Identification key for drosophilid species (Diptera, Drosophilidae) exotic to the Neotropical Region and occurring in Brazil

Keven Yuzuki¹, Rosana Tidon¹* ©
¹Universidade de Brasília, Instituto de Ciências Biológicas, Brasília, DF, Brasil.

ARTICLE INFO
Article history:
Received 20 October 2019
Accepted 07 December 2019
Available online 31 January 2020
Associate Editor: Claudio Carvalho
Keywords:
biological invasions,
Drosophila,
invasive species,
Scaptodrosophila,
Zaprionus.

Abstract
Thirteen species of drosophilid exotic to the Neotropical Region are recorded in Brazil, and some of them are highly invasive and threaten significantly fruit cultures. We provide an illustrated key for identifying these species, and briefly discuss their taxonomic status, distribution, and occurrence in the Neotropics. The key should not only support newcomers to the study of Drosophila but also facilitate their identification by those interested in insects associated with cultivated areas.

Introduction

The Taxonomic Catalog of the Brazilian Fauna (TCBF) records 305 drosophilid species in this country (Tidon et al., 2019). Most are neotropical and ecologically restricted to a particular type of vegetation. Thirteen of these species, however, are exotic to the Neotropical Region and widely distributed in the world. Some (e.g., Drosophila melanogaster Meigen and D. simulans Sturtevant) possibly arrived in Brazil in the 16th century, transported by slave ships from Africa. Others reached the country later, throughout trade ships and airplanes. From the late 20th century, four new arrivals in the Neotropics were accurately recorded in the earlier stages of invasion: D. malerkotliana Parshad and Paika (Val and Sene, 1980), Zaprionus indianus Gupta (Vilela, 1999), D. nasuta Lamb (Vilela and Goñi, 2015) and D. suzukii Matsumura (Deprá et al., 2014).

The impacts of biological invasions have been widely recognized since the seminal book The ecology of invasions by animals and plants (Elton, 1958). Ecological interactions between invasive and native species, like predation and competition, often affect the population dynamics (births, deaths, migration) of native species and bring severe negative consequences for biodiversity (Millennium Ecosystem Assessment, 2005). Moreover, invasive species can also cause economic troubles. In Brazil, annual losses to major crops caused by alien species are estimated to about US$1.6 billion (ca. 16% caused by dipterans), and for USA and India this value is even higher (Oliveira et al., 2013). Therefore, it is crucial to understand the biology and distribution of exotic species (Sakai et al., 2001).

In Brazil, drosophilid communities have been studied by several independent research groups, covering the Amazonian and Atlantic forests (Medeiros and Klaczko, 2004; Penariol and Madi-Ravazzi, 2013; Coutinho-Silva et al., 2017; Santa-Brígida et al., 2017), the Cerrado biome (Tidon, 2006; Blauth and Gottschalk, 2007), Caatinga (Rohde et al., 2010; Garcia et al., 2014; Oliveira et al., 2016), araucarias (Cavasini et al., 2014), pampas (Poppe et al., 2016) and urban sites (Ferreira and Tidon, 2005; Gottschalk et al., 2007). Exotic species are recorded in all drosophilid assemblages, and their relative abundance depends on many factors, as vegetation type, the season of the year, and disturbance (Mata et al., 2015).

Taxonomic identification based on morphological characters is an effective way of determining many drosophilid species, especially the non-natives in a particular region. However, there is a lack of

https://doi.org/10.1590/1806-9665-RBENT-2019-100
© 2020 Sociedade Brasileira de Entomologia Published by SciELO - Scientific Electronic Library Online. This is an open-access article distributed under the terms of the Creative Commons Attribution License (type CC-BY), which permits unrestricted use, distribution and reproduction in any medium, provided the original article is properly cited.
identification resources that can be easily used by non-specialists. The primary dichotomous key for drosophilids in Brazil (Freire-Maia and Pavan, 1949) attended several generations of researchers, and certainly contributed for spreading the study of these flies in the country. However, it does not include the recently introduced species and needs to be taxonomically upgraded (e.g. *Drosophila mirim* was synonymized as *Scaptodrosophila latifasciaeformis*). Here, we provide an illustrated identification key for 13 exotic drosophilid species recorded in Brazil and briefly discuss their taxonomic status, distribution, and occurrence in the Neotropics.

### Material and Methods

We analyzed specimens of 11 among the 13 non-neotropical drosophilids occurring in Brazil and collected data of *Drosophila virilis* and *Scaptodrosophila lebanonensis* from the literature (Table 1). The illustrations were hand-made utilizing a *camera lucida* coupled to a Leica MZ75 stereoscope and followed traditional China ink scientific illustration methods reassembling those from Bächli et al. (2004). The morphological terms used in the dichotomous key are also based mainly on Bächli et al. (op cit.).

The dichotomous key does not consider the degree of phylogenetic correlation, but rather the difficulty of identifying each specimen. Thus, the species with the most striking morphological characteristics (*Z. indianus* with their bright stripes and *D. busckii* with their mesonotum patterns) were placed at the first steps of the key. Those specimens that required the rigorous analysis of bristles or sex combs (*Scaptodrosophila* genus and *melanogaster* species group) were left for the end section of the key.

The characters addressed here to identify females of *D. melanogaster* and *D. simulans* are useful for lab routine or identifying flies in the field, but insufficient for a taxonomic study because the black pigmentation on each tergite is highly variable according to genotype and grow temperature (Moreteau et al., 1995). For more accurate techniques such as egg-shape inspection or wing and thorax size ratio see Moreteau et al. (op cit.).

Identification key for non-neotropical drosophilid species occurring in Brazil

1. Presence of stripes on mesonotum....................................................2
   - Absence of stripes on mesonotum............................................3

2. Yellowish fly, with two silvery-white stripes bordered by black across the head (Fig. 1A). Four stripes across the mesonotum and two in the scutellum (Fig. 1B). Two reduced prescutellar setae. Profemur with a row of strong setae, each one arising from a small tubercle with another setula (Fig. 1C). Costal index about 2.6. Subapical setae on fourth and fifth abdominal tergites arising from blackish spots.......................... *Zaprionus indianus*
   - Yellowish fly with three dark-brown stripes across the mesonotum, median one forked in posterior half (Fig. 1D). Pleura with two horizontal stripes (Fig. 1E). Costal index about 3.1. Abdomen with dark bands interrupted in the middle and narrowed at the sides (Fig. 1F).............................. *Drosophila busckii*

3. Dark brown fly. Carina longitudinally grooved (Fig. 1G). Basal scutellar setae divergent (Fig. 1H). Wing crossveins slightly shaded (Fig. 1I). Costal index about 3.0. Abdominal tergites 2-6 completely dark .......................................................... *Drosophila virilis*
   - Basal scutellar setae convergent (Fig. 1J)...............................4

4. Presence of cuneiform setae on the inner side of profemur (Fig. 2A)..........................................................5
   - Absence of cuneiform setae on the inner side of profemur ....... ..........................................................6

5. Face region with a silvery-shining pigmentation (Fig. 2B), this area is more easily visualized in dry preserved males. Pleura with a wide, slightly brownish stripe (Fig 2C). Costal index about 3.1 .................................................. *Drosophila nasuta*
   - Male protarsomeres 1 and 2 with a dense brush of long hairy setae (Fig. 2D). Wings with crossveins and tips of longitudinal veins slightly shaded (Fig. 2E), costal index about 4.4. Abdominal bands medially interrupted with triangular marginal bands (Fig. 2F).......................................................... *Drosophila immigrans*

6. Presence of prescutellar setae on mesonotum (Fig. 2G). Light hyaline wings. Sex combs absent (*Scaptodrosophila* genus)..........................................................7
   - Absence of prescutellar setae on mesonotum. Males with sex combs on protarsus (*melanogaster* species group)..................8

7. Light yellow fly. Costal index about 1.5. Abdomen deep dark (Fig. 2H).................................................. *Scaptodrosophila latifasciaeformis*
   - Dark brown fly. Costal index about 2.1 Large brown abdominal bands .......................................................... *Scaptodrosophila lebanonensis*

8. Male protarsus with two small rows of 3-4 peg-like setae forming a sex comb (Fig. 2I). Male wings with a large subdiscal black spot (Fig. 3A), costal index about 3.5. Females with a large serrated oviscapt (Fig 3B)............................... *Drosophila suzukii*
   - Male protarsus with a single row of peg-like setae forming a sex comb (Fig. 3C). Costal index 2.4. Male epandrial posterior lobe small and nearly triangular (Fig. 3D). Female abdomen with

### Table 1

Non-neotropical species of Drosophilidae recorded in Brazil.

| Genus        | Subgenus     | Species                  | Source       |
|--------------|--------------|--------------------------|--------------|
| *Drosophila* | Dorsilopha   | *D. busckii* Coquillet   | collection   |
|              | Drosophila   | *D. immigrans* Sturtevant| collection   |
|              |              | *D. nasuta* Lamb         | lab strain   |
|              |              | *D. virilis* Sturtevant  | literature*  |
|              | Sophophora   | *D. ananassae* Deleschall| lab strain   |
|              |              | *D. kikkawai* Burla      | collection   |
|              |              | *D. malekotiana* Parshad and Paika | lab strain |
|              |              | *D. melanogaster* Meigen | lab strain   |
|              |              | *D. simulans* Sturtevant | lab strain   |
|              |              | *D. suzukii* Matsumura   | collection   |
| **Scaptodrosophila** |          | *S. lebanonensis* Wheeler | literature** |
|              |              | *S. latifasciaeformis* Duda| collection   |
|              |              | *Z. indians* Gupta       | collection   |

* description and Miller et al. (2017) ** description and Bächli et al. (2005).
its large dark bands on the sixth tergite running to its ventral margin (Fig. 3E).…………………………Drosophila melanogaster

- Male protarsus with a single row of peg-like setae, forming a sex comb (Fig. 3C). Costal index 2.3. Male epandrial posterior lobe very large and roundish with an amber like color (Fig. 3F). Female abdomen pigmentation border line making an angle with the sixth tergite margin (Fig. 3G) ..............................................................Drosophila simulans

Drosophila melanogaster - Male protarsus with several transverse rows of short setae on the ventral surface, forming an indistinct sex comb (Fig. 3H). Costal index 1.5 ........................................Drosophila ananassae

- Male protarsus with three small rows of 2-3 peg-like setae, forming a sex comb (Fig. 3I). Costal index 1.7............................................................ Drosophila malerkotliana

- Male protarsus with two rows of peg-like setae, forming a sex comb (Fig. 3J). Costal index 1.9.................. Drosophila kikkawai

Figure 1. Zaprionus indianus, Drosophila busckii and D. virilis. A. Head of Z. indianus in frontal view, showing the two silvery stripes bordered by black. B. Thorax of Z. indianus in dorsal view, showing the four silvery stripes bordered by black. C. Proferm of Z. indianus, showing the row of characteristic strong setae. D. Thorax of D. busckii in dorsal view, showing its characteristic dark stripes, the middle one bifurcating at the base. E. Thorax of D. busckii in lateral view with its characteristic dark stripes. F. Abdomen of D. busckii, showing the bands interrupted in the middle. G. Head of D. virilis in frontal view, showing its carina with a longitudinal groove at midline. H. Divergent basal scutellar setae. I. D. virilis wing, showing the shaded crossveins. J. Convergent basal scutellar setae setae. Bar = 1mm. Illustrations of D. virilis were based on published images without scale (Miller et al., 2017).
Figure 2. Drosophila nasuta, D. immigrans, Scaptodrosophila latifasciaeformis, and D. suzukii. A. Proemur with a row of cuneiform setae. B. Head of D. nasuta in frontal view, showing the characteristic silvery pigmentation in the face region. C. Thorax of D. nasuta in lateral view, showing the large brownish stripe on half dorsal area of pleura. D. D. immigrans protarsomeres, showing the brush like thin setae. E. D. immigrans wing, showing the shaded cross veins and ends of longitudinal veins. F. D. immigrans abdomen, showing the bands interrupted in the middle. G. Prescutell lar setae. H. S. latifasciaeformis dark abdomen. I. D. suzukii protarsus with sex combs. Bar = 1mm.
Figure 3. *Drosophila suzukii*, *D. melanogaster*, *D. simulans*, *D. ananassae*, *D. malerkotliana* and *D. kikkawai*. A. *D. suzukii* male spotted wing. B. *D. suzukii* female abdomen, showing the serrated oviscap. C. *D. melanogaster* and *D. simulans* protarsus sex comb. D. *D. melanogaster* male epandrial posterior lobe. E. *D. melanogaster* female abdomen in lateral view, showing the large dark bands on the sixth tergite running to its ventral margin. F. *D. simulans* male epandrial posterior lobe. G. *D. simulans* female abdomen in lateral view, showing the pigmentation border line making an angle with the sixth tergite margin. H. *D. ananassae* protarsus sex combs. I. *D. malerkotliana* protarsus sex combs. J. *D. kikkawai* protarsus sex combs. Bar = 1mm.
Discussion

Potentially colonizer drosophilids had attracted the attention of researchers for over five decades (Dobzhansky, 1965; Lewontin, 1965; David and Tsacas, 1981; Parsons, 1983), and it is well established that these flies can be used as models in studies of biological invasions (Gilbert et al., 2016). The species registered here are widely distributed not only in South America but also in other regions of the world (Bächli, 2019). The section below provides information about the origin (David and Tsacas, 1981), distribution (Brake and Bächli, 2008; Bächli, 2019), and general characteristics of each species.

Genus Drosophila Fällen

The genus Drosophila includes approximately half of the 4,000 species in the family Drosophilidae. Its members have adapted to and radiated in a variety of niches (Markow and O’Grady, 2008), and currently divided into nine subgenera (O’Grady and DeSalle, 2018).

Subgenus Dorsilopha Sturtevant

This subgenus of oriental origin (Toda, 1986) consists of only four species, including the cosmopolitan Drosophila busckii. While many common drosophilids prefer decaying fruit, D. busckii larvae seem to have a broader niche (Atkinson and Shorocks, 1977) and were recorded feeding on many different vegetables (Valadão et al., 2019), animal excrement and meat (Sturtevant, 1921). This species is very abundant in temperate places, where its competitive ability is apparently higher (David and Tsacas, 1981). In Brazil, D. busckii is rare in natural habitats but can be found in disturbed areas (Sene et al., 1980).

Subgenus Drosophila Fällen

This is the largest subgenus of Drosophila, supporting about 80% of its ca. 2000 species. Therefore, this subgenus is organized in 47 species groups, which are an informal taxonomic rank (Sturtevant, 1942) that organize the diversity within large clades of drosophilids.

The immigrans species group, probably of oriental origin, currently contains about 100 nominal species and two of them are recorded in Brazil. The cosmopolitan Drosophila immigrans is abundant in the Palearctic and Nearctic Regions (David and Tsacas, 1981) and has been collected in Brazilian natural and modified environments since the pioneer studies of Pavan (1959). In this country, the abundance of D. immigrans seems to be low at warmer areas (Sene et al., 1980) but increases in the colder southern regions (Hochmüller et al., 2010). Drosophila nasuta, on the other hand, is widespread and abundant in the tropical parts of Africa (David and Tsacas, op cit.) and has been recently recorded in the Neotropics (Vilela and Goifi, 2015). In forest patches located in the Brazilian savanna, where D. immigrans remains rare (data not shown), D. nasuta can reach 20% relative abundance of drosophilids during Summer months (Leão et al., 2017). These findings support the hypothesis raised by David and Tsacas (op cit.) that D. immigrans is cold-adapted, whereas D. nasuta is a tropical species.

The virilis species group consists of about thirteen described species that are typically found in a boreal distribution (Markow and O’Grady, 2006). The group appears to have originated in Asia as a species of the temperate deciduous forest associated predominantly with riparian communities (Throckmorton, 1975). Only Drosophila virilis Sturtevant has been recorded worldwide in wine production areas as well as in breweries (Bächli et al., 2004).

Subgenus Sophophora Sturtevant

This subgenus currently contains 344 species organized in nine species groups. The Drosophila melanogaster species group, the largest of this subgenus, contains almost 200 species widely distributed in the Oriental Region and adjacent areas, but some lineages reached the African continent and radiated. Six species of this group are recorded in Brazil.

The sibling African species Drosophila melanogaster and D. simulans probably are the most studied examples of widespread drosophilids (Capy et al., 2004). D. melanogaster first colonized Eurasia (10,000–15,000 years ago) and later spread to America and Australia. It is generally admitted that this human commensal species travel easily with fruit shipments, mostly as larvae or pupae on rotting material. D. simulans expanded worldwide more recently, probably a few centuries ago, establishing in natural and disturbed environments throughout the invaded areas. In Brazil, both species arrived probably as a result of the slave trade. Currently, D. simulans is a widespread species in all sorts of environments, whereas D. melanogaster is rare in natural habitats (Sene et al., 1980).

Drosophila ananassae, probably native of the Orient, is a peridomestic species occurring in tropical and subtropical areas of the world. In Brazil, it is rare in natural environments but can be found in open types of vegetation (Sene et al., 1980). We have been collecting this species in urban orchards, near Brasilia.

Drosophila malerkotliana, also native of the Orient, was described from the Malerkota region in India by Parshad and Paika, in 1964. Besides being widespread in the Orient, it also occurs in Africa and Americas, where it was introduced in recent decades (Val and Sene, 1980; Sene et al. 1980; David and Tsacas 1981; Castrezana et al., 2010). In Brazil, it occurs in both natural environments (Medeiros and Klaczko, 2004; Torres and Madi–Ravazzi, 2006; Tidon, 2006; Schmitz et al., 2010), and urbanized sites (Gottschalk et al., 2007).

Finally, a species that is currently meriting the status of cosmopolitan is D. suzuki, known as the spotted-wing Drosophila due to the dark spot on the male wings. Probably native of East Asia, this species has spread to western regions: it was found in Hawaii in the early 1980s and more recently in North America and Europe, where it has reached invasive pest status (Asplén et al., 2015). The female has a long and narrow ovipositor used to infest soft-skinned fruit crops and causing enormous economic damage on commercial plantations; hence, the spotted-wing Drosophila has become an agricultural pest in several countries worldwide (Walsh et al., 2011). In Brazil, this cold-adapted species was first detected in the southern region in February 2013 (Deprá et al., 2014). As conjectured by Vilela and Mori (2014), who recorded this species in Southeast Brazil, D. suzuki is probably expanding its territory to other South American areas through the trade of cultivated soft skin fruits and the use of small wild fruits as breeding sites. Although Southern Brazil is the most climatically favorable area for D. suzuki development (Benito et al., 2016), it has already been found in natural vegetation of the tropical Brazilian Savanna, at low abundances (Leão et al., 2017).

Genus Scaptodrosophila Duda

The genus Scaptodrosophila, initially described as a subgenus of Drosophila, was formally elevated to generic rank by Grimaldi (1990). Probably originated in tropical Asia, Scaptodrosophila currently includes...
almost 300 species distributed in Asia, New Guinea, Australia, and Africa, with few species in the Americas and Europe. Two species of this genus have reached the Neotropical Region. *Saptodrosophila latifasciaeformis* is a widespread species in tropical and subtropical areas of the world. In Brazil, it was described by Dobzhansky and Pavan (1943) as *Drosophila mirim* and has been collected in all types of vegetations (Sene et al., 1980), including mangroves in the southern region of the country (Schmitz et al., 2010). *S. lebanonensis*, later described as *Drosophila galloby* Lourenço and Mourão (1992) and synonymized by Bächli et al. (2005), was recorded in southern Neotropical region in 1960 and we have no notice of other records in the Neotropical region after then.

**Genus Zaprionus**

*Zaprionus* is an Afrotropical genus that extended its distribution to the Australian, Oriental and Palearctic regions. *Zaprionus indius* constitutes one of the most successful colonizing species of this genus (Chassagnard and Tscas, 1993), probably because of its broad niche-width characteristics: it utilizes diverse food resources and displays adaptation to variable climatic conditions (Parkash and Yadav, 1993). The first record of *Z. indius* in Brazil was in São Paulo State (Vilela, 1999) and, after that, the species was found in many Brazilian regions (Galego and Carareto, 2010). In natural areas where environmental conditions are similar to those observed in its original area in Africa, *Z. indius* dominates drosophilid assemblages during the wet season (Tidon et al., 2003). It also predominates in fig plantations: among 125,00 drosophilids captured in São Paulo State, 83,339 were identified as *Z. indius* (Roque et al., 2017). This species is highly adaptable (Mata et al., 2010) and deserves to be monitored.

**Final Remarks**

Most drosophilids approached in this study are widely distributed thought natural populations in many Brazilian biomes, and two species in particular, *Drosophila suzukii* and *Zaprionus indius*, can cause great impact on cultivated areas. The identification key provided here should not only support newcomers to the study of *Drosophila* but also the professional that will be dealing with the elimination of the pests affecting plantation, who generally will not be *Drosophila* experts.

**Acknowledgments**

We are grateful to B.F.D. Leão and F. Roque for collecting the specimens and taxonomic advices, to C.R. Vilela and C.H. Lue for suggestions on earlier versions of this manuscript, and to two anonymous referees for their valuable recommendations. This paper was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, grant number 88887.136269/2017-00) and by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant numbers 309973/2017-1 and 441581/2016-1).

**References**

Ashburner, M., 1989. *Drosophila: A Laboratory Handbook*, Cold Spring Harbor, New York.

Asplen, M. K., Anfora, G., Biondi, A., Choi, D. S., Chu, D., Daane, K. M., Gibert, P., Gutierrez, A. P., Hoelmer, K. A., Hutchison, W. D., Isaacs, R., Jiang, Z. L., Kárpáti, Z., Kimura, M. T., Pascual, M., Philips, C. R., Plantamp, C., Ponti, L., Vétek, G., Vogt, H., Walton, V. M., Yu, Y., Zappalà, L., Desneux, N., 2015. Invasion biology of spotted wing *Drosophila* (Drosophila suzukii): a global perspective and future priorities. J. Pest Sci. 88, 469–494. https://doi.org/10.1007/s10340-015-0681-z.

Atkinson, W., Shorrocks, B., 1977. Breeding site specificity in the domestic species of *Drosophila*. Oecologia 29, 223-232. https://doi.org/10.1007/BF00345697.

Bächli, G., 2019. TaxoDros: The Database on Taxonomy of Drosophilidae. Available in: https://www.taxodros.uzh.ch/search/dist_reg.php (accessed 8 February 2019).

Bächli, G., Haring, E., Vilela, C. R., 2005. On the phylogenetic relationships of *Saptodrosophila rutifrons* and *S. lebanonensis* (Diptera, Drosophilidae). Bull. la Société Entomol. Suisse. 78, 349-364.

Bächli, G., Vilela, C., Escher, S. A., Saura, A., 2004. The Drosophilidae (Diptera) of Fennoscandia and Denmark Fauna Entomologica Scandinavica, vol. 39, Brill: Nederland, pp. 1-362.

Benito, N. P., Lopes-da-Silva, M., Santos, R. S. S., 2016. Potential spread and economic impact of invasive *Drosophila suzukii* in Brazil. Pesqui. Agropecu. Bras. 51, 571-578. https://doi.org/10.1590/S0100-204X2016000500018.

Blauth, M. L., Gottschalk, M. S., 2007. A novel record of Drosophilidae species in the Cerrado biome of the State of Mato Grosso, west-central Brazil. Drosoph. Inf. Serv. 90, 90-96.

Brake, I., Bächli, G., 2008. Drosophilidae (Diptera). World Catalog of Insects, v. 9. Apollo Books, Stenstrup.

Capy, P., Gibert, P., Boussy, I., 2004. *Drosophila melanogaster*, *Drosophila simulans*: So Similar, So Different. Springer, Netherlands.

Castrezena, S., Faircloth, B. C., Cowem, P. A., 2010. *Drosophila* collection in Los Angeles, California. Drosoph. Inf. Serv. 93, 91.

Cavasini, R., Buschini, M., Machado, L., Mateus, R., 2014. Comparison of Drosophilidae (Diptera) assemblages from two highland Araucaria forest fragments, with and without environmental conservation policies. Braz. J. Biol. 74, 761-768. https://doi.org/10.1590/1519-6984.00113.

Chassagnard, M.-T., Tsasas, L., 1993. Le Sous-genre *Zaprionus* S. Str.: définition de groupes d’espèces et révision du sous-groupe vittiger (Diptera: Drosophilidae). Ann. Soc. Entomol. Fr. 29, 173-194.

Costa, B., Rohde, C., Valente, V., 2003. Temperature, urbanization and body color polymorphism in South Brazilian populations of *Drosophila kikkawai* (Diptera, Drosophilidae). In: Herzing Ser. Zool. 93, 381–393. https://doi.org/10.1590/S0073-47122003004000005.

Coutinho-Silva, R. D., Montes, M. A., Oliveira, G. F., Carvalho-Neto, F. G., Rohde, C., Garcia, A. C. L., 2017. Effects of seasonality on drosophilids (Insecta, Diptera) in the northern part of the Atlantic Forest, Brazil. Bull. Entomol. Res. 107, 634-644. https://doi.org/10.1017/S0007469217000190.

David, J. R., Tscasas, L., 1981. Cosmopolitan, subcosmopolitan and widespread species: different strategies within the Drosophilidae family (Diptera). C. R. Séances Soc. Biogog. 57, 11-26.

Deprá, M., Poppe, J. L., Schmitz, H. J., De Toni, D. C., Valente, V. L. S., 2014. The first records of the invasive pest *Drosophila suzukii* in the South American continent. J. Pest Sci. 87, 379–383. https://doi.org/10.1007/s10340-014-0591-5.

Dobzhansky, T., 1965. “Wild” and “Domestic” species of *Drosophila*. In: Baker, H.G., Stebbins, G.L. (Eds.), The Genetics of Colonizing Species. Academic Press, London, pp. 533-551.

Dobzhansky, T., Pavan, C., 1943. Studies on Brazilian species of *Drosophila* kikkawai (Diptera, Drosophilidae). Heringa Ser. Zool. 93, 381–393. https://doi.org/10.1590/S0073-47122003004000005.

Dobzhansky, T., 1965. “Wild” and “Domestic” species of *Drosophila*. In: Baker, H.G., Stebbins, G.L. (Eds.), The Genetics of Colonizing Species. Academic Press, London, pp. 533-551.

Dobzhansky, T., Pavan, C., 1943. Studies on Brazilian species of *Drosophila*. Bol. Fac. Filos. Ciências e Let. da Univ. São Paulo. Biol. Geral 36, 7-72.

Elton, C. S., 1958. The Ecology of Invasions by Plants and Animals. University of Chicago Press, Chicago.

Ferreira, L. B., Tidon, R., 2005. Colonizing potential of Drosophilidae (Diptera) assemblages from two highland Araucaria forest fragments, with and without environmental conservation policies. Braz. J. Biol. 74, 761-768. https://doi.org/10.1590/1519-6984.00113.
Tidon, R., Gottschalk, M. S., Schmitz, H. J., Martins, M. B., 2019. Drosophilidae, Catálogo Taxonômico da Fauna do Brasil. Available in: http://fauna.jbrj.gov.br/fauna/faunadobrasil/2 (accessed 4 February 2019).

Tidon, R., Leite, D. F., Leão, B. F. D., 2003. Impact of the colonisation of *Zaprionus* (Diptera, Drosophilidae) in different ecosystems of the Neotropical Region: 2 years after the invasion. Biol. Conserv. 112, 299-305. https://doi.org/10.1016/S0006-3207(02)00322-1.

Toda, M. J., 1986. Drosophilidae (Diptera) in Burma. I: the subgenus *Dorsilopha* Sturtevant of the genus *Drosophila*, with descriptions of two new species. Kontyu 54, 282-290.

Torres, F. R., Madi-Ravazzi, L., 2006. Seasonal variation in natural populations of *Drosophila* spp. (Diptera) in two woodlands in the State of São Paulo, Brazil. Iheringia Ser. Zool. 96, 437-444. https://doi.org/10.1590/S0073-47212006000400008.

Val, F. C., Sene, F. M., 1980. A newly introduced *Drosophila* in Brazil (Diptera, Drosophilidae). Pap. Avulsos Zool. 33, 293-298.

Valadão, H., Proença, C. E. B., Kuhlmann, M. P., Harris, S. A., Tidon, R., 2019. Fruit-breeding Drosophilids (Diptera) in the Neotropics: playing the field and specialising in generalism? Ecol. Entomol. 44 (6), 721-737. https://doi.org/10.1111/een.12769.

Vilela, C. R., 1999. Is *Zaprionus indianus* Gupta, 1970 (Diptera, Drosophilidae) currently colonizing the Neotropical Region? Drosoph. Inf. Serv. 82, 37-39.

Vilela, C. R., Goñi, B., 2015. Is *Drosophila nasuta* Lamb (Diptera, Drosophilidae) currently reaching the status of a cosmopolitan species? Rev. Bras. Entomol. 59, 346-350. https://doi.org/10.1016/j.rbe.2015.09.007.

Vilela, C. R., Mori, L., 2014. The invasive spotted-wing *Drosophila* (Diptera, Drosophilidae) has been found in the city of São Paulo (Brazil). Rev. Bras. Entomol. 58, 371-375. https://doi.org/10.1590/0085-562620140000400004.

Walsh, D. B., Bolda, M. P., Goodhue, R. E., Drea, B. J., Lee, J., Bruck, D. J., Walton, V. M., O’Neal, S. D., Zalom, F. G., 2011. *Drosophila suzukii* (Diptera: Drosophilidae): invasive pest of ripening soft fruit expanding its geographic range and damage potential. J. Integr. Pest Manag. 40, 55-64. https://doi.org/10.1603/IPM10010.