. manakins, Pipridae) ingest fruits and seeds whereas “mashers” (e.g. tanagers, Thraupinae) only swallow fruit juices and spit out fruit fibre and seeds, often while in fruiting plants (Moermond & Denslow, 1985; Levey, 1987).

Although many pteropodid bats are spat-producers, they also swallow and later defaecate small seeds such as those of *Ficus* species (Tang *et al.*, 2007). Some pteropodids are known to defaecate seeds in flight, including *Cynopterus* spp., *Rousettus amplexicaudatus* and *Pteropus vampyrus* in Indonesia and Malaysia and *Pteropus poliocephalus* in Australia (Phua & Corlett, 1998; Shilton *et al.*, 1999). Also, as documented by Shilton *et al.* (1999), pteropodids such as *Cynopterus sphinx* sometimes retain viable fig seeds in their intestinal tracts for more than 12 h and are thus potentially important long-distance seed dispersers, particularly in island archipelagoes. Overall, however, many pteropodid bats are sedentary feeders and probably deposit a higher proportion of the seeds they ingest under the canopies of fruiting trees compared with phyllostomids (Cox *et al.*, 1992; Kalko *et al.*, 1996; McConkey & Drake, 2006).

An additional difference between phyllostomid and pteropodid bats that could influence their importance during plant succession is that these two groups of bats feed heavily on fruits produced by different families of plants (Figs. 3 and 4). Throughout this review, we follow traditional convention (e.g. Gorchov *et al.*, 1995; Jordano, 1995; Dennis & Westcott, 2006; Lobova, Geiselman, & Mori, in press) and use plant family as our basic taxonomic unit. By doing this, we do not mean to imply that bats eat most or all fruits produced by many of these large families. In nearly all cases, bats feed on only a subset of genera and species in each family. The Piperaceae seems to be one of the few exceptions to this (Lobova *et al.*, in press). Based on the number of genera providing fruit eaten by phyllostomid bats, the top five plant families are Cactaceae, Arecaceae (= Palmae), Sapotaceae, Moraceae, and Myrtaceae (Fig. 3A). We will call these “major plant families for bats” in this review. Many genera of columnar cacti in Tribes Pachycereeae and Cereeae produce fruits whose seeds are dispersed by a few species of arid-dwelling phyllostomids as well as by frugivorous birds (Fleming, 1995; Anderson, 2001; Sosa & Fleming, 2002); none of these plants are associated with tropical forest regeneration. Of the other four families, only Moraceae (broadly defined here to include the closely related Cecropiaceae; Zerega *et al.*, 2005) includes plants that commonly occur in early successional habitats. A somewhat different picture emerges, however,

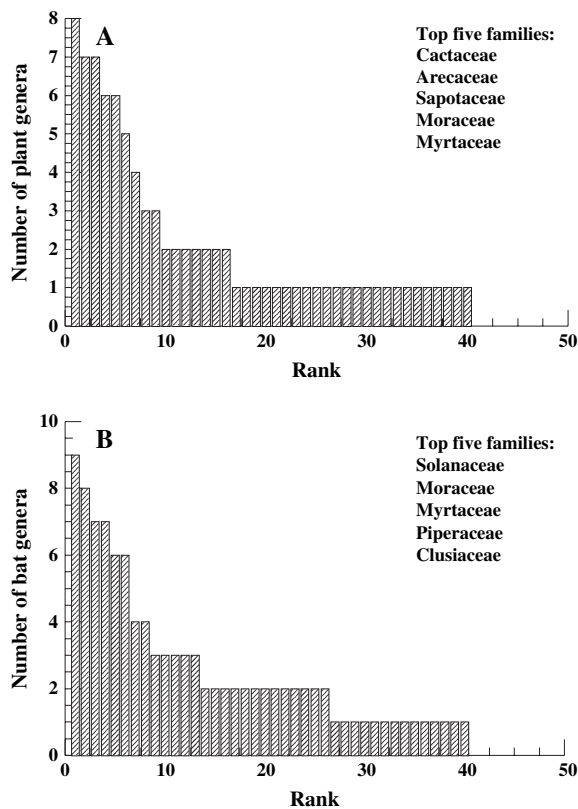


Fig. 3. Rank order of plant families providing fruit for phyllostomid bats. Families are ranked by number of different genera containing bat-dispersed fruits (A) (i.e. the major plant families) and by the number of genera of bats recorded eating fruits in these families. (B) (i.e. the “popular” plant families). Data are from Gardner (1977), Bonaccorso (1979), Fleming (1988), and Gorchov *et al.* (1995).

when we view plant families from the perspective of frugivorous phyllostomid bats (Fig. 3B). By the criterion of number of bat genera known to eat their fruit, the top five plant families are Solanaceae, Moraceae (including Cecropiaceae), Myrtaceae, Piperaceae, and Clusiaceae (= Hypericaceae). We will call these families “popular families for bats” hereafter. Four of these families contain genera whose species are strongly associated with early successional habitats in the neotropics (e.g. *Solanum*, *Cecropia*, *Piper*, and *Vismia*). Thus, fruits of early successional plants are often found in the diets of phyllostomid bats (a thorough review of this topic appears in Lobova *et al.*, in press).

By contrast, in keeping with their preference for fruits produced by forest canopy or subcanopy trees (Banack, 1998; Hodgkison *et al.*, 2003), the major plant families for frugivorous pteropodid bats are generally not associated with early successional habitats. In terms of number of genera, the top five fruit-producing families for pteropodids are Sapotaceae, Anacardiaceae, Meliaceae, Arecaceae, and Rubiaceae (Fig. 4A), and the top five families in terms of bat species eating their fruit are Moraceae (by a large margin), Myrtaceae, Anacardiaceae, Musaceae, and Arecaceae (Fig. 4B). Of these families, only species of Moraceae (e.g.

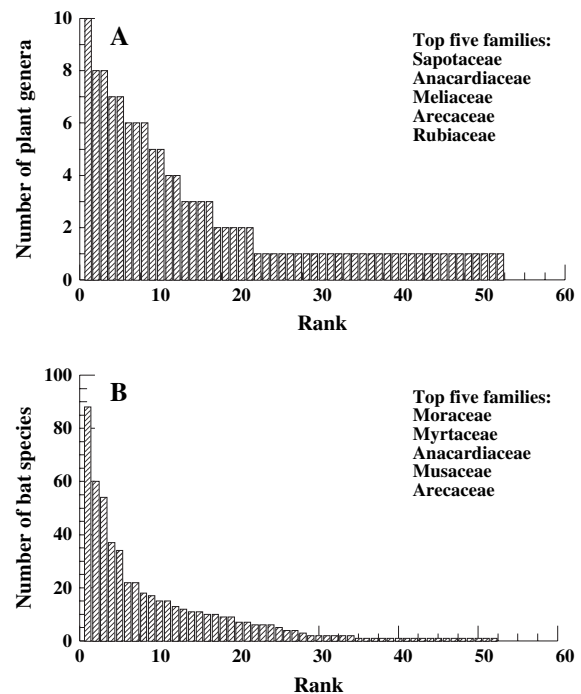


Fig. 4. Rank order of plant families providing fruit for pteropodid bats. Families are ranked by number of different genera containing bat-dispersed fruits. (A) (i.e. the major plant families) and by the number of species of bats recorded eating fruits in these families. (B) (i.e. the “popular” plant families). Data are from Appendix 1 in Mickleburgh, Hutson & Racey (1992).

Ficus) appear to be important in early succession in the Paleotropics. Only Moraceae and Myrtaceae make the “popular” lists of both phyllostomid and pteropodid bats. Strikingly missing from the list of “popular” pteropodid fruit families are early successional plants in the pantropical families Solanaceae and Piperaceae. Given these differences in plant lists, we hypothesize that phyllostomid bats play a much more important role in the early stages of tropical forest succession than pteropodid bats. This is not to say that pteropodid bats are not important seed dispersers for fleshy-fruited plants. They clearly are, especially on isolated oceanic islands (Cox *et al.*, 1991; Pierson & Rainey, 1992; Banack, 1998; Meehan, McConkey & Drake, 2002). Instead, this hypothesis emphasizes the fact that pteropodids interact with somewhat different guilds of tropical plants than phyllostomid bats. They are primarily canopy/subcanopy fruit-eaters whereas phyllostomid bats typically eat both understorey and canopy/subcanopy fruits.

III. QUESTION 1: COMPARED WITH FRUGIVOROUS BIRDS, HOW IMPORTANT ARE FRUIT-EATING BATS IN TROPICAL SUCCESSION?

In addition to fruit-eating bats, most tropical habitats contain a high diversity of frugivorous birds and mammals

(see Primack & Corlett, 2005). What are the relative contributions of frugivorous bats and birds to soil seed banks? Moreover, are there functional differences between these groups of volant seed dispersers that might influence their role in tropical succession? It is not our purpose in this review to compare extensively the roles of frugivorous bats and birds, but it is necessary to address some major differences between these groups in order to highlight the specific ecological role played by bats in tropical succession.

Aspects of foraging behaviour that determine the effectiveness of animals as seed dispersers include the proportion of fruit crops they remove, how far they carry seeds from fruiting plants, how they treat seeds in the mouth or gut, and where they actually defaecate or spit out seeds (McKey, 1975; Howe, 1986). Of these variables, available data indicate that bats and birds differ significantly only in where they deposit seeds. Both groups are capable of eating large proportions of fruit crops (e.g. Fleming *et al.*, 1985; Davidar & Morton, 1986; Fleming & Williams, 1990; Foster, 1990; Ortiz-Pulido & Rico-Gray, 2000), and both tend to treat seeds gently in their mouths and guts (e.g. Fleming, 1988; de Figueiredo & Perin, 1995; Naranjo, Rengifo & Soriano, 2003; Verdu & Traveset, 2004; Tang *et al.*, 2007). The two groups differ in that bats tend to defaecate or spit out seeds during flight (Charles-Dominique, 1986; Corlett, 1998, 2006; Whittaker & Jones, 1994); birds typically defaecate seeds while perched (Charles-Dominique, 1986; Corlett, 2006). Birds often stay longer in fruiting trees and are more likely to deposit seeds under the canopies of these trees than are frugivorous phyllostomid bats (e.g. Bronstein & Hoffmann, 1987; Kalko *et al.*, 1996). Reflecting this, Gorchoy *et al.* (1993) reported that birds were much less likely to deposit seeds in clear-cut strips in Peruvian lowland primary forest than bats.

In addition to their tendency to defaecate seeds in flight, many bats use one or more feeding roosts each night where they deposit the vast majority of seeds they ingest (e.g. Fleming, 1981, 1988). Located up to hundreds of meters from fruiting plants, these deposition sites can be fatal for early successional seeds whenever they involve bowers of dense vegetation (Fleming, 1981). Bats have also been reported to use regular flight paths on a nightly basis so that their movement (and therefore seed dispersal) through the environment is non-random (Janzen *et al.*, 1976). Both of these tendencies increase the heterogeneity of seed shadows created by bats, which in turn increases the probability that dispersed seeds will suffer from density-dependent mortality when deposited in clumps (Howe, 1989). The few seeds dropped during flight, however, may experience an enhanced probability of survival and germination. An experimental test of this idea would be enlightening.

A crucial aspect of both the colonization and directed dispersal hypotheses is that seeds arrive in areas where they are likely to become established. Given the low dietary overlap between bats and birds in Neotropical (Gorchoy *et al.*, 1995; Kalko *et al.*, 1996) and Paleotropical (Hodgkison *et al.*, 2003) rain forests, we might expect these groups to generate seed shadows that differ qualitatively and quantitatively. Behavioural differences between bats and birds may further differentiate their dispersal qualities. Recently

disturbed areas are amenable to the survival of the seeds of early successional plants because of favorable light regimes and low levels of intra- and interspecific competition (e.g. Vazquez-Yanes & Orozco-Segovia, 1982; Orozco-Segovia & Vazquez-Yanes, 1989). These areas, however, are often undesirable habitats for animal dispersers due to low resource availability and greater exposure to predators. If they do not deposit seeds under the parent tree, birds generally carry fruit to a perch or nest before dropping or defaecating seeds (Charles-Dominique, 1986; McClanahan & Wolfe, 1993; Corlett, 1998). As a result, they are less likely than bats to deposit seeds in forest clearings or in open sites (Gorchoy *et al.*, 1993; Whittaker & Jones, 1994; Parrotta, Knowles & Wunderle, 1997; Medellín & Gaona, 1999; but see Ingle, 2003) whereas bats drop some seeds during flight despite their tendency to deposit the majority at feeding roosts (Thomas *et al.*, 1988; Banack *et al.*, 2002; Hodgkison *et al.*, 2003). Thus, bat-dispersed seeds may be more likely to reach highly disturbed areas that lack perching and nesting sites than bird-dispersed seeds. Given this difference, we might expect bats to be more important seed-dispersers than birds during the initial stages of succession.

IV. QUESTION 2: ARE FRUGIVOROUS BATS EQUALLY IMPORTANT SEED DISPERSERS DURING SUCCESSION IN THE NEW AND OLD WORLD TROPICS?

(1) New World tropics

Phyllostomid bats clearly play an important role in both primary and secondary succession in the neotropics. A classic example of their role in primary succession comes from a study of plant succession on floodplains along the Rio Manu in the Peruvian Amazon (Foster, Arce & Wachter, 1986). Close to the river on newly exposed sand, seedlings of *Cecropia*, *Cedrela*, *Tessaria*, *Urera*, *Trema*, *Muntingia*, and *Ficus insipida*, among others, are common, and bats disperse 10 of 38 forest species that become established there. In terms of biomass, two bat-dispersed species, *Cecropia 'tessmannii'* and *F. insipida* dominate early succession along the Rio Manu. As forest development progresses, bird- or non-volant-mammal-dispersed species become more common, but even at 500 years post-disturbance, two of the four species of forest giants (*Dipteryx alata* and *Poulsenia armata*) are bat-dispersed whereas the other two species (*Ceiba pentandra* and *Luehea* sp.) are wind-dispersed. Foster *et al.* (1986, p. 365) concluded that "... wind and bat-dispersal is the most effective way for large or fast-growing trees to reach areas with long-term lack of competition and thus achieve individual or collective dominance... [T]hese mechanisms are much more likely than birds or non-flying mammals to get seeds out of the forest and onto the beach edge, or into the river with later deposition downstream".

Numerous studies of neotropical secondary succession also indicate that bat dispersal is a critical component of its early stages (e.g. Uhl *et al.*, 1981; Uhl & Jordan, 1984; Uhl,

1987; Uhl, Buschbacher & Serrao, 1988) (Table 2). In his comprehensive study of forest succession following slash-and-burn agriculture in Amazonia, for example, Uhl (1987) reported two bat-dispersed species of *Vismia* (Hypericaceae, now Clusiaceae) as the overwhelmingly dominant pioneer trees colonizing disturbed land in the first five years of succession. Over 90% of individuals ≥ 2 m in height present during the first year of succession in this study belonged to species in the “popular” phyllostomid families (Fig. 3B). Likewise, Uhl *et al.* (1988) emphasized the dominance of phyllostomid-dispersed plant species during early succession in eastern Amazonia. Comparisons of light-, moderate- and heavy-use sites by humans showed that species of *Cecropia*, *Solanum* and *Vismia* dominated different-aged sites within each of these categories and that *Solanum crinitum* and *Cecropia* spp. were the only trees present on heavy-use sites. In their discussion of impediments to regeneration, they reported that the results of bird censuses and mist-netting indicated that $< 6\%$ of bird species in the area were potential seed vectors due to their avoidance of open areas.

Numerous other New World studies have demonstrated the ubiquity of bat-dispersed plants in early successional sites. *Vismia* and *Cecropia* were the dominant genera in terms of density and basal area in 9–14-year-old forest stands that had been disturbed by slash-and-burn agriculture in lowland tropical rainforests of the upper Rio Negro, Venezuela (Saldarriaga *et al.*, 1988). Similar results were reported for abandoned terra firme sites north of Manaus in central Amazonia (Mesquita *et al.*, 2001). *Cecropia* was also the dominant genus, accounting for 35% of individuals ≥ 5 cm in diameter at breast height (DBH) in the overstorey, in early successional sites (i.e. 1–5 years since disturbance) along the Rio Negro in Bolivia (Toledo & Salick, 2006).

Guariguata (2000) reported that *Cecropia* spp. were numerically dominant in the soil seed bank in a Costa Rican wet forest and accounted for 33–69% of the total seedlings that germinated, depending on season. *Cecropia* spp. also comprised 78% of the total viable seeds in the soil after burning in a lowland Amazonian forest (Uhl *et al.*, 1981). At 22 months post-burning, *Cecropia* spp. represented 78% of the total living plant biomass at one site. Species of *Cecropia* and *Solanum* have also been noted to dominate early successional lowland forests in Guatemala (Snedaker, 1970) and Surinam (Boerboom, 1974).

According to Hartshorn (1980), *Cecropia* occurs only in forest gaps ≥ 400 m² in lowland rain forest at La Selva, Costa Rica. Similarly, Denslow (1980) referred to *Cecropia* as a “large-gap specialist”. Thus, it is likely that the relatively large areas often disturbed by human activity favour the dominance of *Cecropia* and other sun-loving, bat-dispersed plants in New World early successional forests. Laurance *et al.* (2006), for example, monitored densities of 52 tree species in fragmented and continuous patches of Amazonian rain forest over a 17-year period and found that the density of some species, including bird-dispersed *Cecropia sciadophylla* and bat-dispersed *Vismia* spp., increased more than 1000 times at the edge of fragments. Laurance *et al.* (2006) attributed this increase to bird- and bat-dispersal in addition to increased mortality rates of trees at the edges of fragments that provided new establishment sites. Studies in Mexico, Guatemala, and Bolivia indicate that bats that specialize on fruits of early successional plants (e.g. *Carollia perspicillata* and *Sturnira lilium*) forage in high numbers in lowland tropical forest fragments (Estrada, Coates-Estrada & Merritt, 1993; Schulze, Seavy & Whitacre, 2000; Arteaga, Aguirre & Moya, 2006).

Table 2. Examples of dominant (i.e. high density or high basal area) plant families during early succession at a variety of forest sites in the New and Old World tropics. The most “popular” families providing fruits for bats are indicated in bold (see Figs 3B and 4B)

Location	Successional status (yrs post-disturbance)	Dominant family (Genus: # of spp.)	Source	Notes
New World				
Peru	Primary (~1)	Moraceae (<i>Cecropia</i> : 2)	Foster <i>et al.</i> (1986)	
Venezuela	Secondary (2–5)	Moraceae (<i>Cecropia</i> : > 2) Clusiaceae (<i>Vismia</i> : 2)	Uhl & Jordan (1984)	Dominant year 2 Dominant years 3–5
Colombia	Secondary (9–14)	Clusiaceae (<i>Vismia</i> : 1)	Saldarriaga <i>et al.</i> (1988)	
Bolivia	Secondary (1–5)	Moraceae (<i>Cecropia</i> : 2) Ulmaceae (<i>Trema</i> : 2) Piperaceae (<i>Piper</i> : 1)	Toledo & Salick (2006)	Overstorey dominant Overstorey dominant Understorey dominant
Brazil	Secondary (2–8)	Solanaceae (<i>Solanum</i> : 3)	Uhl <i>et al.</i> (1988)	
Venezuela	Secondary (1–5)	Clusiaceae (<i>Vismia</i> : 2)	Uhl (1987)	
Old World				
Krakatau	Primary (~110)	Moraceae (<i>Ficus</i> : 24)	Whittaker & Jones (1994)	
Cameroon	Secondary (0–5)	Moraceae (3 genera)	Carriere <i>et al.</i> (2002a, b)	
Uganda	Secondary (1–9)	Fabaceae (> 3 genera)	Lwanga (2003)	
Tonga	Secondary (< 27)	Anacardiaceae (<i>Rhus</i> : 1)	Franklin <i>et al.</i> (1999)	
Samoa	Secondary (5)	Euphorbiaceae (<i>Macaranga</i> : 1)	Hjerpe <i>et al.</i> (2001)	
Borneo	Secondary (1–4)	Euphorbiaceae (<i>Macaranga</i> : 9)	Cleary & Priadjati (2005)	
Borneo	Secondary (3)	Ulmaceae (<i>Trema</i> : 1)	Ohtsuka (1999)	
Borneo	Secondary (8–13)	Euphorbiaceae (<i>Macaranga</i> : > 5)	Bischoff <i>et al.</i> (2005)	
Australia	Secondary (10)	Sapindaceae (<i>Guioa</i> : 2)	White <i>et al.</i> (2004)	

In addition to depositing seeds of early successional plants in abandoned agricultural lands and around the edges of forest fragments, phyllostomid bats also deposit many seeds of these species under and around isolated fruiting trees in pastures. Galindo-Gonzalez, Guevara & Sosa (2000), for example, reported that faecal samples from four species of phyllostomid bats captured under isolated fruiting *Ficus* trees as well as from seed traps were dominated by seeds of Piperaceae, Moraceae, and Solanaceae. From this they concluded that bats (and birds) play an important role in the maintenance of plant diversity in fragmented landscapes.

In summary, species from four of the five most “popular” plant families tend to dominate early stages of both primary and secondary succession in the New World (Table 2). These results clearly support the hypothesis that frugivorous phyllostomid bats play an important role in forest regeneration in the neotropics.

(2) Old World tropics

The available evidence appears to indicate that, compared with the neotropics, bats often play a less significant role in early succession in the Old World tropics.

A classic example of primary succession in the Old World is the reforestation of the islands of Krakatau after they were sterilized by volcanic eruptions in 1883. As described by Whittaker & Jones (1994), the earliest animal-dispersed plants included four species of *Ficus* (Moraceae), *Macaranga tanarius* (Euphorbiaceae), and *Melastoma affine* (Melastomataceae). Of these, either birds or bats could have brought in seeds of *Ficus* and *Melastoma*; only birds disperse seeds of *Macaranga*. Early surveys indicated that fruit-eating birds, including fruit pigeons, bulbuls, and the shining starling (*Aplonis metallica*), were resident on Krakatau by 1908. The first pteropodid bat, *Cynopterus sphinx*, colonized the islands between 1908 and 1919 and has been resident ever since; *Rousettus amplexicaudatus* was noted living in a cave on one island in 1933; and a colony of the large *Pteropus vampyrus* was first recorded in 1985. By 1992, 124 plant species dispersed either by bats or birds occurred on Krakatau. Of these, 43 species could have been brought in by either group, 31 species were brought in by birds and subsequently dispersed within the islands by bats, and 50 species were solely bird-dispersed (Whittaker & Jones, 1994). In addition to ≥ 13 species of *Ficus*, known or suspected bat-dispersed colonist plants include *Cyrtandra sulcata* (Gesneriaceae), *Melastoma malabathricum* (Melastomataceae), *Pipturus argenteus* (Urticaceae), and three species of *Solanum* (Solanaceae). Species of *Melastoma*, *Pipturus*, and *Solanum* are also known to be bird-dispersed in Southeast Asia (R. Corlett, *personal communication*). Interestingly, bats also brought two early successional New World fruits that are widespread as ornamentals in tropical Asia – *Muntingia calabura* (Elaeocarpaceae) and *Piper aduncum* – to Krakatau. Both of these fruits are dispersed by birds and bats in the New World (e.g. Fleming *et al.*, 1985). Overall, except for species of *Ficus*, a majority of the animal-dispersed plants on Krakatau were brought there by birds. Therefore, unlike the situation in Amazonia, primary succession on Krakatau was more bird-

dependent than bat-dependent, although, as Shilton & Whittaker (in press) point out, individuals of early colonizing figs brought to Krakatau by vagrant bats prior to 1900 could have served as “recruitment foci” for other species of bat- or bird-dispersed plants.

Studies of secondary succession in Africa, Asia, and Australia also indicate that bat-dispersed species are not among the most common plants during forest regeneration. Corlett (2002) has suggested that, generally, the role of the relatively few extant Asian fruit bats in early succession is limited because the majority of pioneer plants in this region are bird-dispersed (also see Grubb, 1998). Likewise, Franklin (2003) indicated that species of the widespread genus *Macaranga* (Euphorbiaceae), whose trees superficially resemble the neotropical pioneer genus *Cecropia* and which is the “best-described pioneer genus for Australasian rainforests”, is bird-dispersed.

Numerous studies have indicated that, unlike the situation in the New World, the majority of Old World early successional plants occur in families other than the most “popular” pteropodid families (Table 2; Fig. 4B). White *et al.* (2004) examined seed dispersal and seed banks in three isolated rain forest patches in lowland tropical Australia. Of the 71 early successional species dispersed by either ‘flight’ or ‘varied mechanisms’, only nine (12%) belonged to the popular families for pteropodids, and only four of these (5%) belonged to the major families (Fig. 4A). None of these species contributed more than 5% of the colonizing individuals to any of the three sites, and all of them are likely to be bird-dispersed.

Similarly, studies in Southeast Asia that have examined plant community composition in forests of various successional stages are notable for the absence of families with pteropodid-dispersed species (e.g. Turner & Corlett, 1996; Ohtsuka, 1999; Cleary & Priadhati, 2005). In a study comparing primary and secondary lowland rainforests in Borneo, Bischoff *et al.* (2005) reported that Meliaceae was the fifth most dominant family in terms of abundance on the list for early successional forests and was the only family containing species dispersed by pteropodids in their study. Davies & Semui (2006) described patterns of succession in Malaysia along an edaphic gradient in which none of the major pteropodid fruit families were present. Seventy two per cent of the tree species in early successional forest at a montane forest site in central Philippines are bird-dispersed (Hamann & Curio, 1999).

Several studies from Africa also show a low representation of pteropodid food plants in early successional plant communities. Lwanga (2003) included 19 pioneer species in his study of forest succession in upland tropical rainforest in Uganda. Of these, only two species belong to the five most popular families (Fig. 4B): *Ficus exasperata* (Moraceae) and *Rhus natalensis* (Anacardiaceae). Neither of these species is likely to be an important bat fruit (Mickleburgh *et al.*, 1992; Shanahan *et al.*, 2001b). In their analysis of long-term vegetation dynamics in an upland rainforest in Uganda, Sheil, Jennings & Savill (2000) described 55 pioneer species, of which only seven (13%) belong to the most popular families and eight (15%) belong to the major families for pteropodids (Fig. 4A); most of these are figs that are eaten by

a wide variety of birds, bats, and primates (Shanahan *et al.*, 2001a, b). In a study describing forest types along a successional gradient in a lowland rainforest in West Africa, Nansen, Tchabi & Meikle (2001) reported that early successional forests were dominated by six species, two of which belong to popular families: *Ficus exasperata* (Moraceae) and *Lannea nigrilana* (Anacardiaceae). Again, neither of these species is likely to be bat-dispersed; *L. nigrilana* is a bird-dispersed shrub (Parmentier, 2003).

This is not to say that bats do not disperse some early successional plants in the Old World but that they are often not included in the most popular or top five family lists. Phua & Corlett (1989), for example, reported a native pioneer, *Adinandra dumosa* (Theaceae), as the most common fruit in the diet of *Cynopterus brachyotis* in Singapore. Thirty-nine of 40 faecal samples and 93 % of the seeds collected along bat flight paths belonged to *A. dumosa*. Carriere *et al.* (2002a) found that about 70% of the total seed rain underneath remnant trees at 500 m in southern Cameroon came from *Musanga cecropioides* (Moraceae), the African equivalent of *Cecropia*. This pioneer tree is widespread throughout the African tropics and is dispersed by a wide range of animals, including bats. None of the other major families for pteropodids, however, were represented in seed rain at these disturbed sites, in strong contrast to the neotropical situation (e.g. Galindo-Gonzalez *et al.*, 2000).

Finally, there have been several examples of Old World fruit bats consuming invasive pioneer species from the New World. Phua & Corlett (1989) reported *Cecropia peltata* and *Muntinga calabura* in the diet of *Cynopterus brachyotis* in Malaysia. Winkelmann *et al.* (2003) found seeds of *Piper aduncum* in faecal samples collected from *Macroglossus minimus* in Papua New Guinea. Interestingly, this was the first report of frugivory in this nectar-feeding bat. In areas where they are available, pteropodid bats clearly recognize New World bat fruits as food and are important agents for increasing their abundance and distribution in the Old World tropics. In this way, they are dispersing early successional (non-native) species.

In summary, except for Moraceae, bat-dispersed plants rarely dominate early stages of succession in the Old World (Table 2). These results appear to support the hypothesis that frugivorous phyllostomid bats play a more important role in the early stages of forest regeneration than pteropodid bats.

(3) The importance of figs as bat food in a successional context

In their review of the consumption of figs by birds and mammals, Shanahan *et al.* (2001b) provide strong evidence that *Ficus* is an important food source for frugivores throughout the tropics. Our brief review of the fruit diets of phyllostomid and pteropodid bats clearly supports this view. Figs form the core diet (*sensu* Fleming, 1986) of most members of the phyllostomid subfamily Sternodermatinae, which contains 10 genera and 59 species weighing from 5 to about 70 g (Handley, Wilson & Gardner, 1991; Kalko *et al.*, 1996; Wendeln *et al.*, 2000; Simmons, 2005). This subfamily

contains most of the frugivorous species of Phyllostomidae. Likewise, figs are consumed by most species of pteropodids, including species across this family's size spectrum (Mickleburgh *et al.*, 1992; Uzzurum, 1995; Hodgkison *et al.*, 2003). Containing about 750 species, the genus *Ficus* encompasses a diverse array of life forms – from forest understorey geophytes to canopy-dwelling hemi-epiphytes – and some species are early successional shrubs or trees (Janzen, 1979; Corner, 1988; Berg, 1990). In the New World, *F. insipida* is a bat- (and sometimes fish-) dispersed pioneer species that becomes a canopy tree in early successional forests (e.g. Foster *et al.*, 1986; Banack *et al.*, 2002). In the Old World, Corlett (2006) indicated that three *Ficus* species of the dioecious subgenus *Sycomorus* (*F. fistulosa*, *F. hispida*, and *F. variegata*) are bat-dispersed, early successional species in Hong Kong and elsewhere in Southeast Asia and Australasia (e.g. Spencer & Fleming, 1989). Although they never come to dominate disturbed areas in a manner similar to that of *Cecropia*, *Solanum*, *Piper*, and *Vismia*, bat-dispersed figs nonetheless are sometimes important pioneer species that can serve as “recruitment foci” for other early successional plants (e.g. Whittaker & Jones, 1994; Nepstad *et al.*, 1996; Galindo-Gonzalez *et al.*, 2000; Guevara, Laborde & Sanchez-Rios, 2004). When they eat fruits of early successional species of *Ficus*, therefore, phyllostomid and pteropodid bats both play important roles in tropical succession.

(4) What accounts for differences between phyllostomid and pteropodid bats as dispersers of early successional plants?

We have proposed that fruit-eating phyllostomid and pteropodid bats differ in their importance as dispersers of the seeds of early successional plant species. Bat-dispersed seeds of a few key genera of plants often dominate early stages of primary and secondary succession in the Neotropics, but a similar pattern does not appear to characterize early stages of primary and secondary succession in the Paleotropics (Table 2). Why are there no bat-dispersed ecological equivalents of *Cecropia*, *Solanum*, *Piper*, and *Vismia* in the Old World tropics? For the first three genera, confamilial (*Musanga*) or congeneric (*Piper*, *Solanum*) taxa do exist in the Old World, but they are either bird-dispersed (*Musanga*, *Piper*; Snow, 1981; Fleming, 2004) or are not particularly important members of early successional plant communities (*Solanum*).

We propose that a major reason for this is that the evolution of frugivory in the two families has followed different trajectories: frugivory in phyllostomids has followed a “bottom up” trajectory whereas pteropodid frugivory has followed a “top down” trajectory. Here we mean that frugivory in phyllostomids initially involved feeding on small, soft, and small-seeded fruits of understorey plants such as *Piper* and *Solanum*, in much the same manner as species of *Carollia* do today [see discussion on the utility of viewing *Carollia* as the ancestral fruit-eating phyllostomid in Freeman (2000)]. Both of these plant genera are species-rich in the neotropics and are common shrubs and treelets in

both disturbed and undisturbed habitats (Croat, 1978; Gentry, 1982; Gentry & D'Arcy, 1986; Fleming, 2004; Jaramillo & Callejas, 2004). Bats of the genera *Carollia* and *Sturnira* are the primary dispersers of seeds of *Piper* and *Solanum*, respectively, and their elevational distributions in the Andes and elsewhere closely match the distributions of these two plant genera (Fleming, 1986). If this scenario is correct, it is likely that frugivory in phyllostomids could have initially started in secondary growth and later moved into primary growth and canopy tree fruits with the evolution of stenodermatines whose skulls are better-equipped to deal with harder and/or more fibre-rich fruits of figs and other canopy fruits than *Carollia* (Freeman, 2000; Dumont, 2004). Pteropodids, on the other hand, likely entered frugivory "from the top down" by initially feeding on canopy fruits, especially figs, which are more speciose in the Old World tropics (Zerega *et al.*, 2005), and then generalizing from there. If most secondary growth plants in the paleotropics were ancestrally bird-dispersed, and fleshy-fruited understorey plants in dipterocarp-dominated Southeast Asian rain forests were initially scarce (Wong, 1986; Ashton and the CTFS working group, 2004; LaFrankie *et al.*, 2006), then canopy-fruit feeding and eating larger, harder fruits may be ancestral in pteropodids. In support of this, Dumont's (2004) morphological analysis of the skulls of frugivorous bats indicates that, controlling for body size, the lower jaws of pteropodids have higher coronoid processes for generating stronger bite forces than phyllostomid jaws. Except for figs, association with early successional fruit species may be a derived condition in this family. If true, this evolutionary scenario could explain why phyllostomids are more important for the early stages of forest regeneration than pteropodids; they simply have had a longer evolutionary association with secondary fruits.

V. QUESTION 3: WHAT ARE THE ECONOMIC AND CONSERVATION IMPLICATIONS OF THESE DIFFERENCES?

Recent massive land-clearing and loss of old growth forest in the tropics has revealed the need to improve restoration and conservation programs (Lamb, Erskine & Parrotta, 2005). Managers working in these fields depend on ecologists to develop a strong ecological framework for informed decision-making. The concept of successional change is a major link between theoretical ecology and the applied fields of restoration and conservation ecology (Young, Peterson & Clary, 2005). Understanding the role of frugivorous bats in successional change in the tropics will be an important step toward improving conservation and restoration efforts.

A growing body of research describes current threats to the existence of New and Old World frugivorous bats (Cheke & Dahl, 1981; Cox *et al.*, 1991; Fujita & Tuttle, 1991; Cosson, Pons & Masson, 1999; Schulze *et al.*, 2000; Medellín, 2003; Nyhagen *et al.*, 2005). The implications for plants dependent on these bats for dispersal partially depend on the successional status of the plant. Loss of

effective dispersal agents for early successional species may contribute to cases of 'arrested succession' where regenerating forests become dominated by aggressive grasses, herbs, and shrubs that inhibit tree seedling survival and growth (Chapman & Chapman, 1999; Hooper, Legendre & Condit, 2004; also see Mesquita *et al.* (2001) for differences between *Cecropia* and *Vismia* in facilitating the establishment of early successional plants). On the other hand, late successional species deprived of effective dispersal agents may represent the "living dead". Threats to plants dependent on pteropodids for seed dispersal services in vulnerable island regions may be especially severe due to typically depauperate disperser faunas (e.g. Fujita & Tuttle, 1991; Pierson & Rainey, 1992; Elmqvist *et al.*, 1992; Meehan *et al.*, 2002; McConkey & Drake, 2006). Despite their locally greater abundance and diversity, mainland phyllostomid bats also face extensive habitat destruction (Cosson *et al.*, 1999; Schulze *et al.*, 2000; Estrada & Coates-Estrada, 2002; Medellín, 2003). The threat to frugivorous bats in the neotropics may be exacerbated by their relatively high degree of feeding specialization (Fleming, 2005).

Differences in fruit choice and their roles in forest regeneration between phyllostomid and pteropodid bats also have important economic consequences. Identification of the botanical products dependent on pollination and seed dispersal services provided by frugivorous and nectarivorous bats in the Old World tropics has helped elucidate their value from an economic and conservation perspective. Fujita & Tuttle (1991) found that 289 plant species in 59 families rely on flying foxes for seed dispersal, pollination, or both. Sixty-five per cent of these species are used to make 448 products for human use ranging from medicines and foods to wood products and dyes (see Table 1 in Fujita & Tuttle, 1991). The economically valuable plants dispersed by pteropodids are predominately late successional species. Timber and other wood products account for 23% of the total number of products derived from plants visited by pteropodids (Fujita & Tuttle, 1991). Extinction of dispersal agents of these trees would have dramatic impacts on forest dynamics because the number of new recruits would decline, leading to reduced abundance in the short term and possibly extinction in the long term. Populations of the local guilds of organisms that utilize these trees would also suffer from their decline.

To our knowledge, no similar study has been conducted on the economic "contributions" of phyllostomid bats, but the situation is likely to be somewhat different. Due to their preference for smaller-seeded, often early successional plants, phyllostomids play a less important role in the dispersal of primary forest species important to the timber industry. The main timber species in neotropical forests belong to Meliaceae, especially *Cedrela* and *Swietenia* spp., both of which are wind-dispersed. Data from Jansen & Zuidema (2001) show that less than 2 % by volume of important neotropical timber (measured as species from which over 100 m³ was exported by ITTO-Member Countries during 1994–1996) comes from the major families for phyllostomids (Table 3; Fig. 3A). The situation is similar in Asia and Australia with less than 4% by volume of regionally important timber species belonging to the major

Table 3. Regionally important timber species (measured as > 100 m³ exported by ITTO-member countries during 1994–1996) belonging to the top five families for bats listed in Figs 3A and 4A. Data are from Jansen & Zuidema (2001). Genera or species that are bat-dispersed are indicated by an asterisk (*)

Region	Volume (× 1000 m ³)
Tropical America	
<i>Bagassa guianensis</i> (Moraceae)	82.9
<i>Brosimum utile</i> (Moraceae)*	75.7
<i>Pouteria</i> spp. (Sapotaceae)*	2.9
Total volume of important timber species in top five families for phyllostomids = 1.6%	
Tropical Asia and Australia	
<i>Pouteria</i> spp. (Sapotaceae)*	504.0
<i>Palaquium</i> spp. (Sapotaceae)*	302.4
<i>Buchanania</i> spp. (Anacardiaceae)	277.4
<i>Mastisciodendron</i> (Rubiaceae)	172.0
Total volume of important timber species in top five families for pteropodids = 3.7%	
Tropical Africa	
<i>Mitragyna ciliata</i> (Rubiaceae)	2,167.2
<i>Entandophragma</i> spp. (Meliaceae)	2,050.8
<i>Tieghemelia</i> spp. (Sapotaceae)	1,314.3
<i>Chlorophora excelsa</i> (Moraceae)*	1,181.1
<i>Khaya</i> spp. (Meliaceae)	805.9
<i>Baillonella toxisperma</i> (Sapotaceae)	789.1
<i>Antiaris africana</i> (Moraceae)*	435.8
<i>Aningeria</i> spp. (Sapotaceae)	227.8
<i>Nauclea diderrichii</i> (Rubiaceae)*	97.5
<i>Lovoa trichilioides</i> (Meliaceae)	54.9
<i>Guarea cedrata</i> (Meliaceae)	38.8
Total volume of important timber species in top five families for pteropodids = 34.3%	

families for pteropodids (Fig. 4A). In sharp contrast, about 34% by volume of important African timber species belonged to the major families for pteropodids, but most of the important timber species in these families are not dispersed by bats (Table 3). Based on these data, the direct economic “contributions” of phyllostomids as seed dispersers are less valuable than those of pteropodids. The dispersal of seeds from non-timber species, however, represents an important ecological contribution, and the economic value of facilitation of forest regeneration by phyllostomids should not be overlooked or undervalued.

Conservation of volant vertebrate frugivores is especially important because early successional forests are often dependent on seed input from outside areas because of an often depleted soil seed bank and the absence of parent plants in the immediate area (Duncan & Chapman, 1999; Slocum, 2001; Zahwai & Augspurger, 2006). Turnbull, Crawley & Rees (2000) suggested that early successional habitats are commonly seed-limited. A similar conclusion for succession in central Amazonia was reached by Mesquita *et al.* (2001) and for secondary rainforest on Tonga, Western Polynesia (Franklin & Rey, 2007). Some evidence suggests that primary forest trees can be planted as “reforestation facilitators” or “recruitment foci” to acceler-

ate forest regeneration by attracting animal dispersers and increasing seed rain from primary forest species (Vieira, Uhl & Nepstad, 1994; Guevara *et al.*, 2004). Man-made “tree islands” in abandoned pastures can have a similar effect (Zahwai & Augspurger, 2006). Understanding which trees attract dispersal agents that facilitate natural succession in the region is a promising strategy for efficiently restoring degraded lands.

Although disturbances at a variety of spatial and temporal scales have played an important role in primary and secondary succession throughout the tropics (Whitmore & Burslem, 1998), large areas of deforestation and forest fragmentation that currently threaten the survival of vertebrate frugivores (and pollinators) are of relatively recent occurrence in the tropics. Historically, disturbances in the tropics consisted of relatively localized and often small-scale habitat loss (i.e. treefall gaps, landslides, and fires). In addition, bats in some regions of both the New and Old World tropics periodically experience intense disturbances from seasonal cyclones, especially on Pacific islands and in the Caribbean Sea (Pierson & Rainey, 1992; Gannon & Willig, 1994; Banack, 1998; Jones *et al.*, 2001; Rodriguez-Duran & Vazquez, 2001; McConkey *et al.*, 2004). None of these disturbances seriously threatened the survival of fruit-eating bats. Modern human activities such as timber harvesting, agriculture and mining, however, have now led to the destruction of enormous tracts of forest worldwide (Chapman *et al.*, 1999; Myers *et al.*, 2000). As a result, the amount of land in both the New and Old World tropics undergoing early succession has recently increased drastically. This has generated a great demand for effective conservation and restoration activities often conducted with extremely tight budgets and little time to deliver results.

The degree to which expanding early successional forests will influence communities of frugivorous bats is poorly known. On the one hand, increased area in early successional stages will likely increase the abundance of bats that feed in those areas, such as species of *Carollia* and *Sturnira*, due to increased food availability (Fleming, 1988). However, these bats and other species that typically inhabit late successional forests require intact forest for alternative foods as well as for roosting and refuge habitat (Estrada *et al.*, 1993; Schulze *et al.*, 2000; Evelyn & Stiles, 2003). Thus, the conservation of large tracts of primary forest is ultimately needed to conserve succession-promoting bats.

VI. CONCLUSIONS

(1) Frugivorous animals clearly facilitate tropical forest regeneration and help to maintain species diversity by introducing seeds from outside disturbed areas. Frugivorous phyllostomid bats in the neotropics appear to be particularly important in the early stages of forest succession because of the great importance of fruits of early successional shrubs and trees in their diets. Old World pteropodid bats seem to play a somewhat different role in tropical forest regeneration and maintenance of species diversity because they often feed on hard, large-seeded fruits

of forest canopy trees. Pteropodids thus help to promote the regeneration of late successional plant species. Bats of both families are important dispersers of early and late successional fig species.

(2) Differences in the relative importance of these two families in early tropical forest succession reflect their different evolutionary histories. Basal frugivorous phyllostomids were small and initially fed on soft, many-seeded fruits of early successional shrubs and trees; derived frugivores feed on the more fibrous fruits of canopy trees. Basal frugivorous pteropodids were somewhat larger and initially fed on canopy fruits, including many species of figs. In the Old World tropics, consumption of early successional fleshy fruits, most of which are bird-dispersed, likely is a derived condition.

(3) Because of differences in their fruit choices, bats in these two families provide somewhat different ecological 'services' for tropical forests. Phyllostomid bats are important facilitators of early forest regeneration and provide only an indirect benefit to the recruitment of commercially valuable timber trees. By dispersing the seeds of canopy trees, pteropodid bats provide a direct benefit to many economically valuable plants, including timber trees in some cases. Because of their important ecological services, frugivorous bats world-wide deserve considerable conservation attention. Overall, the population and community dynamics of tropical forests would likely be very different in the absence of frugivorous bats.

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