Niche shift of tephritid species after the Oriental fruit fly (*Bactrocera dorsalis*) invasion in La Réunion

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**Abstract**

**Aim:** In a context of successive fruit fly invasions (Tephritidae), this study investigated how the top invader, *Bactrocera dorsalis*, displaced established fruit fly populations. We focused, particularly, on how this invasion impacted the host range and climatic niche of each resident species.

**Location:** La Réunion, France, Indian Ocean.

**Methods:** We collected fruit from more than 100 plant species across the island, in cultivated and non-cultivated areas at different altitudes in order to monitor the emergence of fruit flies. Fruit collection was conducted over two field campaigns: from 2001 to 2009, before the *B. dorsalis* invasion; and from 2018 to 2019, after the *B. dorsalis* invasion. We compared the distribution and host range of fruit fly species for the two periods.

**Results:** Our results confirmed the generalist character of *B. dorsalis*, with the infestation of 52 out of 112 of the fruit species collected in the field. After the *B. dorsalis* invasion, we observed a shift in the host range and spatial distribution of established tephritids. The host range of specialist species that only share a few host species with *B. dorsalis* did not change significantly. On the contrary, we observed a significant shift in diversity or proportion of host range and climatic niches for the generalist species, such as *Bactrocera zonata*, *Ceratitis quilicii* and *Ceratitis capitata*.

**Main conclusions:** We provide evidence of the competitive displacement induced by *B. dorsalis* on other established species. The coexistence between *B. dorsalis* and generalist *Ceratitis* species seems possible because they have different responses to climatic conditions or the capacity to exploit other host fruit species. In contrast, the coexistence of *B. zonata* with *B. dorsalis* seems to be compromised because both species have similar ecological requirements. This research provides useful information for managing invasions, particularly since understanding competitive displacements is essential for the identification of empty niches and for modelling potential species distribution.

**KEYWORDS**

*Bactrocera zonata*, biological invasions, *Ceratitis*, community structure, competitive displacement, fruit fly, host range
INTRODUCTION

Biological invasions are now a major threat to biodiversity (Millennium Ecosystem Assessment (Program), 2005; Murphy & Romanuk, 2014). They can lead to a decrease in gene pools by causing the extinction of native species and alter habitat and ecosystem functions (Simberloff et al., 2013; Vilà et al., 2010). Biological invasions disrupt ecosystem services, such as provisioning services, which also has an important economic impact (Colautti et al., 2006; Olson, 2006; Pimentel et al., 2001; Pimentel, Zuniga, & Morrison, 2005).

Invasive species can interact with established species at different trophic levels. Authors frequently describe interspecific competition, which is widespread among insects and is one of the primary biotic factors that significantly influence their distribution, abundance, and diversity in ecological communities (Denno et al., 1995; Reitz & Trumble, 2002). One of the potential outcomes of an interspecific competition event is the competitive displacement of one of the species. DeBach (1966) defined the competitive displacement principle as follows: ‘different species having identical ecological niches cannot coexist for long in the same habitat’. The superior competitor can cause the local extinction of the weaker competitor, although this is rare, that is competitive exclusion. In general, the less competitive species uses ‘refuge niches’, and coexistence continues. Competitive displacement is generally observed between closely related species. In most cases, it is triggered by the invasion of an exotic species, which displaces an indigenous species or an established exotic species (Reitz & Trumble, 2002). Different niche-based hypotheses have attempted to explain mechanisms of successful biological invasions and coexistence. For example, the use of an empty niche by an invader species may reduce competition with native species and allow the coexistence of species. On the contrary, if non-native species are superior competitors, they may compete for resources and cause a niche shift or the competitive exclusion of the native species, which is less common (Amarasekare, 2003; Blonder, 2018; Musseau et al., 2016; Peterson, Rice, & Sexton, 2013; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013). Moreover, the outcome of interspecific competition can be modulated by abiotic conditions, such as temperature and humidity (Rwomushana, Ekesi, Ogol, & Gordon, 2009; Tilman, Mattson, & Langer, 1981). Thus, differential climatic tolerance among competitors can allow species coexistence across environmental gradients (Czárrán, 1991).

Duyck and Quilici (2006) define an invasive series as a succession of invasions by closely related taxa in the same territory. In this case, the new invader often replaces the existing species as the dominant species (Duyck et al., 2004; Vila & Weiner, 2004). Invasive series have been observed in the fruit fly community (Diptera: Tephritidae) in La Réunion (Indian Ocean), where nine fruit fly species of economic importance coexist. This community consists of generalist species: *Bactrocera dorsalis*, *B. zonata*, *Ceratitis catioirii*, *C. capitata*, and *C. quilicii*, whose larvae feed on the fruit of various plant families. Furthermore, there are more specialized species, such as *Dacus demmerezi*, *Dacus ciliatus* and *Zeugodacus cucurbitae*, whose larvae feed predominantly on the fruit of Cucurbitaceae; and *Neoceratitis cyanescens*, whose larvae feed on the fruit of the Solanaceae family. Apart from the two endemic species, *C. catioirii* and *D. demmerezi*, fruit flies have successively invaded La Réunion. As far as the generalist species are concerned, *C. capitata* was introduced in 1939 and *C. quilicii* (formerly *Ceratitis rosa*) in 1955. As these species became widespread on the island, the endemic species, *C. catioirii*, became rarer (White, De Meyer, & Stonehouse, 2000). *Bactrocera zonata* invaded La Réunion in 2000. This species became competitively dominant over the other established species, thus, modifying the host range of the other three generalist species (Charlery de la Masselière et al., 2017; Joomaye, Price, & Stonehouse, 2000). A previous study, based on experimental tests of exploitative competition between larvae of *B. zonata*, *C. quilicii*, *C. capitata* and *C. catioirii* showed that the competitive hierarchy of fruit flies reflected their order of invasion (Duyck & Quilici, 2006; Duyck et al., 2004).

*Bactrocera dorsalis* is the most recent tephritid invader in La Réunion and it was first detected in May 2017. This species is native to India, Southeast Asia and southern China. It is unusually polyphagous and is regarded as one of the top invaders in the world (Clarke et al., 2005). It has spread rapidly throughout Africa. It was first detected in Kenya in 2003 (Lux, Copeland, White, Manrakhan, & Billah, 2003), and has since invaded all countries in sub-Saharan Africa, the Indian Ocean Islands in the Malagasy subregion (De Villiers et al., 2015; Zeng et al., 2019). It was detected in Comoros in 2005, Mayotte in 2007, Madagascar in 2010, Mauritius in 2015 and La Réunion in 2017 (De Meyer et al., 2012; Mauremootoo, Pandoo, Bachraz, Buldowoo, & Cole, 2019). Despite the disastrous economic impact due to loss of fruit production and the associated export markets, the invasion of *B. dorsalis* provides a unique opportunity for observing and evaluating the role of niche differentiation in community assembly in real-time. The impact of *B. dorsalis* on *Cera ditis* species has been observed in other regions, where the dominance of *B. dorsalis* caused a niche displacement but never to the point of extinction because established insect populations were generally maintained in ‘refuge niches’ (Duyck, Sterlin et al., 2004; Ekesi, Billah, Nderitu, Lux, & Rwomushana, 2009; Hassani et al., 2016; Mwatawala et al., 2009a, 2009b). So far, no studies have described the effect of the introduction of *B. dorsalis* on the population dynamics and host range of a resident *B. zonata* population. In La Réunion, the changes in the Tephritidae community caused by the invasion of *B. dorsalis* are hard to predict because they depend on the structure of the invaded community and the invader’s competitiveness in specific environmental conditions.

A comparative analysis of interspecific interactions before and after the invasion is necessary to determine how invasive species impact the ecological network. However, few studies include a detailed description of the community structure prior to invasion (Charlery de la Masselière et al., 2017). In La Réunion, this comparison is possible because long-term field databases were compiled from 2001 to 2009 (after *B. zonata*, but before the *B. dorsalis* invasion) and recent data were collected in 2018 (one year after the *B. dorsalis* invasion) and 2019. Drawing on the existing databases, we determined how the top invader, *B. dorsalis*, affected a resident fruit fly community.
We focused on the following points: i) the distribution and host range of this polyphagous species in La Réunion; ii) How the host range has evolved and iii) how the climatic niche of each species changed after this invasion.

2 | METHODS

2.1 | Study site

La Réunion is located in the Southern Indian Ocean (55°30′E; 21°10′S), approximately 700 km off the coast of Madagascar and covers an area of 2,512 km². This volcanic island is mountainous, rising to an altitude of 3,100 m, with very rugged topography and a heterogeneous climate. It has a humid tropical climate with two main seasons: a dry season, from May to October, mainly cold and dry with trade winds; and a wet season, from November to April, which is hotter and wetter with light winds. There are two main climatic zones delimited by the central mountain range. The east is exposed to trade winds and has high precipitation (more than 2–3 m per year). In contrast, in the west, the coast is characterized by less humid, even arid, climatic conditions (less than 1 m per year) (Grünberger, 1989).

2.2 | Sampling

We collected fruit samples to monitor Tephritidae infestation in La Réunion. This allowed us to establish a specific link between the host plant and fruit fly species, which is not possible when adult flies are caught with a trap. Agents from CIRAD (a French Agricultural Research Centre for International Development) conducted campaigns from 2001 to 2009. After the invasion of B. dorsalis, a further field campaign was conducted in 2018 and 2019. No field collection was conducted between 2009 and 2018. During this period, we consider that the fruit fly community was stable because no new species were introduced (fruit fly and parasitoid species) and the studied abiotic parameters did not change significantly (Appendix S1). Field collection covered the entire island and included cultivated, ornamental and wild plant species. Fruits were randomly collected regardless of the presence or absence of potential punctures. Whenever possible, 15 fruit samples were collected per plant species, site and date. We collected a total of 8,657 individual fruits between 2001 and 2009 in 212 sites, and 10,839 individual fruits in 2018 and 2019 in 172 sites. We collected fruit from 70 potential host plants in the first period and 112 potential host plants in the last period (Table 1). Forty-eight host plant species were the same for both periods.

2.3 | Laboratory rearing of fruit flies

At the end of each day of field sampling, fruits were taken to the laboratory and subjected to a standardized protocol (Boinahadjii et al., 2019; FAO/IAEA, 2019; Leblanc, Vueti, Drew, & Allwood, 2012; N’Dépo, My, & NL, 2019). Fruits were weighed and individually placed in plastic boxes, containing sand as a pupation substrate, and covered with fine-mesh cloth. Fruit samples were kept in a maturation room at 25°C ± 2°C and 70% ± 20% humidity until pupation. These conditions were chosen because they are favourable to the proper development of all fruit fly species of economic importance in La Réunion (Duyck & Quilici, 2002; Duyck, Sterlin, et al., 2004). Over a 3-week period, fruit samples were regularly inspected and the sand was sifted for Tephritidae pupae. Pupae were kept in a climatic room in plastic boxes until emergence. They were taxonomically identified to species level. We collected data on the number of emerging individuals of each fruit fly species for the different fruit (species and weight), site and date. We calculated (a) the infestation rate as the number of fruit fly individuals per kg of collected fruits and (b) the proportion of infested fruit as the number of fruits with at least one fruit fly emergence divided by the number of fruits collected. The proportion of co-infestation was defined as the number of individual fruits with two or more fruit fly species out of the total number of infested fruits.

2.4 | Statistical analysis

Statistical analyses were performed with R version 3.6.2 (R Core Team, 2019). Unless indicated otherwise, data are presented as means ± SE. Carpomya vesuviana was only observed once on Ziziphus mauritiana and was not included in the following analyses.

2.4.1 | Host range

Only the 48 species that were the same for both periods were kept for analyses (see Appendix S2 for the geographic distribution of samples). For each fruit fly species and each sampling period, the extent of the host niche was calculated as the number of host plant species and by estimating host richness with a Jackknife estimator. Host diversity was also measured with the Shannon index. To estimate changes in the host niche between the first and the second sampling period, we calculated two dissimilarity indexes: Index of Sorensen (Sørensen, 1948), which measures dissimilarity based on presence/absence data (host diversity) and Bray–Curtis (Bray & Curtis, 1957) based on abundance data (host proportion).

We constructed two matrices of interaction between fruit flies and host plant species, one for the historical sampling period (2001–2009) and one for the recent sampling period (2018–2019). For each matrix, rows were normalized by dividing the infestation rate of one fruit fly species for a given host plant species by the global infestation rate of the fruit fly species. We used the ‘ggbipart’ package to create the bipartite network diagram and the ‘FactoMineR’ package for the principal component analysis (PCA) from the two interaction matrices.

For each resident species (except C. catioirii), we realized a generalized linear mixed model (GLMM) with a negative binomial to test
# TABLE 1 Collected plant species in La Réunion in 2018 and 2019 to study the Tephritidae host range

| Family                  | Latin name                                | English name                  | Status         | Weight (g) | N  |
|-------------------------|--------------------------------------------|-------------------------------|----------------|------------|----|
| Anacardiaceae           | Anacardium occidentale L.                  | Cashew nut                    | Cultivated     | 1 166      | 15 |
|                         | Mangifera indica L.                       | Mango                         | Cultivated     | 64 049     | 233|
|                         | Spondias dulcis Parkinsonia               | Jew plum                      | Cultivated     | 2 431      | 42 |
|                         | Spondias mombin L.                        | Yellow mombin                 | Cultivated     | 738        | 60 |
| Annonaceae              | Annona cherimola Mill.                    | Custard apple                 | Cultivated     | 36 145     | 27 |
|                         | Annona muricata L.                        | Surinam apple                 | Cultivated     | 4 042      | 9  |
|                         | Annona reticulata L.                      | Bullock’s heart               | Cultivated     | 3 622      | 19 |
|                         | Cananga odorata (Lam.) Hook. f. & Thomson | Ylang-Ylang                   | Ornamental     | 241        | 60 |
| Aphiioiaceae            | Aphiioi theiformis (Vahl) Bennia           | Endemic                       |                | 145        | 45 |
| Apocynaceae             | Carissa carandas L.                       | Karanda                       | Ornamental     | 186        | 45 |
|                         | Cascabela thevetia (L.) Lippold           | Yellow oleander               | Ornamental     | 39         | 106|
|                         | Ochrosia borbonica J.F.Gmel.              |                                |                | 1 936      | 2  |
| Areaceae                | Phoenix dactylifera L.                    | Date                          | Naturalized    | 592        | 30 |
| Boraginaceae            | Cordia sebestena L.                       | Geiger tree                   | Ornamental     | 779        | 90 |
|                         | Ehretia cymosa Thonn.                     | Naturalized                   |                | 2          | 15 |
| Bromeliaceae            | Ananas comosus (L.) Merr.                 | Pineapple                     | Cultivated     | 6 808      | 13 |
| Cactaceae               | Hylocereus undatus (Haw.) Britton & Rose  | Dragon fruit                  | Cultivated     | 4 706      | 13 |
|                         | Opuntia ficus-indica (L.) Miller          | Sweet prickly pear            | Naturalized    | 1 558      | 35 |
| Caricaceae              | Carica papaya L.                          | Papaya                        | Cultivated     | 19 931     | 35 |
| Chrysobalanaceae        | Chrysobalanus icaco L.                    | Coco plum                     | Cultivated     | 216        | 15 |
| Clusiaceae              | Calophyllum inophyllum L.                 | Alexandrian Laurel            | Ornamental     | 997        | 30 |
|                         | Clusia xanthochymus Hook.f.               | False mangosteen              | Cultivated     | 900        | 8  |
| Combretaceae            | Terminalia catappa L.                     | Indian almond                 | Ornamental     | 19 382     | 588|
| Cucurbitaceae           | Coccinia grandis (L.) Voigt.              | Ivy gourd                     | Invasive (5)   | 1 275      | 105|
|                         | Cucumis sativus L.                        | Cucumber                      | Cultivated     | 2 192      | 15 |
|                         | Cucurbita moschata Duchesne               | Pumpkin                       | Cultivated     | 870        | 51 |
|                         | Cucurbita pepo L.                         | Zucchini squash               | Cultivated     | 2 561      | 30 |
|                         | Lagenaria siceraria (Molina) Standl.      | Bottle gourd                 | Cultivated     | 4 486      | 16 |
|                         | Lagenaria sphaerica (Sond.) Naudin        | Wild melon                    | Naturalized    | 3 750      | 10 |
|                         | Momordica charantia L.                    | Bitter gourd                 | Invasive (5), Cultivated | 3 560 | 295|
|                         | Sechium edule (Jacq.) Sw.                 | Chayote                       | Invasive (4), Cultivated | 22 842 | 118|
| Ebenaceae               | Diospyros blancon A.DC.                  | Velvet apple                  | Cultivated     | 3 423      | 30 |
|                         | Diospyros kaki L. f.                      | Persimmon                     | Cultivated     | 10 457     | 135|
|                         | Diospyros nigra (J.F.Gmel.) Perrier       | Black sapote                 | Invasive (4), Cultivated | 5 603 | 60 |
| Euphorbiaceae           | Jatropha curcas L.                        | Pignut                        | Naturalized    | 198        | 15 |
| Fabaceae                | Inga laurina (Sw.) Willd.                 | Sackycac                      | Cultivated     | 691        | 30 |
|                         | Pithecellobium dulce (Roxb.)              | Guamuich apes-earring         | Naturalized    | 275        | 30 |

(Continues)
| Family                | Latin name | English name    | Status            | Weight (g) | N  |
|----------------------|------------|-----------------|-------------------|------------|----|
| Goodeniaceae         | Scaevola taccada (Gaertn.) Roths.* | Beach naupaka    | Indigena          | 199        | 145 |
| Lauraceae            | Persea americana Mill.* | Avocado          | Cultivated        | 23 815     | 73  |
| Laureae              | Litsea glutinosa (Lour.) C.B.Rob. | Indian laurel    | Invasive (5)      | 44         | 30  |
| Lythraceae           | Punica granatum L. | Pomegranate      | Cultivated        | 2,175      | 16  |
| Malpighiaceae        | Bunchosia armeniaca (Cav.) DC. | Peanut Butter Fruit | Ornamental       | 282        | 30  |
| Melastomataceae      | Cidia hirta (L.) D. Don | Koster’s curse   | Invasive (5)      | 16.9       | 30  |
| Meliaceae            | Azadirachta indica A.Juss. | Neem             | Naturalized       | 540        | 30  |
| Monnimiaceae         | Tambourissa elliptica (Tul.) A. DC. | Endemic |            | 302        | 15  |
| Moraceae             | Artocarpus altillus (Parkinson) Fosberg | Breadfruit | Cultivated | 886        | 1   |
|                      | Ficus benghalensis L. | Banyan           | Ornamental        | 37         | 15  |
|                      | Ficus carica L.* | Fig              | Cultivated        | 1 910      | 60  |
|                      | Ficus lateriflora Vahl.* | Endemic |            | 100        | 15  |
|                      | Ficus mauritiana Lam.* | Endemic |            | 1 856      | 30  |
|                      | Ficus pumila L. | Creeping Fig     | Naturalized       | 1 506      | 60  |
|                      | Ficus sycomorus L. | Sycamore Fig     | Cultivated        | 80         | 15  |
| Moraceae             | Musa acuminata Colla | Banana           | Cultivated        | 6 751      | 64  |
| Myrtaceae            | Eugenia brasiliensis Lamark* | Spanish cherry | Naturalized       | 44         | 15  |
|                      | Eugenia uniflora L. | Brasilian cherry | Naturalized       | 546        | 120 |
|                      | Plinia cauliflora (Mart.) | Jabuticaba | Cultivated        | 198        | 30  |
|                      | Psidium cattleianum Sabine* | Strawberry guava | Invasive (5), Cultivated | 15 886     | 1,041 |
|                      | Psidium guajava L.* | Common guava     | Cultivated        | 28 709     | 550 |
|                      | Syzygium cumini (L.) Skeels | Java plum | Invasive (4)      | 346        | 75  |
|                      | Syzygium cymosum (Lam.) DC.* | Endemic |            | 386        | 38  |
|                      | Syzygium jambos (L.) Alston* | Rose-apple | Invasive (5)      | 11 028     | 570 |
|                      | Syzygium malaccense (L.) Merr. & L. M. Perry* | Malay apple | Naturalized | 917        | 25  |
|                      | Syzygium samarangense (Blume) Merr. & L. M. Perry* | Java apple | Naturalized | 3 322      | 165 |
| Oleaceae             | Ligustrum sp. | Privet           | Invasive (4)      | 1          | 15  |
|                      | Noronhia emarginata (Lam.) Thouars* | Madagascar olive | Naturalized      | 632        | 30  |
| Onagraceae           | Fuchsia boliviana Carriére | Bolivian fuchsia | Invasive (5)     | 17         | 15  |
| Oxalidaceae          | Averrhoa bilimbi L.* | Cucumber tree    | Cultivated        | 1 632      | 55  |
| Passifloraceae       | Averrhoa carambola L.* | Star fruit       | Cultivated        | 4 402      | 63  |
|                      | Passiflora edulis Sims | Passionfruit | Naturalized     | 1 803      | 30  |
|                      | Passiflora foetida L. | Wild maracuja    | Naturalized       | 60         | 30  |
|                      | Passiflora mollissima (Kunth) L.H.Bailey* | Banana passionfruit | Invasive (5) | 2 614     | 60  |
|                      | Passiflora quadrangularis L. | Giant Granadilla | Cultivated      | 91         | 1   |
|                      | Passiflora sp.* | Passionfruit     | Naturalized       | 900        | 15  |

(Continues)
| Family          | Latin name                  | English name               | Status        | Weight (g) | N  |
|-----------------|-----------------------------|---------------------------|---------------|------------|----|
| Passifloraceae  | *Passiflora suberosa* L. ²  | Corkystem passionflower   | Invasive (4)  | 142        | 96 |
| Phytoleacceae   | *Phytolacca americana* L.  | Pokeweds                   | Naturalized   | 24         | 30 |
| Polygonaceae    | *Coccoloba uvifera* L. ³   | Seagrape                   | Naturalized   | 268        | 60 |
| Primulaceae     | *Ardisia crenata* Sims     | Christmas berry            | Naturalized   | 35         | 1  |
| Rhamnaceae      | *Ziziphus mauritania* Lamarck² | Indian jujube             | Cultivated    | 2 428      | 105|
| Rosaceae        | *Eriobotrya japonica* (Thunb.) Lindley¹ | Loquat                   | Invasive (5)  | 4 481      | 359|
|                 | *Malus pumila* Borkh.²     | Apple tree                 | Cultivated    | 1 016      | 23 |
|                 | *Prunus persica* (L.) Batsch² | Peach tree                | Cultivated    | 10 008     | 268|
|                 | *Prunus* sp. L. ³          | Plum tree                  | Cultivated    | 3 789      | 83 |
|                 | *Pyrus* sp. L. ³           | Pear                       | Cultivated    | 7 669      | 78 |
| Rubiaceae       | *Bertiera rufa* DC.         |                           | Endemic       | 2          | 15 |
|                 | *Coffee* sp. L. ³          | Coffee                     | Cultivated    | 885        | 193|
| Rutaceae        | *Citrus aurantifolia* (Christm.) Swing. x *Fortunella* sp.² | Limequat               | Cultivated    | 5 613      | 11 |
|                 | *Citrus clementina* Hort. ex Tan.² | Clementine             | Cultivated    | 648        | 80 |
|                 | *Citrus limon* (L.) Burm. f. | Lemon tree                | Cultivated    | 1 196      | 3  |
|                 | *Citrus maxima* (Burm.) Merr. |                         | Cultivated    | 702        | 1  |
|                 | *Citrus paradisi* Macfad.   | Grapefruit                 | Cultivated    | 1 956      | 2  |
|                 | *Citrus reticulata* Blanco  | Mandarin tree              | Cultivated    | 5 732      | 30 |
|                 | *Citrus reticulata* Blanco x *Citrus sinensis* (L.) Osb.² | Tangor                 | Cultivated    | 9 230      | 51 |
|                 | *Citrus sinensis* (L.) Osbeck² | Orange tree              | Cultivated    | 6 281      | 75 |
|                 | *Citrus tangerina* Hort. ex Tan.² | Orange tree             | Cultivated    | 354        | 104|
|                 | *Murraya paniculata* (L.) Jacq.² | Jessamine orange         | Invasive (4), Ornamental | 149    | 120|
| Salicaceae      | *Dovyalis hebecarpa* (Gardner) Warburg² | Ceylon gooseberry      | Cultivated    | 397        | 45 |
|                 | *Flacourtia indica* (Burman f.) Merrill² | Governor’s plum        | Ornamental    | 920        | 108|
| Sapindaceae     | *Dimocarpus longan* Lour.   | Longan                     | Cultivated    | 230        | 30 |
|                 | *Litchi chinensis* Sonnerat² | Litchi                   | Cultivated    | 1 071      | 181|
| Sapotaceae      | *Chrysophyllum cainito* L.²  | Star-apple                 | Cultivated    | 1 222      | 15 |
|                 | *Labourdonnaisia calophylloides* Bojer | Endemic               | Endemic       | 12         | 1  |
|                 | *Mimusops coriacea* (A.DC.) Miq.² | Monkey’s apple           | Ornamental    | 2 497      | 75 |
|                 | *Mimusops elengi* L.²       | Spanish cherry             | Cultivated    | 287        | 59 |
| Sapindaceae     | *Sideroxylon borbonicum* DC. | Spanish cherry            | Endemic       | 2          | 7  |
| Solanaceae      | *Capsicum frutescens* L.²   | Chilli                     | Cultivated    | 318        | 73 |
|                 | *Solanum betaceum* Cav.²    | Tomato tree                | Cultivated    | 2 705      | 56 |
|                 | *Solanum lycopersicum* L.²  | Tomato                     | Cultivated    | 2 075      | 91 |
|                 | *Solanum mauritianum* Scop.² | Bugweed                   | Invasive (5)  | 940        | 270|
|                 | *Solanum melongena* L.²     | Eggplant                   | Cultivated    | 3 289      | 27 |
Climatic range

Climatic data (maps with mean annual temperature and mean annual precipitation) were drawn from the AWARE Atlas (https://smart.is.re/p/AWARE), which was developed by CIRAD in La Réunion. We used precipitation and temperature as environmental predictors. These factors impact fly development (Eskafi & Fernandez, 1990; Mahmoud, 2016; Shoukry & Hafez, 1979; Teruya, 1990; Vargas, Walsh, Jang, Armstrong, & Kanehisa, 1996; Yang, Carey, & Dowell, 1994) and, therefore, influence the distribution and abundance of Tephritidae (De Villiers et al., 2015; Duyck, et al., 2004; Ni et al., 2012). Extrapolated temperature data were derived from 73 meteorological stations evenly distributed across La Réunion and collected between 1997 and 2017. Precipitation data were obtained from 143 stations and collected between 1986 and 2016 by Météo-France and CIRAD. Prior to the analysis of climatic niches, we analysed data from METEOR (https://smart.is.re/METEOR) to verify the absence of climatic changes between the two studied periods. METEOR provides information on daily temperature, precipitation.

2.4.2 | Climatic range

Climatic data (maps with mean annual temperature and mean annual precipitation) were drawn from the AWARE Atlas (https://smart.is.re/p/AWARE), which was developed by CIRAD in La Réunion. We used precipitation and temperature as environmental predictors. These factors impact fly development (Eskafi & Fernandez, 1990; Mahmoud, 2016; Shoukry & Hafez, 1979; Teruya, 1990; Vargas, Walsh, Jang, Armstrong, & Kanehisa, 1996; Yang, Carey, & Dowell, 1994) and, therefore, influence the distribution and abundance of Tephritidae (De Villiers et al., 2015; Duyck, et al., 2004; Ni et al., 2012). Extrapolated temperature data were derived from 73 meteorological stations evenly distributed across La Réunion and collected between 1997 and 2017. Precipitation data were obtained from 143 stations and collected between 1986 and 2016 by Météo-France and CIRAD. Prior to the analysis of climatic niches, we analysed data from METEOR (https://smart.is.re/METEOR) to verify the absence of climatic changes between the two studied periods. METEOR provides information on daily temperature, precipitation.
and solar radiation. We selected data for 30 sites in 10 different municipalities and for three different elevation ranges (0–300 m; 301–600 m and > 600 m), and compared mean values for the two studied periods (Appendix S1).

We only studied the climatic range for generalist fruit fly species because of the uneven distribution of the host fruit of specialist species (Cucurbitaceae and Solanaceae). To study the distribution of each fruit fly species, we reduced the data set and focused on host fruit with high infestation rates and broad distribution across the island. We kept data from: *Prunus persica*, *Psidium cattleianum*, *Psidium guajava*, *Syzygium jambos* and *Terminalia catappa* for *B. dorsalis*, *B. zonata*, *C. quilicii* and *C. catioirii*; and data from *Eugenia uniflora*, *Murraya paniculata*, *Passiflora suberosa* and *T. catappa* for *C. capitata*.

For each fruit fly species and each studied period, we used a generalized linear mixed model with negative binomial distribution to test the influence of temperature and precipitation on the infestation rate. Host plant species, seasons (winter or summer), and sites were added as random factors.

For each fruit fly species, a niche comparison between the two studied periods was performed using the ‘ecospat’ package (Cola et al., 2017). Niche functions in the ‘ecospat’ package provide tools to quantify and compare species niches with an ordination approach. Niche was described in relation to precipitation and temperature. The global overlap between niches was calculated using metrics of Schoener’s D or Hellinger’s I, ranging from 0 (no overlap) to 1 (complete overlap) (Broennimann et al., 2012). We performed tests of niche equivalency and similarity. The niche equivalency test assesses, through 1,000 random permutations of occurrences between ranges, whether the two niches are equivalent. The niche similarity test assesses, through 1,000 random shifts of the niches within available conditions in the study area, whether the species niches are more or less similar than expected by chance.

3 | RESULTS

3.1 | Tephritidae community structure

Among the nine tephritid species analysed in this study, three were found mostly on Cucurbitaceae (*D. ciliatus*, *D. demmerezi* and *Z. cucurbitae*), one mostly on Solanaceae (*N. cyanescens*) and the others (*B. zonata*, *C. capitata*, *C. catioirii*, *C. quilicii* and after 2017, *B. dorsalis*) on plants from various families (Figure 1). During the first studied period, the generalist species, *C. quilicii* and *C. capitata*, had a close host niche and shared 18 host plant species. *Bactrocera zonata* shared 10 species with *C. quilicii* and 8 with *C. capitata* before 2017 (Figure 1a). After the *B. dorsalis* invasion, we observed several modifications in the network configuration: *C. quilicii* and *C. capitata* shared only eight host plant species, while *B. dorsalis* had a host niche that was very close to that of *C. quilicii* and shared 20 host plant species. All seven host plant species infested by *B. zonata* were shared with both *C. quilicii* and *B. dorsalis* in 2018–2019 (Figure 1b).

On infested fruit, 18.9% of samples hosted two or more species (co-infection) in 2001–2009 and 9.5% in 2018–2019. For example, we observed a decrease in co-infection in *B. dorsalis’* main fruit hosts: from 23.3% to 10.4% for *Mangifera indica*, from 24.4% to 10.3% for *Psidium guajava* and from 28.1% to 11.1% for *Terminalia catappa*. In 2001–2009, data for co-infested fruits reveals that 35% were infested simultaneously by *B. zonata/C. quilicii*, 16% by *Z. cucurbitae/D. ciliatus*, 16% by *C. capitata/C. quilicii*, 8% by *Z. cucurbitae/D. demmerezi*, 6% by *Z. cucurbitae/D. ciliatus/D. demmerezi* and 6% by *B. zonata/C. capitata/C. quilicii*. In 2018–2019, 68% of co-infested fruit was simultaneously infested by *B. dorsalis/C. quilicii*, 11% by *B. dorsalis/B. zonata* and 5% by *Z. cucurbitae/D. ciliatus*.

3.2 | Host range

The principal component analysis (PCA, Figure 2) allowed us to determine specific host plant species of fruit flies in 2001–2009 and 2018–2019. According to axis 1 (Figure 2a,c), *C. quilicii* and *B. dorsalis* host diversity was high and included many species, such as *Annona reticulata*, *Carica papaya*, *Eriobotrya japonica*, *Eugenia uniflora*, *Ficus carica*, *Malus pumila*, *Pyrus sp.* and *P. cattleianum*. Axis 2 (Figure 2b,d) shows that *C. capitata’s* host diversity included *Coffea sp.*, *Mimusops elengi*, *Murraya paniculata*, *Passiflora suberosa* and *Pithecellobium dulce*. Axis 3 (Figure 2b,d) distinguishes *B. dorsalis* and *B. zonata* (2001–2009) host range according to *Citrus reticulata*, *Diospyros blancoi*, *Persea americana*, *Syzygium malaccense* and *Syzygium samarangense*. *Dacus ciliatus*, *D. demmerezi*, and *Z. cucurbitae* have very similar host diversity. Moreover, the PCA revealed differences in host diversity between the two studied periods for generalist but not specialist species.

3.2.1 | *Bactrocera dorsalis*

Among the 112 potential host plant species sampled, 52 were infested by *B. dorsalis* (Table 2). This tephritid was found in fruit from many cultivated species of economic importance in La Réunion, such as *Ananas comosus* (23.1% infested fruit, 1.5 flies/kg, *N* = 13), *Carica papaya* (5.7% of infested fruit, 2.1 flies/kg, *N* = 35), *Hylocereus undatus* (76.9% of infested fruit, 43.1 flies/kg, *N* = 13), *Litchi chinensis* (1.66% of infested fruit, 1.34 flies/kg, *N* = 181), *Mangifera indica* (45.5% of infested fruit, 38.4 flies/kg, *N* = 233) or *Musa sp.* (32.8% infested fruit, 62.4 flies/kg, *N* = 64). Some species in gardens and urban areas had high infestation rates, for example, *Anacardium occidentale* (73.3% infested fruit, 73.8 flies/kg, *N* = 15), *Chrysobalanus icaco* (60% infested fruit, 124.9 flies/kg, *N* = 15), *Diospyros blancoi* (43.3% infested fruit, 139.7 flies/kg, *N* = 30) or *Terminalia catappa* (43.5% infested fruit, 131.8 flies/kg, *N* = 588). This species also infested naturalized and invasive species, such as *Syzygium jambos* (44.2% infested fruit, 140.7 flies/kg, *N* = 570), *Syzygium samarangense* (29.7% infested fruit, 61.4 flies/kg, *N* = 165) or *Psidium cattleianum* (27.3% infested fruit, 67.4 flies/
kg, \( N = 1,041 \)). Lastly, some endemic species were also infested by \( B. \) dorsalis, such as \( Ficus \) lateriflora (13.3\% infested fruit, 19.9 flies/kg, \( N = 15 \)) or \( Aphloia \) theiformis (8.9\% infested fruit, 27.6 flies/kg, \( N = 45 \), Table 2). Although \( B. \) dorsalis preferred sweet fruit, we observed a slight infestation on samples from the Curcubitaceae and Solanaceae families, such as \( Monodora \) charantia (0.7\% infested fruit, 2.8 flies/kg, \( N = 295 \)), \( Sechium \) edule (1.7% infested fruit, 0.1 flies/kg, \( N = 118 \)), \( Solanum \) betaceum (1.8% infested fruit, 0.4 flies/kg, \( N = 56 \)), and \( Solanum \) lycopersicum (1.1% infested fruit, 3.9 flies/kg, \( N = 91 \)).

### 3.2.2 Bactrocera zonata

Diversity and richness of \( B. \) zonata’s host range were reduced by half after the \( B. \) dorsalis invasion and only seven host plant species were detected in 2018–2019 (Table 3). Jackknife estimation of species richness decreased from 16.0 ± 1.4 in 2001–2009 to 12.0 ± 2.2 in 2018–2019.

The dissimilarity indexes of Bray–Curtis (0.66) and Sorensen (0.44) suggested that the host niche changed (in terms of infestation rate) between the two periods. Of the 15 species in \( B. \) zonata’s host range, six were the same for both sampling periods. In 2001–2009, \( B. \) zonata’s host diversity was characterized by \( C. \) reticulata, \( D. \) blanchoi, \( P. \) americana, \( S. \) malaccense and \( S. \) samarangense (Figures 1a, 2). In 2018–2019, these species were absent from its host range and \( T. \) catappa was the main host plant species (Figure 1b).

We also observed a significant decrease in the infestation rate of selected host plant species (\( P. \) persica, \( P. \) cattleianum, \( P. \) guajava, \( S. \) jambos and \( T. \) catappa) between the two periods from 91.20 ± 4.89 fruit flies/kg to 1.33 ± 0.32 fruit flies/kg (\( Z = 5.403; p < .001 \)).

### 3.2.3 Ceratitis quilicii

The species richness of the host range was similar for the two periods (Table 3). Jackknife estimation of species richness was 28.0 ± 2.0 in 2001–2009 and 29.0 ± 2.4 in 2018–2019.

The dissimilarity indexes of Bray–Curtis (0.66) and Sorensen (0.44) suggested that the host niche changed (in terms of diversity and proportion of species) between the two periods. Of the 28 species in \( C. \) quilicii’s host range, 18 were the same for both sampling periods.

In 2001–2009, \( P. \) cattleianum, \( M. \) panicalata and \( P. \) mollissima were important host plant species of \( C. \) quilicii in terms of infestation rate (Figure 1a). In 2018–2019, \( P. \) persica and \( E. \) japonica were the main host plant species (Figure 1b).

We also observed a significant decrease in the infestation rate of selected host plant species (\( P. \) persica, \( P. \) cattleianum, \( P. \) guajava, \( S. \) jambos and \( T. \) catappa) between the two periods from 73.80 ± 3.13 fruit flies/kg to 23.86 ± 1.54 fruit flies/kg (\( Z^2 = 6.092; p = .014 \)).
### Table 2: Fruit fly emergence according to host plants collected in 2018 and 2019 in La Réunion

| Family          | Latin name                  | N  | Pupae | B.d | B.z | C.cap | C.qui | C.cat | Z.c | D.c | D.d | N.c |
|-----------------|-----------------------------|----|-------|-----|-----|-------|-------|-------|-----|-----|-----|-----|
| Anacardiaceae   | Anacardium occidentale      | 15 | 114.1 | 73.3| 73.8|       | 1.3  | 0.1  |     |     |     |     |
| Mangifera indica | 233                        | 69.5| 45.5  | 38.4| 3.4 | 0.3  | 1.7  | 4.1  |     |     |     |     |
| Spondias dulcis | 42                         | 17.3| 7.1   | 7.0 |     |       | 11.1 | 2.7  |     |     |     |     |
| Spondias mombin | 60                         | 59.6| 15.0  | 39.3|     |       |       |       |     |     |     |     |
| Anonaceae       | Annona muricata             | 9  | 4.7   | 11.1| 0.2 |       | 11.1 | 2.7  |     |     |     |     |
| Annona reticulata | 19                         | 18.2| 5.3   | 7.2 |     |       | 10.5 | 9.7  |     |     |     |     |
| Cananga odorata | 60                         | 95.3| 8.3   | 53.9|     |       |       |       |     |     |     |     |
| Aphloiacae      | Aphloia theiformis          | 45 | 62.2  | 8.9 | 27.6|       |       |       |     |     |     |     |
| Apocynaceae     | Cascabela thevetia          | 106| 46.0  | 5.7 | 10.8| 1.9  | 11.9 |       |     |     |     |     |
| Arecaceae       | Phoenix dactylifera         | 30 | 1.7   | 3.3 | 1.7 |       |       |       |     |     |     |     |
| Bromeliaceae    | Ananas comosus              | 13 | 2.6   | 23.1| 1.5 |       |       |       |     |     |     |     |
| Cactaceae       | Hylocereus undatus          | 13 | 62.9  | 76.9| 43.1|       |       |       |     |     |     |     |
| Caricaceae      | Carica papaya               | 35 | 7.6   | 5.7 | 2.1 |       |       | 14.3 | 1.6 |     |     |     |
| Chrysobalanaceae| Chrysobalanus icaco         | 15 | 365.4 | 60  | 124.9|       |       |       |     |     |     |     |
| Clusiaceae      | Calophyllum inophyllum      | 30 | 30.0  | 3.3 | 2.0 | 3.3  | 1.0  |       |     |     |     |     |
| Garcinia        | xanthochymus                | 8  | 70.0  | 37.5| 35.6|       |       |       |     |     |     |     |
| Combretaceae    | Terminalia catappa          | 588| 291.9 | 43.5| 131.8| 4.6  | 6.0  | 12.4 |     |     |     |     |
| Cucurbitaceae   | Coccinia grandis            | 105| 317.7 |     |     |     |     | 41.0 | 201.6| 1.0 | 2.4 |     |
| Cucumis sativus | 15                         | 86.2|     |     |     |     |       | 33.3 | 17.8 | 53.3 | 53.4| 13.3 |
| Cucurbita moschata | 51                        | 600.9|     |     |     |     |       | 33.3 | 147.7| 35.3 | 189.1| 7.8  |
| Cucurbita pepo  | 30                         | 26.9|     |     |     | 3.3  | 12.9 | 13.3 | 10.5 |     |     |     |
| Lagenaria sicaria | 16                        | 14.7|     |     |     | 6.3  | 6.7  | 12.5 | 3.1  |     |     |     |
| Momordica charantia | 295                      | 311.5| 0.7  | 2.8 |     |     |       | 28.5 | 134.6| 6.8 | 18.5| 5.8  | 12.9 |
| Family       | Latin name | N  | Pupae | B.d | B.z | C.cap | C.qui | C.cat | Z.c | D.c | D.d | N.c |
|-------------|------------|----|-------|-----|-----|-------|-------|-------|-----|-----|-----|-----|
|             |            |    |       |     |     |       |       |       |     |     |     |     |
| Ebenaceae   | Diospyros  | 30 | 247.2 | 43.3| 139.7|       |       |       |     |     |     |     |
|             | blanco²    |    |        |     |     |       |       |       |     |     |     |     |
|             | Diospyros  | 135| 26.1  | 14.8| 9.2 | 0.7   | 0.1   | 0.7   | 0.9 | 4.4 | 2.5 |     |
|             | kaki       |    |        |     |     |       |       |       |     |     |     |     |
| Fabaceae    | Inga       | 30 | 28.9  | 3.3 | 5.8 |       |       |       |     | 10 | 17.4|     |
|             | laurina¹   |    |        |     |     |       |       |       |     |     |     |     |
| Lauraceae   | Persea     | 73 | 91    | 11.0| 6.9 |       |       |       |     |     |     |     |
|             | americana  |    |        |     |     |       |       |       |     |     |     |     |
| Moraceae    | Ficus      | 60 | 159.7 | 30  | 49.2|       |       |       |     | 15.0| 10.5|     |
|             | carica      |    |        |     |     |       |       |       |     |     |     |     |
|             | lateriflora¹| 15 | 19.9  | 13.3| 19.9|       |       |       |     |     |     |     |
|             | mauritiana | 30 | 16.7  | .   | .   |       |       |       |     | 6.7 | 11.9|     |
| Musaceae    | Musa       | 64 | 93.6  | 32.8| 62.4|       |       |       |     | 13.3| 47.6| 6.7 |
|             | acuminata  |    |        |     |     |       |       |       |     | 34.8|     |     |
| Myrtaceae   | Eugenia    | 120| 192.2 | 4.2 | 11.0|       |       |       |     | 10.5|     |     |
|             | uniflora   |    |        |     |     |       |       |       |     |     |     |     |
|             | Psidium    | 1,041| 177.2 | 27.3| 67.4| 0.2   | 0.3   | 0.2   | 0.2 | 15.7| 26.2|     |
|             | cattleyanum|    |        |     |     |       |       |       |     |     |     |     |
|             | guajava    | 550| 120.8 | 19.3| 44.2| 0.4   | 0.2   | 0.5   | 0.3 | 22.7| 16.1| 0.2 |
|             | guajava    |    |        |     |     |       |       |       |     |     |     |     |
|             | Syzygium   | 570| 305.1 | 44.2| 140.7|0.4 | 0.2   | 0.4   | 0.2 | 15.3| 22.1| 0.5 |
|             | jambos     |    |        |     |     |       |       |       |     |     |     |     |
|             | malaccense | 25 | 36.0  | 20  | 30.5|       |       | 4.0   | 1.1 |     |     |     |
|             | samarangense| 165| 115.6 | 29.7| 61.4|       |       | 4.8   | 3.6 |     |     |     |
| Oleaceae    | Noronhia   | 30 | 4.7   | 3.3 | 1.6 |       |       |       |     |     |     |     |
|             | emarginata²|    |        |     |     |       |       |       |     |     |     |     |
| Oxalidaceae | Averrhoa   | 55 | 0.6   | 1.8 | 0.6 |       |       |       |     |     |     |     |
|             | bilimbi    |    |        |     |     |       |       |       |     |     |     |     |
|             | carambola  | 63 | 1.8   | 1.6 | 0.5 |       |       | 3.2   | 0.7 |     |     |     |
| Passifloraceae | Passiflora | 60 | 62.7  |     |     |       |       |       |     | 23.3| 18.0|     |
|             | molissima  |    |        |     |     |       |       |       |     |     |     |     |
|             | suberosa   | 96 | 993.3 |     |     |       |       | 43.8  | 74.7|     |     |     |
| Polygonaceae | Coccoloba | 60 | 11.2  | 5.0 | 11.2|       |       |       |     |     |     |     |
|             | uvifera¹   |    |        |     |     |       |       |       |     |     |     |     |

(Continues)
| Family          | Latin name              | N     | Pupae | B.d | B.z | C.cap | C.qui | C.cat | Z.c | D.c | D.d | N.c |
|-----------------|-------------------------|-------|-------|-----|-----|-------|-------|-------|-----|-----|-----|-----|
| Rhamnaceae      | Ziziphus mauritiana     | 105   | 97.6  | 25.7| 68.8| 1.0   | 0.4   | -     | -   | -   | -   | -   |
| Rosaceae        | Eriobotrya japonica     | 359   | 153.6 | 5.0 | 9.2 | -     | -     | -     | -   | -   | -   | -   |
|                 | Malus pumila            | 23    | 46.3  | 17.4| 10.8| -     | -     | -     | -   | -   | -   | -   |
|                 | Prunus persica          | 268   | 221.4 | 26.9| 34.8| -     | -     | -     | -   | -   | -   | -   |
|                 | Prunus sp.              | 83    | 108.2 | 7.2 | 6.9 | -     | -     | -     | -   | -   | -   | -   |
|                 | Pyrus sp.               | 78    | 42.2  | 12.8| 6.5 | -     | -     | -     | -   | -   | -   | -   |
| Rubiaceae       | Coffea sp.              | 193   | 65.7  | -   | -   | -     | -     | -     | -   | -   | -   | -   |
| Rutaceae        | Citrus aurantiifolia x  | 11    | 62.1  | 36.4| 48.0| -     | -     | -     | -   | -   | -   | -   |
|                 | Fortunella sp.          |       |       |     |     |       |       |       |     |     |     |     |
|                 | Citrus clementina       | 80    | 2.3   | -   | -   | -     | -     | -     | -   | -   | -   | -   |
|                 | Citrus reticulata x     | 51    | 6.8   | -   | -   | -     | -     | -     | -   | -   | -   | -   |
|                 | Citrus sinensis         | 75    | 2.3   | 9.3 | 1.4 | -     | -     | -     | -   | -   | -   | -   |
|                 | Citrus tangerina        | 104   | 3.8   | -   | -   | -     | -     | -     | -   | -   | -   | -   |
|                 | Murraya paniculata     | 120   | 1,137.5 | - | - | - | 44.2 | 789.6 | 3.3 | 26.8 | - | - | - |
| Salicaceae      | Dovyalis hebecarpa alt. | 45    | 37.8  | 4.4 | 10.1| -     | -     | -     | -   | -   | -   | -   |
| Sapindaceae     | Flacourtia indica alt.  | 108   | 31.5  | 0.9 | 5.4 | -     | 0.9   | 1.1   | 3.7 | 5.4 | -   | -   |
| Sapotaceae      | Litchi chinensis       | 181   | 1.6   | 1.7 | 1.3 | -     | -     | -     | -   | -   | -   | -   |
|                 | Chrysophyllum cainito   | 15    | 27.8  | -   | -   | -     | -     | -     | -   | 20  | 13.9| -   |
|                 | Mimusops carlceae alt. | 75    | 9.2   | 4.0 | 5.6 | -     | -     | -     | -   | 20  | 13.9| -   |
|                 | Mimusops elengi        | 59    | 13.9  | -   | -   | -     | 1.7   | 13.9  | -   | -   | -   | -   |
| Solanaceae      | Capsicum frutescens    | 73    | 47.2  | -   | -   | -     | 4.1   | 15.7  | -   | -   | -   | 6.8 |
|                 | Solanum betaceum alt.  | 56    | 9.2   | 1.8 | 0.4 | -     | -     | -     | -   | -   | -   | 3.6 |
|                 | Solanum lycopersicium  | 91    | 24.1  | 1.1 | 3.9 | -     | 1.1   | 0.5   | -   | -   | -   | 13.2|

(Continues)
3.2.4 | *Ceratitis capitata*

Host range species richness was similar for the two periods (Table 3). Jackknife estimation of species richness was $32.0 \pm 2.6$ in 2001-2009 and $29.0 \pm 3.3$ in 2018-2019.

The dissimilarity index of Bray–Curtis (0.67) and Sorensen (0.51) suggested a shift in host range (in terms of diversity and proportion of species) between the two periods. Of the 27 species in *C. capitata*’s host range, 16 were the same for both sampling periods. Moreover, of the five characteristic species observed in 2001–2009, only *M. paniculata* and *P. suberosa* were very important host plant species in 2018–2019 (Figure 2). They represent 90% of infestations (fruit flies/kg, Figure 1b). *Coffea sp., M. elengi* and *P. dulce* were host plants in both periods, but the proportion of infested fruits was lower in 2018–2019.

We also observed a significant decrease in the infestation rate of selected host plant species (*Coffea sp., E. uniflora, M. paniculata, P. suberosa, T. catappa*) between the two periods ($\chi^2 = 17.504; p < .001$) from $157.85 \pm 10.02$ fruit flies/kg to $43.20 \pm 16.57$ fruit flies/kg.

3.2.5 | *Ceratitis catoirii*

This rare endemic species was only observed in 77 fruits (of the 6,929 fruit samples collected, vegetables excluded) between 2001 and 2009 and in 5 fruits (of a total of 8,276 fruit samples, vegetables excluded) in 2018–2019. The species richness of the host range was similar for the two periods (Table 3). Jackknife estimation of species richness was $7.0 \pm 1.4$ in 2001–2009 and $5.0 \pm 1.4$ in 2018–2019. *Ceratitis catoirii* was mainly observed in *Z. mauritiana* during the first sampling period and in *T. catappa* during the second sampling period (Figure 1).

3.2.6 | Other Tephritidae species

Diversity and species richness of the host range was similar for the two periods for *D. ciliatus, D. demmerezi, Z. cucurbitae* and *N. cyanescens* (Table 3, Figure 1a, 1b). Nevertheless, we observed some differences in host niche in terms of diversity and proportion of species (Bray–Curtis: 0.29–0.84 and Sorensen: 0.38–0.50), probably due to the lower host diversity.

3.3 | Geographic and climatic distribution

3.3.1 | *Bactrocera dorsalis*

One year after it was first detected, *B. dorsalis* was found all over the island, at a range of from 0 to 1,600 m, the maximal altitude sampled (Figures 3a and 4a). The number of flies per kg significantly increased with temperature ($Z = 3.124; p = .002$). Precipitation had no impact on the number of flies per kg ($Z = -0.706; p = .480$).
### TABLE 3  Diversity index of host range according to fruit fly species and studied period

|                | Species richness | Jackknife estimation | Dissimilarity | Common species between the two periods |
|----------------|------------------|----------------------|---------------|---------------------------------------|
|                | 2001–2009        | 2018–2019            | 2001–2009     | 2018–2019                             |
| **B. dorsalis**| 2.69             | 30                   | 39.0 ± 3      | -                                     |
| **B. zonata**  | 1.61             | 7                    | 16.0 ± 1.4    | 12.0 ± 2.2                            |
| **C. capitata**| 1.66             | 18                   | 32.0 ± 2.6    | 29.0 ± 3.3                            |
| **C. catoirii**| 0.11             | 3                    | 7.0 ± 1.4     | 5.0 ± 1.4                             | 0.99          | 0.50 | 3/5  |
| **C. quilicii**| 2.53             | 23                   | 28.0 ± 2.0    | 29.0 ± 2.4                            | 0.66          | 0.44 | 19/28 |
| **D. ciliatus**| 1.74             | 6                    | 10.0 ± 1.4    | 9.0 ± 1.7                             | 0.46          | 0.38 | 6/8  |
| **D. demmerezi**| 1.41            | 4                    | 6.0 ± 0.0     | 5.0 ± 1.0                             | 0.84          | 0.45 | 4/6  |
| **Z. cucurbitae**| 1.41            | 7                    | 11.0 ± 1.4    | 11.0 ± 2.0                            | 0.46          | 0.50 | 6/10 |
| **N. cyanescens**| 1.14            | 6                    | 9.0 ± 1.0     | 7.0 ± 1.0                             | 0.29          | 0.53 | 5/9  |

**FIGURE 3**  Distribution of samples infested by (a) *B. dorsalis*, (b, c) *B. zonata*, (d, e) *C. quilicii*, and (f, g) *C. capitata* during the 2001–2009 period (b, d, f) and 2018–2019 period (a, c, e, g) in La Réunion.
3.3.2 | *Bactrocera zonata*

*Bactrocera zonata* was found on the coast in fruit harvested at low altitude between 0 and 600 m (Figure 3b,c). During the period 2001–2009, infestation rate significantly increased with temperature \( Z = 3.495; P < .001 \) and decreased with precipitation \( Z = -2.251; p = .024 \). In 2001–2009, temperature had a positive effect on infestation rate \( Z = 4.251; p < .001 \), but not precipitation \( Z = -1.054; p = .292 \).

The niche equivalency test showed that the ecological niche was similar for the two studied periods (Niche overlap \( D = 0.61, I = 0.78 \), \( P_D = 0.06, P_I = 0.06 \), Figure 4b).

3.3.3 | *Ceratitis quilicii*

*Ceratitis quilicii* was present throughout the island and found in fruit harvested between 0 and 1,580 m altitude (Figure 3d,e). During the period 2001–2009, infestation rate significantly decreased with temperature \( Z = -3.472; p < .001 \) and precipitation \( Z = -2.216; p = .027 \).

In 2001–2009, temperature had a negative effect on infestation rate \( Z = -2.835; p = .004 \), but not precipitation \( Z = -1.150; p = .250 \).

The niche equivalency test showed that the ecological niche was significantly different between the two studied periods (Niche overlap \( D = 0.51, I = 0.67 \), \( P_D = .35, p_i < .001 \)). For the second sample period, *C. capitata* was less present in sites with higher temperatures (lower altitude) than for the first period (Figure 4c).

3.3.4 | *Ceratitis capitata*

*Ceratitis capitata* was more frequent in the west of the island and found in fruit harvested between 0 and 850 m altitude (Figure 3f, g). During the period 2001–2009, temperature \( Z = 0.084; p = .933 \) and precipitation \( Z = -0.834; p = .404 \) had no significant impact on infestation rate. In 2001–2009, precipitation had a negative effect on the infestation rate \( Z = -1.999; p = .046 \), but not temperature \( Z = -0.294; p = .768 \).

The niche equivalency tests showed that the ecological niche differed significantly between the two studied periods (Niche overlap \( D = 0.24, I = 0.034 \), \( p_D = <.001, p_i < .001 \), Figure 4). For the second sampling period, *C. capitata* was found in sites with lower precipitation and temperature than for the first period (Figure 4e).

3.3.5 | *Ceratitis catoirii*

*Ceratitis catoirii* was found in the north and south of the island in fruit harvested between 0 and 760 m altitude. There were not enough data to study the preference and niche modification of this rare endemic species (Figure 4d).

4 | DISCUSSION

One and two years after the *Bactrocera dorsalis* invasion, respectively, we observed a shift in the host range and spatial distribution of the established species. In the case of specialist species, which shared few host plant species with *B. dorsalis*, no significant change in host range was observed. On the contrary, generalist species such as *B. zonata*, *C.quilicii* and *C. capitata* modified their host range (diversity and proportion) and we observed a shift in their climatic niches.

4.1 | Host range of *B. dorsalis*

Our results confirm the generalist character of *B. dorsalis* in La Réunion. Of the 112 species tested, 52 were infested by *B. dorsalis* belonging to 23 families. In La Réunion, these species’ primary

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**FIGURE 4** Mean of precipitation and temperature of sample sites collected in 2001–2009 and 2018–2019. Samples were infested by (a) *B. dorsalis*, (b) *B. zonata*, (c) *C. quilicii*, (d) *C. catoirii* and (e) *C. capitata*. All samples are represented in (f) including uninfested fruits. Orange points correspond to the fruits collected in 2001–2009 and green points to fruits collected in 2018–2019.
host plants (as a function of number of infested fruit, infestation rate measured by number of fruit flies per kg and abundance) were *Mangifera indica*, *Terminalia catappa*, *Syzzygium jambos*, *Psidium cattleianum* and *Psidium guajava*. These plant species are regularly cited as essential hosts for this invasive species in different sites (Goergen, Vayssières, Gnanvosou, & Tindo, 2011). Their nutritional value maximizes larval development and survival in generalist species (Hafsi et al., 2016).

The invasion of *B. dorsalis* considerably increased the impact of fruit flies on agriculture in La Réunion because it infested new plant species not previously affected by the established species. These include *Ananas comosus*, *Hylocereus undatus*, *Litchi chinensis* or *Musa* sp. In addition, after the invasion, an increase in the number of infestation rates on *M. indica* was also observed.

*Bactrocera dorsalis* infestations were also observed on some cultivated Cucurbitaceae and Solanaceae species, such as *Momordica charantia*, *Sechium edule*, *Solanum betaceum* and *Solanum lycopersicum*, but to a lesser extent. Similar results showing low *B. dorsalis* infestation on these plants have also been recorded in other studies (Clarke et al., 2005; Goergen et al., 2011). Several factors could explain the relatively low infestation rates observed in these plant species, for example, female preference for oviposition, less efficient larval development or interspecific interactions. The specialist species (*Z. cucurbitae*, *D. ciliatus*, *D. demmerezi* and *N. cyaneascens*) were found to infest a high proportion of Cucurbitaceae and Solanaceae fruit. They may have had direct interactions with the generalist species and, thus, may have been in direct competition for access to resources.

In addition to cultivated species, many wild species were infested by *B. dorsalis*. Both invasive species (for example, *P. cattleianum* or *S. jambos*) and endemic species (for example, *Aphloia theiformis* or *Ficus lateriflora*) were affected. Wild and cultivated host plants (in orchards or gardens) cover a large part of the island. The subtropical climate means that fruiting periods overlap the whole year round (Quilici & Jeuffrault, 2001). Wild species could potentially serve as reservoir hosts, which would allow fruit fly populations to persist in space and time, where or when the preferred plant host species are not available. These results reveal the importance of monitoring non-cultivated hosts when control strategies are developed for a particular fruit crop.

### 4.2 Host range shift

Changes in the host range of established species have been observed in different ways. *Ceratitis* species had the same host plant diversity in 2018–2019. A decline in the host plant range of these species and reduced infestation rates had already been observed on mango, guava and Indian almond species after the arrival of *B. zonata* (Charlery de la Masselère et al., 2017). Therefore, the *Ceratitis* species were not fundamentally impacted by the invasion of *B. dorsalis* with regard to these host plants. Nevertheless, we observed differences in host composition for *C. quilicier* between the two periods studied. In addition, *C. capitata* became rarer in some plants, which had previously been major hosts, such as *Coffee sp.*, *Mimusops elengi* and *Pithecellobium dulce*. These results are in accordance with other studies showing that invasive *Bactrocera* species can displace *Ceratitis* species from their preferred host plants (Duyck, Sterlin, et al., 2004; Ekesi, Mohamed, & De Meyer, 2016; Mwatawala et al., 2009a, 2009b). For example, *B. zonata* previously impacted the host range of *Ceratitis* species in La Réunion (Charlery de la Masselère et al., 2017); *B. dorsalis* displaced *C. cosyra* in Kenya (Ekesi et al., 2009) and *C. capitata* in Hawaii (Keiser et al., 1974), and became the predominant fruit fly pest of mango and guava in both countries. Our findings reveal two different types of response for *Ceratitis* species: *C. capitata* found an ecological refuge in host plants with small berries rarely infested by *B. dorsalis*, such as *Muraya paniculata* and *Passiflora suberosa*, while the *C. quilicier* host range largely overlaps that of *B. dorsalis*. This overlap is also illustrated by the high proportion of co-infestation between *B. dorsalis* and *C. quilicier* (68% of co-infested fruits).

*Bactrocera zonata* suffered a significant decrease in host species diversity and infestation rates. Two years after the *B. dorsalis* invasion, this species was very rare in all fruit samples collected. The competitive superiority of *B. dorsalis* is not surprising. In 2004, this species was already ranked as one of the top invaders and competitors among tephritid species (Duyck, et al., 2004). *Bactrocera dorsalis* has already caused the competitive displacement of other *Bactrocera* species, such as *B. tryoni*, *B. kirki* and *B. perfusca* in French Polynesia (Allwood & Drew, 1997; Leblanc & Putoa, 2000). Many researchers have demonstrated that an invader is competitively superior to the native or established species that it displaces (Duyck, Sterlin, et al., 2004; Reitz & Trumble, 2002). The intensity of the *B. dorsalis* invasion on the *B. zonata* population and its almost immediate impact were unexpected. Our results suggest that *B. zonata* may even be suffering from a process of competitive exclusion. In the literature, competitive exclusion is rarer than displacement (DeBach, 1966). In fruit flies, the only case of exclusion was reported for *C. capitata* in Mauritius because of pressure from successive invasions of different species over the years (Duyck, Sterlin, et al., 2004). *Bactrocera zonata* has proven to be more sensitive than *Ceratitis* species to the invasion of *B. dorsalis*. One hypothesis could be that these closely related species suffered from greater competition because their niches were too similar. For a stable coexistence, species require different niches. Species that are ecologically too similar cannot coexist (Burns & Strauss, 2011; Macarthur & Levins, 1967; Peterson et al., 2013).

### 4.3 Climatic niche shift

In our study, in addition to the host range shift, we observed a shift in the climatic niches after the *B. dorsalis* invasion. *Ceratitis quilicier* and *C. capitata* were less present at low altitude (higher temperature) and *C. capitata* was less present in the east of the island (higher humidity) following the *B. dorsalis* invasion. Similar niche partitioning associated with the *B. dorsalis* invasion was observed in Eastern Central Tanzania, where *C. rosa* became predominant at a higher
elevation (Geurts, Mwatwala, & De Meyer, 2012) and in Hawaii, where C. capitata populations were only maintained in peach and other fruit at high elevations (Keiser et al., 1974), while B. dorsalis was dominant in lowlands.

These results seem to demonstrate that established species are found in areas where they perform better (i.e., climatic optimum). They avoid areas colonized by B. dorsalis. Bactrocera dorsalis has an extensive ecological niche, both in terms of temperature and precipitation. Its niche (from 2018–2019 data) overlaps with that of other established species observed prior to 2009. Nevertheless, data collected showed a higher infestation rate in lowlands, corresponding to the optimum temperature for larval development, which is between 25°C and 30°C (Rwomushana, Ekesi, Ogol, & Gordon, 2008).

Ceratitis capitata was less abundant in humid and warm areas of the island after the B. dorsalis invasions. Duyck and Quilici (2006) showed that this species is more adapted to a dry climate than other Ceratitis species. It can tolerate all temperatures between 15 and 30°C, although it develops more slowly than C. quilicii in lower temperatures. The infestation rate of C. quilicii decreased at low altitude after the invasion of B. dorsalis. This appears to be consistent with the fact that this species has a higher tolerance to low temperatures; its temperature threshold for larval development is 3.1°C (Duyck & Quilici, 2006). Thus, this observed shift could be due to niche-dependent competition, whereby each species becomes dominant in its optimum environment. Numerous models have shown that the environment has a considerable impact on the outcome of competition and tends to shift the balance in favour of one of the species (Snyder, 2008; Velázquez, Garahan, & Eichhorn, 2014). Climatic niche displacement was probably one parameter that allowed the coexistence of B. dorsalis and the two Ceratitis species.

Bactrocera zonata has a climatic niche similar to that of B. dorsalis with an optimal development temperature between 25°C and 30°C (De Villiers et al., 2015; Duyck, Sterlin, et al., 2004; Ni et al., 2012). However, B. zonata is more sensitive to cold than the other two species, with a 12.6°C temperature threshold for larval development (Duyck & Quilici, 2006; Duyck, Sterlin, et al., 2004). In La Réunion, this species probably did not have the opportunity to escape from B. dorsalis at higher altitudes.

### 4.4 The competitive displacement

Although we have no direct evidence of the impact of B. dorsalis on other species, we have a large amount of evidence regarding the competitive displacement induced by B. dorsalis on other established species. Before B. dorsalis was introduced in La Réunion, the coexistence of tephritid species was linked to the differentiation of climatic niche and host range, as demonstrated in studies by Duyck and colleagues (Duyck et al., 2008; Duyck & Quilici, 2006). However, the invasion of B. dorsalis affected this balance. We have shown that the coexistence between B. dorsalis and C. quilicii was possible because the species have a different response to temperature; that is, C. quilicii demonstrates a niche shift to a higher altitude than B. dorsalis. The coexistence of C. capitata with B. dorsalis and the other resident species was possible because of its ability to develop at a lower temperature (high altitude) and to exploit fruit species that are not host to other fruit fly species.

Bactrocera zonata and B. dorsalis have similar ecological requirements for climatic and host range. Both species prefer high temperatures and have a similar range of host plants, such as mango, Indian almond or guava. In La Réunion, the coexistence of B. zonata with B. dorsalis seems to be compromised (DeBach, 1966; Hardin, 1960). However, other studies showed that the coexistence of these two species is possible in other parts of the world, including non-native areas like Sudan (Agarwal et al., 1999; Mahmoud et al., 2020).

According to climatic models, B. zonata seems a little less sensitive to dry stress than B. dorsalis (De Villiers et al., 2015; Ni et al., 2012). We suppose that differences in tolerance allow the coexistence of B. dorsalis and B. zonata within the limits of climatic suitability for B. dorsalis.

Many parameters could influence the competitive outcomes. For example, previous studies have shown that oviposition competition occurs between adult females. Liu et al. (2017) showed that B. dorsalis species has a clear advantage when competing with C. capitata for egg-laying. Aggressive behaviour has been observed in some fruit fly species, including B. dorsalis. Females are reported to defend their oviposition sites from other females (Benelli, 2014; Shelly, 1999) and may be the cause of agonistic interference competition. In addition, competition between females for egg-laying sites could be an issue if B. dorsalis has a greater capacity for locating or exploiting the resource or if B. dorsalis uses the resource at an earlier stage than other fruit fly species (Rwomushana et al., 2009). In the case of co-inestation of the same fruit, interactions between larvae could create interference or competition (Duyck et al., 2008; Rwomushana et al., 2009; Shen et al., 2014). In larval competition, the short duration of larval development of Bactrocera species appears to be an advantage (Duyck, David, & Quilici, 2007).

Other mechanisms could promote coexistence or competitive displacement, such as apparent competition. This occurs when a natural enemy increases in number or becomes more efficient at attacking a given species in the presence of a third species (Holt, 1977). Some cases of niche shift, which were interpreted as competitive displacement, may actually involve apparent competition (David et al., 2017). In La Réunion, generalist species share the same parasitoid, Fopius arisanus. This parasitoid could have a different effect on fruit fly species that coexist in the same biotope (Rousse, Gourdon, & Quilici, 2006).

### 5 CONCLUSION

Our results have implications for control programmes. Integrated information on interaction networks, including competition, is a necessary step for identifying empty niches and modelling potential species distribution. On the basis of the hypothesis of
hierarchical competition in Tephritidae, it would be interesting to determine whether or not the presence of B. dorsalis limits the invasion by B. zonata. In addition, eradication programmes may have unexpected impacts on non-target species, especially through indirect effects. For example, local eradication of B. dorsalis could lead to an increase in B. zonata populations because of reduced competition.

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**BIOSKETCH**

The research team works on the ecological dynamic in insular biotope. The team's work aims to improve knowledge of the biology, ecology and genetics of populations of arthropods of agricultural interest, to identify the structuring factors of plant and arthropod communities in agroecosystems or natural ecosystems. Tephritidae is one of the models of study followed for many years in La Réunion.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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