Bulletin of Entomological Research

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Host plant ranges of fruit flies (Diptera: Tephritidae) in Madagascar

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Research Paper

Cite this article: Rasolofoarivao H, Raveloson Ravaomanarivo LH, Delatte H (2022). Host plant ranges of fruit flies (Diptera: Tephritidae) in Madagascar. *Bulletin of Entomological Research* **112**, 1–12. https://doi.org/10.1017/S0007485321000511

Received: 10 March 2021
Revised: 19 May 2021
Accepted: 14 June 2021
First published online: 20 September 2021

Keywords:
Agroecological regions; altitudinal gradients; fruit flies; host plant; Tephritidae

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Abstract

Agriculture is one of the major farming activities, representing 32% of the gross domestic product of Madagascar and 74.3% of the population is involved in this activity. Fruit flies of the Tephritidae family are considered as the most destructive pests for agriculture in the country, nevertheless, few data exist on host plants and distribution of those pests. In the present study, we address those questions by conducting a large survey between November 2016 and July 2018 across the six agroecological regions of Madagascar. Fruit and vegetable were sampled from 198 plant species (wild and cultivated) and represented 37,965 fruits from all regions of Madagascar. The infestation index ranged from 0.06 to 538.46 pupae/kg, the infestation percentage was up to 54.84% in some samples, 63 plant species were considered as host of Tephritidae. Twelve fruit fly species were identified, seven of which were previously described as endemic, five species could be considered as widespread (altitudinal gradients between 1 and 1634 m asl) and major pests in Madagascar: *Ceratitis malgassa* (23 plant species from 12 families), *Neoceratitis cyanescens* (16 plant species from one family), *Bactrocera dorsalis* (18 plant species from 12 families), *Dacus demmerezi* (ten plant species from one family), *Dacus vertebratus* (six species from one family). Those results are of importance for implementation of control measures.

Introduction

Agriculture in Madagascar is one of the major farming activities owing to the relatively heavy economic value of the products and improving food security (FAO, 2018). The diverse agro - climatic conditions and altitude (from 0 to 2, 876 m asl) enable the year-round production of a wide range of horticultural crops. In Madagascar, fruit and vegetable crops hold a key position in smallholder agricultural production systems due to the number of farmers involved. Agricultural areas represent 70% of the total land area and approximately, around 2 million hectares are cultivated annually (FAO, 2018). Agriculture employed approximately 74.3% of the local population and accounted for 32% of the gross domestic products (GDP) in 2016 (FAO, 2018).

Malagasy farmers do not cultivate fruit crops on a large scale as monoculture. Most fruit trees are cultivated for local markets and are scattered around villages and hamlets, and referred to as 'family agriculture'. More than 40 cultivated species (tropical and temperate) of fruits are grown in Madagascar, of which many species were introduced during the colonial era (Perrier de la Bathie, 1931). Smallholder farmers supply fruits and vegetables consumed in urban regions, most of which are sold through the informal sector. The majority produced is for local consumption. Few species of fruit or vegetables are of great economic significance as export products, such as cocoa *Theobroma cacao* Linnaeus (Malvaceae), coffee *Coffea* Linnaeus sp (Rubiaceae), lychee *Litchi chinensis* Sonnen (Sapindaceae), pepper *Capsicum* Linnaeus sp (Solanaceae) and spices.

Tephritidae are considered as one of the most destructive pest in horticulture in the continental island. Thirty-two species of frugivorous Tephritidae (De Meyer, 1998; De Meyer *et al.*, 2012) belonging to six genera were recorded from Madagascar: *Carpophthoromyia* Austen (one species), *Ceratitis* MacLeay (ten species), *Neoceratitis* Hendel (two species), *Bactrocera* Macquart (three species), *Dacus* Fabricius (11 species) and *Trirhithrum* Bezzi (five species). In addition to representatives of these main frugivorous genera, there are also other species belonging to lesser important genera: *Celidodacus madagascariensis* Hering, *Taomyia marshalli* Bezzi, *Taomya mauritiana* sp. nov., *Taomyia ocellata* Lamb and *Taomyia pictipennis* Hancock. Nevertheless, among this vast diversity, only four species are considered economically important. It includes three native species, *Ceratitis malgassa* Munro, *Neoceratitis cyanescens* Bezzi, *Dacus demmerezi* Bezzi (Dubois, 1965) and one exotic species *Bactrocera dorsalis* Hendel (Raoelijaona *et al.*, 2012). The Malagasy fruit fly species *C. malgassa* is endemic to Madagascar (De Meyer *et al.*, 2012). *Neoceratits cyanescens* a major

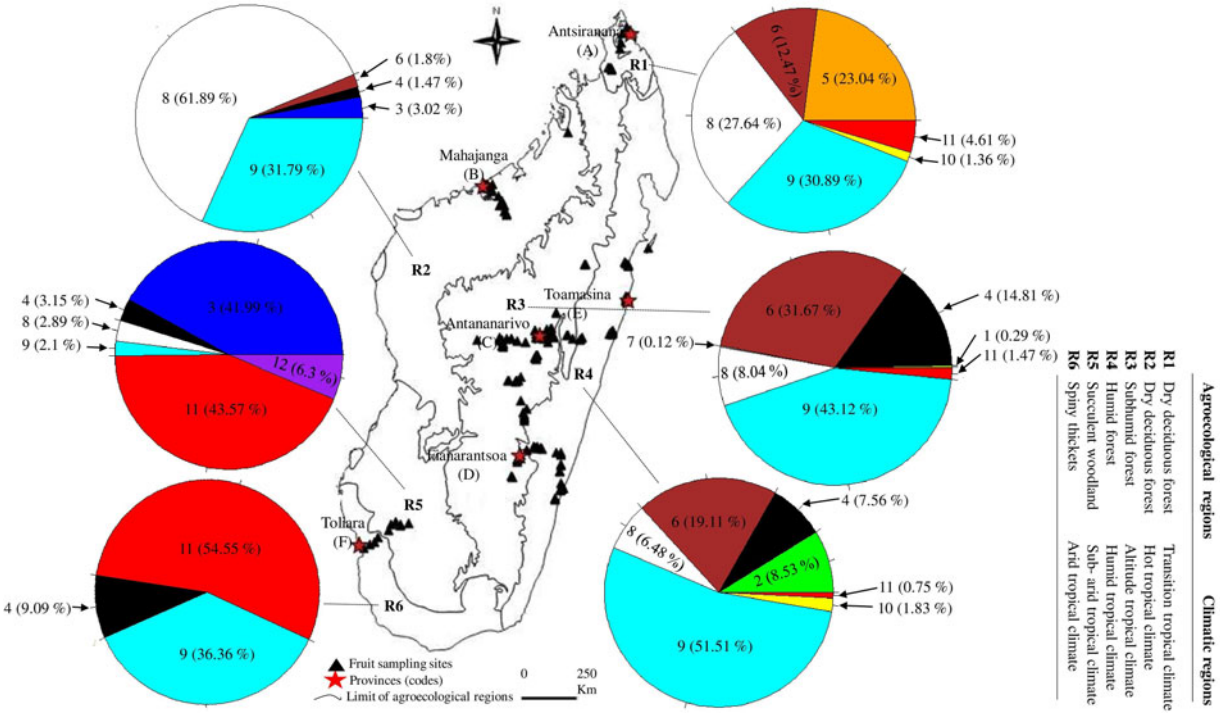

Figure 1. Proportion (% of adults) and geographic distribution of Tephritidae species across agroecological and climatic regions of Madagascar. (1) *C. argenteostriata*, (2) *C. capitata*, (3) *C. cosyra*, (4) *C. malgassa*, (5) *C. pedestris*, (6) *N. cyanescens*, (7) *T. crescentis*, (8) *B. dorsalis*, (9) *D. demmerezi*, (10) *D. quilicii*, (11) *D. vertebratus*, (12) *D. xanthaspis*.

pest of Solanaceae and *D. demmerezi*, the Indian Ocean cucurbit fly, are probably native of Madagascar and were probably introduced from Madagascar to the Mascarenes (Etienne, 1982).

The invasive oriental fruit fly, *B. dorsalis*, previously recognized as *Bactrocera invadens* Drew, Tsura & White was first detected in Madagascar in 2010 near Toamasina (Raoelijaona *et al.*, 2012). This species was recorded in Africa mainland since 2003 (Lux *et al.*, 2003). Soon after its discovery in Kenya, *B. dorsalis* spread throughout Africa, as well as in the Indian Ocean Islands nearby Madagascar, where it was recorded in Comoro islands in 2005, then Mayotte in 2007 (De Meyer *et al.*, 2009, 2012). Other exotic polyphagous Tephritidae of major economic impacts are present on the island, most of the records date back from the 1950s such as the mango fruit fly *Ceratitis cosyra* Walker and the Mediterranean fruit fly *Ceratitis capitata* Wiedemann (Dubois, 1965; De Meyer, 2000).

Fruit production losses by *C. malgassa* were previously estimated between 70 and 80% on plum *Prunus domestica* Linnaeus (Rosaceae), 80% on peach *Prunus persica* Linnaeus (Rosaceae) 'paiso gasy' variety, and 70% on citrus *Citrus* Linnaeus sp (Rosaceae) (Dubois, 1965). The only recent survey made was done by the local extension services (DPV, Direction de la Protection des Végétaux) that estimated direct damages due to *B. dorsalis* to reach up to 50% of the commercial production in five regions of Madagascar (Raoelijaona *et al.*, 2012), but nothing more precise had been conducted in the other regions of the country.

Despite the presence of fruit fly pests and quarantine species on the island, few studies have examined their ecology and distribution. Previous inventory results provided a list of Tephritidae species from Madagascar most often made by trapping systems or fruit surveys on a very small part of the country (Dubois, 1965; Hancock, 1984; De Meyer *et al.*, 2012). The aim of this study was to obtain data on the host plant ranges, diversity and geographic distribution of all frugivorous tephritids throughout the different agroecological regions.

Materials and methods

Ecology and climatic conditions of the sampled regions

Madagascar (covering an estimated area of 592,000 km^2) is a continental island situated in the Indian ocean separated from the east of Africa by the Mozambique Channel (about 400 km away). The country is divided into seven agroecological and climatic regions (R1–R7, fig. 1) ranging from humid eastern lowland forest to spiny thickets in the south west. The seventh agroecological zone (R7) is a mangrove covering around 320,000 ha (Iltis, 1995). The Highland stretches from the North to the South along more than 1000 km and occupies the interior of the island above 800 m asl of altitude. The climate is subtropical with a hot and rainy season between November to March (austral summer) and a cooler dry season from April to October (austral winter). Climate varies from one region to another (fig. 1). The day temperature varies from 5.5 °C (winter, on Highland) to 41.5 °C (summer in the South west lowlands), the minimum night temperature can reach −1 °C (during winter, but rarely) in the Vakinankaratra region. Annual rainfall ranges from 350 to 3500 mm. Administratively, Madagascar is divided into six provinces (fig. 1) which are subdivided into 22 regions, about 119 districts and 800 municipalities.

Fruits and vegetables areas in Madagascar

Fruit and vegetable crops are distributed across all regions of Madagascar. Most fruit species can be grown on the Highland

https://doi.org/10.1017/S0007485321000511 Published online by Cambridge University Press

due to the subtropical climate. The most common fruit species grown in the region of Analamanga (Highland) are Japanese persimmon *Diospyros kaki* Thunberg (Ebenaceae), guava *Psidium guajava* Linnaeus (Myrtaceae), loquat *Eriobotrya japonica* (Thunberg) Lindley (Rosaceae), goldenberry *Physalis peruviana* Linnaeus, (Solanaceae). The temperate fruits are mostly cultivated in Vakinankaratra region (Highland) such as strawberry *Fragaria* Linnaeus sp (Rosaceae), apple *Mallus domestica* Borkhausen (Rosaceae), apricot *Prunus armeniaca* Linnaeus (Rosaceae), plum *P. domestica*, peach *P. persica* and pear *Pyrus communis* Linnaeus (Rosaceae). Grapes *Vitis vinifera* Linnaeus (Vitaceae) grown for wine production are mainly cultivated in Ambalavao (Fianarantsoa region, middle altitude). The eastern coastal region (Toamasina) is suitable for all tropical fruits, including bullock's heart *Annona reticulata* Linnaeus (Annonaceae), sugar-apple *Annona squamosa* Linnaeus (Annonaceae), jackfruit *Artocarpus heterophyllus* Lamarck (Moraceae), banana *Musa* Linnaeus sp (Musaceae), citrus species *Citrus* sp, lychee *L. chinensis*. Production of papaya *Carica papaya* Linnaeus (Caricaceae), banana *Musa* sp (available all year-round) and citrus *Citrus* sp are found both on the Highland and on the coast. The western and north west regions (Mahajanga, Antsiranana) has spontaneously cashew nut *Anacardium occidentale* Linnaeus (Anacardiaceae), mango *Mangifera indica* Linnaeus (Anacardiaceae), marula *Sclerocarya birrea* (A. Richard) Hochstetter (Anacardiaceae), jew plum *Spondias dulcis* Solander ex Parkinson (Anacardiaceae), tamarind *Tamarindus indica* Linnaeus (Fabaceae), monkey orange *Strychnos spinosa* Lamarck (Loganiaceae), common jujube *Ziziphus jujuba* Miller (Rhamnaceae), lemon *Citrus limon* (Linnaeus) Burman (Rutaceae) and others species of citrus *Citrus* sp. The main mango production areas are the western (Mahajanga), northern (Ambanja, Ambilobe) and southern (Toliary) regions. The south area is dominated by the wild marula *S. birrea* and especially the cactus *Opuntia* Miller sp (Cactaceae).

The family of Cucurbitaceae is represented by 27 genera of which eight are endemic (Keraudren-Aymonin, 1966). Cultivation of cucurbits is practiced throughout the island with native seeds and available throughout the year. The south and west regions are very poor in vegetable crops, most of the production is made on the Highland. Cucurbitaceae are the main crops that are often intercropped with root crops and fruit trees. The Solanaceae, such as tomato *Lycopersicum esculentum* Miller (Solanaceae) and varieties of peppers are grown everywhere but mainly in the province of Antananarivo and Antsiranana and grown throughout the year.

Sampling sites and sampling fruits surveys

Fruit sampling was carried out from November 2016 to July 2018. Sampling covered all the different regions and agroecological zones of the island. Fruits of cultivated and wild plant species were collected from fields, orchards and wild areas and sites were chosen because of their accessibility (supplementary table S1).

Species fruiting period varies during the year. In order to maximize the number of different fruit species sampled, sampling were repeated twice or three times per year across the six agroecological regions. All sites were georeferenced with a GPS device (Garmin©). A sampling point (indicated by black triangle in fig. 1) corresponds to a location or site; two locations are at least 1 km apart. The number of fruits collected per sample was according to fruit availability and abundance during the sampling period. Fruits were sampled randomly in each site, most of them were collected from trees and only a few, very recently fallen (less than a day, as not rotten), were collected on the ground. Then, they were individually weighed and placed separately in perforated tagged transparent plastic bags. In order to avoid damage on fruits (or larvae inside the fruit that would need to pupate during the fruit transport to the lab) during transport, each bag was filled with sand at the bottom.

Fruit fly rearing

All samples were transported to the rearing unit at the DPV laboratory of Antananarivo, where they were labeled, and individually transferred to incubation buckets. Small size fruits of less than 5 g in weight were grouped together in batches and placed in plastic buckets covered by fine mesh (11 cm × 6 cm, diameter × depth). Larger fruits were kept in individual buckets (26 cm × 11 cm, diameter × depth). All fruits were weighed, counted and noted. The bottom of each incubation bucket was filled with a 2 cm layer of river sand, so that the last stage larvae could easily drop into the sand and pupate. Every 3 days, the sand was sieved to collect pupae. Pupae were then placed in small hatching cups covered by tissue with a moist cotton inside. The number of newly emerging fruit flies was recorded for all fruits; this procedure was repeated until no pupa was collected during approximately about 6 weeks after field sampling. Rearing was held at room condition.

Fruit fly and host plant identification

All adults were counted, sexed, and preserved in 96% ethanol for later identification. Different types of morphometric keys were used to identify the emerging fruit fly species, White and Elson-Harris (1992), De Meyer (2000) and Virgilio *et al.* (2014) accessed online (http://keys.lucidcentral.org/keys/v3/fruitflies/). In case of any doubts, sample specimens were sent to RMCA (Royal Museum of Central Africa, Belgium) for confirmation under the help of Dr M. De Meyer.

At the same time of sampling, photographs of tree, leaves, fruit and if possible inflorescences were taken for plant specimen identification. Indigenous plant species were identified by botanical expert using photographs and herbarium at the Biologie et Ecologie Végétale laboratory (University of Antananarivo). Botanical plant names corresponded to those found in the 'Catalogue of the vascular plants of Madagascar' (Phillipson *et al.*, 2006).

Infestation level

Two parameters were evaluated for all the sampled fruit fly species. The infestation index was determined as the number of adult or pupa per kg of fruit, a fruit was considered infested when at least one pupa was found. The incidence was evaluated as the number of positive fruits per 100 (% F+ or infestation percentage) of incubated fruit samples, in this case, one sample was equal to one fruit incubated. Incidence was not calculated for small size fruits which were held together in batches and did not allow to have a precise incidence evaluation.

Statistical analysis

Statistical analysis was performed on the interaction between host plants, altitudes, provinces, agroecological and climatic divisions on the distribution and diversity of fruit fly species on the island. To visualize the web interaction between fruit fly species and host plant species, a network was drawn with 'plotweb' function in the

https://doi.org/10.1017/S0007485321000511 Published online by Cambridge University Press

package 'bipartite' (Dormann *et al.*, 2009). Altitudinal gradients were divided into three classes: low altitudes from 0 to 499 m asl, medium altitudes from 500 to 1000 m asl, high altitudes over 1000 m asl.

Incidence and infestation indexes were used to compare infestations level in different fruit species. Analysis of variance (ANOVA) was performed using the general linear model (glm function, quasipoisson family, link identity) procedure and mean separations were done using the Chi square test (Chisq function).

All the statistical analyses and graphs (all at 5% threshold) were performed with R software version 3.5.1 (R Core Team, 2018).

Results

Host range of fruit flies

Over the sampling period, 37,965 fruits in total, weighing 636.92 kg were collected from 198 plant species belonging to 59 families. A total of 191 georeferenced sites were sampled across six agroecological regions, with 8 sites in R1, 25 sites in R2, 83 sites in R3, 60 sites in R4, 7 sites in R5, and 8 sites in R6, respectively (fig. 1, supplementary table S1). Sample size consisted of two to 3401 fruits per plant species (supplementary table S2). The incubation of these fruits produced 10,302 pupae from which emerged 6021 fruit flies (table 1) corresponding to a rate of adult emergence of 58.42%.

Among the 198 plant species (18,285 cultivated fruits and 19,680 wild fruits) inventoried, 63 species were identified as hosts for fruit fly species (table 1). Nevertheless, there was a significant difference (Deviance = 413,766, Df = 62, $P < 2.2 \times 10^{-16}$) between the number of pupa recovered from the 63 host plant species. Abundance of host plant varied from four to 41 host plant species and from three to seven fruit fly species between agroecological regions (fig. 1, supplementary table S2).

The infestation index ranged from 0.06 (*Artocarpus altilis* (Parkinson) Fosberg (Moraceae)) to 538.46 (*Solanum tuberosum* Linnaeus (Solanaceae)) pupae/kg. Among the 5627 samples incubated, 1085 were positive for fruit fly emergence, in some samples up to 54.84% (*Solanum muricatum* Aiton (Solanaceae)) tested positive for fruit flies (table 1).

No adult fruit fly was obtained from pupae of some plant species such as *A. squamosa*, *A. altilis* and *Capsicum frutescens* Linnaeus (Solanaceae) (table 1).

Ten plant species (*Xylopia* Linnaeus sp (Annonaceae), *Dracaena reflexa* Lamarck (Asparagaceae), *Citrullus* Schrad sp (Cucurbitaceae), *Cucumis* Linnaeus sp (Cucurbitaceae), *Cucumis* Linnaeus sp1 (Cucurbitaceae), non-identified species (Meliaceae), *Ficus polita* Vahl (Moraceae), *Podocarpus gaussenii* Woltz (Podocarpacae), *Rubus myrianthus* Baker (Rosaceae), *S. tuberosum*) were identified as new hosts to fruit flies, only one of which (fruit of the *S. tuberosum*) is an exotic species (table 1).

A reduced number of pupae was observed from fruit grown for export such as *L. chinensis:* 0.75 pupae/kg, among which only three adults were emerged from 309 fruits incubated (table 1).

Diversity of fruit fly species

In total 12 fruit fly species was identified in our samples; those 12 fruit fly species were collected in different sites and host plants and in different proportions (fig. 1 and 2, table 1, supplementary table S1): *Ceratitis argenteostriata* De Meyer & Freidberg (ten adults), *C. capitata* (79 adults), *C. cosyra* (187 adults), *C. malgassa* (605 adults), *C. pedestris* Bezzi (85 adults), *N. cyanescens* (1341 adults), *Trirhithrum crescentis* Hancock (four adults), *B. dorsalis* (1001 adults), *D. demmerezi* (2362 adults), *D. quilicii* White (22 adults), *D. vertebratus* Bezzi (245 adults) and *D. xanthaspis* Munro (24 adults). Fifty-six (56) adults were not Tephritidae species.

Ceratitis malgassa was retrieved from 12 families and 23 plant species (fig. 2), but none from vegetables. *Bactrocera dorsalis* was recorded from 18 species of 12 plant families (fig. 2), with few records (four species/two families) from vegetable species (one adult emerged from 183 fruits incubated of *Cucurbita pepo* Linnaeus (Cucurbitaceae), two from 245 fruits of *Sechium edule* (Jacquin) Swartz (Cucurbitaceae), 11 from 592 fruits of *L. esculentum*, two from 3401 fruits of *Solanum nigrum* Linnaeus (Solanceae)). *Bactrocera dorsalis* was also found in indigenous wild fruits: a non-identified plant species from Ankarafantsika Park; site B01 (86.96 adults/kg, 20% of positive fruits) and *F. polita* from urban area, site C23 and E34 (63.78 adults/kg, 6.67% of positive fruits).

Mango (*M. indica*, 22.01% of positive fruits) and tropical almond (*Terminalia catappa* Linnaeus (Combretaceae), 16.08% of positive fruits) were highly infested by *B. dorsalis*. Fruits belonging to the family of Myrtaceae such as *Psidium friedrichsthalianum* (Berg) Niedenzu (40% of positive fruits), the citrus *Citrus paradisi* Macfadyen (Rutaceae) (23.08% of positive fruits) and temperate fruits *P. communis* (22.22% of positive fruits) were infested by *C. malgassa* (table 1).

All species of *Dacus* sampled in this study were found in cucurbits species (table 1), such as, *D. demmerezi* found on species of Cucurbitaceae (ten species). Plant species of those families were very abundant on the island and cultivated throughout the year (supplementary table S2). *Dacus vertebratus* was found on six species of cucurbits and *D. xanthaspis* emerged only from a single species of wild cucurbits (*Citrullus* sp).

Neoceratitis cyanescens attacked 16 species, all belonging to the Solanaceae family (fig. 2, table 1).

The other species of Tephritidae were retrieved from a few host plants with short fruiting periods (1–5 months/year excepted *T. catappa* which fruiting throughout the year) in the year (table 1, supplementary table S2): *C. argenteostriata* found in *R. myrianthus* (Mar., June, Nov., Dec.), *C. capitata* only found in two plant species (*Mimusops coriacea* (A. de Candolle) Miquel (Sapotaceae) and *T. catappa*), *C. cosyra* only from the fruits of two Anacardiaceae species (*M. indica* and *S. birrea*), *C. pedestris* in *S. spinosa* (Feb.), *T. crescentis* in *Coffea sp* (Jan., Mars, Apr., July, Nov.), *D. quilicii* in *Luffa cylindrica* Roemer (Cucurbitaceae) (Feb., Apr., June), and *D. xanthaspis* in *Citrullus* sp (Mar. to June).

Geographic distribution of fruit flies

Infestation level varied between 169/191 infested sites (Deviance = 595,235, Df = 168, $P = 2.2 \times 10^{-16}$) and six provinces (Deviance = 55,838, Df = 5, $P = 1.97 \times 10^{-14}$) of sampling. The highest average of pupae/kg was retrieved from sites of the Antananarivo region (in average 66.48 ± 4.34 pupae/kg).

The overall sampling revealed that Tephritidae was spread across the six agroecological and climatic regions (fig. 1). High significant variations for pest infestation levels were observed among altitudinal gradients (Deviance = 49,780, Df = 2, $P =$

https://doi.org/10.1017/S0007485321000511 Published online by Cambridge University Press

Table 1. List of plant species identified as hosts of Tephritidae, infestation level, incidence, diversity and abundance of fruit flies

Host plant species	No. pupae	No. adult	No. pupae / kg	No. fly / kg	*Ceratitis argenteostriata*		*Ceratitis capitata*		*Ceratitis cosyra*		*Ceratitis malgassa*		*Ceratitis pedestris*		*Neoceratitis cyanescens*		*Tirithrum crescentis*		*Bactrocera dorsalis*		*Dacus demmerezi*		*Dacus quilici*		*Dacus vertebratus*		*Dacus xanthaspis*	
					T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+
Mangifera indica	1231	480	12.43	4.85					27	2.56	2	0.43							451	22.01								
Sclerocarya birrea	202	160	32.63	25.85					160	40.91																		
Spondias dulcis	16	6	1.26	0.47							2	1.03							4	1.03								
Annona senegalensis	5	3	0.65	0.39							2	6.67							1	6.67								
Annona squamosa	1	0	0.20	0.00																								
Xylopia sp	1	1	9.01	9.01							1																	
Dracaena reflexa	2	2	6.10	6.10															1									
Terminalia catappa	426	223	109.91	57.53			49	9.09			10	2.80							129	16.08								
Citrullus colochynthis	46	24	7.95	4.15																					24	14.04		
Citrullus lanatus	6	5	0.35	0.29																	4	3.70			1	3.70		
Citrullus sp	235	169	99.79	71.76																	7	4.17			138	54.17	24	4.17
Cucumis sativus	1021	606	43.74	25.96																	542	38.65			64	4.29		
Cucumis sp	47	22	67.05	31.38																	22	33.33						
Cucumis sp1	27	13	5.77	2.78																	3	6.67			10	20.00		
Cucurbita maxima	1202	726	34.47	20.82																	718	32.67			8	1.33		
Cucurbita pepo	1186	667	74.61	41.96															1	0.56	666	46.63						
Luffa cylindrica	32	22	4.67	3.21																			22	6.25				
Momordica charantia	114	63	192.57	106.42																	63	24.14						
Sechium edule	475	334	13.93	9.80															2	0.41	332	31.95						
Trichosanthes cucumerina	11	5	3.72	1.69																	5	21.05						
Diospyros kaki	45	31	4.29	2.96							26	9.09							2	1.14								
Persea americana	4	2	0.29	0.15							2	3.77																
Strychnos spinosa	94	85	24.30	21.98									85	23.08														
Non identified	14	4	304.35	86.96															4	20.00								
Artocarpus altilis	2	0	0.06	0.00																								
Ficus polita	154	90	109.14	63.78															90	6.67								
Psidium cattleyanum	49	32	10.63	6.94							30	12.00							2									
Psidium friedrichsthalianum	20	13	16.46	10.70							13	40.00																
Psidium guajava	641	421	22.52	14.79							230	14.40							182	7.82								

(*Continued*)

Table 1. (*Continued.*)

Host plant species	No. pupae	No. adult	No. pupae / kg	No. fly / kg	*Ceratitis argenteostriata*		*Ceratitis capitata*		*Ceratitis cosyra*		*Ceratitis malgassa*		*Ceratitis pedestris*		*Neoceratitis cyanescens*		*Trirhithrum crescentis*		*Bactrocera dorsalis*		*Dacus demmerezi*		*Dacus quilici*		*Dacus vertebratus*		*Dacus xanthaspis*	
					T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+	T	% F+
Syzygium jambosa	33	21	11.65	7.42							21	9.20																
Syzygium malaccense	1	1	0.42	0.42							1	1.75																
Averrhoa carambola	6	1	0.76	0.13							1	0.75																
Podocarpus gaussenii	20	17	14.15	12.03							17																	
Eriobotrya japonica	283	171	25.25	15.26							71	3.87							98	9.79								
Mallus domestica	26	10	9.15	3.52							10	8.47																
Prunus domestica	4	1	1.82	0.45															1	0.93								
Prunus persica	160	70	19.02	8.32							54	13.53							16	2.94								
Pyrus communis	46	20	13.76	5.98							20	22.22																
Rubus myrianthus	12	10	28.57	23.81	10																							
Coffea sp	5	5	4.63	4.63							1						4											
Citrus paradisi	43	9	5.42	1.14							9	23.08																
Citrus reticulata	97	23	13.95	3.31							19	11.02																
Citrus sinensis	324	65	10.70	2.15							60	6.12							3	0.92								
Litchi chinensis	3	3	0.75	0.75							3																	
Mimusops coriacea	77	30	73.90	28.79			30	17.86																				
Capsicum annum	11	10	9.25	8.41											10	3.25												
Capsicum bacatuum	6	5	28.71	23.92											5	25.00												
Capsicum chinense	6	5	15.71	13.09											5	1.08												
Capsicum frutescens	2	0	7.02	0.00																								
Capsicum sp	11	8	11.59	8.43											8	5.48												
Lycopersicum esculentum	771	558	72.80	52.69											547	27.11			11	0.79								
Lycopersicum esculentum C.	237	175	170.26	125.72											175	27.96												
Solanum betaceum	14	5	4.23	1.51											5	4.60												
Solanum indicum	390	317	118.65	96.44											317	25.17												
Solanum macranthum	27	16	15.24	9.03											16													
Solanum mauritianum	121	85	70.27	49.36											85													
Solanum melongena	59	35	6.48	3.84											35	5.56												
Solanum muricatum	75	40	37.44	19.97											40	54.84												
Solanum nigrum	108	83	73.77	56.69											81				2									

Solanum pseudocapsicum	2	1	17.09	8.55		1
Solanum seaforthianum	2	2	14.60	14.60		2
Solanum torvum	4	4	20.20	20.20		4
Solanum tuberosum	7	4	538.46	307.69		4

T: total number of adult of fruit fly species/host plant.
Fruit flies are ordered alphabetically by family, tribe and scientific name.
Positive fruits (% F+): percentage of infested fruit sample (one sample = one incubated fruit).

2.61×10^{-15}) and agroecological regions (Deviance = 63,564, Df = 5, $P < 2.2 \times 10^{-16}$).

Five species (*C. capitata*, *C. cosyra*, *C. pedestris*, *D. quilicii*, and *D. xanthaspis*) were found only in coastal regions at altitudes below 500 m asl (figs 1 and 3). *Ceratitis capitata* was limited mainly on three sites (E18, E22, E38) from eastern warm and humid coast, the third site E38 was situated in Sainte-Marie Island. *Ceratitis cosyra* and *D. quilicii* were found below 500 m asl of altitude in two distinct climatic and agroecological regions; *C. cosyra* was distributed in R2 (site B14 of mango orchard) and R5 (site F02, F05 and F06) where climates are dry and sub-arid, and altitudes are ranking from 20 to 465 m asl; *D. quilicii* was found in sites R1 (A07 at 336 m asl) and R4 (E20 at 20 m asl) with dry and humid climates, respectively. *Ceratitis pedestris* was found in site (A08) from northern dry region at altitude 37 m asl and *D. xanthaspis* in the southern region in the sub-arid climate (site F02) at 465 m asl of altitude.

C. argenteostriata and *T. crescentis* were found only in Highland (Ambatolampy district) at high altitudes (1467 to 1556 m asl) with a tropical altitudinal climate (figs 1 and 3).

The other five species (*C. malgassa*, *N. cyanescens, B. dorsalis, D. demmerezi, D. vertebratus*) were widespread and infested fruits over an altitudinal range of 1–1634 m asl (figs 1 and 3).

Globally, *C. malgassa* and *B. dorsalis* were the two dominant species in fruit crops, their distributions were variable along the altitudinal gradients (Deviance = 9909.3, Df = 2, $P = 1.13 \times 10^{-14}$ and Deviance = 2777.1, Df = 2, $P = 0.01$, respectively). *Ceratitis malgassa* was found in 56 sites and *B. dorsalis* was found in 33 sites of the 191 monitored sites. Highest numbers of *B. dorsalis* were collected at low altitude (3.56% of *C. malgassa* and 29.61% of *B. dorsalis* at altitude ≤500 m asl). In contrast, *C. malgassa* appeared to be dominating at high altitude (15.01% of *C. malgassa* and 8.05% of *B. dorsalis* at altitude >500 m asl).

The species *N. cyanescens* had significatively higher infestation levels at high altitude (altitude ≥1000 m asl) than at lower altitude (altitude ≤500 m asl) (Deviance = 95,995, Df = 2, $P < 2.2 \times 10^{-16}$). Within southern regions (R5 and R6), no adult of *N. cyanescens* was obtained from 339 collected fruits of Solanaceae (fig. 1). *Dacus demmerezi* was found across the country in all regions without distinction (Deviance = 182.55, Df = 2, $P = 0.84$).

Dacus vertebratus occupied all regions (excepted R2) and all altitudinal gradients (from 13 to 1421 m asl) in 12 sites. The total number of adults collected from R5 (164/254 adults) was higher than in other regions (Deviance = 2250.4, Df = 2, $P = 0.02$).

Interaction between fruit fly species

Two or three fruit fly species were found emerging from the same fruit and this was the case of seven fruit fly species from 43 fruits of ten host plant species (fig. 4). The invasive species, *B. dorsalis* shared the same host plant fruit with other polyphagous species (figs 2 and 4): *C. capitata* (*T. catappa*, $n = 2$ fruits), *C. cosyra* (*M. indica*, $n = 9$ fruits) and *C. malgassa* (*D. kaki*, $n =$ one fruit; *P. guajava*, $n = 12$ fruits; *E. japonica*, $n = 6$ fruits; *P. persica*, $n =$ 2 fruits). In those fruits, the infestation indexes by *B. dorsalis* varied between 16.43 and 244.90 adults/kg, higher or equal to those of *Ceratitis* species (from 9.39 to 224.49 adults/kg).

A co-infestation of *C. capitata* and *C. malgassa* was also recorded from two samples of fruits of *T. catappa* with similar infestation indexes, 109.38 adults/kg.

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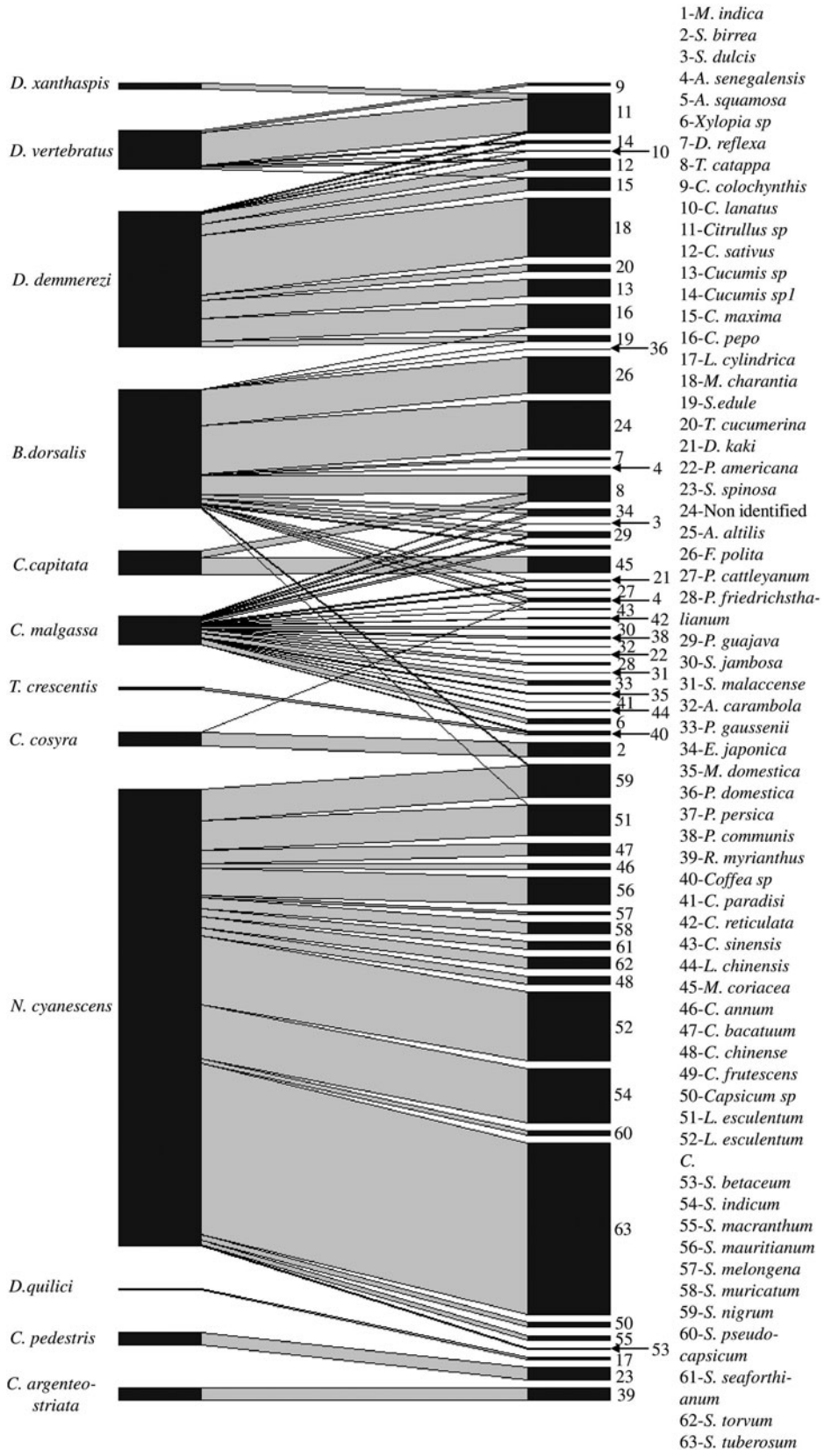

Figure 2. Network of interaction between fruit fly species and host plant species, line thickness represents the total number of adult of fruit flies/kg of fruits.

Dacus demmerezi was found in co-infestation with *D. vertebratus* in four species of Cucurbitaceae ($n = 10$ fruits) and with *D. xanthaspis* in one species (n = one fruit). Generally, *D. demmerezi* was found dominant in cultivated fruits (*Cucumis sativus* Linnaeus (Cucurbitaceae), 38.65% positive fruits) and *D. vertebratus* in wild species (*Citrullus sp*, 54.17% positive fruits) (table 1).

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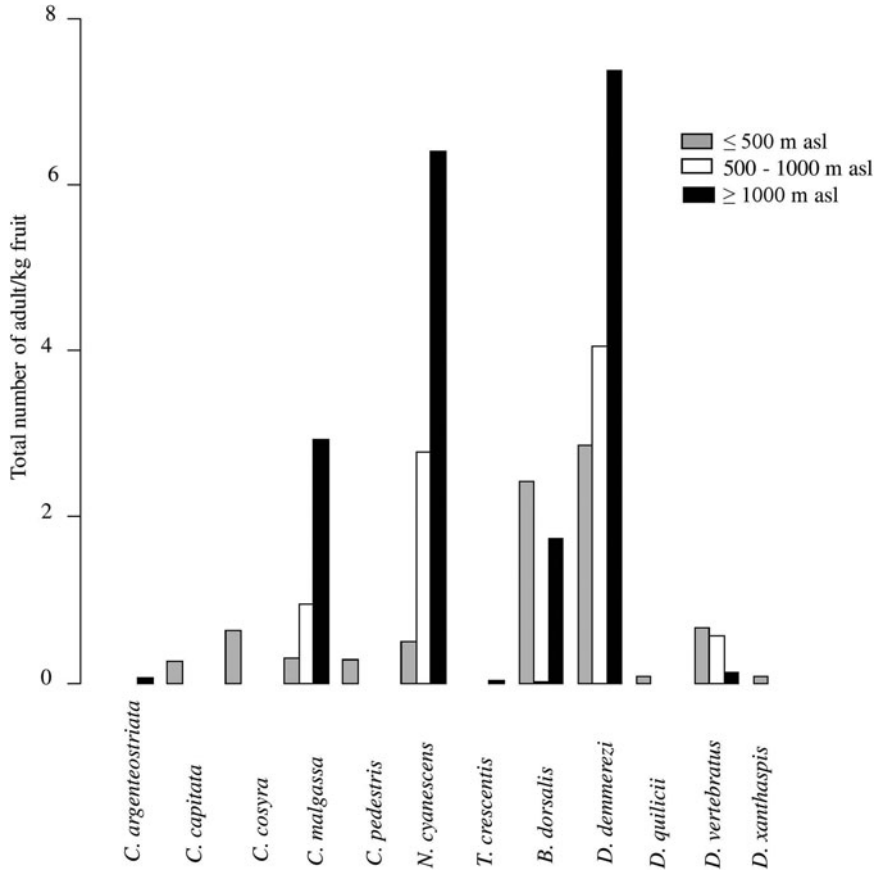

Figure 3. Infestation index (total number of adults/kg of fruits) of each of fruit fly species recorded in all host plant species (pooled data) in relation to the altitudinal gradient.

Discussion

Diversity of frugivorous Tephritidae species in Madagascar

To our knowledge, this is the first study recording host range of Tephritidae of economic importance throughout all agroecological zones of Madagascar. This extensive survey made on 37,955 fruits was able to document 12 fruit fly species and their hosts, seven of which are endemic to Madagascar (*C. argenteostriata*, *C. malgassa*, *N. cyanescens*, *T. crescentis, D. demmerezi*, *D. quilicii* and *D. xanthaspis*) and the five remaining being non-indigenous (*C. capitata*, *C. cosyra*, *C. pedestris, B. dorsalis* and *D. vertebratus*). According to De Meyer *et al.* (2012), the family of frugivorous Tephritidae comprised 32 species in Madagascar with 23 endemic species. The 20 species remaining were not retrieved during our survey as their host plants might not have been sampled, or because they might be rare or highly localized.

A comparison with the results from Afrotropical region suggests that the actual fruit fly diversity may be even lower. Fruit grown for export (*T. cacao*, *Coffea* sp, *L. chinensis*, *Capsicum* sp) were of minor importance as hosts with low infestation rate, with only one species per host plant observed. However, according to White and Elson-Harris (1992), Sub-Saharan Africa is a reservoir of 915 fruit fly species from 148 genera, nearly, 299 of these species are considered as pests by feeding on fruits of economic importance. *Theobroma cacao* and *Coffea arabica* Linnaeus (Rubiaceae) host three species of *Ceratitis* in Kenya with considerable damage (Copeland *et al.*, 2006). Three fruit fly species: *C. capitata*, *C. cosyra* and *C. rosa* Karsch are reported to attack *L. chinensis* in South Africa (Grové *et al.*, 2002); and in La Réunion, *B. dorsalis* and *C. quilicii* De Meyer, Mwatawala & Virgilio were also recorded as a pest on this plant (Moquet *et al.*, 2021). Commercial species of pepper and chilies are known to host *C. cosyra* and *B. dorsalis* in west and central African countries (Goergen *et al.*, 2011; Badii *et al.*, 2015); *C. capitata*, *N. cyanescens* and *B. dorsalis* in some of the islands of the Indian Ocean (Franck and Delatte, 2020).

Host plant use

Among the sampled fruits of the 198 plant species, 63 (31.66%) plant species from 23 plant families were positive to fruit fly, ten of which are indigenous species of the island and nine species are new fruit fly hosts compared with existing records in the Indian Ocean islands and in the world. Within the 99 collected plant species previously recognized as potential hosts of Tephritidae (supplementary table S2), 40 of them were found free of Tephritidae despite repeated sampling. Nevertheless, for some of them, the low number of fruits sampled (no. <10) does not allow any statement on their suitability as hosts in our sampling conditions.

Status of monophagous/polyphagous

Among the 12 species of Tephritidae found in this study, five species were widely found with high infestation indexes and can be considered as major pests in Madagascar: *C. malgassa*, *N. cyanescens*, *B. dorsalis, D. demmerezi,* and *D. vertebratus*.

Because of their wide range of host plants and occurrence on the island, *C. malgassa* (12 families/23 host species), and *B. dorsalis* (12 families/18 host species) can be considered the most

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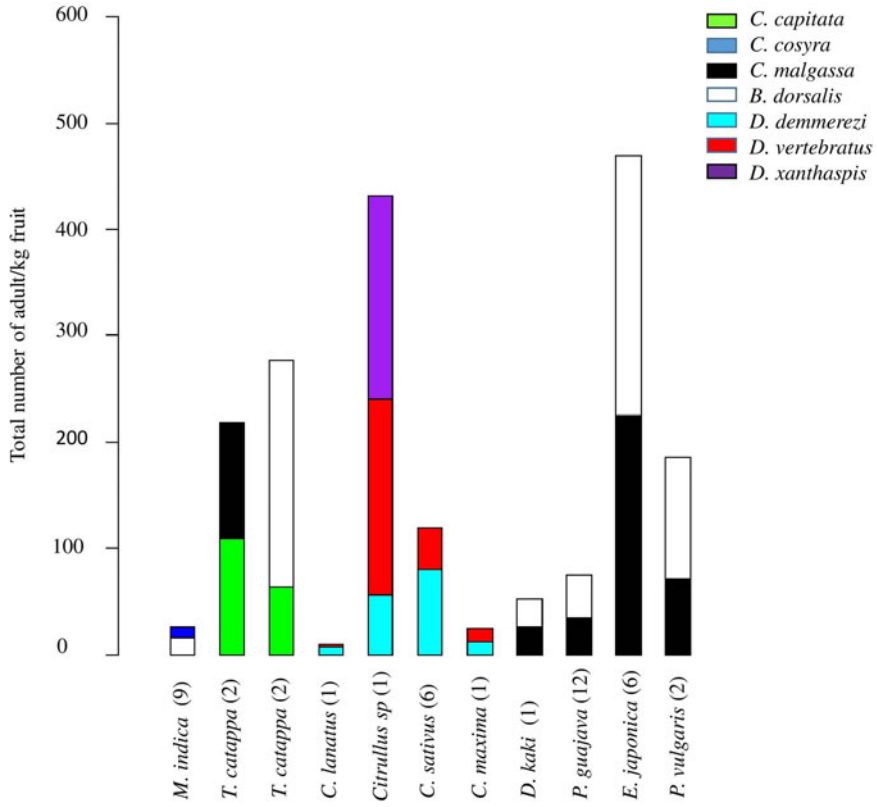

Figure 4. Total number of adults/kg of fruits for fruits of the ten plant species co-infested by two or three fruit fly species. Plants species of fruit and vegetable crops are ordered by family and species name. Numbers of positive fruits per species are presented in brackets.

'polyphagous' species present in Madagascar. *Ceratitis malgassa* is native from Madagascar, it was recorded, but never found in the other Indian Ocean islands (Comoros, Mayotte and Mauritius) (Franck and Delatte, 2020), it could be particularly well adapted to the ecosystems of the island.

Fruit species belonging to major economic crops such as mango (*M. indica*), mostly occurring in low altitudes showed the highest infestation by *B. dorsalis*. Furthermore, temperate fruits, such as apple (*M. domestica*), peach (*P. persica)* and pear (*P. communis*) had very low infestation levels by *B. dorsalis*. *Bactrocera dorsalis* is known as a pest with the broadest host range of any known species of *Bactrocera* genus, Mwatawala *et al.* (2006*a*) have shown that *B. dorsalis* only occurs in low numbers and only during a short seasonal period in the high-altitude areas where temperate fruit species are grown.

Not only exotic crops were found infested by *B. dorsalis* but also a few indigenous species with high rates of infestations showing its capacity to adapt to novel environments and hosts.

Bactrocera dorsalis was also found on cucurbit crops but in low number, confirming that the host status for certain members of the Cucurbitaceae is uncharacteristic of this fruit fly species as observed in Tanzania (Mwatawala *et al.*, 2009). Furthermore, a few adults of *B. dorsalis* emerged from Solanaceae species, which is not corroborated in a study performed in Ghana, where bell pepper (*Capsicum annum* Linnaeus (Solanaceae)) and tomato (*L. esculentum*) were highly preferred by *B. dorsalis* (Badii *et al.*, 2015). Despite its polyphagous trait, *B. dorsalis* preferred fruit crops other than Cucurbitaceae and Solanaceae in Madagascar, and this could be linked to interactions with other fruit fly species present on those crops.

Three fruit fly species could be classified as 'oligophagous', *N. cyanescens* associated with Solanaceae crops, *D. demmerezi* and *D. vertebratus* with Cucurbitaceae crops. *Neoceratitis cyanescens* was found only in Solanaceae species. This fruit fly species invaded also the islands surrounding Madagascar: Mauritius, Comoros, Mayotte and la Réunion, where *N. cyanescens* had been described attacking also only species of Solanaceae (Franck and Delatte, 2020).

Dacus demmerezi, is endemic to Madagascar, it was only found in cucurbits in Reunion Island and Mauritius (Franck and Delatte, 2020; Moquet *et al.*, 2021).

Dacus vertebratus was also only found in cucurbits in our study. Following the wide distribution of *D. vertebratus* (12 sites spread in five agroecological regions) and its large host use of cucurbit hosts (50% of the cucurbits species sampled in this study), this species could be considered as one of the major pest species on cucurbit on the island. *Dacus vertebratus* is also known as an important pest of cucurbits in Africa where it is the dominant fruit fly species attacking water melon and cucumber varieties (Badii *et al.*, 2015).

Four endemic species (*C. argenteostriata*, *T. crescentis, D. quilicii* and *D. xanthaspis*) occurred in relatively low abundances in terms of infestation of fruits (below around 10 adults/kg, excepted for *C. argenteostriata* found in *R. myrianthus*). They also have very narrow host range, with only one host plant species found per fruit fly species, for example, *C. argenteostriata* was found only once on an endemic and wild species *R. myrianthus*, which fruits are mostly eaten by lemurs or birds. For those reasons, these species could be considered as species with lesser economic importance, and are probably 'monophagous' species.

Distribution of fruit fly species

Five species (*C. malgassa*, *N. cyanescens*, *B. dorsalis*, *D. demmerezi*, and *D. vertebratus*) were found in all agroecological regions

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and able of infesting fruits over an altitudinal range of 1 to 1634 m asl. The highest infestations levels were found in Antananarivo, the capital of the island, which might be partly due to human transportation of infested fruits. The capital is very populated, receiving fruits and vegetables from all over the regions. A similar situation is often found for frugivorous pests being moved along with human activities (Putulan *et al*., 2004).

The polyphagous invasive fruit fly *B. dorsalis* was found in the highest number of sites of collected fruit species (33 sites) and has a wide host range (18 host plant species).

Both *C. malgassa* and *B. dorsalis* showed a similar regional distribution, but highest numbers of *B. dorsalis* were collected at low altitude (<500 m asl), while *C. malgassa* appeared to be dominating at higher altitudes (>1000 m asl). Similarly, Vargas *et al.* (1983) demonstrated that fruit infestation by *B. dorsalis* in native and exotic forests on Kauai Island was moderate at middle (579–800 m asl) altitude and low at high altitude (>800 m asl). A similar pattern was found in La Réunion with *B. dorsalis,* dominating all other species, but being less abundant at higher altitudes (Moquet *et al*., 2021).

The majority of minor occurrence fruit fly species (*C. capitata*, *C. cosyra*, *C. pedestris*, *D. quilicii*, and *D. xanthaspis*) were found in the coast region. Geurts *et al.* (2012) observed a spatial increase in diversity and population density of Tephritidae species at lower altitude below (581 m asl) in the Morogoro mountains of Tanzania. Altitude by itself does not determine fruit fly distribution but associated with other factors such as weather and host plants availability play an important role (Mwatawala *et al*., 2006*b*; Geurts *et al*., 2012). Indeed, the diversity of Tephritidae was very poor in the dry southern region (only three species and five host plants recorded) with arid tropical climate and thickets of spiny plants. This very dry weather not allowing constant availability of potential host fruits may have been largely unfavorable for the establishment of a large diversity of fruit fly species.

Ceratitis argenteostriata and *T. crescentis* were collected above 1000 m asl, where the temperature can fall −1 °C at night during the austral winter. Both of these species are endemic of the island and might have developed specific adaptations to this kind of weather. This is the first record of the potential hosts of these two species, indeed no record from host existed for *C. argenteostriata*, it had only been described from trimedlure trapped specimens in Japanese persimmon (*D. kaki*) ochard from the Highland area (De Meyer and White, 2016).

Trirhithrum is an afrotropical genus. Six species are now known from the Malagasy subregion, five of which are restricted to Madagascar (Hancock, 1984). Most of the species of *Trirhithrum* genus are monophagous, which is most probably the case for *T. crescentis*. Indeed, the availability of its main hosts *Coffea* sp was the most important factor contributing to the presence of *T. crescentis* in a given area in Madagascar.

The Strychnos fruit fly *C. pedestris,* was rare in our study on the country, it is widespread in the southern half of Africa, its country of distribution includes Angola, Zambia, Zimbabwe, South Africa and Madagascar and its hosts are various species of the genus *Strychnos* Linnaeus (Loganiaceae) (Hancock, 1984).

Ceratitis capitata, in our case, was only found on two plant species in low numbers from three sites restricted in the eastern region of Madagascar. In many countries this species is often considered as highly polyphagous with almost 400 host plants known worldwide (Liquido *et al*., 1998, 2015; Copeland *et al*., 2002; Moquet *et al*., 2021). This limited distribution range could be due to environmental factors unfavorable to the establishment of this species (Vera *et al*., 2002) and/or to a recent phenomenon of displacement following the invasion of *B. dorsalis* on the island. Unfortunately, we do not have any detailed records of its abundance before the invasion of *B. dorsalis.*

Ceratitis cosyra was found in a few areas at low altitude. However, studies done in Tanzania by Mwatawala *et al.* (2006*b*) have shown that *C. cosyra* was the most abundant species at 781 m asl and 1105 m asl and has also been reported from Kenya at 700 m asl (Rwomushana *et al*., 2008), in equivalent latitudinal ranges. It was demonstrated that the distribution of *C. cosyra*, however, appears to be more related to host plants than climate, following a similar pattern of distribution of their host plant (De Villiers *et al*., 2013). Mango (*M. indica*) are known to be important hosts for *C. cosyra*. When mango is not available, *C. cosyra* shifts to alternative host plants including wild fruits such as marula (*S. birrea*) (Copeland *et al*., 2006).

Co-occurrence between species of fruit flies in sampled fruit

In fruits of which *C. malgassa* and *B. dorsalis* species coexisted, the average number of *B. dorsalis* adults/kg of fruit was higher than that of *C. malgassa*. Those results might indicate the existence of potential interactions between both species. Nevertheless, further experiments in controlled conditions are needed.

In the coastal regions, *B. dorsalis* shared the same host fruit with other pre-established species such as *C. capitata* and *C. cosyra.* Nevertheless, high populations of both *C. capitata* and *C. cosyra* had never been reported, even in the first records made by Dubois (1965), where he mentioned the absence of heavy damage attributed to both species on fruits, but with *C. malgassa* well developed in coast areas. The arrival of *B. dorsalis* might have negatively impacted both species that were already in low abundance.

Conclusion

Madagascar has a wide diversity of plant species that can support indigenous and exotic tephritid fruit fly species. More extensive sampling, targeting specific regions should be considered in order to complete host plant range of Tephritidae on the island, especially for the low abundance species. Five Tephritidae fruit fly species were found in all agroecological regions of Madagascar and considered as major pests of many horticultural crops among which *B. dorsalis* was the most abundant.

The majority of farmers do not apply any control against fruit flies despite the high presence of *B. dorsalis* in fruits (Rasolofoarivao, pers. comm.). Furthermore, little information is available on the natural enemies attacking Tephritidae pests in Madagascar. Historically, many hymenopteran parasitoids (*Dirhinus gifardii* Silvestri (Chalcididae), *Fopius arisanus* Sonan (Braconidae), *Opius concolor* Szépligeti (Braconidae), *Opius longicaudatus* Ashmead (Braconidae), *Opius oophilus* Fullaway (Braconidae)) were introduced into Madagascar from Hawaii for control of *C. malgassa* (Dubois, 1965; Fischer and Madl, 2008) but no updated studies to evaluate their installation or/and impacts on fruit fly populations have been made since their introduction. The future perspective of this study will be to identify native or exotic parasitoid species in order to provide a complete set of potential strategies for future biological control programs.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485321000511

https://doi.org/10.1017/S0007485321000511 Published online by Cambridge University Press

Acknowledgements. The authors are grateful to the master II students (Herinandrasana P. and Rasolofondrainibe T.) from the University of Antananarivo, Département d'Entomologie and Mze Hassani I. from Institut National de Recherche pour l'Agriculture, la Pêche et l'Environnement (INRAPE) Comoros who assisted in the field and laboratory work. We would like to acknowledge the DPV for lending a laboratory to carry out fruit fly rearing. We thank De Meyer M. and Virgilio M. from RMCA, Belgium who gave a valuable support about fruit fly identification. This work was funded by Union Européenne (FEDER INTERREG V), Conseil Régional de la Réunion and CIRAD, under EPIBIO-OI 'EPIdémiosurveillance et BIOcontrole dans le Sud-Ouest de l'Océan Indien' project.

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