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Niche partitioning via host plants and altitude among fruit flies following the invasion of *Bactrocera dorsalis*

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Abstract

1. Invasions by exotic species in areas already occupied by related species may lead to extinction or niche partitioning. *Bactrocera dorsalis* has invaded the Comoros archipelago in 2005 where other tephritids were already present.

2. The host ranges of fruit flies in the Comoros were studied by conducting a seven-year survey on the three islands of the archipelago with a substantial sampling effort comprising 91 plant species from 37 families.

3. The results showed that 45 fruit species in 16 families were infested by tephritid species. Eight fruit fly species were detected in the sampled fruits, but 78% of the individuals were identified as *B. dorsalis*, confirming its dominance and polyphagous status.

4. More than ten years after its invasion, *B. dorsalis* has replaced *Ceratitis capitata* as the dominant fruit fly species on several species such as mango and citrus. The coexistence between *B. dorsalis* and *C. capitata* seems possible due to the capacity of the latter to exploit different niches, i.e. higher altitudinal ranges and a few host fruit species (among which, chillies and coffee berries) constituting a refuge niche.

5. Information about coexistence between *B. dorsalis* and other tephritids is useful for the management and better estimates of invasion risks and associated biosecurity measures.

KEYWORDS

B. dorsalis, host-plant range, interspecific competition, niche differentiation, Tephritidae

INTRODUCTION

Tephritid fruit flies (Diptera: Tephritidae) are important, worldwide pests because their larval stages consume a wide range of fruit and vegetable crops (White & Elson-Harris, 1992). The extent of losses caused by these pests depends on the tephritid species, the species of fruit or vegetable, and the location (Mwatawala et al., 2009). In the last century in Africa, tephritid damages to fleshy fruits were mainly caused by a limited number of highly polyphagous species, most of them belonging to the genus *Ceratitis* Macleay, such as *Ceratitis capitata* Wiedemann that was reported from 100 host plant species in 30 families in Africa (Copeland et al., 2002).

A number of Tephritidae are well-known for being invasive and have expanded their distribution beyond their native ranges, and many species in the genus *Bactrocera* have invaded areas occupied by native *Ceratitis* spp. (Duyck et al., 2004, 2022). Because of their wide host range and invasive potential, several *Bactrocera* spp. are considered a serious threat to horticultural crops (Clarke et al., 2005). In

Africa, only a few indigenous *Bactrocera* spp. are known, and none is of great economic importance except for the olive fruit fly, *Bactrocera oleae* Gmelin, which is a notorious pest of cultivated olives in the Mediterranean region (Mwatawala et al., 2007; White & Elson-Harris, 1992).

In the last two decades, some species of *Bactrocera* have invaded many African countries and islands (Duyck et al., 2004; Ekesi et al., 2016; Moquet et al., 2021; Rasolofoarivao et al., 2021). Based on phylogenetic and biogeographic data, *Zeugodacus cucurbitae* Coquillett, formerly known as *Bactrocera cucurbitae* (De Meyer et al., 2015), is the oldest case of an Asian species being introduced into Africa (Mwatawala et al., 2007). *Bactrocera zonata* Saunders has probably been in Egypt since the early or mid-twentieth century but was initially misidentified as *B. pallida* (Abuel-Ela et al., 1998). Two other *Bactrocera* spp., *Bactrocera latifrons* Hendel and *Bactrocera dorsalis* Hendel, have recently invaded Africa. *B. latifrons*, which is associated with hosts in the Solanaceae, was recorded in Tanzania in 2006 (Mwatawala et al., 2007). *B. dorsalis*, which was initially described as *B. invadens* (Drew et al., 2005), was first detected in Kenya in 2003 (Lux et al., 2003) and has rapidly spread across the African continent (Manrakhan et al., 2015). Based on similarities in morphology, molecular structure, and chemoecology, as well as on sexual compatibility, *B. invadens* was synonymized with *B. dorsalis* (Schutze et al., 2015).

In Africa, local studies have indicated that *B. dorsalis* is the dominant tephritid on a wide variety of hosts (Ekesi et al., 2006; Mwatawala et al., 2006; Rwomushana et al., 2008) and has high infestation rates on mango and other commercial fruits (Vayssières et al., 2005). In tropical Asia, *B. dorsalis* attacks 124 host plant species in 42 families (Drew, 1989). *B. dorsalis* has been recorded on more than 40 cultivated and wild host plants and causes substantial damage to mango and guava fruits in Africa and Indian Ocean islands (Ekesi et al., 2006; Goergen et al., 2011; Rwomushana et al., 2008; Moquet et al., 2021; Rasolofoarivao et al., 2021). In these areas, *B. dorsalis* has displaced several species of *Ceratitis*, such as C. *rosa* Karsch, C. *quilicii* De Meyer et al., C. *cosyra* (Walker), and C. *capitata*, on a number of hosts (Ekesi et al., 2009, 2016; Moquet et al., 2021).

Polyphagous *Bactrocera* have usually invaded areas where other polyphagous tephritids already occur (Duyck et al., 2004). Interspecific competition, via exploitative competition in fruits, interference between adults (Duyck, David, Junod, et al., 2006) is usually observed with a reduction of niche and abundance of the already present species (Charlery de la Masselière, Ravigné, et al., 2017; Moquet et al., 2021; Vargas et al., 1995). Niche partitioning, i.e. the process driving competing species into different patterns of resource use or different niches, and by which resident and introduced species may coexist (Denno et al., 1995; Reitz & Trumble, 2002) has been observed among Tephritidae to be driven by abiotic factors such as temperature and rainfall (Duyck, David, & Quilici, 2006) and by host range, the main resource for which competition occurs being the host fruit (Prokopy & Roitberg, 1984). Complete exclusion after tephritid invasion seems rare but niche partitioning can be asymmetric in favour of the invasive species that the resident species are only able to use a few species, that is defined as a refuge niche (David et al., 2017). A well-documented case is the reduction in the host

range of *C. capitata* after invasion by *B. dorsalis* in Hawaii where in lowlands, *C. capitata* persists only on coffee which is considered a refuge host (Reitz & Trumble, 2002).

The Comoros Archipelago in the Mozambique Channel is composed of four main islands, one of which, Mayotte, is under French administration. The remaining three islands (Grande Comore, Anjouan, and Mohéli) form the Comoros Union (or Comoros). *Bactrocera dorsalis* was detected in 2005 on Grande Comore and in 2007 on Mayotte Island (De Meyer et al., 2012). In Comoros, a wide variety of fruits are important for local consumption and subsistence farming. This variety of fruits also represent a substantial food source for fruit flies (De Meyer et al., 2012). In 2012, De Meyer et al. noted the presence of ten species of fruit flies in Comoros, namely *B. dorsalis*, *C. capitata*, *Ceratitis malgassa* Munro, *N. cyanescens* Bezzi, *Dacus bivittatus* Bigot, *D. ciliatus* Loew, *D. etiennellus* Munro, *Trirhithrum nigerrimum*, *D. punctatifrons* Karsch, and *D. vertebratus* Bezzi. A few years later, Hassani et al. (2016) mentioned five of these species collected through trapping and suggested that *C. malgassa* may be extinct in the country.

Although fruit flies are a major problem in Comoros, their host range is poorly known. Mangoes and citrus, however, were known to be highly infested by *C. capitata* before the invasion of *B. dorsalis* (Hassani et al., 2016). The knowledge of the host range and economic significance of invasive fruit fly species in Comoros are also limited. *Neoceratitis cyanescens* was mentioned on *Solanaceae* in Mayotte and on three other islands in Comoros (Kassim & Soilihi, 2000). According to Wuster (2005), soursop fruit (*Annona muricata*) was attacked by *Ceratitis* spp. in Anjouan, Mohéli, and Grande Comore. De Meyer et al. (2012) observed *D. bivittatus* and *D. vertebratus* on cucurbit fruits on Anjouan Island. In addition, Hassani et al. (2016) reported that the population densities of *B. dorsalis* and *C. capitata*, collected with traps, were increasing with the presence of main host fruits such as mango, guava, and citrus in the study sites. Host plants of Tephritidae including *B. dorsalis* can be present only in certain altitudes but the main factors allowing niche partitioning among Tephritidae regarding altitude are the different abilities to develop under different abiotic conditions, such as temperature and humidity (Duyck, David, & Quilici, 2006). This is also the case between *B. dorsalis* and *C. capitata* in Comoros where Hassani et al. (2016) showed that *B. dorsalis* was more abundant in low altitude areas, while *C. capitata* was more abundant in medium altitude areas, suggesting niche partitioning regarding altitude between the two species.

The main objectives of this study were to determine the host ranges of the different tephritid species in Comoros and to understand their distribution according to host and altitude.

MATERIALS AND METHODS

Study sites

This research was conducted on the three islands of the Comoros: Grande Comore, Anjouan and Moheli from June 2013 to July 2020. Grande Comore is the main island for agricultural activities with
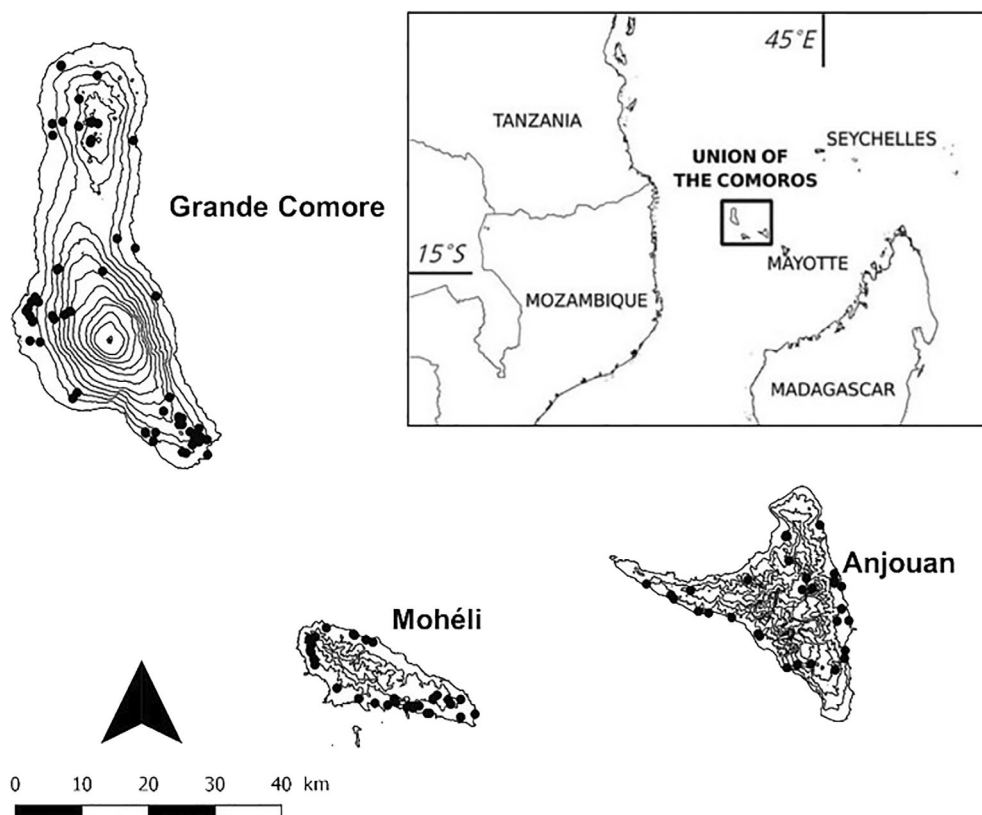
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3

FIGURE 1 Map showing the 147 sites in Comoros Islands where fruits were sampled to determine the host range of the different Tephritidae species. The inset shows the location of the Union of Comoros Islands in the Indian Ocean

Moroni as the main port of entry, and is situated at about 80 km from Anjouan, while Mohéli is about 40 km from the other two islands (Figure 1). The maximum altitudes are 2361, 1575, and 860 m for Grande Comore, Anjouan, and Mohéli, respectively. Whereas, altitudes go up to 860 m in Moheli, we have not been able to sample at more than 300 m, due to a scarcity of fruit resources at higher altitudes. Although these three volcanic islands have slightly different climatic conditions, they have a hot and rainy season from November to April (28°C–32°C and 376–1018 mm in lowlands) and a cool and dry season from May to October (24°C–27°C and 38–942 mm in lowlands).

Sampling

Cultivated and wild fruits were collected in cultivated fields, backyard gardens, and roadsides covering most parts of these islands from sea level to 887 m asl from June 2013 to July 2020 (Figure 1, Table S1). The methods of fruit collection, transport, and incubation in the laboratory were as previously described (Copeland et al., 2002). Fruits at all stages of development were randomly sampled from the plants, and very recently fallen fruits without decomposition or attack by soil organisms were occasionally collected from the ground. Host plants were identified in the field using the manuals of Quilici and Jeuffrault (2001). A sample is defined as a fruit collection from a given place at a

given date (one plant per sample). Number of fruits per sample varied highly regarding the fruit size and fruit availability. Number of fruits and samples per plant are given in Supporting Information tables (-Tables S2–S4). Fruit samples were transported to the rearing rooms at the National Research Institute of Agricultural, Fisheries and Environment (INRAPE) Entomology and Plant health laboratories in Moroni. The main goal was to collect a large number of fruit species and samples to cover the host range diversity of all tephritid species of economic importance. For each sampling site, GPS coordinates and elevation were recorded. A total of 12, 974 fruits from 763 different samples and weighing 572 kg in total were collected across Comoros from June 2013 to July 2020 (66 sites, 40 sites and 42 sites, respectively from Grande Comore, Anjouan and Moheli). These represented 91 fruit species from 37 families (Tables S2–S4).

Incubation of fruit samples

Fruit samples were weighed and placed individually in box waiting for pupation of larvae and emergence of adults for species identification. The bottom of each boxes was covered with a layer of sterilized volcanic sand sifted at 2 mm, to allow pupation of mature larvae (Woods et al., 2005; Rwomushana et al., 2008), with dimensions of 12 × 7 × 9 cm, 11 × 9.5 × 8 cm, or 7 × 7 × 4 cm, depending on fruit size. The lids were perforated and covered with muslin. The boxes with

fruits were placed in a room at 25°C ± 3°C with a relative humidity of 71% ± 10% and a photoperiod of 12:12 ± 1 h (L:D), which allow the development of all studied species. Pupae were collected by sieving the sand after 1 and 2 weeks of incubation, respectively. All of the pupae collected from an individual fruit were placed in one transparent box with a perforated lid. After adult emergence, tephritids were placed after one week in 95% alcohol, sexed, and identified. An identification key of Comoros fruit flies was initially prepared based on the study of Comoros Archipelago tephritid diversity (De Meyer et al., 2012). The field guide to the management of economically important tephritid fruit flies in Africa (Ekesi & Billah, 2006) was also used. All identified species were sent to Cirad La Réunion for morphological and genetic confirmation by barcoding.

Statistical analysis

To understand the interaction between host specialization and altitude, we choose to study Grande-Comore island in detail because of the presence of higher number of host fruit species, the greater number of samples collected and the higher gradient regarding altitude compared to the other islands. In order to ensure that infestation rates were sufficiently representative of the field, we only used samples > = 10 (98 samples were not used in the analysis) and calculated the number of infested fruits / total number of fruits collected for each host plant species.

Modularity is a good proxy of interaction niches in ecological networks for coexisting species or populations and simplify the description and understanding of an ecological system, by representing not each and every species, but aggregating their interactions (Dormann & Strauss, 2014). The modules represent interacting groups with within-module interactions more prevalent than between-module interactions (Dormann & Strauss, 2014). In order to understand how the interactions between Tephritid species and host are partitioned in the community, we measured modularity, using Beckett (2016) algorithm, as implemented in the function *computeModules* from the package bipartite (Dormann et al., 2008) in R version 4.1.0 (R Core Team, 2021). Five modules were identified for all interactions between Tephritidae and their host fruit species in Grande-Comore.

We then analysed infestation rates (number of infested samples over total samples collected for each fruit species) by generalized linear mixed-effects models (GLMMs) with a binomial error (Bolker et al., 2009). Fruit fly species, group of host plants identified for each module, altitude, and interactions between these variables were defined as fixed effects, while host plant species and samples were defined as random effects.

RESULTS

Tephritidae infestation

Of the 91 fruit species collected, 45 species in 16 families were infested by fruit flies, of which 27 by *B. dorsalis*. Tephritid infestation rates differed between fruit species ($\Delta Dev_{90,30,058} = 472.7$, $p < 0.0001$). The main families infested were Anacardiaceae, Annonaceae, Combretaceae, Cucurbitaceae, Myrtaceae, Rutaceae, and Solanaceae.

Among wild plants, fruit infestation was highest for *Annona senegalensis* (86%), *Terminalia catappa* (62%) *Momordica charantia* (54%), *Syzygium jambos* (53%), *Solanum mauritianum* (50%), *Psidium guajava* (42%), and *Psidium cattleyanum* (40%). Among crops, fruit infestation was highest for *Citrullus lanatus* (80%), *Prunus persica* (39%), *Citrus reticulata* (34%), *Mangifera indica* (25%), *Cucurbita maxima* (20%), and *Spondias edulis* (17%) (Supporting Information Table S1, Figure 2).

Tephritid species and host plant use

A total of eight species of fruit flies were obtained from the fruits sampled in Grande Comore (Table S2): *B. dorsalis*, *C. capitata*, *D. ciliatus*, *D. bivittatus*, *D. punctatifrons*, *D. etiennellus*, *N. cyanescens*, *T. nigerrimum*; four species of fruit flies in Anjouan (Table S3): *B. dorsalis*, *C. capitata*, *N. cyanescens*, *T. nigerimum*, and three species of fruit flies in Moheli (Table S4): *B. dorsalis*, *C. capitata*, *D. ciliatus*. Of all the samples collected in the three islands, 24% were infested by *B. dorsalis*, 5% by *C. capitata*, 4% by *N. cyanescens*, 3% by *D. ciliatus*, 2% by *B. bivittatus* and 1% by *D. punctatifrons*. Only one sample was found infested by *D. etiennellus* (on *Cucurbita pepo* in Grande Comore). This species was not considered in further analyses and figures.

On the three islands, *B. dorsalis* was able to infest a total of 27 host plant species while *C. capitata* was able to infest 15 host plant species. Fourteen plants were exclusive to *B. dorsalis* (mainly from the families Anonaceae, Myrtaceae, Rosacea, and Rutaceae) and only three exclusive to *C. capitata* (*Averrhoa carambola*, *Capiscum fructescens*, and *Saba comorensis*) while they shared five plants together, four others being also shared with *N. cyanescens* and/or *T. nigerrimum* (Figure 2, Figure 3). *B. dorsalis* and *C. capitata* dominated, respectively, on 21 and five of their host fruits. (Figure 2). *Neoceratitis cyanescens* was found on 11 host plants, eight of which were shared with other species but dominated on eight Solanaceae species (Figure 2, Figure 3). *Dacus bivittatus*, *D. ciliatus*, and *D. punctatifrons* shared eight species of Cucurbitaceae, of which four were dominated by *Dacus bivittatus* and four by *D. ciliatus* (Figure 2, Figure 3). Only *Citrullus lanatus* was exclusive to *D. bivittatus*, *Cucumis anguria* and *Cucumis melo exlusive* of *D. ciliatus* and no exclusive host to *D. punctatifrons*. Interestingly, *Dacus bivittatus* was also found on fruits of *Solanum tuberosum* (Figure 2, Figure 3).

Niche partitioning among Tephritidae via host fruit and altitude

Regarding the interaction between host fruit and Tephritidae species in Grande-Comore, the network analysis was significantly modular ($Q = 0.61$) and composed of five modules (Figure 4). This analysis
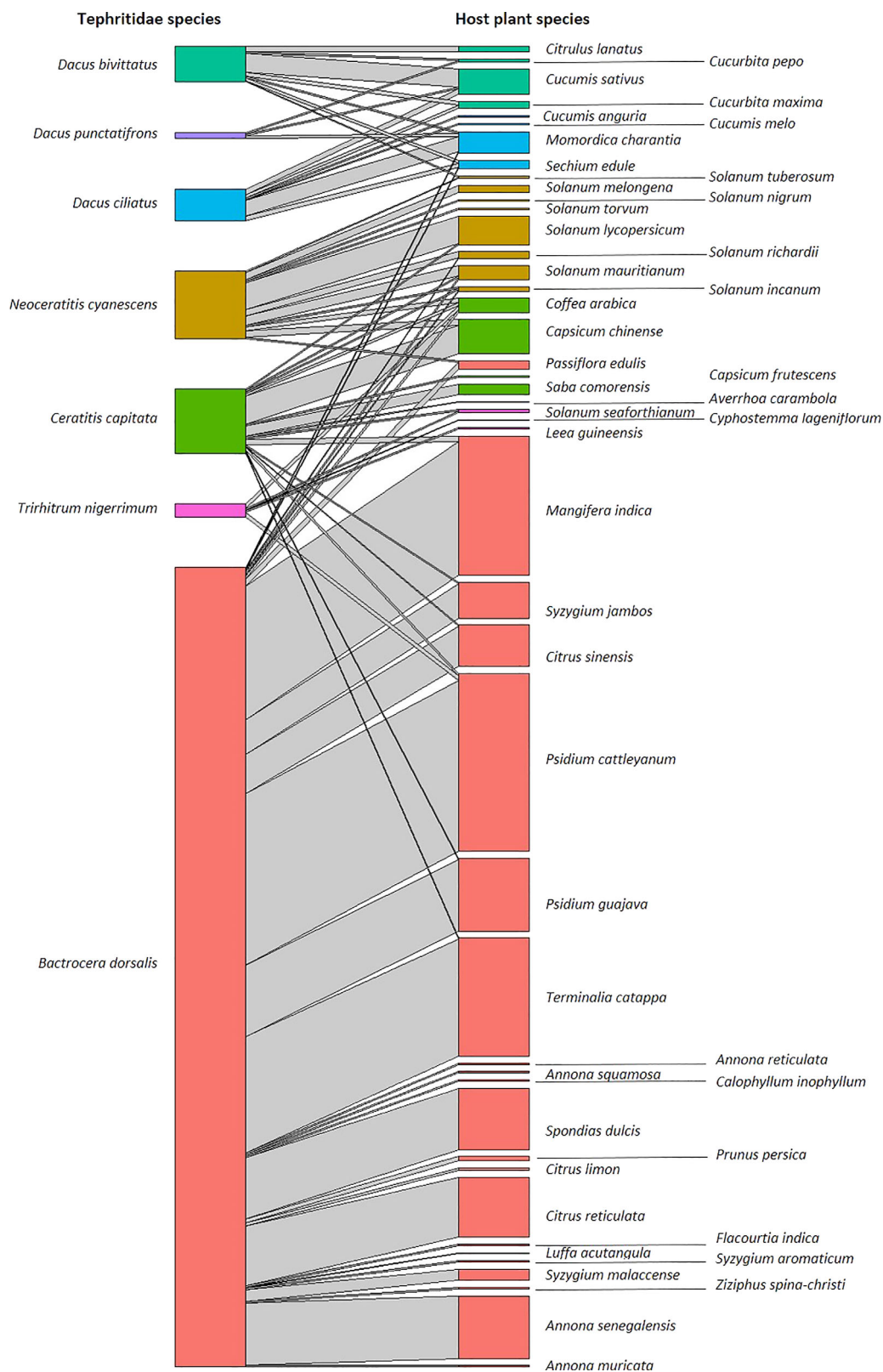
FIGURE 2 Network of interaction between fruit fly species and host plant species for the three islands of Comoros, and line thickness is proportional to number of infested fruits by each Tephritidae species. The different colours correspond to the tephritid species most commonly found in that host. For the different host plant species (the right-hand boxes), colours correspond to the tephritid species, the most present in that host
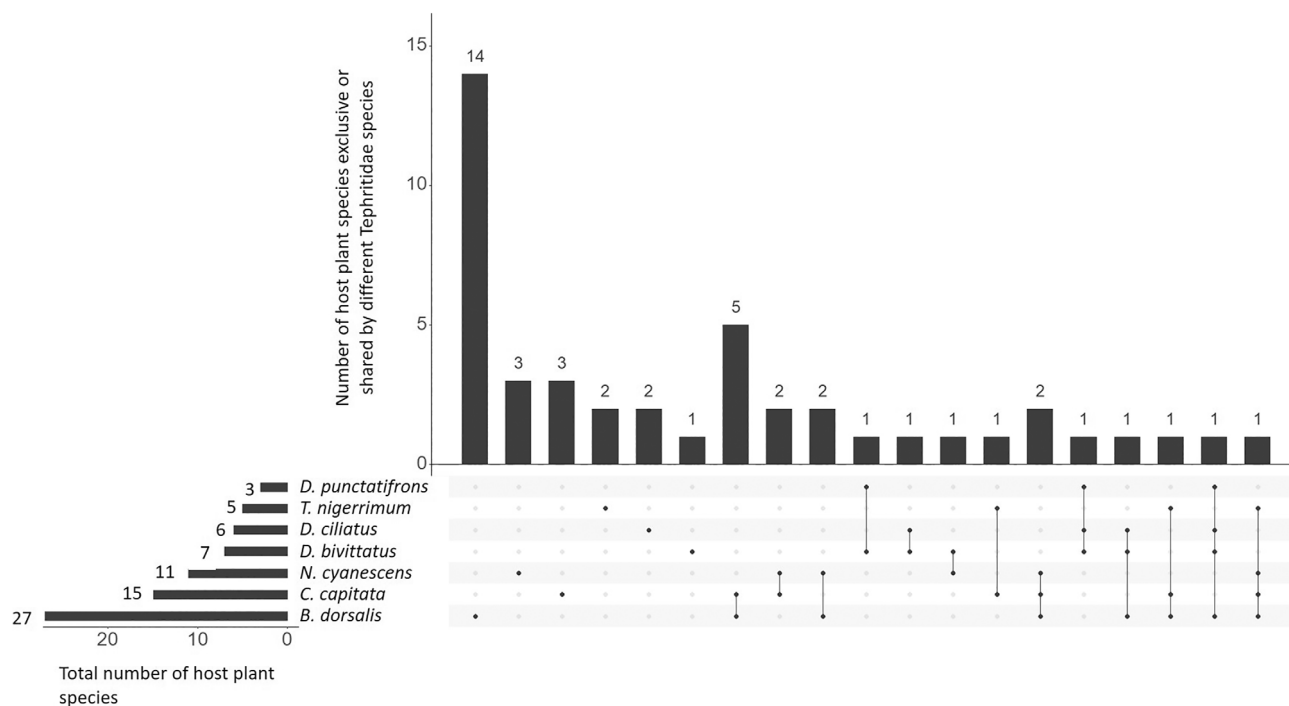
FIGURE 3 Total, exclusive, and shared species of host plants of the different Tephritidae species on the three islands of Comoros. The upper panel corresponds to the number of host plant species exclusive of one Tephritidae species (left-hand side of the panel), or shared by different combination of two, three, or four Tephritidae species (right-hand side of the panel) denoted by the filled and joined dots in the lower right panel. The lower left panel corresponds to the total number of host plant species for each Tephritidae species

highlights how the interactions between Tephritidae species and host are partitioned in the community. Module 1 includes only *B. dorsalis*, which is found on a wide range of fruit families (Figure 4). Module 2 is composed solely of *Solanaceae* crops, which are almost exclusively hosts of *N. cyanescens*. Module 3 contains four fruit species associated with two tephritid species, *C. capitata* and *T. nigerrimum*. Modules 4 and 5 comprises only host plants of the *Cucurbitaceae* family. However, module 4 is dominated by *D. bivittatus*, while module 5 includes *D. ciliatus* and *D. punctatifrons*.

Fruit flies infestation rates were significantly influenced by fruit fly species (GLMM, $\Delta Dev_{6,17,284} = 1851.7$, $p < 0.0001$) and the interaction between fruit fly species and plant group ($\Delta Dev_{24,17,284} = 818.4$, $P < 0.0001$). Fruit flies infestation rates were also significantly influenced by altitude and the quadratic term for altitude ($\Delta Dev_{1,17,259} = 10.0$, $P = 0.001$), as well as by the interaction between altitude and Tephritidae species ($\Delta Dev_{6,17,253} = 14.8$, $p = 0.021$). Nevertheless, there was no significant interaction between host plant group and altitude, once Tephritidae species was considered ($\Delta Dev_{21,17,225} = 5.1$, $P = 0.99$). Therefore, although there is a large and significant effect of altitude that is different for each fruit fly, each species behaves in the same way with respect to altitude within its host range. In the fruits of Module 1 (almost exclusive hosts of *B. dorsalis*), the infestation rate of *B. dorsalis* was highest between 0 and 300 m altitude and then decreased gradually from 300 to 800 m (Figure 5). Infestation rates of *N. cyanescens* decreased quickly from sea level to 250–300 m in both Module 2 (almost exclusive hosts of *N. cyanescens*) and Module 3 (main

host of *C. capitata* and *T. nigerrimum*). In Module 3, the infestation rate of *C. capitata* increased from sea level to 400 m, while the infestation of *T. nigerrimum* remained low (<0.1), and increased slightly with altitude. Infestation rates by *D. ciliatus* decreased quickly from sea level to 300 m in both Module 4 (main hosts of *D. bivittatus*) and Module 5 (shared host with *D. punctatifrons*). *Dacus bivittatus* showed the highest levels of infestation around 600 m altitude in Module 4 while *D. punctatifrons* showed low levels of infestation throughout the altitudinal range.

DISCUSSION

Tephritidae species and host range

Among the 91 plant species sampled in this study on the three islands of the Comoros, 45 cultivated and wild plant species in 16 families were infested by fruit flies. From all our samples performed over seven years, eight Tephritidae species were found: *B. dorsalis*, *C. capitata*, *D. ciliatus*, *D. bivittatus*, *D. punctatifrons*, *D. etiennellus*, *N. cyanescens*, *T. nigerrimum*. All these species were previously described in Comoros (De Meyer et al., 2012; Hassani et al., 2016). Nevertheless, two other frugivorous species *C. malgassa* and *D. vertebratus*, not found in the current fruit collection, were described from these islands but in low numbers from specimen collected in 2004 (De Meyer et al., 2012). Almost ten years after *B. dorsalis* invasion in Comoros with a two-year Tephritidae trapping survey, Hassani
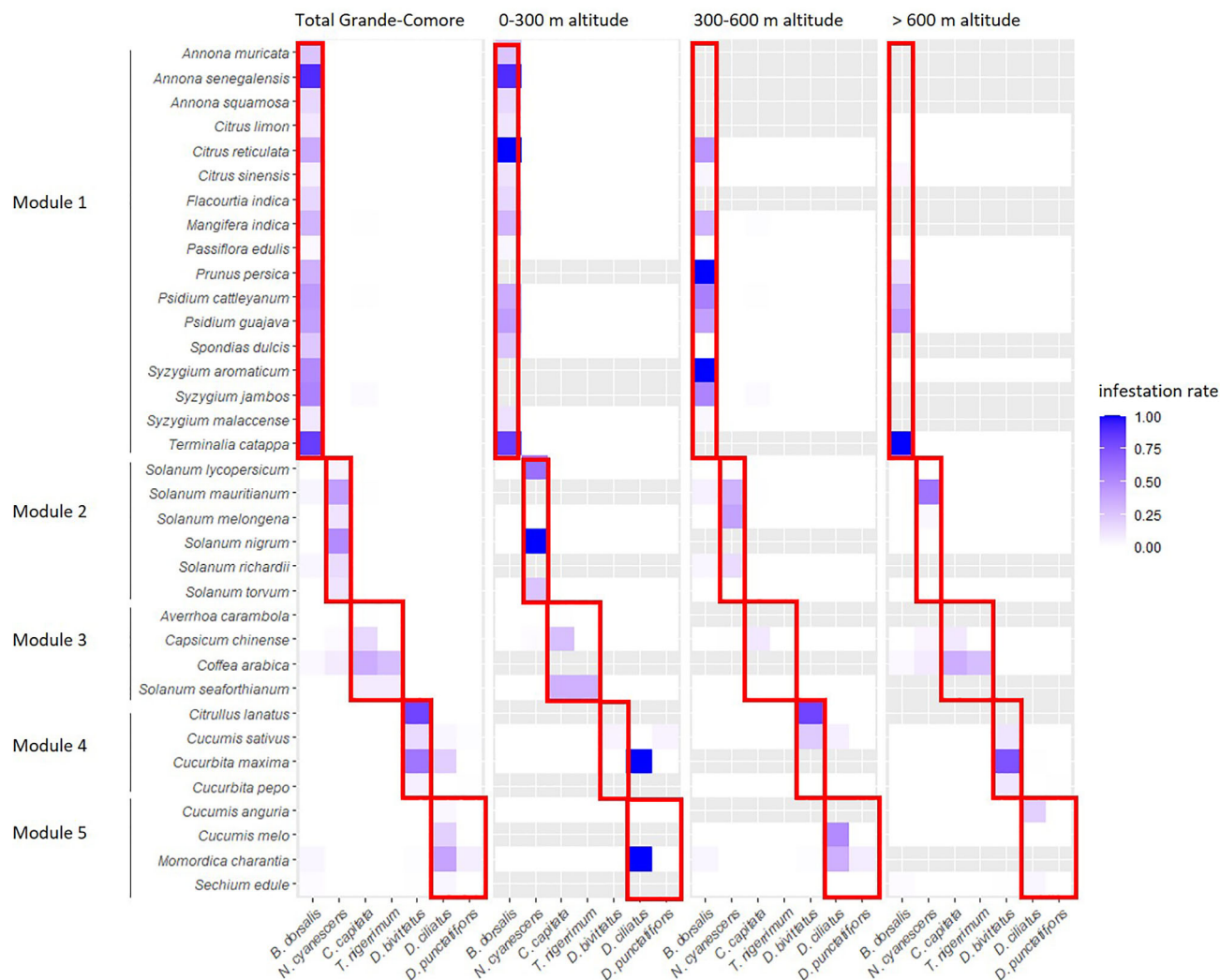
FIGURE 4 Infestation rate of the different Tephritidae species in the different host plants in Grande-Comore (left panel). Using the same modules, data are detailed for 0–300 m, 300–600 m and > 600 m altitude. Five modules were identified using Beckett (2016) algorithm (Dormann et al., 2008, see methods for details) for all interactions between Tephritidae and their host fruit species in Grande-Comore. Order of rows and columns are defined by modules in red and are kept for the three altitude sections. The modules represent interacting groups with within-module interactions more prevalent than between-module interactions (Dormann & Strauss, 2014). Absence of fruit in a given altitude is represented by light grey

et al. (2016) also failed to trap *C. malgassa* using trimedlure traps. We can hypothesize that both species might have been outcompeted by other Tephritidae species occupying the same niche and might be in such low numbers that were not detectable in the previous (Hassani et al., 2016) and current study, or might be extinct from the Comoros.

From all the Tephritidae species, *B. dorsalis* had the largest host range with a total of 27 out of 45 infested plant species collected. Host fruits include host plants from seven families. This species was dominant on 20 host fruits and 14 of its hosts were exclusive. The most common host fruits of *B. dorsalis* found in Comoros such as *Mangifera indica*, *Terminalia cattapa* or *Psidium cattleyanum*, are also the most common hosts of *B. dorsalis* described in the world (Clarke et al., 2005; Rwomushana et al., 2008; Moquet et al., 2021).

While *C. capitata* is considered as a polyphagous species able to infest a wide variety of species (Copeland et al., 2002) it has only been

found on 15 host species in our study (in low numbers), and being dominant on only five hosts including coffee berry and two species of chilli. *Trirhithrum nigerrimum*, also considered as polyphagous (White et al., 2003) was retrieved in our study in very low quantity and only in 5 host plants.

While tephritids are typically non-dispersive, especially when hosts are plentiful, some individuals may travel up to 12 km (Froerer et al., 2010). As our methodology involved collecting fruits, this provides direct estimates of the ability of fruit fly species to grow in a given host plant at a given altitude. Long distance dispersal is more often linked to human translocation of fruits, such as in cases of invasions between islands (Duyck et al., 2004). In different islands, host range of a given tephritid species can be different because of the differences in presence and abundance of host plant species but also linked to the presence and abundance of other fruit fly species that
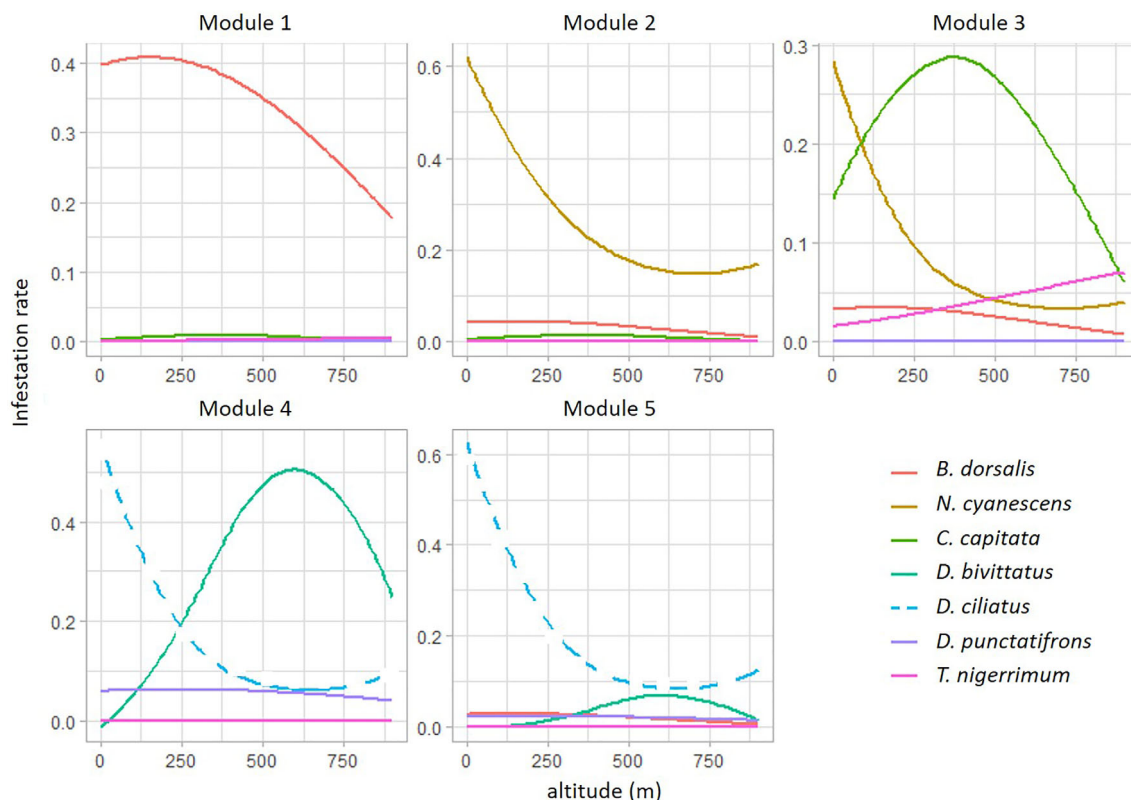
FIGURE 5 Relationship between infestation rate of each Tephritidae species and altitude predicted from model for each group of host plant (see Figure 4)

interact via exploitative competition but also interference competition (Duyck, David, Junod, et al., 2006). The length of time after the onset of the invasion may also affect host range choice, with newly introduced species being primarily associated with their preferred hosts and the host range gradually expanding as the abundance of the tephritid population increases (Moquet et al., 2021).

Niche partitioning regarding host range and altitude

While niches of the eight species overlap, there is a clear niche partitioning regarding host range for most of the species. *Ceratitis capitata* is known to be able to infest a wide variety of host species around the world, nevertheless, in the present study, it was only found dominant on a few small or toxic fruit species shared with *T. nigerrimum*. The usual described main hosts in the tropics of *C. capitata* (from the literature) are from Myrtaceae, Anacardiaceae, and Rutaceae families, which are occupied and dominated by *B. dorsalis* in Comoros. Niche partitioning between *B. dorsalis* and *C. capitata* in Comoros is also linked to altitude as already suggested by Hassani et al. (2016). Previous studies showed that *B. dorsalis* prefers warmer environment compared to *C. capitata* (De Meyer et al., 2010; De Villiers et al., 2015; Vera et al., 2002). The distribution and population dynamics of tephritids are closely related to influence of temperature and rainfall, and have a direct impact on tephritids life

history traits (Duyck, David, & Quilici, 2006). This dominance of *B. dorsalis* and potential refuge niche of *C. capitata* in higher altitude or on fruits such as coffee berry has been observed in Hawaii after *B. dorsalis* invasion (Vargas et al., 1995). A very similar pattern was recently documented in La Réunion and in numerous African countries where *B. dorsalis* significantly reduced host range and climatic niche of species already present such as *C. capitata*, *C. quilici*, *C. cosyra* (Ekesi et al., 2009; Rwomushana et al., 2008; Mwatawala et al., 2009; Moquet et al., 2021).

In its refuge niche, partly on several Solanaceae, *C. capitata* may also compete for resources with *N. cyanescens*, specialist of this family (Brévault et al., 2008). However, these two species have different distributions regarding to altitudes, *N. cyanescens* being more present in lowland areas.

While the three cucurbit fruit flies recorded in this study may interact, there is an important and significant niche partitioning linked to altitude. Indeed *D. bivittatus* was found more in lowlands and *D. ciliatus* in higher altitudes. *Dacus punctatifrons*, while widespread in Africa (De Meyer et al., 2012) was found in very low number in Comoros. The latter species is dominated by the two other cucurbit infesting species and seems to have no private niche regarding to host plants, nor altitudes, and it could be in the process of extinction. A similar low level of the indigenous fruit fly *D. etiennelus* has been observed, which seems in a process of extreme population decrease that might also lead this species to extinction.

Competitive replacement by *B. dorsalis*

Nutrient composition of host fruits of Tephritidae explains their suitability for larvae as it greatly affects larval growth, developmental time, and survival (Krainacker et al., 1987; Hafsi et al., 2016). Larval development is correlated with female preference (Charlery de la Masselière, Facon, et al., 2017) and explains mainly host range in the field (Facon et al., 2021). Host fruit specialization is therefore partly explained by their fundamental niche (Charlery de la Masselière, Facon, et al., 2017; Hafsi et al., 2016) and by interaction among species such as interspecific competition (Charlery de la Masselière, Ravigné, et al., 2017; Facon et al., 2021; Moquet et al., 2021). *Ceratitis capitata* was probably present on a wide range of host plants in Comoros before the invasion by *B. dorsalis*. While we have no direct data on that from the present study, we were able to trace different mentions of *C. capitata* on major host fruits in Comoros from the literature (see the Introduction section). Furthermore, a recent study in laboratory showed that larvae of *C. capitata* were able to exploit a wide range of host fruits and had a good fitness on most infested fruits by *B. dorsalis* found in the present study such as Indian almond, mango, guava, or strawberry guava (Hafsi et al., 2016). These hosts are also among the preferred egg-laying hosts of *C. capitata* in laboratory conditions (Charlery de la Masselière, Facon, et al., 2017). This wide fundamental niche is however counterbalanced by the fact that *C. capitata* is a weak competitor in terms of exploitative competition in fruits and interference between females (Duyck, David, Junod, et al., 2006). This competitive disadvantage is probably linked to the small body size of this species compared to other polyphagous invasive Tephritidae (Duyck et al., 2007).

The potential competitive displacement by *B. dorsalis* has led to an apparent specialization of *C. capitata* on a refuge niche on a few host fruits where it is still dominant. Some of these fruits such as coffee berry and the two species of chilli are known to contain toxic compounds and are particularly of small size. Larvae of *C. capitata*, may need less resource and accomplish quickly their development compared to larvae of bigger size polyphagous species (Duyck et al., 2007). While the small size body of *C. capitata* appears a disadvantage in term of competition with *B. dorsalis* in fruits containing a lot of resource, it is probably an advantage in its refuge niche. *C. capitata* is also know have a refuge niche in coffee berry and chilli in Hawaii and La Réunion (Moquet et al., 2021; Vargas et al., 1995).

While *T. nigerrimum* is also considered as polyphagous (White et al., 2003), it is only present on a few species, some shared with *C. capitata*. The other species are known to be specialized on Cucurbitaceae and Solanaceae, being rarely present on hosts of other families.

Description of the detailed host ranges of Tephritidae in Comoros is important for pest management. For instance, trapping or releases of parasitoid to manage populations of *B. dorsalis* would need to be done close to its most highly infested hosts. Moreover, some general useful principles for biosecurity can be drawn from our study. Compared to *C. capitata*, the risk of introduction of *B. dorsalis* is probably lower in cooler climate as its infestation rate decreased with altitude (Hassani et al., 2016) but global potential geographical distribution of *B. dorsalis* may be impacted by climate change (Qin et al., 2019). For countries where *B. dorsalis* is already present, the risk of invasion by *C. capitata* is probably weaker as fewer host fruit species would be available, or climate would be less favourable to start new populations where *B. dorsalis* is less present. The habitat with the most abundant and accessible resource may act as an invasion filter in which potential invasive species need to be competitively superior to already establish species, before spreading to other habitats (David et al., 2017).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Abuel-Ela, R.G., Hashem, A.G. & Mohamed, S.M.A. (1998) *Bactrocera pallidus* (Perkins and may) (Diptera: Tephritidae), a new record in Egypt. *J. Egypt. Ger. Soc. Zool. (Entomol.)*, 27, 221–129.

Beckett, S.J. (2016) Improved community detection in weighted bipartite networks. *Royal Society Open Science*, 3, 140536.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135.

Brévault, T., Duyck, P.F. & Quilici, S. (2008) Life-history strategy in an oligophagous tephritid: the tomato fruit fly, *Neoceratitis cyanescens*. *Ecological Entomology*, 33, 529–536.

Charlery de la Masselière, M., Facon, B., Hafsi, A. & Duyck, P.-F. (2017) Diet breadth modulates preference - performance relationships in a phytophagous insect community. *Scientific Reports*, 7, 16934.

Charlery de la Masselière, M., Ravigné, V., Facon, B., Lefeuvre, P., Massol, F., Quilici, S. et al. (2017) Changes in phytophagous insect host ranges following the invasion of their community: long-term data for fruit flies. *Ecology and Evolution*, 7, 5181–5190.

Clarke, A.R., Armstrong, K.F., Carmichael, A.E., Milne, J.R., Raghu, S., Roderick, G.K. et al. (2005) Invasive phytophagous pests arising through a recent tropical evolutionary radiation: the *Bactrocera dorsalis* complex of fruit flies. *Annual Review of Entomology*, 50, 293–319.

Copeland, R.S., Wharton, R.A., Luke, Q. & De Meyer, M. (2002) Indigenous hosts of *Ceratitis capitata* (Diptera: Tephritidae) in Kenya. *Annals of the Entomological Society of America*, 95, 672–694.

David, P., Thébault, E., Anneville, O., Duyck, P.-F., Chapuis, E. & Loeuille, N. (2017) Impacts of invasive species on food webs. *Advances in Ecological Research*, 56, 1–60.

De Meyer, M., Delatte, H., Mwatawala, M., Quilici, S., Vayssieres, J.F. & Virgilio, M. (2015) A review of the current knowledge on *Zeugodacus cucurbitae* (Coquillett) (Diptera, Tephritidae) in Africa, with a list of species included in *Zeugodacus*. *Zookeys*, 540, 539–557.

De Meyer, M., Quilici, S., Franck, A., Chadhouliati, A.C., Issimaila, M.A., Youssoufa, M.A. et al. (2012) Records of frugivorous fruit flies (Diptera: Tephritidae: Dacini) from the Comoro archipelago. *African Invertebrates*, 53, 69–67.

De Meyer, M., Robertson, M.P., Mansell, M.W., Ekesi, S., Tsuruta, K., Mwaiko, W. et al. (2010) Ecological niche and potential geographic distribution of the invasive fruit fly Bactrocera invadens (Diptera, Tephritidae). *Bulletin of Entomological Research*, 100, 35–48.

De Villiers, M., Hattingh, V., Kriticos, D.J., Brunel, S., Vayssières, J.-F., Sinzogan, A. et al. (2015) The potential distribution of *Bactrocera dorsalis* considering phenology and irrigation patterns. *Bulletin of Entomological Research*, 106, 1–15.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology*, 40, 297–331.

Dormann, C., Gruber, B. & Fründ, J. (2008) Introducing the bipartite package: Analysing ecological networks. *R News*, 8, 8–11.

Dormann, C.F. & Strauss, R. (2014) A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, 5, 90–98.

Drew, R.A.I. (1989) The tropical fruit flies (Diptera: Tephritidae: Dacinae) of the Australasian and Oceanian regions. *Corrigendum to Memoirs of the Queensland Museum*, 28, 664–664.

Drew, R.A.I., Tsuruta, K. & White, I.M. (2005) A new species of pest fruit fly (Diptera: Tephritidae: Dacinae) from Sri Lanka and Africa. *African Entomology*, 13, 149–154.

Duyck, P., David, P. & Quilici, S. (2007) Can more *K* -selected species be better invaders? A case study of fruit flies in La Réunion. *Diversity and Distributions*, 13, 535–543.

Duyck, P.-F., David, P., Junod, G., Brunel, C., Dupont, R. & Quilici, S. (2006) Importance of competition mechanisms in successive invasions by polyphagous tephritids in La Réunion Island. *Ecology*, 87, 1770–1780.

Duyck, P.-F., David, P. & Quilici, S. (2004) A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology*, 29, 511–520.

Duyck, P.F., David, P. & Quilici, S. (2006) Climatic niche partitioning following successive invasions by fruit flies in La Réunion. *Journal of Animal Ecology*, 75, 518–526.

Duyck, P.-F., Jourdan, H. & Mille, C. (2022) Sequential invasions by fruit flies (Diptera: Tephritidae) in Pacific and Indian Ocean islands: a systematic review. *Ecology and Evolution*, 12, e8880. https://doi.org/10.1002/ece3.8880

Ekesi, S. & Billah, M.K. (2006) *A field guide to the Management of Economically Important Tephritid Fruit Flies in Africa*. Nairobi, Kenya: International Centre of Insect Physiology and Ecology.

Ekesi, S., Billah, M.K., Nderitu, P.W., Lux, S.A. & Rwomushana, I. (2009) Evidence for competitive displacement of *Ceratitis cosyra* by the invasive fruit fly *Bactrocera invadens* (Diptera: Tephritidae) on mango and mechanisms contributing to the displacement. *Journal of Economic Entomology*, 102, 981–991.

Ekesi, S., De Meyer, M., Mohamed, S.A., Virgilio, M. & Borgemeister, C. (2016) Taxonomy, ecology and management of native and exotic fruit fly species in Africa. *Annual Review of Entomology*, 61, 219–238.

Ekesi, S., Nderitu, P.W. & Rwomushana, I. (2006) Field infestation, life history and demographic parameters of *Bactrocera invadens* Drew,

Tsuruta & White, a new invasive fruit fly species in Africa. *Bulletin of Entomological Research*, 96, 379–386.

Facon, B., Hafsi, A., Charlery de la Masselière, M., Robin, S., Massol, F., Dubart, M., Chiquet, J., Frago, E., Chiroleu, F., Duyck, P.F. & Ravigné, V. (2021) Joint species distributions reveal the combined effects of host plants, abiotic factors and species competition as drivers of species abundances in fruit flies. *Ecology Letters*, 24, 1905–1916.

Froerer, K.M., Peck, S.L., McQuate, G.T., Vargas, R.I., Jang, E.B. & McInnis, D.O. (2010) Long-distance movement ofBactrocera dorsalis(Diptera: Tephritidae) in Puna, Hawaii: how farcanthey go? *American Entomologist*, 56, 88–95.

Goergen, G., Vayssieres, J.F., Gnanvossou, D. & Tindo, M. (2011) *Bactrocera invadens* (Diptera: Tephritidae), a new invasive fruit fly pest for the afrotropical region: host plant range and distribution in west and Central Africa. *Environmental Entomology*, 40, 844–854.

Hafsi, A., Facon, B., Ravigné, V., Chiroleu, F., Quilici, S., Chermiti, B. et al. (2016) Host plant range of a fruit fly community (Diptera: Tephritidae): does fruit composition influence larval performance? *BMC Ecology*, 16, 40.

Hassani, I.M., Raveloson-Ravaomanarivo, L.H., Delatte, H., Chiroleu, F., Allibert, A., Nouhou, S. et al. (2016) Invasion by *Bactrocera dorsalis* and niche partitioning among tephritid species in Comoros. *Bulletin of Entomological Research*, 6, 1–10.

Kassim, M. & Soilihi, A.M. (2000) Fruit flies in the Federal Islamic Republic of the Comoros. In: Price, N.S. & Seewooruthun, I. (Eds.) *Proceedings of the Indian Ocean commission, regional fruit Fly symposium*. Mauritius: Indian Ocean Commission, pp. 71–72.

Krainacker, D.A., Carey, J.R. & Vargas, R.I. (1987). Effect of larval host on life-history traits of the mediterranean fruit fly, *Ceratitis capitata*. *Oecologia* 73, 583–590.

Lux, S.A., Copeland, R.S., White, I.M., Manrakhan, A. & Billah, M.K. (2003) A new invasive fruit fly species from the *Bactrocera dorsalis* (Hendel) group detected in East Africa. *Insect Science and its Application*, 23, 355–361.

Manrakhan, A., Venter, J.H. & Hattingh, V. (2015) The progressive invasion of *Bactrocera dorsalis* (Diptera: Tephritidae) in South Africa. *Biological Invasions*, 17, 2803–2809.

Moquet, L., Payet, J., Glenac, S. & Delatte, H. (2021) Niche shift of tephritid species after the oriental fruit fly (*Bactrocera dorsalis*) invasion in La Réunion. *Diversity and Distributions*, 27, 109–129.

Mwatawala, M., De Meyer, M., White, I.M., Maerere, A. & Makundi, R.H. (2007) Detection of the solanum fruit fly, *Bactrocera latifrons* (Hendel) in Tanzania (Dipt., Tephritidae). *Journal of Applied Entomology*, 131, 501–503.

Mwatawala, M.W., De Meyer, M., Makundi, R.H. & Maerere, A.P. (2006) Biodiversity of fruit flies (Diptera, Tephritidae) in orchards in different agro-ecological zones of the Morogoro region, Tanzania. *Fruits*, 61, 321–332.

Mwatawala, M.W., De Meyer, M., Makundi, R.H. & Maerere, A.P. (2009) Host range and distribution of fruit-infesting pestiferous fruit flies (Diptera, Tephritidae) in selected areas of Central Tanzania. *Bulletin of Entomological Research*, 99, 629–641.

Prokopy, R.J. & Roitberg, B.D. (1984) Foraging behavior of true fruit-flies. *American Scientist*, 72, 41–49.

Qin, Y., Wang, C., Zhao, Z., Pan, X. & Li, Z. (2019) Climate change impacts on the global potential geographical distribution of the agricultural invasive pest, Bactrocera dorsalis (Hendel) (Diptera: Tephritidae). *Climatic Change*, 155, 145–156.

Quilici, S. & Jeuffrault, E. (2001) *Plantes-hôtes des mouches des fruits: Maurice*. Réunion, Seychelles: PRF/COI, Imp. Graphica, La Réunion.

R Core Team. (2021) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rasolofoarivao, H., Raveloson Ravaomanarivo, L.H. & Delatte, H. (2021) Host plant ranges of fruit flies (Diptera: Tephritidae) in Madagascar. *Bulletin of Entomological Research*, 112, 1–12.

Reitz, S.R. & Trumble, J.T. (2002) Competitive displacement among insects and arachnids. *Annual Review of Entomology*, 47, 435–465.

Rwomushana, I., Ekesi, S., Gordon, I. & Ogol, C.K. (2008) Host plants and host plant preference studies for *Bactrocera invadens* (Diptera: Tephritidae) in Kenya, a new invasive fruit fly species in Africa. *Annals of the Entomological Society of America*, 101, 331–340.

Schutze, M.K., Aketarawong, N., Amornsak, W., Armstrong, K.F., Augustinos, A.A., Barr, N. et al. (2015) Synonymization of key pest species within the *Bactrocera dorsalis* species complex (Diptera: Tephritidae): taxonomic changes based on a review of 20 years of integrative morphological, molecular, cytogenetic, behavioural and chemoecological data. *Systematic Entomology*, 40, 456–471.

Vargas, R.I., Walsh, W.A. & Nishida, T. (1995) Colonization of newly planted coffee fields: dominance of Mediterranean fruit Fly over oriental fruit Fly (Diptera: Tephritidae). *Journal of Economic Entomology*, 88, 620–627.

Vayssières, J.-F., Goergen, G., Lokossou, O., Dossa, P. & Akponon, C. (2005) A new *Bactrocera* species in Benin among mango fruit fly (Diptera: Tephritidae) species. *Fruits*, 60, 371–377.

Vera, M.T., Rodriguez, R., Segura, D.F., Cladera, J.L. & Sutherst, R.W. (2002) Potential geographical distribution of the Mediterranean fruit fly, Ceratitis capitata (Diptera: Tephritidae), with emphasis on Argentina and Australia. *Environmental Entomology*, 31, 1009–1022.

White, I., Copeland, R. & Hancock, D. (2003) Revision of the afrotropical genus Trirhithrum Bezzi (Diptera Tephritidae). *Cimbebasia*, 18, 71–137.

White, I.M. & Elson-Harris, M.M. (1992) *Fruit flies of economic significance: their identification and bionomics*. Wallingford, UK: CAB International.

Woods, B., Lacey, I.B., Brockway, C.A. & Johnstone, C.P. (2005) Hosts of Mediterranean fruit fly Ceratitis capitata (Wiedemann) (Diptera: Tephritidae) from Broome and the Broome peninsula, Western Australia. *Australian Journal of Entomology*, 44, 437–441.

Wuster, G. (2005) Inventaire des organismes nuisibles aux Comores (phytopathologie). In: *Rapport de mission, Programme Régional de la Protection des Végétaux*, p. 187.

SUPPORTING INFORMATION

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

Appendix Table S1. Sampling sites in the three studied islands

Table S2. List of plant species collected with number of samples, fruits and abundance of each Tephritidae species in the island of Grande-Comore (2013–2018). A sample is defined as a fruit collection from a given place at a given date

Table S3. List of plant species collected with number of samples, fruits and abundance of each Tephritidae species in the island of Anjouan (2013–2018). A sample is defined as a fruit collection from a given place at a given date

Table S4. List of plant species collected with number of samples, fruits and abundance of each Tephritidae species in the island of Moheli (2013–2018). A sample is defined as a fruit collection from a given place at a given date