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1 **Seed dispersal by frugivorous bats in Central Guyana and a description of previously**

2 **unknown plant-animal interactions.**

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4 THOMAS W. B. HORSLEY*, JAKE E. BICKNELL, BURTON K. LIM, AND LOREN K. AMMERMAN.

5 *Department of Biology, Angelo State University, San Angelo, TX 76909, USA (TH and LKA);*

6 *Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation,*

7 *University of Kent, Kent, UK, CT2 7NR (JEB); Department of Natural History, Royal*

8 *Ontario Museum, Toronto, ON M5S 2C6, Canada (BKL).*

9

10 *Corresponding author

11 Thomas Horsley

12 Angelo State University

13 Department of Biology

14 San Angelo, TX, USA 76909

15 twhorsley@gmail.com

16 1-(603)-425-9790

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21 **Bat Seed dispersal in Central Guyana.**

22

23

24   ABSTRACT:

25   Species of bats in the subfamilies Stenodermatinae and Carolliinae are primarily

26   frugivores, and through the ingestion of fruit and defecation of seeds, they play a crucial role

27   in their environment through the dispersal of early successional and pioneer plants

28   contributing to reforestation. These ecosystem services provided by frugivorous bats are

29   becoming more critical with time, as anthropogenic habitat destruction continues to rise. The

30   objective of this study was to survey the plant species dispersed by frugivorous bats in a

31   tropical rainforest in Guyana. Fecal samples were taken from captured frugivorous bats and

32   stomach contents were taken from a representative collection. The four most common bats

33   were *Artibeus planirostris, A. obscurus, A. lituratus,* and *Carollia perspicillata*, which

34   accounted for 67% of total captures in mist nets set in the forest understory. Twenty plant

35   species were identified in fecal and stomach content samples with the most abundant (*Ficus

36   nymphaeifolia, Piper bartlingianum, Cecropia latiloba,* and *C. sciadophylla*) accounting for

37   60% of the total. *Cecropia latiloba*, which is an early colonizer of floodplains throughout the

38   Guiana Shield and Amazon River Basin was previously unknown to be bat dispersed. Seven

39   plant species were documented as being dispersed by nine bat species for the first time.

40   These results enhance our understanding of seed dispersal by Neotropical bats, specifically

41   by revealing previously unknown bat/plant relationships.

42

43   INTRODUCTION

44   Bats are ecologically important as mediators of seed dispersal in tropical forests

45   (Heithaus et al. 1975). This provision of ecosystem services is fundamental to forest

46   dynamics and regeneration. Over 80% of plant species in the Neotropics rely on frugivorous

47 vertebrates for the dispersal of their diaspores (the effective dispersal unit) (Howe and

48 Smallwood 1982). Geiselman et al. (2002 onward) reported a total of 549 species in 191

49 genera forming 62 plant families that are dispersed by bats. In many cases, bats are the sole

50 or primary dispersal agents for numerous tropical plants (Fleming and Heithaus 1981,

51 Fleming 1988, Galindo-González et al. 2000). Lopez and Vaughan (2007) found that five of

52 the six most commonly caught sympatric frugivorous bats in Costa Rica had a diet that was

53 composed of predominately one or two species of plant, however, the frequency and extent to

54 which bats change among food items depends on food resource abundance and competitors

55 (Humphrey and Bonaccorso 1979).

56   Many neotropical phyllostomid bats rely on one or more of the five plant genera

57 *Cecropia, Ficus, Piper, Solanum*, and *Vismia* (Fleming 1986). These bats are critical to the

58 dispersal of these genera (Bonaccorso and Gush 1987); their fruits are nutritionally poor,

59 requiring the consumption of large quantities to meet the bats dietary needs (Fleming 1986).

60 Between foraging bouts, bats carry fruit to feeding roosts where they drop the indigestible

61 material (Nowak 1994), and defecate seeds along the way. This process results in a single bat

62 dispersing up to thousands of diaspores each night.

63   In Guyana, the phyllostomid genera *Artibeus* and *Carollia* are found in

64 disproportionately high abundances compared with other species (Lim and Engstrom 2001a,

65 2005), and are therefore likely important seed dispersers that contribute disproportinately to

66 the local forest dynamics in these relatively undisturbed forests. The objective of this study

67 was to survey the plant species dispersed by frugivorous bats within the Iwokrama Forest in

68 Guyana, with an emphasis on the genera *Artibeus* and *Carollia*. This is the first study of

69 frugivorous bat diet conducted in Guyana.

70 METHODS

71 Study site

72   The Iwokrama Forest is composed of 371,000 ha of largely pristine rainforest located

73 in central Guyana in the Potaro-Siparuni Region (Figure 1). Iwokrama was set aside by the

74 government of Guyana in 1990 under the auspices of the Commonwealth Secretariat

75 (Hawkes and Wall 1993). It is divided into two approximately equal parts: half is strictly a

76 wilderness reserve set aside for the study of biodiversity, whereas the other area is for

77 research in harvest of rainforest resources. A 70 km road passes through the center of the

78 reserve. The Surama Forest is located just outside Iwokrama, bordering the southwest corner.

79 The reserve is characterized by low-lying terra firme tropical rainforest dominated by

80 emergent trees such as *Chlorocardium rodiei*, *Eperua falcata*, *Dicorynia guianensis*, *Mora*

81 *excelsa* and *Swartzia leiocalycina*. Average annual rainfall for the region is approximately

82 3000 mm yr, 400-500 mm during rainy season months (April to July) and 200 mm during

83 most other months. Temperatures range from an average low of 22°C at night during the July

84 wet season to an average high of 36°C in the daytime during the October dry season

85 (Bicknell et al. 2011).

86   In this study, four sites in this region were surveyed for bats. Turtle Mountain (4.731°

87 -58.717°), Kabocalli (4.287° -58.508°), and Sandstone (4.383° -58.921°) are located within

88 Iwokrama; and Rock Landing (4.179° -59.082°) is within the Surama Forest (Figure 1). The

89 Turtle Mountain site is located within a large area of flooded forest adjacent to the Essequibo

90 River. The other sites are subject to flooding from the Essequibo or Burro-Burro Rivers.

91 However, the flooded forest at Turtle Mountain is the most substantial of the surveyed sites.

92   Kabocalli is the only site located within the wilderness preserve of Iwokrama and is the least

93   developed of any site.

94

95   Sampling strategy

96   Bat surveys were conducted in the Iwokrama and Surama Forests during the wet-

97   season in July and August 2013. Turtle Mountain was surveyed for 4 nights (July 20-23),

98   Kabocalli for 5 nights (July 25-29), Rock Landing for 4 nights (August 1-4), and Sandstone

99   for 4 nights (August 6-9). Sites were surveyed using 18 understory mist nets arranged in a

100 100 m grid comprised of three transects through the forest. Pairs of 12 m nets were

101 positioned perpendicular to each other and separated by 50 m along each of the three

102 transects. Nets were opened at 18:00 h and closed at 00:00 h. In the event of ongoing heavy

103 rain, nets were closed. Species were identified using keys developed by Lim and Engstrom

104 (2001b).

105   Fecal samples were collected from captured frugivores. Bats were held in cloth

106 capture bags for no longer than two hours to allow time for individuals to defecate in order to

107 maximize sample yield (Lopez and Vaughan 2004). Bags were cleaned of remnant feces

108 between captures to prevent cross contamination of fecal samples. Bats were released after

109 collection of data and fecal samples, if provided. Voucher specimens were collected of one

110 individual per species per night of surveying to represent the species diversity of bats at each

111 of the four sampling localities, and stomach contents were taken from collected frugivorous

112 individuals for dietary analysis. Stomach content samples were not collected from individuals

113 that had provided an earlier fecal sample. All procedures followed animal research guidelines

114 approved by the American Society of Mammalogists (Sikes et al. 2011) and the Institutional

115   Animal Care and Use Committee at Angelo State University (IACUC Approval Number

116   1312). Specimens were deposited at the Centre for the Study of Biological Diversity in

117   Georgetown, Guyana, Angelo State Natural History Collection in San Angelo, Texas, and the

118   Royal Ontario Museum in Toronto, Ontario. Fecal samples were stored in 2 ml screw-cap

119   microcentrifuge tubes filled with 70% ethanol.

120   Fallen fruit and any fruit available on plants surrounding the bat nets at each site, in

121   addition to available accompanying plant parts, were collected and stored in Whirl-pak™

122   bags containing 70% ethanol for use as a comparative reference source for identification of

123   seeds defecated by bats. Furthermore, any fruit carried into the nets by bats were documented

124   and collected, and the species of bat carrying the fruit was recorded. All collected fruit and

125   fecal samples were identified, and the contained diaspores were dried in order to build a

126   reference collection. Diaspores from collected fecal samples and stomach contents were

127   sorted into morphotypes and identified using a reference collection at Old Dominion

128   University in Norfolk, Virginia. The number of types, number of diaspores of each type, and

129   morphometric data of each type were recorded for each collected sample. Additionally, all

130   diaspore types were photographed for digital documentation. Bat and plant genus

131   associations were tested using a permutation test for independence (Chihara and Hesterberg

132   2011) using a chi-square test function in the coin package in R (Hothorn et al. 2006, 2008).

133

134   RESULTS

135   We accumulated 1,656 net hours of survey effort among the four sites, capturing 241

136   individuals from 26 species of bats. Capture rates ranged from a high of 0.262 captures/nh at

137   Rock Landing to a low of 0.060 captures/nh at Kabocalli. The five most commonly captured

138   species were *Artibeus planirostris* (70), *A. obscurus* (31), *Carollia perspicillata* (31), *A.*

139   *lituratus* (30), and *Rhinophylla pumilio* (15). Overall, 75 fecal samples and 39 stomach

140   content samples were collected from 14 bat species. Collectively, 63 of the combined 114

141   samples contained diaspores. The remaining 51 samples contained a combination of fruit

142   pulp, plant material, and some insect material. Additionally, four fruits were collected from

143   bats carrying them into nets: two *Chrysobalanaceae* species, one dispersed by *A. obscurus*

144   and the other dispersed by *A. lituratus*, *Ficus maxima* dispersed by *A. planirostris*, and *Piper*

145   *bartlingianum* dispersed by *Carollia perspicillata*. Of the 63 samples containing diaspores,

146   *Artibeus lituratus, A. planirostris,* and *A. obscurus* accounted for 27 samples; *Carollia*

147   *perspicillata* accounted for 25 samples; and other bat species (*Artibeus gnomus,*

148   *Phyllostomus hastatus, Platyrrhinus helleri, Rhinophylla pumilio, Sturnira lilium, S. tildae,*

149   and *Vampyressa bidens*) represented 11 samples.

150   Overall, 20 plant species were identified in collected samples, including *Cecropia*

151   *latiloba*, a species previously unknown to be bat dispersed (Figure 2, Table 1) (Lobova et al.

152   2009). *Cecropia latiloba* was dispersed most commonly by *Artibeus planirostris* (three

153   samples) and *A. obscurus* (two samples). However, a single dispersal record also was

154   observed for *A. lituratus*, *C. perspicillata, P. helleri,* and *V. bidens.* Seven bat-dispersed plant

155   species were found to be dispersed by bat species that have not previously been recorded as

156   dispersers of those plant species, and thus are newly recorded bat/plant relationships (Lobova

157   et al. 2009) (Table 1). When considering bat/plant genus associations, there was a significant

158   association between *Artibeus* and *Ficus/Cecropia* and *Carollia* and *Piper/Solanum* ($\chi^2 = 42.1$,

159   df= 3, p<0.001) (Figure 3). *Artibeus* accounted for 83% of *Ficus* records and 74% of

160 *Cecropia* records, and *Carollia* species accounted for 75% of *Piper* records and 100% of

161 *Solanum* records.

162

163 DISCUSSION

164   Overall, *A. lituratus, A. planirostris, and A. obscurus* fed on three plant genera *Ficus,*

165 *Cecropia,* and *Philodendron. Carollia perspicillata* fed on nine genera: *Piper, Solanum,*

166 *Rollinia, Senna, Anthurium, Paullinia, Philodendron, Vismia,* and *Cecropia.* Delaval et al.

167 (2005) attained similar results in their analysis of niche breadth among frugivorous

168 phyllostomid guilds in French Guiana. They found large *Artibeus* species exhibited low niche

169 breadth, foraging on predominantly *Cecropia* and *Ficus* species, and conversely *Carollia*

170 species foraged on a variety of fruits (predominantly *Solanum* and *Piper* species) with a

171 much higher niche breadth. In the current study, minimal dietary overlap occurred between

172 *Artibeus* and *Carollia*, with only two overlapping plant genera, *Philodendron* and *Cecropia.*

173 Furthermore, each of these plant genera was represented by only a single sample in each

174 group of bats: one *Artibeus* sample contained *Philodendron sp.* and a single *Carollia* sample

175 contained *Cecropia latiloba*.

176   *Cecropia latiloba* is one of the most efficient colonizers of flood plains throughout

177 its distribution within the Amazon Basin and the Guiana Shield (Parolin 2002, Lobova et al.

178 2003, Zalamea et al. 2011). The peak flowering and fruiting period of this species is during

179 the wet season, contrary to most other fruit-producing plant species over its range (Milton

180 1991). Fruits of *C. latiloba* mature only at the end of the high water phase, occurring in July

181 and August, and are adapted for aquatic dispersal by fish (Parolin 2002, Parolin et al. 2010).

182 *Artibeus lituratus*, *A. planirostris,* and *A. obscurus* were responsible for six of the nine

183 dispersal records of *Cecropia latiloba* in our study. It is unknown whether foraging on *C.*

184 *latiloba* by bats was opportunistic or preferential. Futhermore, as many bird species are

185 known to consume and disperse *Cecropia* species (Eisenmann 1961) and many *Cecropia*

186 species are known to have multiple animal dispersers (Eisenmann 1961, Fleming and

187 Williams 1990, Lobova et al. 2003, Anderson et al. 2009), future studies are necessary to

188 determine if *C. latiloba* is dispersed by birds in the Iwokrama Forest, and compare the roles

189 and germination rates as a result of fish, bat, and bird dispersal.

190   In the present study, 37% of the fecal/stomach content samples from 9 species of

191 frugivorous bats represented new dispersal records for 7 species of plants, including the first

192 report of *Cecropia latiloba* being bat dispersed (Lobova et al. 2009). Continued dietary

193 research on the bat community within Iwokrama would undoubtedly add to our current

194 understanding of bat/plant interactions in wet and seasonally inundated habitat as well as the

195 ecological contribution of bats during forest regeneration.

206   providing study sites, lodging and support. Lastly, we thank local Amerindian counterparts

207   within Iwokrama/Surama for their assistance on Operation Wallacea Guyana expeditions.

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TABLE 1. *Inventory of Bat Dispersed Plant Species--* The 20 dispersed plant species identified in fecal and stomach content samples of bats collected in 2013 from study sites within the Iwokrama Forest, Guyana. Along with plant species, the number of samples in which each plant species occurred and bat species whose samples contained each plant species are displayed. An asterisk (*) denotes a new record of plant species documented in fecal samples of bat species acting as a dispersal agent, or in the case of *C. latiloba,* a plant species that has been newly discovered to be bat dispersed.

| Plant Species	Total Number of Samples	Bat Species (Number of Samples)
Ficus nymphaeifolia	12	*A. lituratus* (2), *A. obscurus, A. planirostris* (7), *V. bidens** (2)
Piper bartlingianum	12	*C. perspicillata* (8), *R. pumilio, S. tildae* (3)
*Cecropia latiloba**	9	*A. lituratus, A. obscurus* (2), *A. planirostris* (3), *C. perspicillata, P. helleri, V. bidens*
Cecropia sciadophylla	8	*A. lituratus* (4), *A. obscurus, A. planirostris, P. hastatus, S. lilium**
Solanum rugosum	5	*C. perspicillata* (5)
Ficus panurensis	4	*A. gnomus*, A. planirostris** (3)
Rollinia exsucca	4	*C. perspicillata* (4)
Piper trichoneuron	2	*C. perspicillata* (2)
Senna quinquangulata	2	*C. perspicillata* (2)
Anthurium trinerve	1	*C. perspicillata*
Cecropia obtusa	1	*A. obscurus*
Cecropia sp.	1	*A. lituratus*
Ficus insipida	1	*A. planirostris*
Ficus maxima	1	*A. obscurus**
Paullinia sp.	1	*C. perspicillata**
Philodendron guianense	1	*C. perspicillata**
Philodendron sp.	1	*A. lituratus*
Piper anonifolium	1	*C. perspicillata*
Piper hostmannianum	1	*C. perspicillata*
Vismia cayennensis	1	*C. perspicillata*
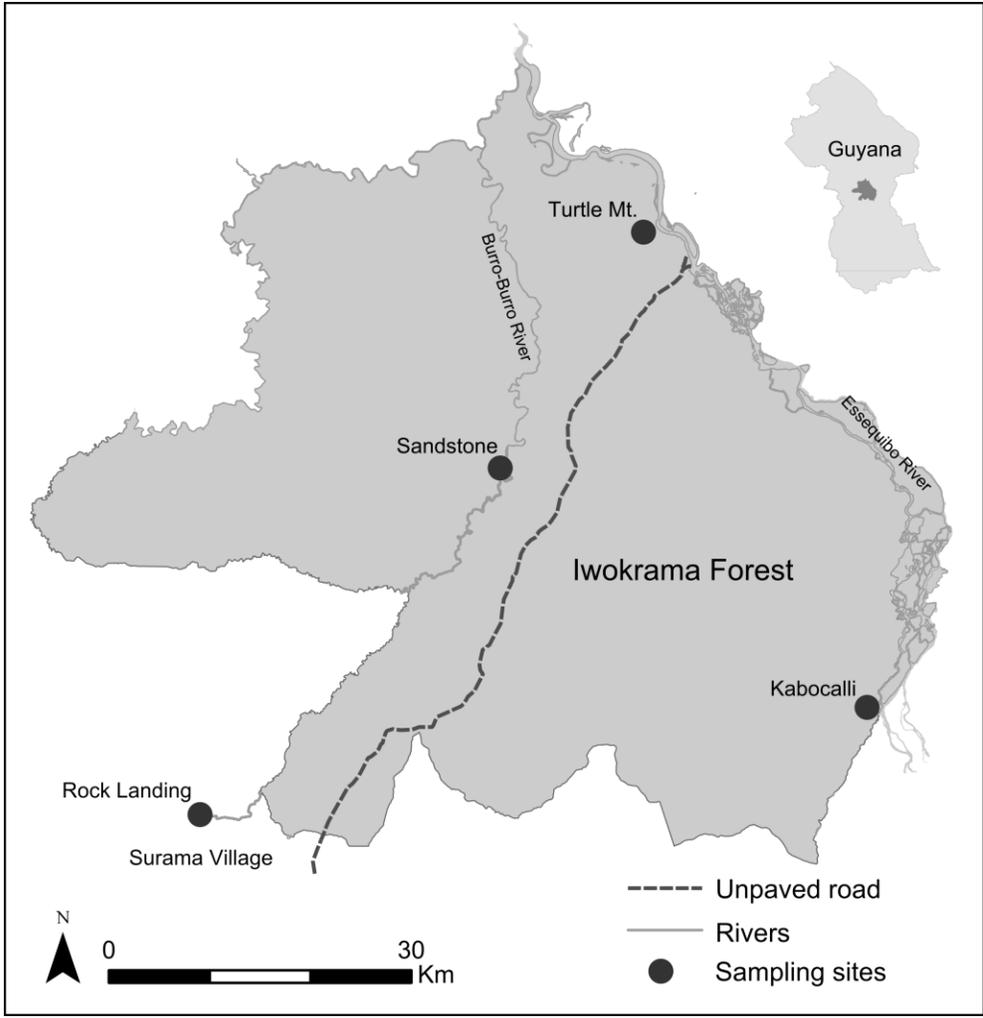
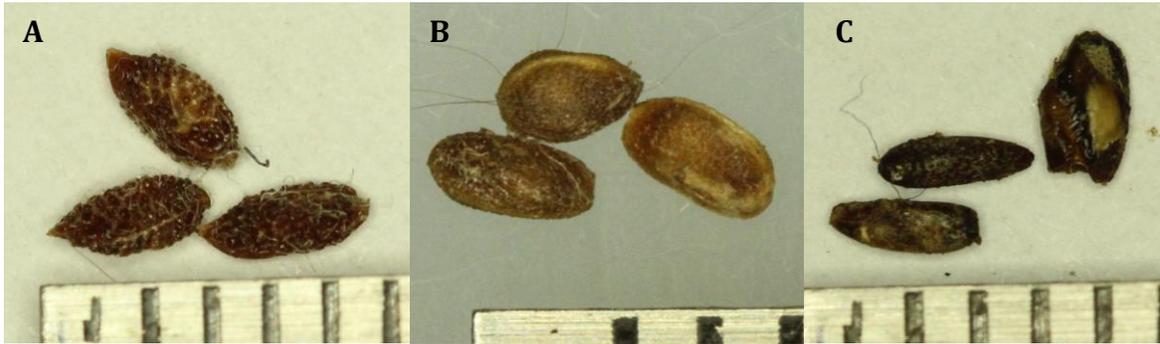FIGURE 1. Map of the Iwokrama Forest in central Guyana with the study sites labeled.

FIGURE 2. Images showing diaspores of *Cecropia sciadophylla* (A), *Cecropia latiloba* (B), and *Cecropia obtusa* (C). Diaspores were isolated from the following collected fecal samples: *C. sciadophylla – Artibeus lituratus*; *C. latiloba – Artibeus obscurus*; and *C. obtusa – Artibeus obscurus*. Samples collected July-August 2013 from the Iwokrama Forest, Guyana. Scales in images in millimeters.
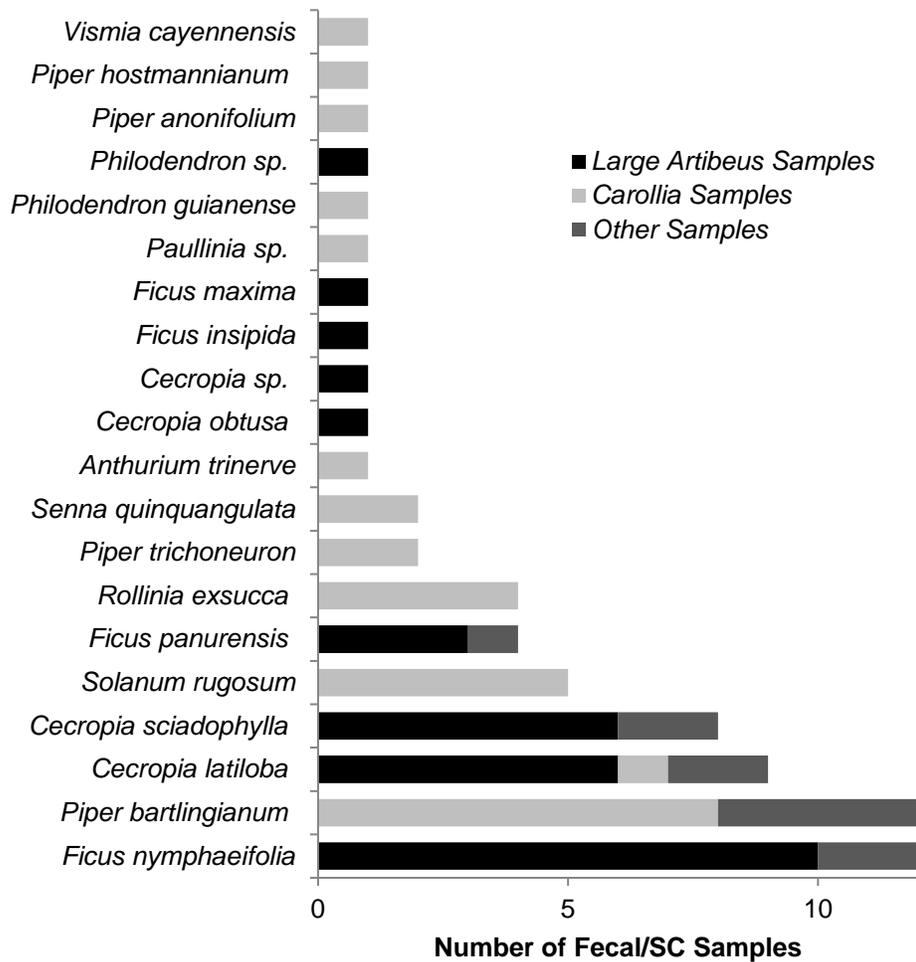
FIGURE 3. Plant species identified in collected fecal and stomach content (SC) samples, and the number of samples in which each plant species occurred from *Artibeus* (black), *Carollia* (light grey), or other bat genera (*Rhinophylla*, *Phyllostomus, Platyrrhinus*, *Sturnira, Vampyressa,* and non-focal *Artibeus*; dark grey). Non-focal *Artibeus* species are represented by a single sample collected from *Artibeus gnomus*, a smaller *Artibeus* species within the subgenus *Dermanura* (Simmons 2005). Samples collected July-August 2013 from the Iwokrama Forest, Guyana.