# SEED DISPERSAL BY FRUGIVOROUS BATS ON LANDSLIDES IN A MONTANE RAIN FOREST IN SOUTHERN ECUADOR

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**Abstract**. Phyllostomid bats are fundamental components of the neotropical mammalian diversity and they have the greatest dietary diversity in any mammalian family. Their tendency to occur in a widespread spectrum of different habitats and their capability to carry seeds long distances makes them essential for the regeneration of disturbed forest areas, like landslides. In this study the seed rain produced by bats and birds in forest slopes and landslides was investigated. A total of 232 faeces by birds and bats accounting a total of 3312 seeds of at least 13 plant families were collected in all seed traps on all sites. The number of bat dispersed seeds on each site was higher than the number of bird dispersed seeds (between 62,5 % to 90,6 % by bats). The chiropterochorous seed rain was composed of 27 different seed morphotypes. The ascertained distribution pattern of the faeces of bats and birds indicates that bats are crossing open areas regularly. This is in marked contrast to the behaviour of birds, which are sojourning at the forest edge. Additionally, faecal samples from frugivorous bats were also analysed, resulting in 18 different seed morphotypes out of 8 plant families. The majority belongs to the families of Piperaceae, Solanaceae and Araceae. In conclusion, the frugivorous phyllostomid bats showed to be essential for the regeneration of neotropical montane forest and the restoration of landslides.

**Key words:** seed dispersal, bats, landslides, montane rain forest, Ecuador.

## INTRODUCTION

Frugivorous bats are a key element for the regeneration of tropical forests and the preservation of the diversity of the flora in the Neotropics (VAN DER PIJL 1972, FLEMING 1991, KALKO 1997). There is no doubt about the importance of those bats for the ecosystem. However, there is little knowledge about competition between bats and birds for example.

About 70 – 98 % of the tree species in tropical lowland forests produce zoochorous seeds and fruits, furthermore many single tree individuals in scattered distribution depending on their dispersion by animals (HOWE & SMALLWOOD 1982, JANSON 1983). In French Guyana about 93 % of all pioneer plant species are dispersed by birds and bats (PRÉVOST 1983, CHARLES-DOMINIQUE 1986) and 96 out of 140 species of neotropical phyllostomid bats are feeding exclusively or at least partly on fruits (FLEMING *et al.* 1987).

Without an existing seedbank, dispersion events are the only source for a natural regeneration and thereby the influence of birds and bats is fundamental for the secondary, successional process (MEDELLIN & GAONA 1999). The zoochorous seed rain often are denser near by the forest than in open areas (GORCHOV *et al.* 1993), but the seed rain caused solely by bats is more intense on open areas because they are crossing such regions more often than birds (CHARLES-DOMINIQUE 1986). As a consequence frugivorous bats are able to connect forest fragments and have a significant influence on the regeneration process (GALINDO-GONZÁLEZ *et al.* 2000).

The present study deals with the influence of the seed rain by frugivorous phyllostomid bats on the regeneration process of landslides in a neotropical montane rainforest in Southern Ecuador.

## MATERIAL AND METHODS

<u>Study Area</u>

The study was realised in a montane rainforest near the Podocarpus National Park in the south of Ecuador. The study area is located at the research centre Estación Cientifica San Francisco ECSF (03°58'06"S and 79°04'35"W), half way between Loja and Zamora, in the province Zamora/Chinchipe. The research centre is situated at the eastern chain of the south Ecuadorian Andes and reaches maximum altitudes of about 3500 m asl. The slopes are generally very steep, on average around 30° with maxima >60° (SCHRUMPF *et al.* 2001). Landslides can be frequently observed even in natural forests. About 3,7 % of the area of the ECSF is covered by landslides (STOYAN 2000). The experimental site covers a slope in NNW to NE position and represents altitudes from 1800 asl (River San Francisco) to 3150 m asl at the top of the highest peak.

The average yearly temperature at the study site is about 17° C at 1950 m asl. Because the experimental site is located at the eastern slope of the Cordillera del Consuelo, the study area receives a pronounced orographic precipitation. A special type of climate without a distinctive dry season predominate this region (BENDIX & LAUER 1992). The yearly precipitation is about 2280 mm, reaching the maximum in June and July with 280 mm monthly.

The forest of the study area can be divided into three units, the "montane broad-leaved forest" (1850 – 2100 m asl), the "upper montane forest" (2100 – 2750 m asl) and the "subalpine-elfin forest" (2750 – 3150m asl) (BUSSMANN 2001). The lower part, between 1800 – 2000 m asl, is highly influenced by anthropogenic activities due to the easier access, and this area is a multiplex mosaic of areas with different successional stages. The data for this study was collected in this lower area.

Seed collection

To collect the seed rain, 128 seed traps with a surface of 1 m² each were constructed. The traps were placed on three different sites in the research area between 1800 m asl and 1900 m asl. 118 seed traps were established on two different landslides and the remaining 10 traps were placed as a reference on a trail inside the forest. Such position was selected because bats are orientating their flight routes on linear structures like rivers, forest borders and trails (CHARLES-DOMINIQUE 1986). The first landslide, the "Orchid-Slide" is situated between 1850 – 1900 m asl in NNW position. The inclination of the slide is about 40° to 60°, increasing in the upper part. This landslide was manmade in 1981 during construction works in this area. Altogether 68 seed traps in a 5 m grid were placed, covering about 5,6 % of the total size of the 1220 m² terrain in the upper part of the landslide, including the border-vegetation. In the "Orchid-Slide" the location of the seed traps were divided in three zones differentiating between border-vegetation, edge and open area. This arrangement leads to 20 traps in the border-vegetation, 17 traps on the edge and 31 traps in the open area.

The second landslide, the "Quebrada-Slide" is situated in S position and was formed in 1998 creating an open area of 334 m² and was classified as an unique slide event (STOYAN 2000). But in 2001 the area became unstable again, increasing the area of the landslide to 1500 m². The inclination of this study site is about 45° to 60°, increasing in the upper part, too. Altogether 50 seed traps in the equivalent 5 m grid were placed, covering about 3,3 % of the total size of the terrain. On this site no subdivisions into different zones were established.

Between October 2002 and January 2003, in four control periods, seed traps were depleted daily. Days with strong rainfalls, which washed away the seeds from the traps, were excluded from the evaluation. But at least 10 days per control period were included in the data analysis. Because the mounting of the seed traps were continued after the start of the first control period, different time space for the data collection for each research site was available, resulting in 51 days of evaluation for the site on the trail and for the "Orchid-Slide" and 34 days of evaluation for the "Quebrada-Slide". The differentiation between faeces from birds and bats was done by means of content, consistence and appearance. Faecal samples were sealed in Eppendorff tubes and labelled. Seeds were later separated for counting and identification in the laboratory. The seeds were identified, using collected reference material and an existing seed-catalogue for bat dispersed plants in the region of the ECSF by MATT (2001), containing 51 seed-morphotypes.

Bat captures

Bats were collected in 18 capture sessions using one or two mist nets (ATX 3 m and 6 m; mesh size 19 mm). Except for two sessions, which took place directly on the investigated landslides, all catching sessions were executed on trails near those sites. The captured bats were identified using field keys by ALBUJA (1999) and TIMM & LAVAL (1998). Faeces were collected while animals were in the net, during subsequent handling or when kept separately in numbered cloth bags for approximately 30 minutes. Faecal samples were examined in the laboratory for seeds and were identified using the catalogue of MATT (2001) and other collected reference material.

## RESULTS

A total f 232 faecal samples by birds and bats were collected in all 128 seed traps on all sites. These samples contained 3312 seeds of at least 13 plant families. The number of bat dispersed seeds on each site was higher than the number of bird dispersed seeds.

During 51 sample days on the trail site, 44 bird faeces and 49 bat faeces were collected using 10 seed traps. These samples contained 1687 seeds of at least 11 plant families. Only 158 seeds (9,4 %) were isolated from faeces by birds.

On the Orchid-Slide during 51 control days, 62 faeces by birds and 41 faeces by bats were collected using 68 seed traps arranged in the three different zones mentioned before. A total of 1569 seeds out of at least

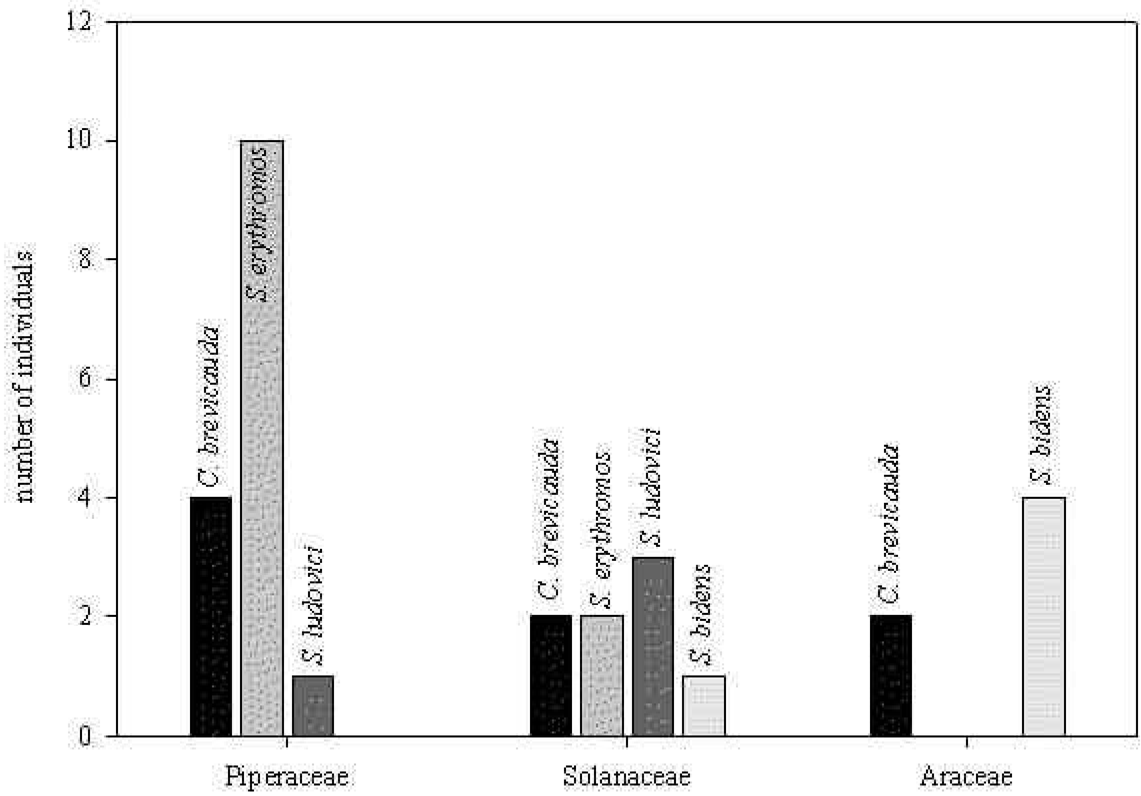


Figure 1. Diet of the four most captured frugivorous bat species

10 plant families were isolated from those samples. Only 289 seeds (18,4 %) were recognized as bird dispersed. There were significantly more faeces produced by birds found in the zone of the border vegetation than in the open area of this slide (*U*=126; p<0,05, Mann-Whitney *U*-Test), resulting in a distribution-index ($s^2/x$) of 1,92. The faeces by bats were distributed more regularly ($s^2/x$=1,09).

On the Quebrada-Slide, about 19 faecal samples by birds and 17 faecal samples by bats were collected during 34 control days, using 50 seed traps. These samples contained 56 seeds belonging to at least 5 plant families. About 21 of the isolated seeds (37,5 %) were found in the faeces of birds.

The bat-produced seed rain contained seeds from at least 12 plant families (Table 1). The most abundant families were Araceae, Clusiaceae, Melastomataceae, Piperaceae and Solanaceae. Mostly just one seed-morphotype was found in the analyzed samples of bat faeces. Only 13 % of the samples contained two different seed-morphotypes, and more than that were never observed.

The average number of seeds dispersed by birds and bats was 3 seeds/day/m² on the trail site, 0,67 on the Orchid-Slide and 0,04 on the Quebrada-Slide.

After a total capture-effort of 945 m²h, 16 of the 18 netting nights were successful, with 62 bats from 12 species. Frugivorous phyllostomids (Stenodermatinae, Carollinae) represented the major part with 39 individuals (62 %) out of six species: *Sturnira erythromos* (15 individuals), *Sturnira ludovici* (9 individuals), *Carollia brevicauda* (8 individuals), *Sturnira bidens* (4 individuals), *Artibeus phaeotis* (2 individuals), *Platyrrhinus infuscus* (1 individual).

Other bats were also captured including 9 insectivorous bats of 4 species, the Vespertilionidae *Lasiurus borealis* (5 bats), *Myotis* spec. (2 bats) and *Eptesicus brasiliensis* (1 bat), and the Phyllostomidae [Phyllostominae] *Micronycteris megalotis* (1 bat), 8 nectarivorous *Anoura caudifer* (Glossophaginae) and 6 blood feeding *Desmodus rotundus* (Desmodontinae).

During mistnetting, 33 faecal samples with seeds from six bat species were collected. The analysis of those samples resulted in 36 seed findings; a seed finding is defined as the verification of a seed morphotype in a faecal sample. The majority of the faecal samples (91 %) contained only one seed morphotype; merely 3 of the sampled faeces contained two different seed morphotypes.

Most of the frugivorous bats captured belong to

Table 1. Number of faeces of bats which contained seeds

| Plant species | Site | | |
|---|---|---|---|
| | trail | Orchid-Slide | Quebrada-Slide |
| | st=10 | st=68 | st=50 |
| | cd=51 | cd=51 | cd=34 |
| **Piperaceae** | | | |
| *Piper* spec. 1 | 1 | - | - |
| *Piper* spec. 2 | 3 | - | - |
| *Piper* spec. 3 | 2 | - | - |
| *Piper* spec. 4 | - | 1 | - |
| *Piper* spec. 5 | - | - | 1 |
| *Piper* spec. 6 | - | - | 1 |
| *Piper* spec. 7 | 1 | - | - |
| *Piper* spec. 8 | 1 | - | - |
| *Piper* spec. 9 | 1 | - | - |
| *Piper* spec. 10 | 1 | - | - |
| *Piper* spec. 11 | - | 1 | - |
| **Solanaceae** | | | |
| Solanaceae ms 1 | 1 | 1 | - |
| Solanaceae ms 2 | 1 | - | 1 |
| Solanaceae ms 3 | - | 1 | - |
| Solanaceae ms 4 | 1 | 1 | - |
| **Actinidiaceae** | | | |
| *Saurauia* spec. | 1 | 5 | - |
| **Araceae** | | | |
| *Anthurium* spec. | 9 | 3 | 4 |
| **Clusiaceae** | | | |
| *Vismia tormentosa* | 5 | 8 | - |
| **Cecropiaceae** | | | |
| *Cecropia* spec. | - | 1 | - |
| **Ericaceae** | | | |
| Ericaceae ms 1 | 3 | 1 | 1 |
| **Moraceae** | | | |
| *Ficus* spec. | - | 3 | 2 |
| **Araliaceae** | | | |
| Araliaceae ms 1 | - | 1 | - |
| **Melastomataceae** | | | |
| Melastomataceae ms | 18 | 6 | - |
| **Onagraceae** | | | |
| Onagraceae ms 1 | 3 | - | - |
| **Siparunaceae** | | | |
| Siparunaceae ms 1 | 1 | - | - |
| **Other** | | | |
| indet. 1 | - | 1 | - |
| indet. 2 | - | 3 | - |
| **TOTAL** | 43 | 37 | 10 |

st=seed traps; cd=control days

species of the "understory-guild" (Matt 2001, Charles-Dominique & Cockle 2001, Bonaccorso 1979): *Sturnira erythromos*, *S. ludovici*, *S. bidens*, *Carollia brevicauda*. As a result the biggest part of the faecal samples and identified seeds belong to this group. Because of the use of ground mounted mist nets the capture success and number of faeces of "canopy-guild" species like *Artibeus phaeotis* and *Platyrrhinus infuscus* was low.

Although the number of captured individuals was not the highest one, *Carollia brevicauda* presented the greatest variety in diet. There were 9 different seed morphotypes found in 8 faecal samples by this species: four *Piper*-species, two Solanaceae-species, *Anthurium* spec. (Araceae), *Vismia tormentosa* (Clusiaceae) and one Melastomataceae-species.

The diet of *Sturnira erythromos* was mainly comprised of four *Piper*-species with a distinct preference for one of them (*Piper* spec. 2). In addition to this two Solanaceae morphotypes were verified.

In the faeces of four individuals of *Sturnira ludovici* two morphotypes of Solanaceae seeds and seeds of *Piper* spec. 6 (Piperaceae), *Saurauia* spec. (Actinidiaceae), *Cecropia* spec. (Cecropiaceae) were found. Two times captured individuals of this species were carrying fruits with them: one time an infructescens of *Piper* spec. and the other time a *Saurauia*-berry.

The faecal samples of all four *Sturnira bidens* contained seeds from *Anthurium* spec. (Araceae). In the faeces of one individual Solanaceae-seeds were additionally found.

## Discussion

The influence of frugivorous bats and birds on the secondary successional process is fundamental for the development of the vegetation (Medellin & Gaona 1999). The main part of the seed rain in disturbed areas is dispersed by birds and bats (Charles-Domonique 1986). These statements are confirmed by the present work, supporting the importance of frugivorous bats as seed dispersers.

In the moist Neotropics, the early successional species that commonly establish in gaps and open areas in or adjacent to forests (e.g. *Piper*, *Solanum*, *Vismia* and *Cecropia*) are primarily (but not exclusively) bat dispersed (Foster *et al.* 1986, Uhl 1987, Gorchov *et al.* 1993, Gorchov *et al.* 1995). Here, bats dispersed more seeds than birds on all investigation sites. Furthermore the seed rain caused by bats is more diverse than the one caused by birds. These results are in accordance with similar works realized in disturbed areas in the

Neotropics (GORCHOV *et al.* 1993, GORCHOV *et al.* 1995, MEDELLIN & GAONA 1999).

Piperaceae-seeds were part of the seed rain on every investigation site. The most morphotypes of this family were found in the trail-site, even with the smallest collection effort (10 seed traps). This observation is an indication for the feeding behaviour especially for frugivorous understory bat species using linear structures like trails as flight routes (CHARLES-DOMINIQUE 1986, CHARLES-DOMINIQUE & COCKLE 2001, MATT pers. comm.). Although the sample size was relatively small, it seems clear that *Sturnira erythromos* and *Carollia brevicauda* are the main dispersion agents for Piperaceae-seeds in the investigated region (see also BIZERRIL & RAW 1997, EMMONS & FEER 1997). FLEMING (1986) proposed that the evolution of feeding habits in frugivorous phyllostomids involved principally the specialization on core plant taxa (e.g. *Carollia* on *Piper*, *Sturnira* on *Solanum* and *Piper*, *Artibeus* on *Ficus*). Furthermore the high number of different morphotypes of Piperaceae-seeds reflects the high diversity of this plant family in the region. To that effect additional research in respect of the ecology and the habitats of the species of this family are suggested.

Seed morphotypes belonging to *Anthurium* spec. (Araceae) were also common in the seed traps of every site. In faecal samples of captured *Sturnira bidens*, seeds of *Anthurium* spec. (Araceae) were identified, confirming this bat species as a specialist for *Anthurium*-fruits, which occurs seasonally in the investigation area (MATT 2001).

Seeds of Melastomataceae are mainly dispersed by birds in disturbed areas (GORCHOV *et al.* 1993, GORCHOV *et al.* 1995), but there are also records of dispersion by bats (HERNÁNDEZ-CONRIQUE *et al.* 1997, GARCIA *et al.* 2000). Seeds of this family were only found in faeces from *Carollia brevicauda*, though they were a steady part of the bat-rated seed rain on the trail and the Orchid-slide.

Many plants, which are part of the seed rain caused by bats, belong to a flora with pioneer-characteristics (e.g. *Piper*, *Saurauia*, Melastomataceae, and Solanaceae - MEDELLIN & GAONA 1999, GORCHOV *et al.* 1993). They can become an essential part for the regeneration of disturbed habitats such like landslides. The zoochorous seed rain on disturbed areas is generally composed of pioneer species. Although this leads only to a low diverse regeneration forest, it is an important step for the following succession, because during this level different species of seed dispersers will appear and consequently start the entry of climax species, which are now able to establish (BROSSET 1996).

Based on the faeces collected as well as by other observations, frugivorous bats were crossing open areas more frequently than frugivorous birds. Similar results are recorded for works realized in the moist neotropical lowland (CHARLES-DOMINIQUE 1986, GORCHOV *et. al.* 1993). This behavioural difference is essential and has important repercussions on seed dispersal: frugivorous birds tend to defecate from a perch, whereas frugivorous Phyllostomidae bats defecate more often during flight (CHARLES-DOMINIQUE & COCKLE 2001). Furthermore the dispersed amount of seeds by several Phyllostomidae species is considerable, because they feed 30 to 40 times in a single night (FLEMING 1986, CHARLES-DOMINIQUE & COCKLE 2001).

It seems there is no difference in those facts between the moist neotropical lowland and the montane regions and it is more likely that frugivorous bats maybe play even a more important role in the neotropical montane forest, because there are more bat dispersed plant species per frugivorous bat species (MATT 2001).

The main focus of this work was concentrated on the aspect of chiropterochory, as a consequence the data set for the group of the frugivorous birds is smaller. A continuation with regard to a completion would be useful and an improvement in respect of the comparableness.

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