

Scientific Note

Stingless bees as collectors of resin from *Bertholletia excelsa* Bonpland (Lecythidaceae)

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Abstract. Stingless bees build their nests using, in general, clay, wax and resins; in addition, these bees also use resins for defense against natural enemies and as an antimicrobial agent. Our goal was to register the stingless bees that collect resin from *Bertholletia excelsa* Bonpland (Lecythidaceae), and the observations were made in the Reserva Particular do Patrimônio Natural Dr. Daisaku Ikeda, Manaus, Amazonas, with five species recorded: *Melipona (Michmelia) seminigra* Friese, 1903, *Trigona albipennis* Almeida, 1995, *Trigona hypogea* Silvestri, 1902, *Trigona williana* Friese, 1900, and *Ptilotrigona lurida* (Smith, 1854) (Hymenoptera: Apidae), the last two species were more frequent. During the observations, the monopoly of resin resources by *T. hypogea*, *T. williana* and *P. lurida*; collection without conflict between *M. seminigra* and *T. albipennis*, and collection with intraspecific conflict between *M. seminigra* individuals were recorded. Bees invest substantial amounts of energy and labor to collect resin from a wide spectrum of different plant species, and the resin must be considered as a necessary resource for the conservation of Amazonian stingless bees.

Keywords: Meliponini, behavior, non-floral resource, resinous plant, Amazon.

In general, stingless bees (Apidae: Meliponini) build their nests using clay, wax and resins (Kerr et al. 1996; Shanahan & Spivak 2021). Resins collected from different plants are commonly mixed with other materials for the construction of nest structures such as the entrance, the access tube, brood disks and honey and pollen pots (Nogueira-Neto 1997; Roubik 2006; Grüter 2020).

Resins are commonly stored in deposits in the nests of stingless bees, who use it in defense against the attack of intruders by placing it on their bodies, and by creating barriers around the entrance to the nest (Roubik 2006; Duangphakdee et al. 2009; Grego et al. 2010; Nunes et al. 2014; Grüter 2020; Melo 2020). In addition, some stingless bees acquire substances derived from collected resins in their cuticular chemical profiles, and use them as an additional agent in protecting colonies against natural enemies (Leonhardt et al. 2009; Leonhardt et al. 2015). These bees seem to have a preference for certain species of resiniferous plants and they often visit antimicrobial plant resins that help them regulate the microbial communities found in the nests (Roubik 1989; Leonhardt & Blüthgen 2009; Drescher et al. 2014; Grüter 2020). The use of antimicrobial resins in nest construction may have been fundamental for the evolution of the sociability of stingless bees (Shanahan & Spivak 2021).

There is a variety of plants that secrete resins, but records of resiniferous trees as a resource for the stingless bees of the Amazon are scarce. Among the resin-producing trees in the region is *Bertholletia excelsa* Bonpland (Lecythidaceae) (FAO 1986; Schöngart et al. 2015), which is popularly known as the Brazil nut tree (Lorenzi 1992). Occurring throughout the Amazon region, it is a large tree that can reach more than 60 m in height and the base of the trunk can be over 4 m in diameter (Lorenzi 1992; Santos et al. 2006). It has great economic importance due to the exploitation of its wood, bark, seed pod and seeds (Wadt & Kainer 2009). Moreover, the species present ecological importance through its several biological interactions (Santos-Silva et al. 2017), cultural importance via food use (Clement 1999), as well as medicinal importance (Lago et al. 2016). Although it is protected by law in Brazil, *B. excelsa* has been affected by extractive pressure, expansion of agricultural activities and logging, which have contributed to add this species on the Red List as a species that is at

risk of extinction (MMA 2008; CNCF 2012; IUCN 2021). Thus, our goal in this study was to register and identify the stingless bees that collect resin from *B. excelsa*, and emphasize the importance of resiniferous plants for Amazonian bees.

The monitoring of the bees was carried out in the Reserva Particular do Patrimônio Natural Dr. Daisaku Ikeda - Instituto Soka Amazônia (3°06'43.9"S, 59°54'31.8"W), which is an urban forest fragment in Manaus, Amazonas state, Brazil. It has an area of 54.06 ha (ICMBIO 2021) composed by ombrophilous forest and alluvial forest, the former with a portion of secondary vegetation. The Brazil nut tree used in the study is located on the right bank of the track that gives access to the banks of the Amazon River (3°06'47.7"S, 59°54'15.3"W). It is one of the oldest trees on the site with a trunk of 6.15 m in circumference (measured using tape measure at a height of 1.20 m from the ground). At the base of the trunk, there are three protruding striae (Fig. 1) that are commonly visited by stingless bees. Although there are other Brazil nut trees in the locality, they did either not have striae or resin during the study.

The observations of the striae of the *B. excelsa* specimen occurred randomly between the months of April to November 2021, with a total of 14 visits, which took place between 9:00 a.m. and 12:30 p.m. The pictures were taken using a smartphone, and the bee specimens were collected for later identification. The identification of the specimens was done using a binocular stereomicroscope (XT-3L-NM-BI, Biofocus). The taxonomical key from Silveira et al. (2002) was used for genera identification. For species identification, specific literature was used: Camargo & Pedro (2004), Oliveira et al. (2013), Camargo & Roubik (1991), and Almeida (1992). Subsequently, the specimens were taken to a specialist to confirm the identification.

The following five species of stingless bees were recorded collecting resin from the Brazil nut tree: *Trigona williana* Friese, 1900 (with 33.3% of the records); *Ptilotrigona lurida* (Smith, 1854) (26.7%); *Melipona (Michmelia) seminigra* Friese, 1903 (20%); *Trigona hypogea* Silvestri, 1902 (13.3%); and *Trigona albipennis* Almeida, 1995 (6.7%) (Hymenoptera: Apidae). No other insects were seen collecting resin during the observation period.



Figure 1. Brazil nut tree (*Bertholletia excelsa*) of the Instituto Soka Amazônia, Manaus, Amazonas state, Brazil. A) Tree in wide view. B) The base of the tree with the three striae (indicated with the yellow arrow).

In most cases, the presence of more than five individuals per species was recorded collecting resin from the striae. It is possible that the behavior of group formation to collect resin is common in some species, since it is one of the main resources for building and protecting their nests. The apparent monopoly of the site of the resin resource presented by *T. hypogea*, *T. williana* and *P. lurida* (Figs. 2A-C, respectively) is not exclusive of these species, this behavior also was observed for *Trigona corvina* Cockerell, 1913 (Hymenoptera: Apidae) (Reyes-González & Zamudio 2020). The dominance of the resin resources is possibly similar to that of food resources, Johnson & Hubbell (1974) describe the behavior, in which interspecifically aggressive species are usually large and commonly forage in groups, visiting and monopolizing clustered resources, and the interspecifically nonaggressive species tend to be smaller and to forage alone or in small groups.

On one occasion, *M. seminigra* and *T. albipennis* were observed collecting resin simultaneously, apparently without any conflict, in the same striae, though maintaining a distance of about five centimeters (Fig. 2D). This distancing from *T. albipennis* may be related to the size of *M. seminigra*, since there is a relationship between larger size and a higher rate of aggressive behavior in some stingless bee species (Leonhardt & Blüthgen 2009). Most often, *M. seminigra* bees collected resin without the presence of other bee species (Fig. 2E). Intraspecific conflicts between *M. seminigra* were witnessed in April and November, in which one of the bees attacked the other in order to gain access to the resin source (Fig. 2F). This behavior was also reported for other species in the studies of Howard (1985) and Leonhardt & Blüthgen (2009).

The striae of the trunk of the Brazil nut tree secreted resin during the entire observation period, though sometimes at a lower rate during the dry season, from July to November in the central Amazon (Asner & Alencar 2010). This fact may be related to the presence of bees on the site, since stingless bee species actively bite resin wounds and are able to stimulate and maintain resin secretion for long periods (Schwarz 1948), despite the lack of studies about the resin productivity of Brazil nut tree throughout the year. Several species, especially *Trigona* Jurine, 1807, such as *Trigona spinipes* (Fabricius, 1793) (Hymenoptera: Apidae), stimulate the secretion of resins by biting buds, young leaves,

flowers and plant bark (Willer & Michener 1973; Santos et al. 2012).

Bees invest substantial amounts of energy and labor to collect resin from a wide spectrum of different plant species (Leonhardt & Blüthgen 2009; Simone-Finstrom & Spivak 2010), because they benefit more from a greater variety of resin resources due to the greater effect against various predators and microorganisms (Drescher et al. 2014). The diversity of tropical bees, such as stingless bees, is not only related to floral resources, but is likely driven by the broad spectrum of plant species that provide non-floral resources such as resin (Roubik 1989; Litman et al. 2011).

Some studies have identified potential plant families that produce resin resources that are collected by stingless bees, such as Hypericaceae [*Vismia guianensis* (Aubl.) Choisy], on the outskirts of Manaus, Amazonas state, Brazil (Kerr et al. 1967); Moraceae (*Castilla elastica* Sessé) in Costa Rica (Howard 1985); Dipterocarpaceae, Myristicaceae, Araucariaceae and Burseraceae in Borneo, Malásia (Leonhardt & Blüthgen 2009); Euphorbiaceae (*Croton yucatanensis* Lundell) in Costa Rica (Reyes-González & Zamudio 2020); and, in this work, bees were recorded collecting resin from Lecythidaceae (*B. excelsa*) in Manaus, Amazonas state, Brazil. *Bertholletia excelsa* also presents itself as a source of pollen for some species of meliponines (Santos & Absy 2010). Despite this record, more studies are necessary to bigger conclusions about the usage and importance of the resin of *B. excelsa* for stingless bees.

It is of great importance to have knowledge of and conserve resiniferous plants since they are an indispensable resource for stingless bees. The loss of biodiversity as a result of anthropogenic actions can limit this resource for them, and can negatively contribute to the destabilization of populations due to the restriction in the variety of resources (Howard 1985; Drescher et al. 2014). Unfortunately, the role and importance of resin still receives little attention and more studies related to the variety of plants that provide such resources are needed (Requier & Leonarth 2020). Therefore, it is important to consider resin as a necessary resource for the conservation of Amazonian stingless bees.

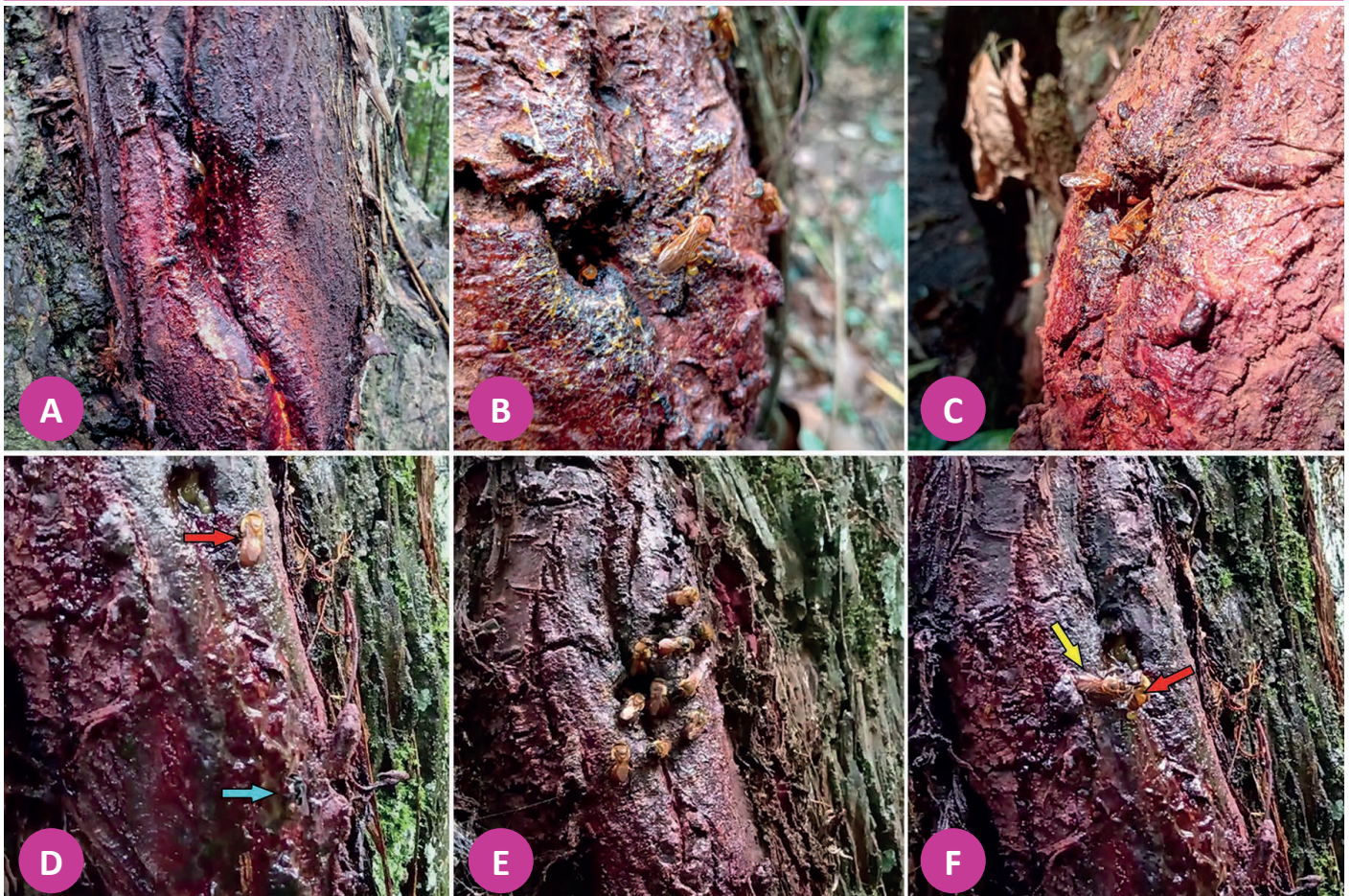


Figure 2. Stingless bees collecting resin from the striae of *Bertholletia excelsa* Bonpland (Lecythidaceae), at the Instituto Soka Amazônia. A) *Trigona hypogea*; B) *Trigona williana*; C) *Ptilotrigona lurida*; D) *Melipona seminigra* (red arrow) and *Trigona albipennis* (blue arrow) collecting on the same stria; E) group of *Melipona seminigra*; F) Conflict between the specimens of *Melipona seminigra* (red arrow marks the bee that is attacking and the yellow arrow the one being attacked).

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Authors' Contributions

IAC and PCSB monitored, recorded and collected specimens; IAC analyzed the data; IAC wrote the text; PCSB revised the entire text. All authors approved the final text.

Conflict of Interest Statement

We have no conflict of interest to declare.

References

- Almeida, M. C. (1992) Quatro espécies novas de *Trigona* (s. str.) (Apidae, Meliponinae) da região neotropical. *Acta Biologica Paranaense*, 21: 181-193. doi: [10.5380/abpr.v21i0.756](https://doi.org/10.5380/abpr.v21i0.756)
- Asner, G. P.; Alencar, A. (2010) Drought impacts on the Amazon forest: the remote sensing perspective. *New Phytologist*, 187(3): 569-578. doi: [10.1111/j.1469-8137.2010.03310.x](https://doi.org/10.1111/j.1469-8137.2010.03310.x)
- Camargo, J. M. F.; Pedro, S. R. (2004) Meliponini neotropicais: o gênero *Ptilotrigona* Moure (Hymenoptera, Apidae, Apinae). *Revista Brasileira de Entomologia*, 48(3): 353-377. doi: [10.1590/S0085-56262004000300012](https://doi.org/10.1590/S0085-56262004000300012)
- Camargo, J. M. F.; Roubik, D. W. (1991) Systematics and bionomics of the apoid obligate necrophages: the *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae). *Biological Journal of the Linnean Society*, 44(1): 13-39. doi: [10.1111/j.1095-8312.1991.tb00604.x](https://doi.org/10.1111/j.1095-8312.1991.tb00604.x)
- Clement, C. R. (1999) Castanha-do-pará: *Bertholletia excelsa*. In: Clement, C. R., Clay, J. W.; Sampaio, P. T. B. (Eds.), *Biodiversidade amazônica: exemplos e estratégias de utilização*, pp. 118-131. Programa de Desenvolvimento Empresarial e Tecnológico, Manaus, AM.
- CNCF - Centro Nacional de Conservação da Flora (2012) *Bertholletia excelsa* Bonpl.: Informações da avaliação de risco de extinção. <http://cncflora.jbrj.gov.br/portal/pt-br/profile/Bertholletia%20excelsa>. Access on: 18.xi.2021.
- Drescher, N.; Wallace, H. M.; Katouli, M.; Massaro, C. F.; Leonhardt, S. D. (2014) Diversity matters: how bees benefit from different resin sources. *Oecologia*, 176(4): 943-953. doi: [10.1007/s00442-014-3070-z](https://doi.org/10.1007/s00442-014-3070-z)
- Duangphakdee, O.; Koeniger, N.; Deowanish, S.; Hepburn, H. R.; Wongsiri, S. (2009) Ant repellent resins of honeybees and stingless bees. *Insectes Sociaux*, 56(4): 333-339. doi: [10.1007/s00040-009-0027-z](https://doi.org/10.1007/s00040-009-0027-z)
- FAO - Food and Agriculture Organization of the United Nations (1986) *Food and Fruit-bearing Forest Species*. 3: Examples from Latin America, Rome, Italy.
- Greco, M. K.; Hoffmann, D.; Dollin, A.; Duncan, M.; Spooner-Hart, R.; Neumann, P. (2010) The alternative Pharaoh approach: stingless bees mummify beetle parasites alive. *Naturwissenschaften*, 97(3):

- 319-323. doi: [10.1007/s00114-009-0631-9](https://doi.org/10.1007/s00114-009-0631-9)
- Grüter, C. (2020) *Stingless Bees: Their Behaviour, Ecology and Evolution*. Switzerland: Springer, Cham. doi: [10.1007/978-3-030-60090-7](https://doi.org/10.1007/978-3-030-60090-7)
- Howard, J. J. (1985) Observations on resin collecting by six interacting species of stingless bees (Apidae, Meliponinae). *Journal of the Kansas Entomological Society*, 58(2): 337-345. <https://www.jstor.org/stable/25084643>
- Hubbell, S. P.; Johnson, L. K. (1977) Competition and Nest Spacing in a Tropical Stingless Bee Community. *Ecological Society of America*, 58(5): 949-963. doi: [10.2307/1936917](https://doi.org/10.2307/1936917)
- ICMBIO - Instituto Chico Mendes de Conservação da Biodiversidade (2021) RPPN Dr. Daisaku Ikeda. <https://www.gov.br/icmbio/pt-br/assuntos/biodiversidade/unidade-de-conservacao/unidades-de-biomas/amazonia/lista-de-ucs/rppn-dr-daisaku-ikeda/rppn-dr-daisaku-ikeda>. Access on: 18.xi.2021.
- IUCN - International Union for Conservation of Nature (2021) The IUCN Red List of Threatened Species. Online version 2021-3. <https://www.iucnredlist.org/search?taxonomies=117302&searchType=species>. Access on: 18.xi.2021.
- Johnson, L. K.; Hubbell, S. P. (1974) Aggression and competition among stingless bees: Field studies. *Ecology*, 55(1):120-127. doi: [10.2307/1934624](https://doi.org/10.2307/1934624)
- Kapyla, M. (1974) Diurnal flight activity in a mixed population of Aculeata (Hym.). *Annual Entomology Fenology*, 40:61-69.
- Kerr, W. E.; Carvalho, G. A.; Nascimento, V. A. (1996) Ninhos de Meliponíneos. In: Kerr, W. E.; Carvalho, G. A.; Nascimento, V. A. (Eds.). *Abelha Urucu: Biologia, Manejo e Conservação*, pp. 33-38. Coleção Manejo da Vida Silvestre 2, Belo Horizonte: Fundação Acangaú.
- Kerr, W. E.; Sakagami, S. F.; Zucchi, R.; Araújo, V. P.; Camargo, J. M. F. (1967) Observações sobre a arquitetura dos ninhos e comportamento de algumas espécies de abelhas sem ferrão das vizinhanças de Manaus, Amazonas (Hymenoptera, Apoidea). *Atas do Simpósio sobre a Biota Amazônica*, 5: 235-309.
- Lago, J. H. G.; Tezoto, J.; Yazbek, P. B.; Cassas, F.; Santos, J. F. L.; Rodrigues, E. (2016) Exudates used as medicine by the “caboclos river-dwellers” of the Unini River, AM, Brazil - classification based in their chemical composition. *Revista Brasileira de Farmacognosia*, 26(3): 379-384. doi: [10.1016/j.bjp.2016.03.001](https://doi.org/10.1016/j.bjp.2016.03.001)
- Leonhardt, S. D.; Blüthgen, N. (2009) A sticky affair: resin collection by Bornean stingless bees. *Biotropica*, 41(6): 730-736. doi: [10.1111/j.1744-7429.2009.00535.x](https://doi.org/10.1111/j.1744-7429.2009.00535.x)
- Leonhardt, S. D.; Wallace, H. M.; Blüthgen, N.; Wenzel, F. (2015) Potential role of environmentally derived cuticular compounds in stingless bees. *Chemoecology*, 25(4): 159-167. doi: [10.1007/s00049-015-0185-6](https://doi.org/10.1007/s00049-015-0185-6)
- Leonhardt, S. D.; Blüthgen, N.; Schmitt, T. (2009) Smelling like resin: terpenoids account for species-specific cuticular profiles in Southeast-Asian stingless bees. *Insectes Sociaux*, 56(2): 157-170. doi: [10.1007/s00040-009-0007-3](https://doi.org/10.1007/s00040-009-0007-3)
- Litman, J. R.; Danforth, B. N.; Eardley, C. D.; Praz, C. J. (2011) Why do leafcutter bees cut leaves? New insights into the early evolution of bees. *Proceedings of the Royal Society B*, 278(1724): 3593-3600. doi: [10.1098/rspb.2011.0365](https://doi.org/10.1098/rspb.2011.0365)
- Lorenzi, H. (1992) *Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil*. Editora Plantarum, Nova Odessa, SP.
- Melo, G. A. R. (2020) Stingless Bees (Meliponini). In: Starr, C. K. (Ed.), *Encyclopedia of Social Insects*, pp. 883-900. Switzerland: Springer: Cham. doi: [10.1007/978-3-030-28102-1](https://doi.org/10.1007/978-3-030-28102-1)
- MMA - Ministério do Meio Ambiente (2008) *Instrução Normativa nº. 6, de 23 de setembro de 2008*. <https://www.ibama.gov.br/component/legislacao/?view=legislacao&force=1&legislacao=114465>. Access on: 18.xi.2021.
- Nogueira-Neto, P. (1997) *Vida e Criação de Abelhas Indígenas Sem Ferrão*. São Paulo: Editora Nogueirapis.
- Nunes, T. M.; von Zuben, L. G.; Costa, L.; Venturieri, G. C. (2014) Defensive repertoire of the stingless bee *Melipona flavolineata* Friese (Hymenoptera: Apidae). *Sociobiology*, 61(4): 541-546. doi: [10.13102/sociobiology.v61i4.541-546](https://doi.org/10.13102/sociobiology.v61i4.541-546)
- Oliveira, F. F.; Richers, B. T. T.; Silva, J. R.; Farias, R. C.; Matos, T. A. L. (2013) *Guia ilustrado das abelhas “sem ferrão” das Reservas Amanã e Mamirauá, Amazonas, Brasil (Hymenoptera, Apidae, Meliponini)*. Tefé: IDSM.
- Requier, F.; Leonhardt, S. D. (2020) Beyond fowers: including non-foral resources in bee conservation schemes. *Journal of Insect Conservation*, 24(1): 5-16. doi: [10.1007/s10841-019-00206-1](https://doi.org/10.1007/s10841-019-00206-1)
- Reyes-González, A.; Zamudio, F. (2020) Competition interactions among stingless bees (Apidae: Meliponini) for *Croton yucatanensis* Lundell resins. *International Journal of Tropical Insect Science*, 40(4): 1099-1104. doi: [10.1007/s42690-020-00160-5](https://doi.org/10.1007/s42690-020-00160-5)
- Roubik, D. (1989) *Ecology and Natural History of Tropical Bees* (Cambridge Tropical Biology Series). Cambridge: Cambridge University Press. doi: [10.1017/CBO9780511574641](https://doi.org/10.1017/CBO9780511574641)
- Roubik, D. W. (2006) Stingless bee nesting biology. *Apidologie*, 37(2): 124-143. doi: [10.1051/apido:2006026](https://doi.org/10.1051/apido:2006026)
- Santos, C. F.; Absy, M. L. (2010) Polinizadores de *Bertholletia excelsa* (Lecythidales: Lecythidaceae): interações com abelhas sem ferrão (Apidae: Meliponini) e nicho trófico. *Neotropical Entomology*, 39(6): 854-861. doi: [10.1590/S1519-566X2010000600002](https://doi.org/10.1590/S1519-566X2010000600002)
- Santos, J. U. M.; Bastos, M. N. C.; Gurgel, E. S. C.; Carvalho, A. C. M. (2006) *Bertholletia excelsa* Humboldt & Bonpland (Lecythidaceae): aspectos morfológicos do fruto, da semente e da plântula. *Boletim do Museu Paraense Emílio Goeldi - Ciências Naturais*, 1(2): 103-112. doi: [10.46357/bcnaturais.v1i2.745](https://doi.org/10.46357/bcnaturais.v1i2.745)
- Santos, A. J. N. D.; Broglio, S. M. F.; Dias-Pini, N. D. S.; Souza, L. A. D.; Barbosa, T. J. D. A. (2012) Stingless bees damage broccoli inflorescences when collecting fibers for nest building. *Scientia Agricola*, 69(4): 281-283. doi: [10.1590/s0103-90162012000400008](https://doi.org/10.1590/s0103-90162012000400008)
- Santos-Silva, L.; Silva, L. C. P.; Corassa, J. N.; Battirola, L. D. (2017) The Brazil nut tree (*Bertholletia excelsa* Humb. & Bonpl. (Lecythidaceae)): Importance and biological interactions. *Scientific Electronic Archives*, 10(6): 71-83.
- Schöngart, J.; Gribel, R.; Fonseca-Junior, S. F.; Haugaasen, T. (2015) Age and growth patterns of Brazil nut trees (*Bertholletia excelsa* Bonpl.) in Amazonia, Brazil. *Biotropica*, 47(5): 550-558. doi: [10.1111/btp.12243](https://doi.org/10.1111/btp.12243)
- Schwarz, H. F. (1948) Stingless bees (Meliponidae) of the Western Hemisphere. *Bulletin of the American Museum of Natural History*, 90: 1-546.
- Shanahan, M.; Spivak, M. (2021) Resin use by stingless bees: a review. *Insects*, 12(8): 719. doi: [10.3390/insects12080719](https://doi.org/10.3390/insects12080719)
- Silveira, F. S.; Melo, G. A. R.; Almeida, E. A. B. (2002) *Abelhas brasileiras: sistemática e identificação*. Belo Horizonte: Ministério do Meio Ambiente/Fundação Araucária.
- Simone-Finstrom, M.; Spivak, M. (2010) Propolis and bee health: the natural history and significance of resin use by honeybees. *Apidologie*, 41(3): 295-311. doi: [10.1051/apido/2010016](https://doi.org/10.1051/apido/2010016)
- Wadt, L. H.; Kainer, K. A. (2009) Domesticação e melhoramento de castanheiras. In: Borém, A.; Lopes, M. T. G.; Clement, C. R. (Eds.), *Domesticação e melhoramento: espécies amazônicas*, pp. 297-317. Viçosa: Editora Universidade Federal de Viçosa.
- Wille, A.; Michener, C. D. (1973) The nest architecture of stingless bees with special reference to those of Costa Rica (Hymenoptera, Apidae). *Revista de Biologia Tropical*, 21(1):1-271. <https://revistas.ucr.ac.cr/index.php/rbt/article/view/26200>