

Invasive Fruit Flies (Diptera: Drosophilidae) Meet in a Biodiversity Hotspot

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ABSTRACT

Oceanic islands' natural ecosystems worldwide are severely threatened by invasive species. Here we discuss the recent finding of three exotic drosophilids in Madeira archipelago - *Acletoxenus formosus* (Loew, 1864), *Drosophila suzukii* (Matsumura, 1931) and *Zaprionus indianus* (Gupta, 1970). *Drosophila suzukii* and *Z. indianus* are invasive species responsible for severe economic losses in fruit production worldwide and became the dominant drosophilids in several invaded areas menacing native species. We found that these exotic species are relatively widespread in Madeira but, at present, seem to be restricted to human disturbed environments. Finally, we stress the need to define a monitoring program in the short-term to determine population spread and environmental damages inflicted by the two invasive drosophilids, in order to implement a sustainable and effective control management strategy.

Key words: Biological invasions, *Drosophila suzukii*, invasive species, island biodiversity, Madeira archipelago, *Zaprionus indianus*.

INTRODUCTION

Oceanic islands are known to contribute disproportionately to their area for Global biodiversity and by harbouring unique evolutionary lineages and emblematic plants and animals (Grant, 1998; Whittaker and Fernández-Palacios, 2007). Nevertheless, many of these organisms are particularly vulnerable to human-mediated changes in their habitats due to their narrow range size, low abundance and habitat specificity (Paulay, 1994). In fact, the present biodiversity crisis is nowhere else more evident than in island ecosystems, where major extinctions occurred following habitat destruction and invasive species introductions (Sax and Gaines, 2008).

Some insect species are among the worst invasive species worldwide being responsible for huge economic losses and severe environmental impacts (Lowe *et al.*, 2000). During the last decades many drosophilid species have spread around the world mostly aided by human transport of goods (Westphal *et al.*, 2008; Hulme, 2009).

Some of those species, like *Drosophila suzukii* and *Zaprionus indianus*, proved to be serious economic threats, being responsible for heavy losses in various flesh fruit cultures in many countries (van der Linde *et al.*, 2006; Cini *et al.*, 2012). For instance, the economic losses caused by *D. suzukii* to fruit production in USA are estimated to cost over 500 million dollars each year (Bolda *et al.*, 2010) and, in Brazil, *Z. indianus* severely impacted fig production leading to annual losses on the order of 50% (Tidon *et al.*, 2003). Furthermore, associated with the economic impacts in colonized regions, these two invasive drosophilids also have significant ecological impacts on native ecosystems that start to become better understood (Galego and Carareto, 2005).

Some oceanic island ecosystems, like Madeira, are vulnerable to the negative effects of invasive pest species due to the particular structure of local economies (often specialized in the production of few goods) and to the high levels of island endemism, where rare endemics may be threatened by the invaders (Reaser *et al.*, 2007). Madeiran native drosophilids, particularly the endemic *D. madeirensis*, may be negatively impacted by invasive drosophilids. This endemic species seems to be strictly associated to the native laurel forest (Laurisilva), has seldom been recorded and is not abundant (Monclús, 1984). Furthermore, the study of life-history traits of *D. madeirensis* indicates that it may be particularly vulnerable to competition from invasive congeners since this species has a poor performance when compared with a closely related species with a wide distribution (Rego *et al.*, 2007).

The aim of our study is to provide information on the recent invasion of Madeira archipelago by three drosophilid species *Acletoxenus formosus* (Loew, 1864), *Drosophila suzukii* (Matsumura, 1931) and *Zaprionus indianus* (Gupta, 1970) and evaluate its potential impact on local economy and on native species.

MATERIAL AND METHODS

Madeira archipelago is located on the Atlantic Ocean, nearly 800 km away from Continental Europe (Portugal). The archipelago is composed by three groups of islands: Madeira Island, Desertas Islands and Porto Santo and its surrounding islets. In Madeira Island there is a variety of native habitat-types from coastal xeric vegetation to altitudinal meadows, but Laurisilva, the native laurel forest, is the most emblematic one, being classified as World Natural Heritage Site due to its outstanding natural value (IUCN, 1999).

Sampling took place in selected sites from different habitat-types throughout Madeira and Porto Santo. Several complementary sampling techniques were used to collect the drosophilid species reported in this study, namely: Ad-hoc direct sampling, Moericke and yellow colour traps. Moericke and colour traps were set in several areas of Madeira, in different habitat-types, as part of an early warning system to detect the presence of exotic species. Ad-hoc direct sampling was applied mostly in flesh fruit cultures throughout Madeira, because the presence of predictable food resources (mature and rotten fruits) allows the attraction of drosophilids.

The specimens collected in this study are deposited in the entomological collection of the Laboratório de Qualidade Agrícola (ICLAM) in Camacha (Madeira, Portugal). The

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study of specimens from previous collections housed in the ICLAM was important by making available information concerning species distribution, thus providing insights on invasion date and dispersal pathways.

In order to evaluate and predict the environmental impact of the three introduced drosophilid species in Madeira archipelago, we applied the Generic Impact Scoring System adapted to the IUCN criteria and categories (GISS-IUCN) (Blackburn *et al.*, 2014), taking in consideration the available information on species biology and colonization history.

RESULTS

In this study we report for the first time the finding of two exotic drosophilid species *A. formosus* and *D. suzukii* in Madeira and confirm the occurrence of the invasive *Z. indianus* in this archipelago (Figs. 1A, 1B, 1C).

The recent finding of the invasive *D. suzukii* in Madeira confirmed the worst expectations of its rapid spread worldwide benefiting from human-aided long distance dispersal (Cini *et al.*, 2012). The species was recorded from distanced locations within Madeira (Fig. 2, Table 1) suggesting the occurrence of multiple infestations following its first introduction. Nonetheless, at present *D. suzukii* seems to be restricted to human disturbed areas since all specimens were collected in vineyards. Further, with the exception of Arco de São Jorge (in north Madeira), this invasive species was not abundant in the invaded areas. At present there is no single record of this species from native habitats despite the occurrence of potential host plants (e.g. *Rubus*, *Sorbus* and *Vaccinium* species).

Another exotic drosophilid, *A. formosus*, is also reported for the first time to Madeira archipelago after being sampled from both Madeira and Porto Santo islands. This species with a remarkable colour pattern was always found in low abundance in man-made habitats, mostly in urban gardens (Fig. 2, Table 1). The larvae of *A. formosus* are predaceous and all the adult specimens were collected near their whitefly prey (e.g. *Trialeurodes vaporariorum*). The study of specimens housed in the entomological collection of ICLAM provided additional information on the ecological associations of *A. formosus* (three whitefly species were recorded as hosts: *Aleyrodes proletella*, *Siphoninus phillyreae* and *Trialeurodes vaporariorum*) and on its introduction history in Madeira (collection specimens date back to mid- and late 90s).

The invasive *Z. indianus* was recorded in several fruit plantations (e.g. banana, grape, mango, pineapple) from sites mostly located in southwestern Madeira (Fig. 2, Table 1). This drosophilid was relatively abundant at Serra de Água (in the center of Madeira) while in most of the other locations only a few specimens were sampled. Population genetic studies on the invasive *Z. indianus* had previously reported this species to Madeira, but no mention was made to species abundance and geographic distribution in this island (Nardon *et al.*, 2005; Yassin *et al.*, 2008). The study of drosophilids housed in the ICLAM allowed the finding of specimens dating back from 1992, a decade before the first reports of the presence of this invasive species in Madeira.

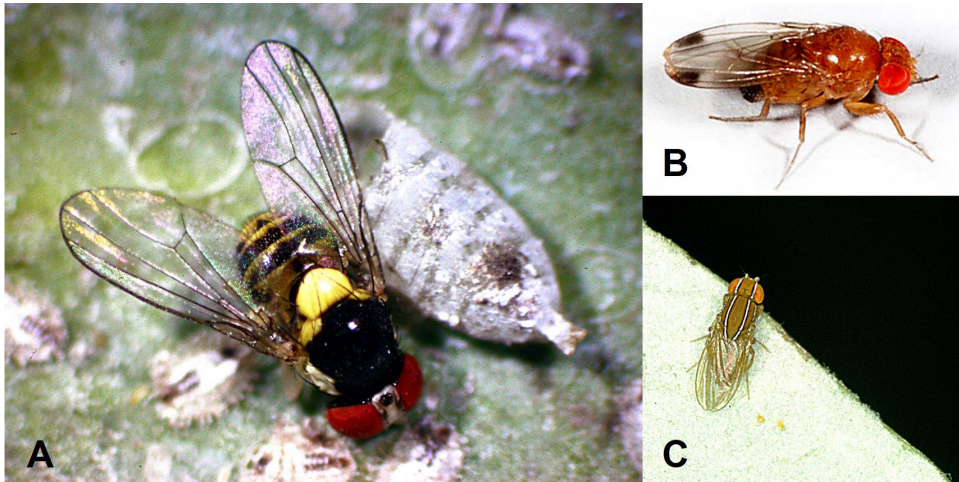


Fig. 1. Drosophilids recently found in Madeira archipelago. A: *Acletoxenus formosus* associated with a colony of the ash whitefly *Siphoninus phillyreae* on pomegranate (photo by AMF Aguiar); B: *Drosophila suzukii* (photo by M Hauser); C: *Zaprionus indianus* (photo by AMF Aguiar).

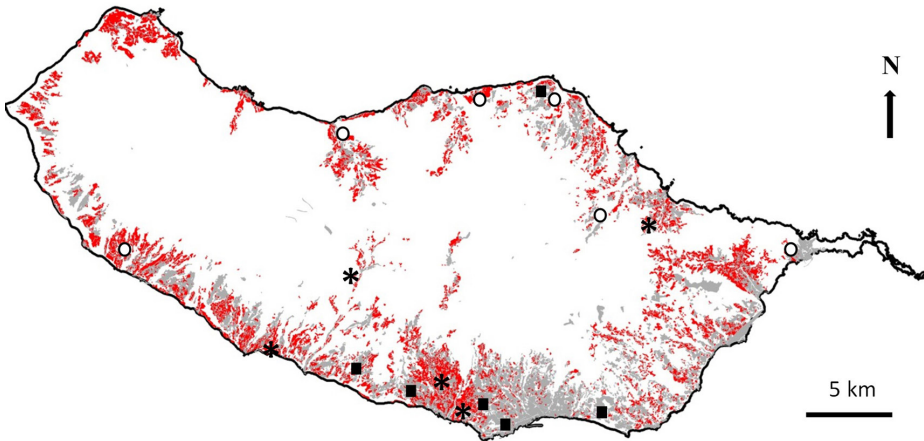


Fig. 2. Distribution of the exotic drosophilids in Madeira Island: *A. formosus* (in squares), *D. suzukii* (in circles) and *Z. indianus* (in asterisks). The geographic distribution of urban areas (in grey) and fruit plantations (in red) are also presented.

The assessment of the ecological impact of the three alien drosophilid species using the GISS-IUCN protocol (Blackburn *et al.*, 2014) allowed us to classify *D. suzukii* and *Z. indianus* as having a moderate impact on natural communities since the decline of population densities in some native species is expected. On the other hand, *A. formosus* may have a minor impact on natural communities since this species seems to be restricted to human disturbed areas in coastal lowlands, not presenting for now a threat to native potential prey (endemic whiteflies).

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Table 1. Records of exotic drosophilids in Madeira with information on sampling dates, locations and techniques applied. The geographical coordinates (in degrees, minutes and seconds) of each sampling site are indicated together with the altitude (in meters) and habitat-type. Site names are listed alphabetically for each species.

Species	Site	Habitat	Lat. (N)	Long. (W)	Altitude	Date	N	Technique
<i>A. formosus</i>	Amparo	Urban garden	32°38'45.67"	16°56'39.88"	160	2.ix.1999	1♂	Direct sampling
	Caldeira	Strawberry plantation	32°39'25.42"	16°59'47.54"	312	12.xi.1998	1♂	Direct sampling
	Campanário	Agricultural land	32°40'12.79"	17°1'44.22"	325	6.x.1994	2♂,2♀	Direct sampling
	Farrobo	Cabbage plantation	32°50'2.40"	16°54'29.34"	270	1.viii.2012	1♂,4♀	Direct sampling
	Ribeiro Salgado	Urban garden	33°2'52.84"	16°21'6.95"	15	22-26.vii.2013	1♂,2♀	Direct sampling
	São Gonçalo	Urban garden	32°38'53.05"	16°52'35.69"	238	9.viii.2006	1♂,2♀	Direct sampling
	São Martinho	Urban garden	32°38'21.16"	16°55'50.70"	64	6.vii-2006	1♂,1♀	Direct sampling
<i>D. suzukii</i>	Arco de São Jorge (M)	Vineyard	32°49'29.62"	16°57'14.44"	134	1.x.2014	11♂,4♀	Colour traps
	Canical	Vineyard	32°44'17.66"	16°44'37.73"	58	25.ix.2014	1♂	Colour traps
	Estreito da Calheta (M)	Vineyard	32°44'5.66"	17°11'11.83"	335	13.x.2014	1♀	Colour traps
	Faial	Vineyard	32°45'32.26"	16°52'27.84"	328	25.ix.2014	4♂,1♀	Colour traps
	São Jorge	Vineyard	32°49'38.93"	16°54'09.94"	256	25.ix.2014	1♂	Colour traps
	São Vicente	Vineyard	32°47'56.44"	17°02'28.15"	90	1-15.x.2014	2♂,3♀	Colour traps
<i>Z. indianus</i>	Câmara de Lobos	Pineapple plantation	32°39'21.17"	16°58'51.96"	148	15.ix.1997	1♂,1♀	Direct sampling
	Ponta do Sol	Banana plantation	32°40'50.65"	17°05'15.79"	30	1992/1993	3♂,6♀	Moericke trap
	Porto da Cruz	Vineyard	32°45'59.36"	16°50'8.09"	233	13.ix.2001	4♂,1♀	Direct sampling
	Quebradas	Mango groove	32°38'51.90"	16°57'44.39"	114	18.xi.1998	1♂,2♀	Direct sampling
	Serra de Água	Agricultural land	32°43'18.00"	17°02'03.79"	400	1992/1993	24♂,20♀	Moericke trap

DISCUSSION

During the last few centuries human-mediated disturbance has led to the homogenization of island biotas worldwide as a result of species introductions and the extinction of endemic life forms (Olden, 2006; Florencio *et al.*, 2013). The recent discovery of two invasive drosophilid species in Madeira archipelago is a matter of concern since both species have potential negative impacts on the economy and on the environment. The worldwide invasion of *D. suzukii* is proving to be a serious issue due to its severe economic impacts on fruit production and the difficulties in managing this fast spreading pest species (Cini *et al.*, 2012). In Madeira, *D. suzukii* is already widespread in the island, but seems to be associated to vineyards where it can be found in low to moderate abundance. This species was most probably introduced in Madeira following the importation of contaminated fruits or plants from mainland Portugal or Spain, which are the main sources of commercial traffic to the archipelago. In Madeira, *D. suzukii* benefited from human-assisted dispersal to spread rapidly throughout the island. The great improvements on Madeira road network made during the last decade, including the construction of many road tunnels, eased considerably the transportation of people and goods to remote areas of the island and also contributed to a significant increase in traffic. Consequently, exotic species, like *D. suzukii*, can be accidentally

transported jointly with commodities to distant locations soon after their arrival on the island. The invasion of Madeira by *D. suzukii* seems to be quite recent since these are the first records of its occurrence after being detected by an early warning system for introduced species managed by the regional agriculture services. The lack of reports on increased economic losses in fruit production during previous years also seems to support our assumptions of a quite recent arrival of *D. suzukii* in Madeira. A study carried out in Trentino (Italy) showed that following the introduction of *D. suzukii*, soft fruit production economic losses have escalated from 0.5 million euros in 2010 to over three million euros in 2011, not considering the management costs of control strategies and societal impacts (De Ros *et al.*, 2013). The impacts of *D. suzukii* on the environment are still poorly understood, but the finding of oviposition on wild hosts (Grassi *et al.*, 2009) clearly highlights a potential negative role on plant reproduction since fruit dispersers generally tend to avoid damaged fruits (García *et al.*, 1999). Since a considerable number of Madeira endemic plants potentially threatened by *D. suzukii* are dispersed by frugivorous birds (e.g. *Rubus grandifolius*, *R. vahlilii*, *Sambucus lanceolata*, *Sorbus maderensis*, *Vaccinium padifolium*), a precautionary principle should be carried out by extending population monitoring of this invasive species to natural areas.

The other invasive drosophilid reported from Madeira, *Z. indianus*, was also recorded from several low-altitude locations (0-250 m a.s.l.) in north and south Madeira associated to a variety of flesh fruit cultures (banana, grape, mango, pineapple). In Tenerife (Canary Islands), *Z. indianus* was found to be abundant at lower altitudes in urban and agricultural ecosystems, less abundant in a well preserved coastal xeric vegetation environment and absent from both the laurel and pine native forests (Báez and Ortega, 1980, 1981). Thus, in the two Macaronesian archipelagos, *Z. indianus* is mainly distributed throughout the milder coastal lowlands where fruit cultures provide an abundant and stable food resource. During the last decades, this African species has undergone a considerable range expansion having colonized Asia, Europe, South and North America (e.g. Vilela, 1999; Yassin and Abou-Youssef, 2004; van der Linde *et al.*, 2006; Carles-Tolrá, 2009). This invasive species is known to have negative impacts on native insects, particularly on other drosophilids. According to Galego and Carareto (2005), the larval residues of *Z. indianus* interfere with the viability and development of other drosophilids and may lead to a decrease of their abundance over time. In fact, in many invaded areas *Z. indianus* became the dominant species accounting in some cases for 90% of all the drosophilids collected (Tidon *et al.*, 2003). Thus, if we take in consideration the early colonization of fruits by *Z. indianus*, its local high abundance and the negative effects on the viability of native species, we may conclude that its overall impact on native communities can be quite severe (Tidon *et al.*, 2003; Leão and Tidon, 2004; Galego and Carareto, 2005).

The exotic *Acletoxenus formosus* was found associated with colonies of their whitefly prey in cultivated areas from Madeira and Porto Santo. The larvae of *A. formosus* are predators and may have a significant impact on the populations of their prey (Arzone, 1998). Amongst the potential prey of *A. formosus* in Madeira, there

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are two species of concern: The endemic whitefly species *Bemisia lauracea* (Martin, Aguiar and Pita, 1996) and *Pealius madeirensis* (Martin, Aguiar and Pita, 1996) which are relatively rare and restricted to Laurisilva (Martin *et al.*, 1996). The present lack of records of *A. formosus* from Madeira native habitats make us believe that this species could be confined to urban and agricultural environments, not posing for now a threat to the Madeiran Laurisilva endemic whitefly species, but further studies are needed to confirm this.

The two invasive drosophilid species *D. suzukii* and *Z. indianus* share some characteristics that contribute for their ecological success: both species are very fecund, have a wide host range, show adaptive flexibility and broad physiological tolerance, and have high dispersal capability by benefiting from human assisted transportation (Leão and Tidon, 2004; Cini *et al.*, 2012). Furthermore, the finding of niche shift capability by *Z. indianus* considerably challenges the accurate prediction of its potential distribution in introduced areas through conventional ecological modelling (da Mata *et al.*, 2010), which may in turn compromise the effectiveness of population control actions.

According with our evaluation using the GISS-IUCN impact assessment protocol (Blackburn *et al.*, 2014), *D. suzukii* and *Z. indianus* were both classified as having a moderate impact on natural communities in Madeira since the decline of population densities in some native species could be expected. However, there is some uncertainty associated to these classifications due to the difficulties in evaluating the role of natural ecosystems' resilience to drosophilid species introductions. If these alien species are able to colonize Madeira Laurisilva their ecological impact will be much more severe and some narrow endemics may be in peril. At this stage, the development of a monitoring scheme to assess the distribution and abundance of *D. suzukii* and *Z. indianus* in Madeira is mandatory. The monitoring of invasive species should be performed not only on cultivated areas but also in native habitats, particularly Laurisilva, coupled with a thorough evaluation of their economic impacts in fruit production and potential ecological repercussions. Furthermore, it is also critical to identify the origin and pathways of invasion in order to prevent recurrent reintroductions. These steps are crucial for the comprehension of the invasion process of *D. suzukii* and *Z. indianus* in Madeira archipelago and for the establishment of efficient and effective integrated management strategies.

ACKNOWLEDGMENTS

The authors wish to thank to Direcção Regional do Ordenamento do Território e Ambiente for allowing the use of geographic information, Enésima Mendonça for providing the maps and Martin Hauser for permission to use his photo of *D. suzukii*. CR and MB were supported by Fundação para a Ciência e a Tecnologia grants SFRH/BPD/91357/2012 and SFRH/BPD/86215/2012, respectively.

REFERENCES

- Arzone, A., 1998, *Acletoxenus formosus* a predator of *Trialeurodes vaporariorum*. *Bollettino di Zoologia Agraria e di Bachicoltura*, 30: 55-60.
- Báez, M., Ortega, G., 1980, Notas taxonómicas y ecológicas sobre el género *Zaprionus* (Diptera, Drosophilidae) en las islas Canarias. *Bulletin de l'Institut Scientifique*, 4: 87-94.
- Báez, M., Ortega, G., 1981, Estudio preliminar sobre la dinámica de las poblaciones de drosophilidos en la isla de Tenerife (Diptera, Drosophilidae). *Vieraea*, 11: 77-96.
- Blackburn, T. M., Essl, F., Evans, T., Hulme, P. E., Jeschke, J. M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Wilson, J. R. U., Winter, M., Genovesi, P., Bacher, S., 2014, A unified classification of alien species based on the magnitude of their environmental impacts. *Plos Biology*, 12(5): 1-11.
- Bolda, M., Goodhue, R. E., Zalom, F. G., 2010, Spotted wing drosophila: potential economic impact of a newly established pest. *Agricultural and Resources Economic Update*, 13: 5-8.
- Carles-Tolrà, M., 2009, *Zaprionus indianus* Gupta: género y especie nuevos para la Península Ibérica (Diptera: Drosophilidae). *Boletín de la Sociedad Entomológica Aragonesa*, 45: 316.
- Cini, A., Loriatti, C., Anfora, G., 2012, A review of the invasion of *Drosophila suzukii* in Europe and a draft research agenda for integrated pest management. *Bulletin of Insectology*, 65: 149-160.
- da Mata, R. A., Tidon, R., Côrtes, L. G., De Marco Jr, P., Diniz-Filho, J. A. F., 2010, Invasive and flexible: niche shift in the drosophilid *Zaprionus indianus* (Insecta, Diptera). *Biological Invasions*, 12: 1231-1241.
- De Ros, G., Anfora, G., Grassi, A., Loriatti, C., 2013, The potential economic impact of *Drosophila suzukii* on small fruits production in Trentino (Italy). *International Organisation for Biological and Integrated Control West Palaearctic Regional Section Bulletin*, 91: 317-321.
- Florencio, M., Cardoso, P., Lobo, J. M., Azevedo, E. B., Borges, P. A. V., 2013, Arthropod assemblage homogenization in oceanic islands: the role of indigenous and exotic species under landscape disturbance. *Diversity and Distributions*, 19: 1450-1460.
- Galego, L. G. C., Carareto, C. M. A., 2005, Intraspecific and interspecific pre-adult competition on the neotropical region colonizer *Zaprionus indianus* (Diptera: Drosophilidae) under laboratory conditions. *Bragantia*, 64: 257-262.
- García, D., Zamora, R., Gómez, J. M., Hódar, J. A., 1999, Bird rejection of unhealthy fruits reinforces the mutualism between juniper and its avian dispersers. *Oikos*, 84: 536-544.
- Grant, P. R. (ed.), 1998, *Evolution on Islands*. Oxford University Press, Oxford, UK, 352.
- Grassi, A., Palmieri, L., Giongo, L., 2009, *Drosophila (Sophophora) suzukii* (Matsumura) Nuovo fitofago per i piccoli frutti in Trentino. *Terra Trentina*, 10: 19-23.
- Hulme, P. E., 2009, Trade, transport and trouble: managing invasive species pathways in an era of globalisation. *Journal of Applied Ecology*, 46: 10-18.
- IUCN, 1999, The Laurisilva of Madeira (Portugal). In: Bureau of the World Heritage Committee. IUCN Evaluation of Nominations of Natural and Mixed Properties to the World Heritage List. The 23rd ordinary session of the World Heritage Committee, Paris, France, 106-111.
- Leão, B. F. D., Tidon, R., 2004, Newly invading species exploiting native host-plants: the case of the African *Zaprionus indianus* (Gupta) in the Brazilian Cerrado (Diptera, Drosophilidae). *Annales de la Société Entomologique de France (N.S.)*, 40: 285-290.
- Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000, *100 of the World's worst invasive Alien species. A selection from the Global Invasive Species Database*. 1st edn. The Invasive Species Specialist Group, Species Survival Commission, IUCN, New Zealand, 12.
- Martin, J. H., Franquinho Aguiar, A. M., Pita, M. T., 1996, Aleyrodidae of Madeira: descriptions of three new species, with notes on a pan-Mediterranean species of *Aleurotrachelus*. *Journal of Natural History*, 30: 113-125.

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- Monclús, M., 1984, Drosophilidae of Madeira, with the description of *Drosophila madeirensis* n. sp.. *Zeitschrift fuer zoologische Systematik und Evolutionsforschung*, 22: 94-103.
- Nardon, C., Deceliere, G., Loevenbruck, C., Weiss, M., Vieira, C., Biémont, C., 2005, Is genome size influenced by colonization of new environments in dipteran species? *Molecular Ecology*, 14: 869-878.
- Olden, J. D., 2006, Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, 33: 2027-2039.
- Paulay, G., 1994, Biodiversity on oceanic islands: its origin and extinction. *American Zoologist*, 34:134-144.
- Reaser, J. K., Meyerson, L. A., Cronk, Q., De Poorter, M., Eldrege, L. G., Green, E., Kairo, M., Latasi, P., Mack, R. N., Mauremootoo, J., O'Dowd, D., Orapa, W., Sastroutomo, S., Saunders, A., Shine, C., Thrainsson, S., Vaiutu, L., 2007, Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation*, 34: 98-111.
- Rego, C., Rose, M. R., Matos, M., 2007, Do species converge during adaptation? A case study in *Drosophila*. *Physiological and Biochemical Zoology*, 80: 347-357.
- Sax, D. F., Gaines, S. D., 2008, Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences*, 105: 11490-11497.
- 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. *Biological Conservation*, 112: 299-305.
- van der Linde, K., Steck, G. J., Hibbard, K., Birdsley, J. S., Alonso, L. M., Houle, D., 2006, First records of *Zaprionus indianus* (Diptera, Drosophilidae), a pest species on commercial fruits from Panama and the United States of America. *Florida Entomologist*, 89: 402-403.
- Vilela, C. R., 1999, Is *Zaprionus indianus* Gupta, 1970 (Diptera, Drosophilidae) currently colonizing the Neotropical region? *Drosophila Information Service*, 82: 37-39.
- Westphal, M. I., Browne, M., Mackinnon, K., Noble, I., 2008, The link between international trade and the global distribution of invasive alien species. *Biological Invasions*, 10: 391-398.
- Whittaker, R. J., Fernández-Palacios, J. M., 2007, *Island Biogeography: Ecology, Evolution and Conservation*. 2nd edn. Oxford University Press, Oxford, UK, 416.
- Yassin, A., Abou-Youssef, A. Y., 2004, A new front for a global invasive drosophilid: the colonization of the Northern-Western desert of Egypt by *Zaprionus indianus* Gupta, 1970. *Drosophila Information Service*, 87: 67-68.
- Yassin, A., Capy, P., Madi-Ravazzi, L., Ogereau, D., David, J. R., 2008, DNA barcode discovers two cryptic species and two geographical radiations in the invasive drosophilid *Zaprionus indianus*. *Molecular Ecology Resources*, 8: 491-501.

Received: January 14, 2016

Accepted: March 29, 2016