Journal of Tropical Ecology

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Research Article

**Cite this article:** Laurindo RS and Vizentin-Bugoni J (2020) Diversity of fruits in *Artibeus lituratus* diet in urban and natural habitats in Brazil: a review. *Journal of Tropical Ecology* **36**, 65–71. https://doi.org/10.1017/S0266467419000373

Received: 24 September 2019
Revised: 11 November 2019
Accepted: 21 November 2019

**Keywords:**
Chiroptera; frugivory; Neotropics; plant–animal interactions; seed dispersal; urbanization

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# Diversity of fruits in *Artibeus lituratus* diet in urban and natural habitats in Brazil: a review

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## Abstract

The great fruit-eating bat (*Artibeus lituratus*) is a large-sized species that forages primarily on fruits. This species is widespread throughout the Neotropics, where it is common in natural areas and also occupies forest patches and cities. In this study, we review the composition of *Artibeus lituratus* diet in Brazil as well as the size of fruits and seeds, plant geographic origin, and sampling methods used in natural *versus* urban habitats. We show that *Artibeus lituratus* is able to consume a higher proportion of exotic fruits with large seeds in urban environments than in natural areas. Fruit diameter was not statistically different between environments, but both fruit and seed diameters are smaller when detected by fecal sampling than by other methods. This difference is likely due to the fact that in natural habitats studies are predominantly based on fecal samples, which hinders the detection of large unswallowed seeds. Consequently, we recommend the use of complementary sampling methods (not only the widely used technique of fecal sorting) in order to produce more accurate descriptions of frugivorous bats' diets. We suggest that the ability to exploit fruits of exotic plant species including the ones with large seeds may be a key trait for the persistence of *A. lituratus* in urban habitats.

Urbanization is one of the most extreme types of land use, and consists in the conversion of natural landscapes into habitats dominated by human constructions, typically harbouring few native plant species in remnants separated by a matrix generally inhospitable for most species (McKinney 2006, 2008; Pauchard *et al.* 2006). By affecting plant diversity, urbanization changes food resources available to animals due to a decline in native species diversity and an increase in exotic plant presence (Alberti *et al.* 2017, Gelmi-Candusso & Hämäläinen 2019). Consequently, changes in plant diversity and composition in urban areas may have important impacts on plant–animal interactions (Gelmi-Candusso & Hämäläinen 2019) and on the capacity of such areas to maintain ecosystem functions such as seed dispersal.

Seed dispersal by frugivorous animals is a key mutualistic interaction that is crucial for the dynamics of plant populations and regeneration of degraded areas, including green areas within cities (Hougner *et al.* 2006). The persistence of frugivorous animals in urban areas depends critically on the availability of fruits in such places, as well as on the ability of frugivores to track resources and be flexible in the use of food resources (Nunes *et al.* 2017, Santini *et al.* 2019).

*Artibeus lituratus* (Phyllostomidae) is a large frugivorous bat, often abundant in continuous preserved areas, forest patches (Muylaert *et al.* 2017) and cities in the Neotropics (Ballesteros & Racero-Casarrubia 2012, Jara-Servín *et al.* 2017, Nunes *et al.* 2017), where it is one of the main seed-dispersing bats (Nunes *et al.* 2017). Despite a preference for *Cecropia* and *Ficus* fruits, *A. lituratus* is known to include in its diet more than 260 fruit species across its range (Parolin *et al.* 2016). This capacity to exploit a broad variety of fruits is one of the characteristics that may favour its tolerance to deep habitat modification such as urbanization (Oprea *et al.* 2009, Nunes *et al.* 2017).

In this context, comparing the resources consumed between natural and urban habitats can provide important insights into the success of some species in persisting in cities. For this study, we compiled data on fruits consumed by *Artibeus lituratus* in urban and non-urban (hereafter, natural) environments in Brazil, and compared these habitat types in terms of fruit and seed traits and sampling techniques.

We found 28 publications by searching online repositories (Supplementary Appendix 1). Searches included combinations of the keywords (in English, Portuguese and Spanish): *Artibeus lituratus*, *bats*, *frugivory*, *diet* and *seed dispersal*. For each of the publications obtained the following information were extracted: identity of the fruits consumed (only those identified at species level); fruit origin (native or exotic) defined according to Reflora (2019); and the sampled environment (urban and natural). We also classified studies according to the methods used to record interactions as: *fecal samples* (seeds taken from feces of individuals captured with

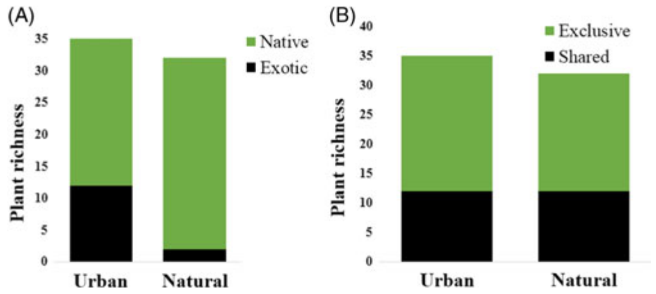


**Figure 1.** (A) Number of exotic and native fruits consumed by the *Artibeus lituratus* in urban or natural environments in Brazil; (B) Number of fruit species consumed per habitat type.

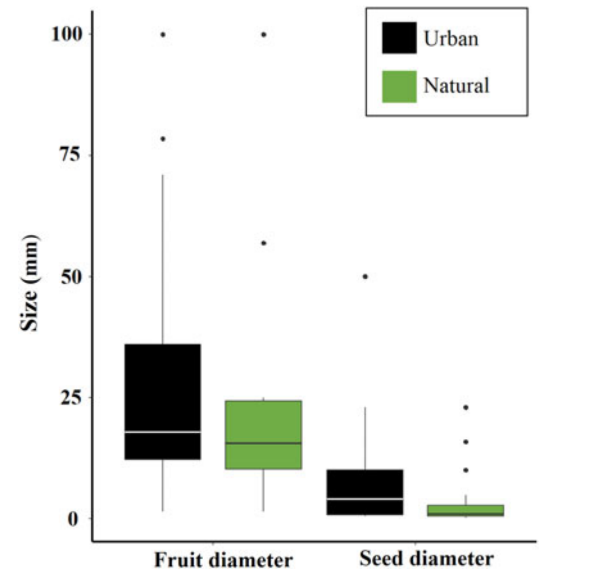


**Figure 2.** Diameter of fruits and seeds consumed by *Artibeus lituratus* in urban and natural habitats in Brazil.

mist net), *roost sampling* (seeds or fruit remains found in daytime shelters), *direct observation* (individuals observed consuming fruits directly on the plant), *carried in the mouth* or *found under feeding perches*. For each fruit species recorded, we compiled data on fruit and seed diameters obtained from the UFLA Mammals Diversity and Systematic Laboratory (LADISMA) seed collection or from the literature (Supplementary Appendix 2 and 3). Differences in fruit diameter between urban and natural habitats and between sampling methods (fecal samples *versus* other methods) were tested using the non-parametric Mann–Whitney test. Differences in seed sizes were tested using one-way ANOVA after log-transformation of variables.

Out of 28 studies, 18 were conducted in natural habitats, nine in urban habitats and one in both. We found 55 fruit species consumed by *Artibeus lituratus*, distributed in 25 genera belonging to 16 families. In natural habitats, 94% of the species consumed ($n = 30$ out of 32) were native, while in urban habitats 66% ($n = 23$ out of 35) were native (Figure 1A). Of the 55 fruit species that are part of the *A. lituratus* diet, 23 species were consumed exclusively in urban habitats, 20 in natural habitats and 12 in both habitat types (Figure 1B, Table 1).

Identification of seeds present in fecal samples was the most commonly used method to describe *A. lituratus* diet (27 out of 28 studies). In urban habitats, eight studies used two sampling methods concomitantly: four studies combined fecal sampling and roost sampling, three studies combined fecal sampling and direct observation, and one study combined direct observation and roost sampling. In natural areas, all studies used fecal sampling but only one study complemented it with direct observations.

In terms of traits, the overall average fruit diameter consumed by *Artibeus lituratus* was 22.52 ± 20.67 mm (mean ± SD). However, the average fruit diameter recorded by fecal analysis (12.29 ± 7.05 mm) and other methods combined (39.98 ± 24.52 mm) was significantly different ($U = 39.50$, $P < 0.01$). Similarly, the average seed diameter recorded using fecal analysis (1.10 ± 0.96 mm), and other methods combined (10.62 ± 5.47 mm) was also significantly different ($F = 91.19$, $P < 0.01$). Between habitats, there was no significant difference in fruits diameter ($U = 0.93$, $P = 0.17$), but seed diameter was significantly larger in urban habitats ($F = 99.8$, $P < 0.01$; Figure 2).

Our results show that *A. lituratus* may consume fruit of at least 12 exotic species in Brazil, which represents a considerable proportion of the resources consumed in urban habitats, when compared with natural areas. This ability to exploit exotic fruits may be key to this species' persistence in habitats with varying degrees of anthropic interference, including large urban centres in Brazil (Nunes *et al.* 2017, Oprea *et al.* 2009). In fact, most exotic plant species found in the *A. lituratus* diet are common in Brazilian cities, where they are frequently used for urban forestry or backyard ornamentation (Petri *et al.* 2018).

Our study also demonstrates that in urban centres *Artibeus lituratus* consumes a high proportion of large seeded fruits with seeds that are too large to be swallowed and, therefore, are not detected in fecal samples. Detection of consumption of fruit with large seeds requires the use of methods such as direct observation and collection of seed in roosts or under feeding perches (Oprea *et al.* 2007, Silvestre *et al.* 2016) in order to achieve a comprehensive description of the species' diet. Thus, diet descriptions based only on fecal analysis, as is the case for most studies conducted in natural habitats (e.g. Laurindo *et al.* 2019), may considerably underestimate the diversity of fruits consumed by *A. lituratus*. Moreover, this is likely to be the case for other frugivorous bat species. Such bias may be especially important in old-growth forests, where large-seeded species often occur (Huston & Smith 1987). Furthermore, frugivorous bats generally take such large-seeded fruits to feeding perches away from the parent plant, likely acting as legitimate seed dispersers of such species (Melo *et al.* 2009).

Because frugivorous bats may travel long distances between roosts, feeding perches and foraging areas (Chaverri *et al.* 2007, Trevelin *et al.* 2013), they can facilitate invasion of exotic plants into natural habitats. In fact, some of the species consumed by *A. lituratus* in urban habitats are invasive in protected areas in Brazil (Ziller & Dechoum 2013), such as *Hovenia dulcis* (Rhamnaceae), which is a frequent invasive species in several Neotropical ecosystems (Zenni & Ziller 2011). On the other hand, seeds of native species can also be carried for long distances from natural to urban habitats, facilitating the regeneration of parks and other urban green areas as well as contributing to the persistence of other frugivorous species in such areas (Hougner *et al.* 2006).

In conclusion, our review summarizes the knowledge on the fruits consumed by *A. lituratus* in urban and natural areas in Brazil. We highlight the lack of studies using methods other than fecal sampling in natural habitats, which likely biases the description of frugivorous bats' diets towards small-seeded species. Therefore, for the most accurate description of frugivorous bats' diets and seeds dispersal networks in natural areas, we recommend that future

https://doi.org/10.1017/S0266467419000373 Published online by Cambridge University Press

**Table 1.** Fruits consumed by *Artibeus lituratus* in urban and natural habitats in Brazil. Sampling method: (1) fecal samples; (2) direct observation; (3) roosts; (4) carried in the mouth; (5) found under feeding perches. The number of studies where each fruit was reported is specified for urban and natural habitats.

| Family/Species | Environment | | Origin | Seed diameter (mm) | Fruit diameter (mm) | Sampling method |
|---|---|---|---|---|---|---|
| | Urban | Natural | | | | |
| **Anacardiaceae** | | | | | | |
| *Mangifera indica* L. | 2 | 0 | Exotic | 50 | 78.57 | 2 |
| **Arecacea** | | | | | | |
| *Livistona chinensis* (Jacq.) R. Br. ex Mart. | 1 | 0 | Exotic | 10 | 13.5 | 3 |
| *Syagrus romanzoffiana* (Cham.) Glassman | 1 | 1 | Native | 23 | 25 | 2 |
| **Calophyllaceae** | | | | | | |
| *Calophyllum brasiliense* Cambess. | 2 | 1 | Native | 16 | 25 | 2 |
| **Caricaceae** | | | | | | |
| *Carica papaya* L. | 2 | 1 | Exotic | 5 | 100 | 2 |
| **Combretaceae** | | | | | | |
| *Terminalia catappa* L. | 1 | 0 | Exotic | 8 | 40 | 4 |
| **Fabaceae** | | | | | | |
| *Inga uruguensis* Hook. & Arn. | 0 | 1 | Native | – | 25 | 2 |
| **Humiriaceae** | | | | | | |
| *Humiriastrum mussungense* Cuatrec. | 0 | 1 | Native | – | – | 4 |
| **Hypericaceae** | | | | | | |
| *Vismia magnoliifolia* Cham. & Schltdl. | 0 | 1 | Native | – | – | 1 |
| *Vismia martiana* Reichardt | 0 | 1 | Native | – | – | 1 |
| **Malpighiaceae** | | | | | | |
| *Byrsonima stipulacea* A.Juss. | 0 | 1 | Native | 10 | 17 | 4 |
| **Melastomataceae** | | | | | | |
| *Miconia cinnamomifolia* (DC.) Naudin | 0 | 1 | Native | 0.3 | 2.54 | 1 |
| **Moraceae** | | | | | | |
| *Ficus eximia* Schott | 1 | 0 | Native | – | 16.5 | 1 |
| *Ficus glabra* Vell. | 1 | 0 | Native | – | – | 1 |
| *Ficus guaranitica* Chodat | 1 | 2 | Native | 0.7 | 18 | 1 |
| *Ficus obtusifolia* Kunth | 0 | 1 | Native | – | 23.4 | 1 |
| *Ficus organensis* (Miq.) Miq. | 1 | 0 | Native | 0.7 | 7 | 1 |
| *Ficus adhatodifolia* Schott in Spreng. | 0 | 1 | Native | – | 25 | 1 |
| *Ficus citrifolia* Mill. | 1 | 0 | Native | 0.7 | 14 | 1 |
| *Ficus crocata* (Miq.) Miq. | 0 | 1 | Native | – | 24.7 | 1 |
| *Ficus enormis* Mart. ex Miq. | 0 | 1 | Native | 1 | 14 | 1 |
| *Ficus gomelleira* Kunth | 0 | 2 | Native | 0.4 | 23 | 1 |
| *Ficus insipida* Willd. | 1 | 3 | Native | 1.7 | 20 | 1 |
| *Ficus luschnathiana* (Miq.) Miq. | 1 | 4 | Native | 0.7 | 12.3 | 1 |
| *Ficus mexiae* Standl. | 0 | 3 | Native | | | 1 |
| *Maclura tinctoria* (L.) D. Don ex Steud. | 2 | 2 | Native | 2.1 | 14.2 | 1 |
| **Musaceae** | | | | | | |
| *Musa paradisiaca* L. | 1 | 0 | Exotic | – | 50 | 5 |
| **Myrtaceae** | | | | | | |
| *Eugenia jambolana* Lam. | 1 | 0 | Exotic | | 40 | 2 |

(*Continued*)

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**Table 1.** (*Continued*)

| Family/Species | Environment | | Origin | Seed diameter (mm) | Fruit diameter (mm) | Sampling method |
|---|---|---|---|---|---|---|
| | Urban | Natural | | | | |
| *Eugenia uniflora* L. | 1 | 0 | Native | 11.4 | 18 | 3 |
| *Myrciaria cauliflora* (Mart.) O.Berg | 1 | 0 | Native | 5.5 | 19 | 2 |
| *Myrciaria jaboticaba* (Vell.) O.Berg | 2 | 0 | Native | 5.5 | 19 | 3 |
| *Psidium guajava* L. | 4 | 1 | Exotic | 3.5 | 57 | 3 |
| *Syzygium jambos* (L.) Alston | 3 | 0 | Exotic | – | 29 | 2, 3 |
| *Syzygium malaccense* L.O | 1 | 0 | Exotic | 17.3 | 71 | 3 |
| **Piperaceae** | | | | | | |
| *Piper aduncum* L. | 1 | 3 | Native | 0.8 | 3 | 1 |
| *Piper arboreum* Aubl. | 0 | 1 | Native | 0.7 | 8 | 1 |
| *Piper gaudichaudianum* Kunth | 2 | 0 | Native | – | 3 | 1 |
| *Piper lindbergii* C.DC. | 0 | 1 | Native | – | – | 1 |
| *Piper umbellatum* L. | 0 | 1 | Native | 0.3 | 3 | 1 |
| **Rhamnaceae** | | | | | | |
| *Hovenia dulcis* Thunb. | 1 | 0 | Exotic | 4 | 6.5 | 1 |
| **Rosaceae** | | | | | | |
| *Eriobotrya japonica* (Thunb.) Lindl. | 4 | 0 | Exotic | 15 | 36 | 2, 3 |
| *Prunus persica* (L.) Batsch | 1 | 0 | Exotic | 7.86 | 41.6 | 3 |
| **Solanaceae** | | | | | | |
| *Solanum asperolanatum* Ruiz & Pav. | 0 | 1 | Native | – | – | 1 |
| *Solanum caavurana* Vell. | 2 | 0 | Native | 2 | 11 | 1 |
| *Solanum erianthum* D. Don | 1 | 0 | Native | – | – | 1 |
| *Solanum gemellum* Mart. ex Sendtn. | 1 | 0 | Native | – | 7 | 1 |
| *Solanum megalochiton* Mart. | 1 | 0 | Native | – | 6.3 | 1 |
| *Solanum paniculatum* L. | 0 | 1 | Native | 1.5 | 10 | 1 |
| *Solanum sisymbriifolium* Lam. | 2 | 0 | Native | – | 17 | 1 |
| *Solanum granulosoleprosum* Dunal | 0 | 2 | Native | 2.5 | 11 | 1 |
| *Solanum rufescens* Dunal | 0 | 1 | Native | – | 11.3 | 1 |
| *Solanum stipulaceum* Willd. ex Roem. & Schult. | 0 | 1 | Native | – | 10 | 1 |
| **Urticaceae** | | | | | | |
| *Cecropia glaziovii* Snethl. | 3 | 7 | Native | 0.62 | 12.62 | 1 |
| *Cecropia hololeuca* Miq. | 3 | 4 | Native | 0.98 | 20.58 | 1 |
| *Cecropia pachystachya* Trécul | 5 | 9 | Native | 0.62 | 1.53 | 1 |

studies include seed collection in daytime roosts and under nocturnal feeding perches. These methods have been used in urbanized areas and successfully detected large-seeded fruits consumed by *A. lituratus* (Melo *et al.* 2009, Silvestre *et al.* 2016). Another alternative technique little explored in studies of Neotropical bats is DNA barcoding, which allows the identification of a broader range of food items including large-seeded species, based also on fecal samples analysis (Lim *et al.* 2018). Finally, we highlight that the ability to use a high diversity of fruits, including exotic species, is remarkable in *A. lituratus*, and is probably linked to its persistence in altered habitats such as urban centres.

**Acknowledgements.** We thank Dr Renato Gregorin and the Mammals Diversity and Systematic Laboratory (LADISMA) of the UFLA for access to the seed collection. We also thank MSc Roberto L. M. Novaes and an anonymous referee for valuable suggestions on the manuscript.

**Financial support.** RSL thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

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## Appendix 1

Original sources of data on the diet of *Artibeus lituratus* in Brazil compiled in this study.

### Urban

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Original sources of fruits and seeds traits.

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## Appendix 3

Fruits consumed by *Artibeus lituratus* in urban and natural habitats in Brazil. For original source of data on interactions see Appendix 1. For original source of data on fruit and seed traits see Appendix 1 and 2.

| Family/Species | Source of data of interaction | Source of data for traits |
|---|---|---|
| **Anacardiaceae** | | |
| *Mangifera indica* L. | 7, 28 | 1 |
| **Arecacea** | | |
| *Livistona chinensis* (Jacq.) R. Br. ex Mart. | 9 | 1 |
| *Syagrus romanzoffiana* (Cham.) Glassman | 28 | 1 |
| **Calophyllaceae** | | |
| *Calophyllum brasiliense* Cambess. | 7, 19, 28 | 1 |
| Caricaceae | | |
| *Carica papaya* L. | 5, 28 | 6 |
| **Combretaceae** | | |
| *Terminalia catappa* L. | 8 | 5, 6 |
| **Fabaceae** | | 1 |
| *Inga uruguensis* Hook. & Arn.*** | 28 | – |
| **Humiriaceae** | | |
| *Humiriastrum mussungense* Cuatrec. | 18 | – |
| **Hypericaceae** | | |
| *Vismia magnoliifolia* Cham. & Schltdl. | 26 | – |
| *Vismia martiana* Reichardt | 18 | – |
| **Malpighiaceae** | | |
| *Byrsonima stipulacea* A.Juss. | 18 | 1 |
| **Melastomataceae** | | |
| *Miconia cinnamomifolia* (DC.) Naudin | 18 | 1 |
| **Moraceae** | | |
| *Ficus eximia* Schott | 6 | 3 |
| *Ficus glabra* Vell.** | 28 | 2 |
| *Ficus guaranitica* Chodat | 6, 12, 25 | 1 |
| *Ficus obtusifolia* Kunth | 21 | 3 |
| *Ficus organensis* (Miq.) Miq. | 6 | 1 |
| *Ficus adhatodifolia* Schott in Spreng. | 27 | 2 |
| *Ficus citrifolia* Mill. | 9 | 1 |
| *Ficus crocata* (Miq.) Miq. | 21 | 3 |
| *Ficus enormis* Mart. ex Miq. | 14 | 1 |
| *Ficus gomelleira* Kunth | 16, 24 | 1, 6 |
| *Ficus insipida* Willd. | 2, 14, 16, 21 | 1 |
| *Ficus luschnathiana* (Miq.) Miq. | 14, 23, 27, 28 | 1 |
| *Ficus mexiae* Standl. | 20, 11 | – |
| *Maclura tinctoria* (L.) D. Don ex Steud. | 4, 12, 27, 28 | 1 |
| **Musaceae** | | |
| *Musa paradisiaca* L. | 5 | |
| **Myrtaceae** | | |
| *Eugenia jambolana* Lam.** | 7 | – |
| *Eugenia uniflora* L. | 5 | 1 |
| *Myrciaria cauliflora* (Mart.) O.Berg**** | 8 | 1 |
| *Myrciaria jaboticaba* (Vell.) O.Berg**** | 5, 9 | 1 |
| *Psidium guajava* L. | 7, 8, 9, 11, 28 | 1 |
| *Syzygium jambos* (L.) Alston | 5, 9, 28 | – |
| *Syzygium malaccense* L.O | 9 | – |
| **Piperaceae** | | |
| *Piper aduncum* L. | 6, 24, 27 | 4, 6 |
| *Piper arboreum* Aubl. | 14 | 4, 6 |
| *Piper gaudichaudianum* Kunth | 1, 6 | 4 |
| *Piper lindbergii* C.DC. ***** | 22 | – |
| *Piper umbellatum* L. | 17 | 4, 6 |
| **Rhamnaceae** | | |
| *Hovenia dulcis* Thunb. | 1 | 1 |
| **Rosaceae** | | |
| *Eriobotrya japonica* (Thunb.) Lindl. | 5, 8, 9, 28 | – |
| *Prunus persica* (L.) Batsch | 5 | – |
| **Solanaceae** | | |
| *Solanum asperolanatum* Ruiz & Pav. | 12 | – |
| *Solanum caavurana* Vell. | 6, 28 | 1 |
| *Solanum erianthum* D. Don | 1 | – |
| *Solanum gemellum* Mart. ex Sendtn. | 1 | – |
| *Solanum megalochiton* Mart. | 1 | 1 |
| *Solanum paniculatum* L. | 17 | 6 |
| *Solanum sisymbriifolium* Lam. | 1, 6 | – |
| *Solanum granulosoleprosum* Dunal | 13, 14 | 1, 6 |
| *Solanum rufescens* Dunal* | 23 | 1 |
| *Solanum stipulaceum* Willd. ex Roem. & Schult. | – | |
| **Urticaceae** | | |
| *Cecropia glaziovii* Snethl. | 6, 9, 10, 15, 16, 18,23, 22, 26, 28 | 1, 6 |
| *Cecropia hololeuca* Miq. | 6, 9, 14, 16, 18, 26, 28 | 1, 6 |
| *Cecropia pachystachya* Trécul | 2, 6, 7, 8, 10, 11, 14, 16, 22, 24, 25, 26, 28 | 1, 6 |

https://doi.org/10.1017/S0266467419000373 Published online by Cambridge University Press