

A study on fruit fly host range reveals the low infestation rate of *Bactrocera dorsalis* (Tephritidae) in Mayotte

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Abstract

1. The oriental fruit fly (*Bactrocera dorsalis*) is one of the world's most invasive and polyphagous fruit pests. It causes severe damage throughout its range and can devastate the entire fruit harvest in unprotected orchards. In 2007, *B. dorsalis* was detected in Mayotte, where it now ranks ninth on the list of fruit fly species of economic importance. This tropical island is a good study area to analyse the host range of *B. dorsalis* and its interactions with other resident fruit fly species.
2. Two field campaigns were carried out from 2012 to 2014 and from 2019 to 2021. We collected fruit from all over the island in cultivated and non-cultivated areas and compared the infestation rates between the two periods.
3. We detected six fruit fly species, including the common species *Dacus ciliatus*, *Neoceratitis cyanescens*, *Ceratitis capitata*, *B. dorsalis* and two rarer species, *Dacus etiennei* and *Trirhithrum nigerrimum*.
4. The most surprising result was the low occurrence of *B. dorsalis*, with only seven host plant species identified out of a total of 84 plant species. Infestation rates were low for these host plant species, even in the case of mango (11.71 flies/kg) and Indian almond (0.97 fly/kg), which are considered to be major host plants of *B. dorsalis*.
5. *Bactrocera dorsalis* seems to have a lower impact in Mayotte than in other parts of the world. We discuss the possible causes of the weak infestation rates observed, which could provide the key to regulating the species on the island.

KEYWORDS

biological invasions, food-web network, Indian Ocean, infestation rates, oriental fruit fly

INTRODUCTION

The oriental fruit fly, *Bactrocera dorsalis* (Hendel, 1912), (Diptera, Tephritidae), endemic to the Indo-Asian region, is one of the world's most invasive and polyphagous pests of fruits and vegetables (White & Elson-Harris, 1992). This fruit fly species has the widest host range within the *Bactrocera* genus and has been recorded on more

than 500 host plants (Allwood et al., 1999; Clarke et al., 2005; Liquido et al., 2015). Its extensive host range allows it to sustain populations both spatially and temporally all year round. *Bactrocera dorsalis* causes crop damage, which can have a major economic impact and lead to the loss of export markets. For example, in some cultivated species, such as mango and guava, up to 100% of fruit can be infested (Badii et al., 2015). *Bactrocera dorsalis* is highly competitive and can displace

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ecological niches of pre-established tephritid species, such as *Ceratitis* sp. or other *Bactrocera* sp. (Sauders, 1841) (Duyck et al., 2004; Ekesi et al., 2016; Hassani, 2017; Moquet et al., 2021; Mwatawala et al., 2006; Rasolofoarivao et al., 2021). This species often becomes the dominant generalist fruit fly species in invaded locations. This has occurred on islands in the Indian Ocean, such as Madagascar, Mauritius and La Réunion (Moquet et al., 2021; Rasolofoarivao et al., 2021; Sookar et al., 2021).

In Mayotte, *B. dorsalis* was first recorded in 2007 (De Meyer et al., 2010, 2012), but its host range, infestation rate and interactions with other species have yet to be investigated. In Mayotte, nine species of Tephritidae were recorded, including one endemic to the archipelago, *Dacus etiennellus* Munro, 1984 (De Meyer et al., 2012). Besides *B. dorsalis*, the known invasive fruit fly pests on the island include *Dacus ciliatus* Loew, 1862, which generally infests Cucurbitaceae (Ryckewaert et al., 2010); *Neoceratitis cyanescens* (Bezzi, 1923), which is found on Solanaceae; and the polyphagous species, *Ceratitis capitata* (Wiedemann, 1824) (De Meyer et al., 2012; Franck & Delatte, 2020). Other fruit fly species have been reported in Mayotte, including *Dacus bivittatus* (Bigot, 1858) and *Dacus vertebratus* Bezzi, 1908, on Cucurbitaceae; and *Trirhithrum nigerrimum* (Bezzi, 1913) and *Ceratitis malgassa* (Munro, 1939), which attack a wide variety of different host plant families (De Meyer et al., 2012; Rasolofoarivao et al., 2021).

Agriculture is one of the principal activities in Mayotte. It provides a livelihood for around 60,000 people, a third of the population (DAAF Mayotte, 2021). Local agriculture supplies about 80% of the fresh fruits and vegetables consumed on the island (SISE/DAAF Mayotte, 2017). Most farmers use traditional agricultural and food systems called 'Mahorais gardens'. These are small-scale agroforestry systems, which are multilayered and include various cultural associations (DAAF Mayotte, 2016). These systems often include fruit trees (mango, orange, etc.), fruit and leaf vegetables, roots and tubers, aromatic plants (vanilla, ylang-ylang, etc.), forage plants and other food crops.

Our aim was to identify the host range of fruit flies of economic importance in Mayotte and to determine the diversity of parasitoids that attack tephritid species. We focused particular attention on *B. dorsalis*, the most recent invasive species recorded on the island. To study the changes in fruit fly infestation over time, we compared infestation rates between two periods: 5–7 years and 12–14 years after the invasion of *B. dorsalis*.

MATERIALS AND METHODS

Study region

Mayotte is part of the Comoros Archipelago. It is located in the Mozambique Channel in the Indian Ocean, about 300 kilometres northwest of Madagascar. Mayotte is split into two main islands, Grande-Terre (or Mahoré) and Petite-Terre (or Pamandzi). Mayotte's climate is tropical and humid with two distinct seasons: a warm humid rainy season from December to March (temperature ranges from

24 to 32°C with 70%–95% humidity), and a cooler dry season from June to September (temperature ranges from 20 to 28°C with 61%–90% humidity) (Météo-France, 2022; Appendix S1, Figure S1). These abiotic factors are highly suitable for the development of tropical fruit flies, especially *B. dorsalis* (De Villiers et al., 2015).

Mayotte has very diverse landscapes, and trees constitute a major component, alternating between forests and 'agroforestry' systems. The dense forest cover represents approximately 13,730 ha or 36.7% of the island's total surface area, whereas the primary forests represent only 5% (Lartigue & Boisseaux, 2020; Appendix S1, Figure S2). Although some fruits were collected in natural forests (*Mimusops comoriensis*, *Ficus sycomorus*, etc.), our study was largely conducted in agroforestry systems, where the dominant woody species are jackfruit (*Artocarpus heterophyllus*), breadfruit (*Artocarpus altilis*), African tulip tree (*Spathodea campanulata*), mango (*Mangifera indica*) and coconut palm (*Cocos nucifera*). There are two main types of agroforestry systems: the first combines crops with a more or less dense cover of fruit species and the second combines food or cash crops (vanilla, turmeric, coffee, etc.) with a cover of forest species (Lartigue & Boisseaux, 2020). Pure vegetable systems are less common, particularly located in the central area of the island. Vegetables are generally grown in the dry season, and the main crops include peppers, tomatoes, cucumbers, zucchini and aubergine.

Sampling

We collected fruit during two separate periods from 2012 to 2014 and from 2019 to 2021. Field campaigns covered the two main islands (Grande-Terre and Petite Terre, Figure 1). When possible, samples were collected every week from January 2012 to March 2013, from April 2019 to July 2020, and from March 2021 to July 2021. We scouted the island to collect any soft-skinned fruit. Additional samplings were conducted in July 2013, January 2014 and December 2020. We took samples of any fleshy fruit species, cultivated or wild. In cultivated areas, we favoured non-treated crops. Fruit was randomly collected from trees or from the ground when ripe, which is when they are most susceptible to fruit fly infestation. Cucurbit fruit was collected in the early stage (when the fruit was small and its skin soft), whereas most other fruit was collected when mature. We collected fruit from 28 plant species during the first period and from 74 plant species during the second period (Table 1). Overall, 18 species were the same for the two sampling periods. A total of 1307 fruits were collected between 2012 and 2014, and 6673 fruits between 2019 and 2021. We focused particularly on host plant species of socioeconomic importance: (i) mango (*Mangifera indica*) from the local variety 'Nounou' and from spontaneous germination; and cultivated Rutaceae (*Citrus reticulata* and *Citrus sinensis*), as potential host plants for the generalist species, *B. dorsalis*; (ii) tomato (*Lycopersicon esculentum*), as a potential host plant of the fruit fly that specialises in Solanaceae, *Neoceratitis cyanescens*; and (iii) cultivated Cucurbitaceae (*Cucumis sativus* and *Cucurbita pepo*), as potential host plants for *Dacus ciliatus* and *D. etiennellus*. For mango, two types of samples were

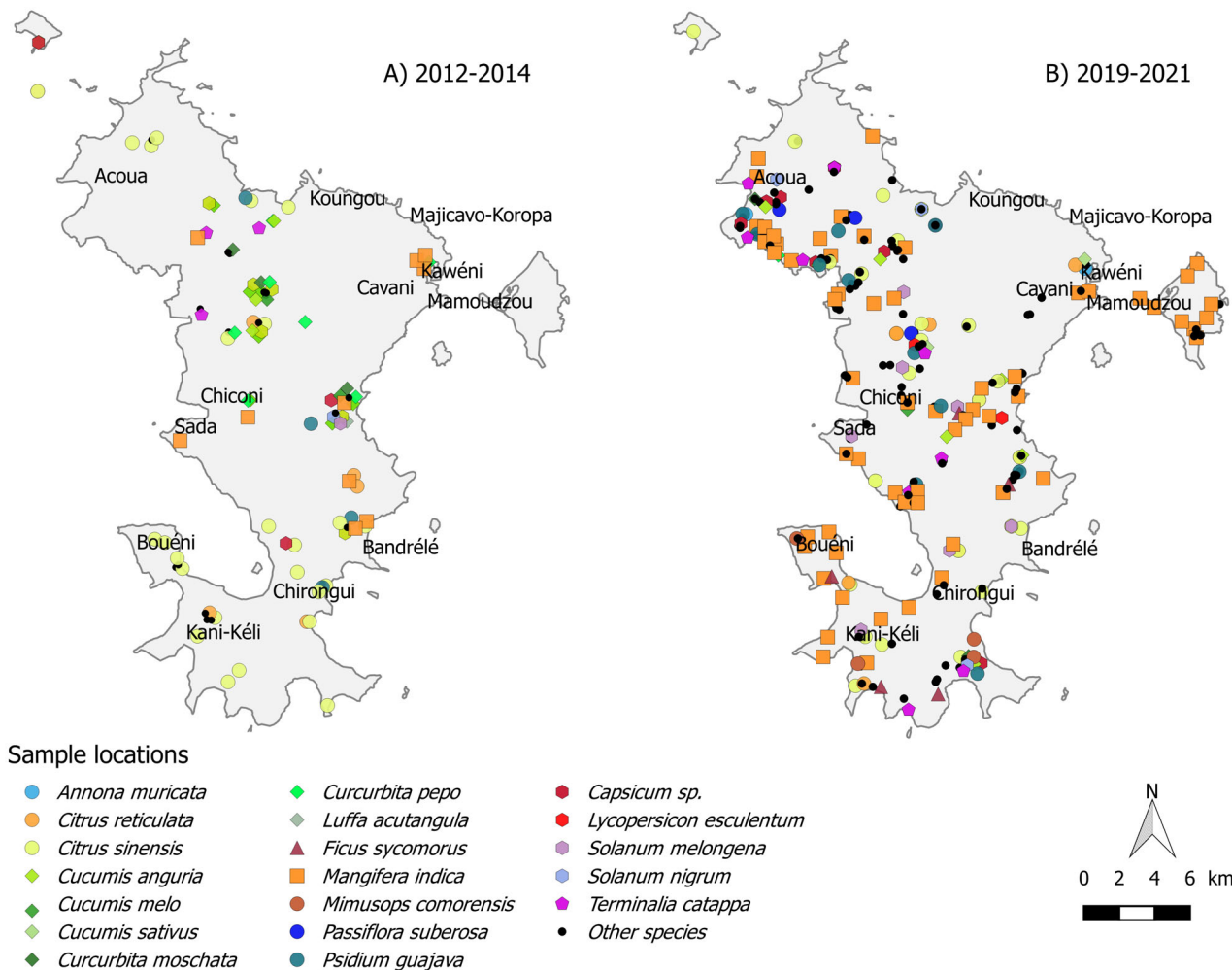


FIGURE 1 Sampling sites for the main plant species collected between (a) 2012 and 2014, and (b) 2019 and 2021.

collected: small immature fruit that had just fallen from the tree (<50 g), and large ripe fruit still on the tree or fleshy fallen (>50 g).

Incubation of fruit samples

In the laboratory, fruits were weighed, placed in plastic boxes with sand as a pupation substrate and covered with fine mesh cloth. We put fruit samples in a maturation room ($28 \pm 2^\circ\text{C}$, $80 \pm 10\%$ RH) until pupation. From 2012 to 2014, fruits from the same species collected on the same date, within the same site, were counted and grouped for weighing and incubation. Since 2019, fruit was weighed and incubated individually. Fruit samples were inspected each week for 3 weeks, and the sand was sifted for pupae. At the end of the incubation period, fruit was opened to check for larvae and pupae. Pupae were kept in a climate room in plastic boxes until fruit flies or parasitoids emerged. Individuals were then sexed and taxonomically identified to species level using morphological characteristics. We calculated the fruit fly infestation rate as the number of individuals per kilogram of collected fruit. Proportions of infested fruits (fruits that allow the development of at least one pupa) were only calculated

for the period 2019–2021, when emergence from individual fruits was recorded. We calculated the parasitism rate as the number of emerged parasitoids over the number of emerged fruit flies.

Comparison of *Bactrocera dorsalis* infestation between the two periods

We compared the infestation rate of *B. dorsalis* for the two sampling periods: 2012–2014 and 2019–2021. We considered the host plant species for which we had enough samples from both collection periods: *C. reticulata*, *C. sinensis*, *M. indica* and *Terminalia catappa*. We used generalised linear mixed effect models (GLMMs), with the period as a fixed effect and plant species as a random factor. Analyses were performed using the R software (R Core Team, 2022).

Network

The function ‘networklevel’ of the ‘bipartite’ package (Dormann et al., 2008, 2009) was used to determine indices describing networks

TABLE 1 Collected plant species in Mayotte during the period 2012–2014 and 2019–2021 to study the Tephritidae host range.

Family	Species name	English name	N		Total weight (g)		Pupae/kg		
			2012–2014	2019–2021	2012–2014	2019–2021	2012–2014	2019–2021	
Anacardiaceae	<i>Mangifera indica</i> ^a	Mango	57	882	16,149	62,065	10.5	18.1	
		Mango small fruits (<50 g)	5	475	15,978	9471	251.5	16.0	
		Mango large fruits (>50 g)	52	407	171	52,594	2.5	18.5	
	<i>Spondias dulcis</i> ^a	Golden apple	0	47	0	4124	–	0	
Annonaceae	<i>Annona cherimola</i> ^a	Cherimoya	0	11	0	142	–	0	
		<i>Annona muricata</i> ^a	Soursop	0	12	0	6398	–	2.5
		<i>Annona reticulata</i> ^a	Custard apple	0	21	0	3510	–	0
		<i>Cananga odorata</i> ^a	Ylang-ylang	0	45	0	212	–	0
Apocynaceae	<i>Petchia erythrocarpa</i>		0	9	0	5.5	–	0	
		<i>Saba comorensis</i> ^a	Bungo fruit	0	45	0	2279	–	0
		<i>Cascabela thevetia</i> ^a	Yellow oleander	0	76	0	932	–	0
Boraginaceae	<i>Cordia myxa</i> ^a	Assyrian plum	0	62	0	137	–	0	
		<i>Ehretia cymosa</i>		0	312	0	121	–	0
Caricaceae	<i>Carica papaya</i> ^a	Papaya	0	69	0	96,812	–	0	
Combretaceae	<i>Terminalia catappa</i> ^a	Tropical almond	41	102	1558	3594	3.2	3.6	
Cucurbitaceae	<i>Citrullus lanatus</i> ^a	Water melon	18	0	2041	0	71.5	–	
		<i>Cucumis anguria</i>	West indian gherkin	12	0	888	0	46.2	–
		<i>Cucumis melo</i> ^a	Muskmelon	14	1	3507	701	36.5	0
		<i>Cucumis sativus</i> ^a	Cucumber	151	16	3463	4044	209.9	9.39
		<i>Cucurbita moschata</i> ^a	Butternut squash	34	41	1056	466	371.2	219.1
		<i>Cucurbita pepo</i> ^a	Zucchini	134	4	3256	2574	401.1	11.3
		<i>Lagenaria siceraria</i> ^a	Calabash	7	0	56	0	857.1	–
		<i>Luffa acutangula</i> ^a	Angled luffa	20	0	343	0	113.7	–
		<i>Momordica charantia</i> ^a	Bitter squash	5	30	30	731	0	28.7
Euphorbiaceae	<i>Jatropha curcas</i>	Physic nut	0	68	0	866	–	0	
		<i>Ricinus communis</i>	Castor oil tree	0	32	0	38	–	0
Fabaceae	<i>Canavalia</i> sp.		0	4	0	121	–	0	
		<i>Cassia fistula</i>	Golden tree	0	15	0	430	–	0
		<i>Pithecellobium dulce</i>	Manila tamarind	0	15	0	194	–	0
		<i>Vigna</i> sp.		0	131	0	31	–	0
Lauraceae	<i>Cinnamomum verum</i>	Cinnamon	0	30	0	15	–	0	
		<i>Litsea glutinosa</i>	Brown bollywood	0	379	0	145	–	0
		<i>Persea americana</i> ^a	Avocado tree	2	15	795	38	0	0
Malvaceae	<i>Cola</i> sp. ^a		0	30	0	1362	–	0	
		<i>Theobroma cacao</i>	Cacao tree	0	4	0	1009	–	0
Melastomataceae	<i>Clidemia hirta</i>	Koster's curse	0	165	0	93.5	–	0	
Monimiaceae	<i>Tambourissa leptophylla</i>		0	1	0	603	–	0	
Moraceae	<i>Artocarpus altilis</i> ^a	Breadfruit	0	5	0	4931	–	0	
		<i>Artocarpus heterophyllus</i> ^a	Jackfruit	0	20	0	5677	–	0
		<i>Morus kagayamae</i>	Japanese mulberry	0	15	0	35	–	0
		<i>Ficus benjamina</i>		0	45	0	21	–	0
		<i>Ficus sycomorus</i> ^a	Sycamore fig	0	104	0	794	–	13.9

(Continues)

TABLE 1 (Continued)

Family	Species name	English name	N		Total weight (g)		Pupae/kg	
			2012– 2014	2019– 2021	2012– 2014	2019– 2021	2012– 2014	2019– 2021
Muntingiaceae	<i>Muntingia calabura</i>	Jamaica cherry	0	15	0	35.5	–	0
Musaceae	<i>Musa</i> sp. ^a	Banana tree	0	12	0	867	–	0
Myrtaceae	<i>Eugenia uniflora</i> ^a	Pitanga	0	27	0	188	–	0
	<i>Psidium cattleianum</i> ^a	Purple guava	0	15	0	91	–	0
	<i>Psidium guajava</i> ^a	Guava	6	58	93	2931	0	36.5
	<i>Syzygium malaccense</i> ^a	Malay rose apple	0	45	0	1519	–	0
Oxalidaceae	<i>Averrhoa bilimbi</i> ^a	Bilimbi	0	131	0	3028	–	0
	<i>Averrhoa carambola</i> ^a	Carambola	2	61	45	2024	0	0.3
Passifloraceae	<i>Passiflora foetida</i>	Bush passion fruit	0	16	0	19	–	0
	<i>Passiflora suberosa</i>	Cork passion fruit	0	30	0	21	–	736.8
Petiveriaceae	<i>Rivinia humilis</i>	Bloodberry	0	45	0	8	–	0
Phyllantaceae	<i>Flueggea virosa</i>	White berry bush	0	195	0	23	–	0
Rhamnaceae	<i>Colubrina asiatica</i>	Asian nakedwood	0	15	0	266	–	0
Rosaceae	<i>Eriobotrya japonica</i> ^a	Japanese medlar	0	15	0	97	–	0
	<i>Rubus alceifolius</i>	Giant bramble	0	15	0	40.5	–	0
Rubiaceae	<i>Coffea</i> sp. ^a	Coffee	0	171	0	671	–	0
	<i>Morinda citrifolia</i>	Indian mulberry	0	27	0	2985	–	0
Rutaceae	<i>Citrus aurantifolia</i> ^a	Lime	0	48	0	1899	–	0
	<i>Citrus hystrix</i>	Kaffir lime	0	26	0	1342	–	0
	<i>Citrus limon</i> ^a	Lemon	32	66	2210	4500	0	0
	<i>Citrus medica</i>		0	4	0	664	–	0
	<i>Citrus reticulata</i> ^a	Tangerine	83	109	8360	10,783	1.7	1.8
	<i>Citrus sinensis</i> ^a	Orange	218	716	31,041	97,814	1.4	0.1
	<i>Citrus sinensis</i> x <i>Citrus limon</i>		18	0	2560	0	0	–
	<i>Citrus x paradisi</i> ^a	Pomelo	1	0	200	0	0	–
	<i>Citrus x tangelo</i> ^a	Tangelo	1	0	65	0	0	–
Sapindaceae	<i>Allophylus bicurris</i>		0	111	0	19	–	0
Sapotaceae	<i>Mimusops comorensis</i>		0	90	0	695	–	214.6
	<i>Mimusops coriacea</i> ^a		0	5	0	189	–	0
Solanaceae	<i>Capsicum</i> sp. ^a	Pepper	35	269	159	466	150.7	195.3
	<i>Lycopersicon esculentum</i> ^a	Tomato	153	126	413	2902	283.3	85.8
	<i>Solanum aethiopicum</i> ^a	Ethiopian nightshade	18	0	148	0	527	–
	<i>Solanum melongena</i> ^a	Eggplant	2	85	55	2211	145.5	28
	<i>Solanum nigrum</i> ^a	Blackberry nightshade	38	95	5	20	2600	0
	<i>Solanum seafortianum</i> ^a	Brazilian nightshade	0	66	0	40	–	0
	<i>Solanum sisymbriifolium</i>	Sticky nightshade	0	15	0	236	–	0
	<i>Solanum torvum</i> ^a	Turkey berry	37	270	43	297	0	0
Verbenaceae	<i>Duranta repens</i>	Golden dewberry	0	232	0	113	–	0
	<i>Lantana camara</i>	Lantana	0	75	0	20	–	0
	<i>Lantana trifolia</i>	Threeleaf shrubverbena	0	45	0	8	–	0

TABLE 1 (Continued)

Family	Species name	English name	N		Total weight (g)		Pupae/kg	
			2012– 2014	2019– 2021	2012– 2014	2019– 2021	2012– 2014	2019– 2021
	<i>Premma serratifolia</i>	Headache tree	0	115	0	10	–	0
Vitaceae	<i>Leea guinensis</i>	Hawaiian holy	0	101	0	39	–	0

Note: N, Number of collected samples; –, No data.

^aHost plants of *B. dorsalis* according to Badii et al., 2015; Franck & Delatte, 2020; Goergen et al., 2011; Moquet et al., 2021; Mwatawala et al., 2006; Ndiaye et al., 2012; Rattanapun, 2009; Rwomushana et al., 2008; Vargas et al., 2007; Zida et al., 2020.

TABLE 2 Infestation rate (number of fly/kg of fruit) of host plants of the Tephritidae of economic importance in Mayotte. Species names are ordered according to their plant family.

Species name	<i>B. dorsalis</i>		<i>C. capitata</i>		<i>D. ciliatus</i>		<i>D. etiennellus</i>		<i>N. cyanescens</i>	
	2012– 2014	2019– 2021	2012– 2014	2019– 2021	2012– 2014	2019– 2021	2012– 2014	2019– 2021	2012– 2014	2019– 2021
<i>Annona muricata</i>	–	0.94	–	0	–	0	–	0	–	0
<i>Citrus reticulata</i>	0	0.19	0	0	0	0	0	0	0	0
<i>Citrus sinensis</i>	0.71	0.05	0	0	0	0	0	0	0	0
<i>Ficus sycomorus</i>	–	18.90	–	0	–	0	–	0	–	0
<i>Mangifera indica</i>	5.14	13.42	0	0	0	0	0	0	0	0
M. indica small fruits (<50 g)	251.46	14.57	0	0	0	0	0	0	0	0
M. indica large fruits (>50 g)	2.50	13.21	0	0	0	0	0	0	0	0
<i>Psidium guajava</i>	0	21.50	0	0	0	0	0	0	0	0
<i>Terminalia catappa</i>	3.21	0	0	0	0	0	0	0	0	0
<i>Mimusops comorensis</i>	–	0	–	429.41	–	0	–	0	–	0
<i>Passiflora suberosa</i>	–	0	–	684.21	–	0	–	0	–	0
<i>Citrullus lanatus</i>	0	–	0	–	29.40	–	2.45	–	0	–
<i>Cucumis anguria</i>	0	0	0	0	24.77	0	0	0	0	0
<i>Cucumis melo</i>	0	0	0	0	17.39	0	2.00	0	0	0
<i>Cucumis sativus</i>	0	0	0	0	98.76	7.67	6.64	0.49	0	0
<i>Cucurbita moschata</i>	0	0	0	0	135.42	214.82	17.99	0	0	0
<i>Cucurbita pepo</i>	0	0	0	0	261.67	11.27	0	0	0	0
<i>Luffa acutangula</i>	0	–	0	–	78.717	–	0	–	0	–
<i>Sechium edule</i>	0	–	0	–	31.26	–	0	–	0	–
<i>Capsicum</i> sp.	0	0	12.56	100.88	0	0	0	0	37.68	10.73
<i>Lycopersicon esculentum</i>	0	0	0	0	0	0	0	0	200.97	65.13
<i>Solanum aethiopicum</i>	0	–	0	–	0	–	0	–	391.89	–
<i>Solanum melongena</i>	0	0	0	0	0	0	0	0	72.73	37.54
<i>Solanum nigrum</i>	0	0	0	0	0	0	0	0	2200.00	0

Note: –, No collection of this fruit was done.

(connectance, links per species, number of compartments, cluster coefficient, nestedness and H2') for each period studied. We tested if the network presented specific patterns or corresponded to what was forecast in the absence of a structuring mechanism, by comparing the indices observed to indices of random webs. Thus, we performed a

t-test using the function 'null.t.test', where the random matrices were based on the function 'r2dtable' (N = 1000). In addition, as explained by Dormann (2022), we also built 1000 null models (function 'nullmodel') and computed indices for each one. We graphically compared the distribution of null-model index values to our observed index

values. We designed the food web for each period with the 'bipartite' package from a matrix of interactions among host plants and emerging fruit fly species.

RESULTS

Tephritidae species richness

Six fruit fly species were collected during the sampling: *B. dorsalis*, *C. capitata*, *D. ciliatus*, *D. etiennellus*, *N. cyanescens* and *T. nigerrimum*. The latter was only observed once on an undetermined fruit on a Solanaceae vine in the 2019–2021 sampling period.

Host range

Potential host fruit was available all year round (Appendix S1, Figure S3). However, in some years of the study (e.g., 2019), less fruit was available for sampling from April to August, probably because of the rainfall deficit (Appendix S1, Figure S1).

Bactrocera dorsalis was observed on seven host plant species (Table 2): soursoup (*Annona muricata*), tangerine (*C. reticulata*), orange (*C. sinensis*), mango (*M. indica*), sycamore fig (*Ficus sycomorus*), guava (*Psidium guajava*) and tropical almond (*T. catappa*). It is worth noting that *B. dorsalis* emerged from tropical almonds during the first sampling campaign, but not in 2019–2021, despite the fact that we collected twice as many samples (Table 1) and took samples on five different occasions (Appendix S1, Figure S3).

Ceratitidis capitata was found in three host plant species belonging to different families: corky passion fruit (*Passiflora suberosa*), Comoros mimusops (*Mimusops comorensis*) and chilli pepper (*Capsicum* sp.).

Dacus ciliatus was observed in all cultivated Cucurbitaceae (*Cucurbita moschata*, *C. pepo* and *C. sativus*), and *D. etiennellus* was found in the fruit of muskmelon (*Cucumis melo*), cucumber (*C. sativus*), squash (*C. moschata*) and calabash (*Lagenaria siceraria*).

Neoceratitidis cyanescens was observed in large numbers on cultivated Solanaceae, such as chilli pepper (*Capsicum* sp.), tomato (*L. esculentum*), Ethiopian nightshade (*Solanum aethiopicum*) and eggplant (*Solanum melongena*).

Infestation rate

There was no significant difference ($z = -1.232$; $p = 0.218$) in the infestation rate of *B. dorsalis* for the two sampling periods (2012–2014 and 2019–2021, Table 2).

Infestation rates and the proportion of fruit infested by *B. dorsalis* varied depending on the host plant. Total infestation rates ranged from 0.10 fly/kg for *C. sinensis* to 20.84 flies/kg for *P. guajava*. In 2019–2020, the proportion of infested fruit ranged from 0.9% for *C. reticulata* to 12.0% for *P. guajava* (Table 3). For *M. indica*, we observed similar results in small fruit (<50 g) and in large fruit (>50 g).

The infestation rate was 11.71 flies/kg and around 5.1% of fruit was infested.

Ceratitidis capitata had a high infestation rate in two wild plant species: *Passiflora suberosa* (684.2 flies/kg) and *Mimusops comorensis* (429.4 flies/kg, Table 2). In 2019–2020, the proportion of infested fruit ranged from 31.3% to 13.0% for *P. suberosa* and *Capsicum* sp., respectively (Table 3).

Dacus ciliatus and *N. cyanescens* had high infestation rates in Cucurbitaceae (from 2.51 to 214.82 flies/kg) and Solanaceae (from 13.67 to 448.98 flies/kg), respectively (Table 2). In 2019–2020, the proportion of fruit infested by *D. ciliatus* ranged from 12.5% for *Cucumis sativus* to 50.0% for *Cucurbita pepo*. For *N. cyanescens*, the proportions of infested fruit were 1.1% for *Capsicum* sp., 30.0% for *S. melongena* and 47.58% for *L. esculentum* (Table 3).

Parasitoids

Only 11 individuals from one parasitoid species were observed in samples from 2019 to 2021. We identified the species *Psytalia insignipennis* using taxonomic criteria. They emerged from six Solanaceae fruit (*S. melongena*) from two sites and probably parasitised *N. cyanescens*. The parasitism rate was 0.3%.

Network

For the two periods studied, we observed three compartments in our networks: (i) one with *B. dorsalis*, (ii) one with *Dacus* species and (iii) one with *C. capitata* and *N. cyanescens*, which only shared one host plant, *Capsicum* sp. (Figure 2). The connectance, the number of links per species and the cluster coefficient were lower than expected with the null model for both networks (Table 4, $p < 0.05$). Nestedness and H2' were higher than expected with the null model for the two networks (Table 4, $p < 0.05$).

DISCUSSION

Our study focuses on the community of Tephritidae species of socio-economic importance between 5 and 14 years after the *B. dorsalis* invasion was reported in 2007 in Mayotte (De Meyer et al., 2012). Our main result shows that the infestation rate of polyphagous fruit fly species, especially *B. dorsalis*, is unexpectedly low in the fruit samples, regardless of the year of collection.

Tephritidae richness and host range

We found six fruit fly species during this study, including four regularly detected species: *D. ciliatus*, *N. cyanescens*, *C. capitata* and *B. dorsalis*. Of the nine species identified on the island in 2012 (de Meyer et al., 2012), *D. vertebratus*, *D. bivittatus* and *C. malgassa* were not observed in our samples.

TABLE 3 Proportion of infested fruits according to fruit fly species and host plants for samples collected in 2019–2020.

Species name	<i>B. dorsalis</i>	<i>C. capitata</i>	<i>D. ciliatus</i>	<i>D. etiennellus</i>	<i>N. cyanescens</i>
<i>Psidium guajava</i>	0.120	0	0	0	0
<i>Annona muricata</i>	0.083	0	0	0	0
<i>Mangifera indica</i>	0.051	0	0	0	0
<i>M. indica</i> small fruits (<50 g)	0.057	0	0	0	0
<i>M. indica</i> large fruits (>50 g)	0.044	0	0	0	0
<i>Citrus reticulata</i>	0.001	0	0	0	0
<i>Ficus sycomorus</i>	0.026	0	0	0	0
<i>Citrus sinensis</i>	0.011	0	0	0	0
<i>Passiflora suberosa</i>	0	0.313	0	0	0
<i>Mimusops comorensis</i>	0	0.187	0	0	0
<i>Capsicum</i> sp.	0	0.130	0	0	0.011
<i>Cucurbita moschata</i>	0	0	0.268	0	0
<i>Cucurbita pepo</i>	0	0	0.500	0	0
<i>Cucumis sativus</i>	0	0	0.125	0.125	0
<i>Lycopersicon esculentum</i>	0	0	0	0	0.476
<i>Solanum melongena</i>	0	0	0	0	0.300

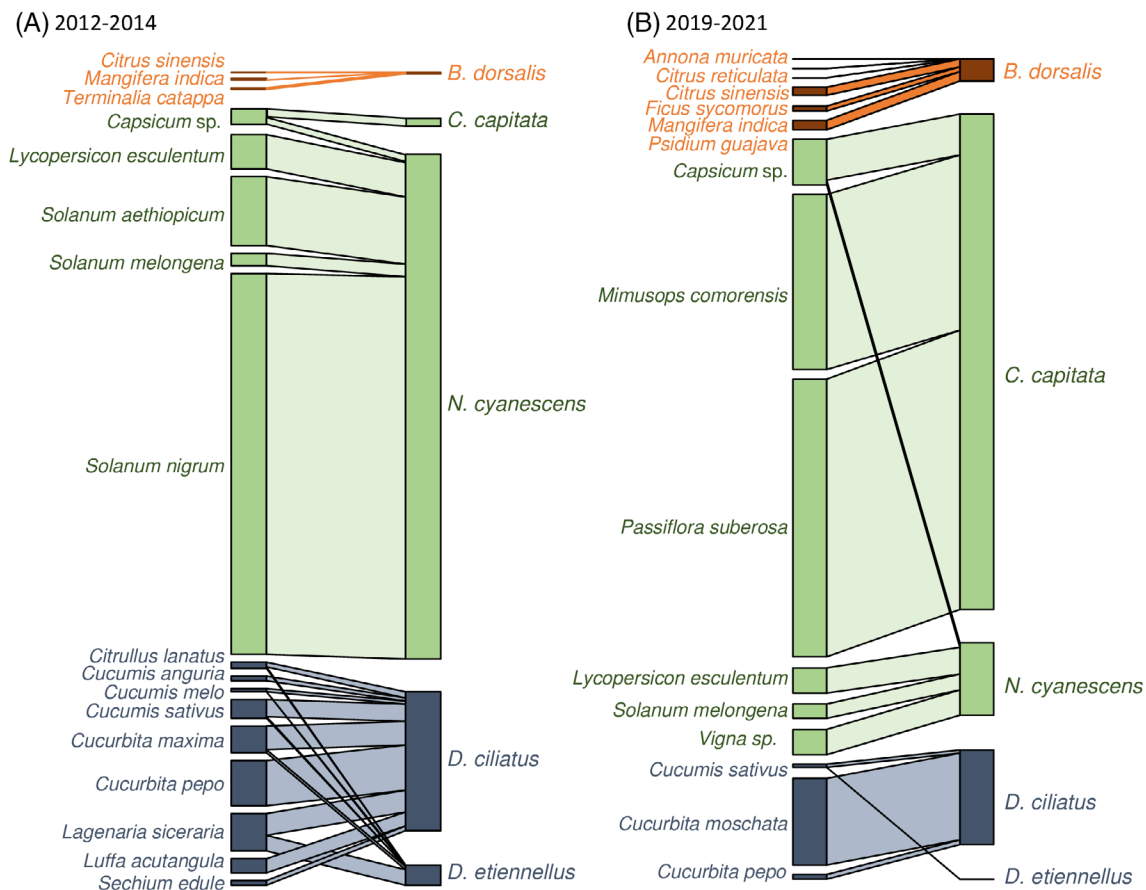
**FIGURE 2** Bipartite network analysis of host–fruit fly associations based on infestation data in Mayotte between (a) 2012 and 2014 and (b) between 2019 and 2021. Edge width is dependent on infestation rate. We represented each network compartment with different colours.

TABLE 4 Network indices calculated from bipartite networks between fruit flies and host plant species in Mayotte between 2012 and 2014 and between 2019 and 2021.

Network indices	2012–2014	<i>p</i> -value	2019–2021	<i>p</i> -value
Connectance	0.27	<0.001	0.26	<0.001
Links per species	1.04	<0.001	0.85	<0.001
Number of compartments	3.00	NA	3.00	NA
Cluster coefficient	0.20	NA	0.20	<0.001
Nestedness	37.9	<0.001	38.3	<0.001
H2'	0.84	<0.001	0.98	<0.001

Dacus ciliatus was observed on Cucurbitaceae. This species is widespread in Africa (De Meyer et al., 2010) and is also present on other Indian Ocean islands, such as Comoros, Mauritius and La Réunion (Hassani et al., 2016; Moquet et al., 2021; Sookar et al., 2021). It was the main species responsible for damage observed on Cucurbitaceae in Mayotte during our surveys. For example, in 2019–2021, almost 25% of squashes were infested by *D. ciliatus*. This species shared host plant species with *D. etiennellus*, which was much less abundant in the host plant species studied. *Dacus ciliatus* remains the fruit fly species with the greatest economic impact in Mayotte because it causes damage to Cucurbitaceae. Control involves heavy chemical pesticide use because there are no effective trapping systems (Alagarmalai et al., 2009; Manrakhan et al., 2017). Trials are being conducted using mechanical methods of protection, such as nets or screenhouses (Vanhuffel & Huat, 2019).

Neoceratitis cyanescens species was observed on Solanaceae with a high level of infestation. Almost 50% of tomatoes were infested by this species, which is the main threat to tomatoes in Mayotte. This oligoleptic species, which originates from the islands in the Indian Ocean, also has a major impact on tomato production in Madagascar and surrounding islands (Hassani et al., 2022; Moquet et al., 2021; Rasolofoarivao et al., 2021; Sookar et al., 2021). As far as *D. ciliatus* is concerned, other agroecological techniques of control must be developed, for example, sanitation and/or nets or screenhouses are being considered.

Two polyphagous species were observed: *B. dorsalis* and *C. capitata*. The first was present in cultivated host plants, such as *M. indica* and *C. sinensis*, while the second was particularly present in wild species, such as *M. comorensis* and *Passiflora suberosa*. Despite the capacity of these two species to infest similar host plants in similar environments (Franck & Delatte, 2020), we did not observe overlapping host ranges in Mayotte. *Bactrocera dorsalis* and *C. capitata* were in a distinct compartment in the bipartite network (Figure 2). This result could be related to the niche partitioning after the *B. dorsalis* invasion or due to other unexplained factors. Interspecific competition and climatic niche partitioning have been documented in several studies, where *B. dorsalis* largely displaced resident *Ceratitidis* species (Ekesi et al., 2009; Hassani et al., 2016; Moquet et al., 2021; Vargas et al., 1995). This could be one of the factors that potentially plays a role in the current host ranges observed for the two species.

The networks of host–fruit fly interactions were highly compartmentalised and specialised with low complexity for the two studied

periods. We observed three compartments: one with *B. dorsalis*, one with *C. capitata* and *N. cyanescens* and one with the *Dacus* species. Consequently, the connectance measuring the proportion of realised interactions, among all the possible interactions in a network, was lower than expected randomly. The H2', a network-level measure of specialisation, was higher than expected randomly. This type of compartmentalised plant–fruit fly web structure was observed in a non-pest Dacine (Tephritidae) in a New Guinea rainforest (Novotny et al., 2005). However, this contrasts with the majority of studies on invasive and agronomic fruit fly pests, where the presence of generalist species appears to induce networks with high connectance (Charlery de la Masselière et al., 2017; Moquet et al., 2021, 2023).

Infestation rate of *Bactrocera dorsalis*

Of the 84 plant species collected during our field sampling, 49 are recorded in the literature as host plants for *B. dorsalis*. However, in our study, only seven were infested by *B. dorsalis*. Observed infestation rates were low, even for fruit species recognised as preferential hosts (>100 flies per kilogram of fruit, Appendix S2), according to Follett's categories (Follett et al., 2021), for example: mango (11.71 flies/kg), guava (20.84 flies/kg) and tropical almond (0.97 fly/kg). Moreover, in 2019–2020, the proportion of infested fruit ranged from 0.9% for tangerine to 12% for guava. For mangoes, the proportion of infested fruit was 5.08%, with similar results on small and large fruit. Our result suggests that the observed impact of *B. dorsalis* was weak compared with other regions invaded by *B. dorsalis* (Appendix S2). In comparison, other studies in the Indian Ocean showed a higher proportion of infested fruits, with 45.5% of mangoes infested in La Réunion (Moquet et al., 2021), 33% in the Comoros (Hassani et al., 2016) and 22% in Madagascar (Rasolofoarivao et al., 2021). Moreover, in our study, we did not observe significant differences in infestation rates between the first and second sampling periods. *Bactrocera dorsalis* populations seemed to stabilise at low incidence during our sampling campaigns (5 and 12 years after the *B. dorsalis* invasion). Many hypotheses, which are not incompatible, could explain these results: (i) poor climatic conditions during sampling, (ii) an equilibrium at low incidence was reached, (iii) a long lag phase before population growth and (iv) invasion by *B. dorsalis* involved a different, potentially less competitive strain than those found on surrounding islands.

Abiotic variables, such as weather parameters, are known to influence *B. dorsalis* population dynamics (Chen et al., 2006; Hassani et al., 2022; Kamala Jayanthi & Verghese, 2011). Previous studies showed positive correlations between *B. dorsalis* population size and rainfall, as well as maximum and minimum temperatures (Kamala Jayanthi & Verghese, 2011; Shukla & Prasad, 1985). Our data do not allow to observe seasonal fluctuations linked to variations in temperature and humidity. Despite a less favourable cold dry season, the temperatures and rainfall recorded by MétéoFrance (temperature between 21.8 and 34°C, rainfall between 0.4 and 479 mm, Appendix S1, Figure S1) seem to correspond to suitable conditions for the development of *B. dorsalis* (De Villiers et al., 2015) and, therefore, do not explain the low infestation rates.

After the expansion stage of a biological invasion event, population densities are supposed to reach an equilibrium, when populations of the invasive species are regulated by interspecific interactions (competition with other fruit flies, natural enemies, etc.), or limited by the carrying capacity of the new environment (Büyükahtakin & Haight, 2018). In our study, the first scenario is less probable because no parasitoids have yet been deliberately introduced into Mayotte. We only detected one indigenous parasitoid species in low abundance (*Psytalia insignipennis* with a parasitism rate of 0.3%), which is not known to infest *Bactrocera* species. Moreover, we noticed the absence of one of the major parasitoid species often used to control *B. dorsalis*: *Fopius arisanus* (Rousse et al., 2005). The competition we observed appeared to be weak. Only *C. capitata*, another polyphagous species, may compete for larval resources. However, this species also had a low infestation rate in Mayotte and we did not observe an overlap in the host range with *B. dorsalis*. Thus, we cannot rule out the possibility that these phenomena could be the result of strong competition shortly after invasion. In La Réunion, for example, competition led to a shift in the host range and spatial distribution of resident fruit fly species less than 2 years after the *B. dorsalis* invasion. Similar observations were noticed before in Madagascar, Comoros, Kenya or Hawaii (Hassani et al., 2016; Keiser et al., 1974; Mwatawala et al., 2009; Rasolofoarivao et al., 2021). Following the invasion, the host range of *C. capitata* was significantly reduced and the species was only found in host plants with small berries, which were rarely infested by *B. dorsalis* (Moquet et al., 2021). Similarly, 5–12 years after the *B. dorsalis* invasion in Mayotte, *C. capitata* was only found in fruit of *Passiflora suberosa*, *Mimosa comorensis* and *Capsicum* sp.

The carrying capacity of the new environment could depend on temporal variations in resource availability. Many studies show a relation between the fruiting period and fruit fly abundance (Abro et al., 2021; Hassani et al., 2016; Tasnin et al., 2021; Theron et al., 2017). Generally, despite a temporary decrease in the population during the season when resources are scarce, the population rises during the fruiting period of the main host plants, especially mango (Bota et al., 2018; Motswagole et al., 2019). Tropical fruit flies have endogenous mechanisms, such as variation in adult longevity and seasonal fecundity to cope with changes in the available breeding resources (Clarke et al., 2022; Tasnin et al., 2021). Thus, although the

decrease in the availability of fruit resources during some parts of the year could influence temporal population dynamics, it is unlikely to explain the overall low infestation rate observed. Indeed, little fruit is available for *B. dorsalis* in Mayotte, even during the favourable periods. We observed that farmers harvested a great deal of fruit before ripening, either because they eat unripe fruit (e.g., banana or mango (Weibel, 1997)), or to prevent human theft and avoid damage by feeding vertebrates (SISE/DAAF Mayotte, 2017). When ripe, the brown lemur (*Eulemur fulvus*, Nègre et al., 2006) or the flying fox (*Pteropus seychellensis comorensis*, Trewhella et al., 2001) eat fruits rapidly, causing considerable losses to farmers (SISE/DAAF Mayotte, 2017). However, this may be good for orchard sanitation, by limiting fruit availability for *B. dorsalis*. It has already been shown that frugivorous predators could be natural enemies of Tephritidae larvae (Drew, 1987). Sanitation is known to be the key to effective integrated pest management (IPM) to control *B. dorsalis* (Vargas et al., 2016). This could partly explain the low infestation rate observed in Mayotte.

Another hypothesis is that *B. dorsalis* has not yet entered the expansion stage of its biological invasion. In some cases, demographic processes can be more complex than the exponential growth of pests after an introduction. There may be a time lag when the exotic species persists in relatively low numbers before population growth (Crooks, 2005). In Tephritidae, a lag phase lasting a number of decades has already been observed for *C. capitata* in a fragmented landscape in Kenya (Copeland et al., 2002). Many mechanisms can account for long lags, such as intraspecific interactions (Allee effect) or genetics (Crooks, 2005). If *B. dorsalis* in Mayotte is in the lag phase, rather than the equilibrium phase, it is important to focus on monitoring population levels to ensure a timely response in the event of a sudden population increase. Lags in population growth and range expansion can impact decision-making processes because the possible consequences of the invasion are underestimated.

We considered a further hypothesis, namely, the genetic origin of the *B. dorsalis* population that invaded Mayotte could be different to that of the population in the Mascarenes (Deschepper et al., 2022). This, combined with the impact of several bottlenecks on the invasive population, could have resulted in the selection of less fit populations (potentially impacted by Allee effects, Stephens & Sutherland, 1999) than those found in other invaded countries. If this is the case, it is important to prevent invasion by a new more virulent *B. dorsalis* strain from other parts of the Indian Ocean.

CONCLUSION

In Mayotte, the infestation rate of *B. dorsalis* was low compared with other regions and had less impact on cultivated species. It is essential to understand why the situation in Mayotte differs from that in other invaded areas. Additional studies are required to test each hypothesis in order to explain the low abundance of *B. dorsalis*. This could provide an important contribution to help manage and regulate the species, which is expanding its geographic range.

AUTHOR CONTRIBUTIONS

Laura Moquet: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Tim Dupin:** Investigation; methodology; writing – review and editing. **Louis Maigné:** Investigation; methodology; writing – review and editing. **Joel Huat:** Conceptualization; funding acquisition; project administration; writing – review and editing. **Thomas Chesneau:** Investigation; methodology; writing – review and editing. **Hélène Delatte:** Conceptualization; investigation; methodology; supervision; validation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest in this publication.

DATA AVAILABILITY STATEMENT

Data are available in CIRAD Dataverse (<https://dataverse.cirad.fr>) <https://doi.org/10.18167/DVN1/HXOZ9Z>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Context of the study of the host range of fruit flies in Mayotte in 2012–2014 and 2019–2021: Meteorological data (Figure S1), land use (Figure S2) and phenology of host plants (Figure S3).

Appendix S2. A literature review of the infestation of *Mangifera indica*, *Psidium guajava* and *Terminalia catappa* by *B. dorsalis* (Table S1).

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