



Distribution and host ranges of *Ceratitis rosa* and *Ceratitis quilicii* (Diptera: Tephritidae) in South Africa

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Research Paper

Cite this article: Tsatsu SK, Sutton GF, Serfontein L, Addison P, De Meyer M, Virgilio M, Manrakhan A (2024). Distribution and host ranges of *Ceratitis rosa* and *Ceratitis quilicii* (Diptera: Tephritidae) in South Africa. *Bulletin of Entomological Research* 1–11. <https://doi.org/10.1017/S0007485324000294>

Received: 19 December 2023

Revised: 2 May 2024

Accepted: 11 May 2024

Keywords:

Africa; Cape fruit fly; ecology; Natal fly

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Abstract

Two fruit fly (Diptera: Tephritidae) species of economic importance: *Ceratitis rosa* Karsch and *Ceratitis quilicii* De Meyer, Mwatawala & Virgilio are present in South Africa. The two species were considered as one species prior to 2016, but were subsequently separated. In this study, the distribution and abundance of the two species were quantified in seven provinces in South Africa through trapping with Enriched Ginger Oil as an attractant. Trapping was conducted over three seasons across two years (2020 and 2021): late summer, autumn-winter, and spring-early summer. Host ranges of the two species were investigated by fruit sampling in and outside of trapping sites. *Ceratitis quilicii* was more widely distributed than *C. rosa* with the latter being recorded in only three north-eastern provinces. There were geographical limits for both species with no records of them in Northern Cape Province. Catches of *C. quilicii* were higher in summer with average temperatures varying from 15 to 27°C while for *C. rosa*, catches remained low and consistent between seasons. *Ceratitis quilicii* catches decreased at lower rates than those of *C. rosa* at temperatures below 15°C. The two species were reared from 13 plant species from nine families. Four of these hosts were infested by both *C. quilicii* and *C. rosa* in the same province where they occurred. Preferred hosts of the two species belonged to the Myrtaceae family. The characterisation of the distribution, abundance and host ranges of these pests will provide a baseline for pest status determination and implementation of management actions.

Introduction

Distribution of insects in space and time is influenced by multiple factors which are classified based on the scale at which their impacts are most significant (Hortal *et al.*, 2010). On a wider scale, abiotic factors would generally have significant effects on distribution of insects whilst on a localised scale, biotic factors and habitat related movement may be more influential (Hortal *et al.*, 2010).

In integrated pest management (IPM), information on the ecology of a pest that encompasses its distribution in space and time is key (Pimentel, 1982). In South Africa, IPM practices are recommended in fruit production areas for insect pests affecting fruit commodities. Fruit industries in South Africa play an important role in the country's economy, with the largest contribution to agricultural exports (Uys, 2016). Effective IPM practices for fruit infesting insect pests are therefore critical to sustain these industries. Fruit flies (Diptera: Tephritidae) are among important insect pests of commercial fruit in South Africa (Prinsloo and Uys, 2015). Five key fruit fly pests of commercial fruit are known to occur in South Africa: *Ceratitis capitata* (Wiedemann), *Bactrocera dorsalis* (Hendel), *Ceratitis cosyra* (Walker), *Ceratitis rosa* Karsch, and *Ceratitis quilicii* De Meyer, Mwatawala & Virgilio (De Meyer *et al.*, 2002; Prinsloo and Uys, 2015; De Meyer *et al.*, 2016).

Ceratitis rosa, the Natal fruit fly, and *C. quilicii*, the Cape fruit fly, were previously considered as one species (*C. rosa* *sensu lato*) but in 2016, they were recognised as two separate species, based on differences in their morphology (males only), physiology and genetics (Virgilio *et al.*, 2013; De Meyer *et al.*, 2015, 2016). *Ceratitis rosa* and *C. quilicii* form part of the FARQ complex (previously FAR complex) (Zhang *et al.*, 2021), a cryptic species complex that currently includes two other member species: *Ceratitis fasciventris* (Bezzi) and *Ceratitis anonae* Graham (Virgilio *et al.*, 2008). *Ceratitis rosa* and *C. quilicii* are the only two species within the FARQ complex that occur in South Africa (De Meyer *et al.*, 2015, 2016).

The ecology of *C. rosa* and *C. quilicii* in South Africa has, to date, been studied only to a limited extent. There have been already indications of parapatric and sympatric distribution of

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these two species in South Africa during a study on the genetic composition of *C. rosa* sensu lato (s.l.) (Virgilio *et al.*, 2013), although these results were based on limited sampling locations (six in total) across the country. In a subsequent study on the population genetic structure of *C. rosa* s.l. in South Africa, *C. quilicii* (then known as *C. rosa* R2) was the only species of the two recorded in the country (Karsten *et al.*, 2016). The latter study was based on a larger survey across the country (22 sampling locations) but it was not clear whether these were samples collected at different times of the year or just once in a location. Sympatric distribution of *C. rosa* and *C. quilicii* in the north eastern provinces of South Africa was however confirmed in another study conducted between 2014 and 2015 (Manrakhan *et al.*, 2017a). In the latter study, the seasonal abundances of the two species were not separately presented. Since the split of *C. rosa* and *C. quilicii*, there has also been little information on separate host lists for each species in South Africa. De Meyer *et al.* (2002) provided an annotated host list of Afro-tropical fruit fly species for *C. rosa* s.l. Museum-stored voucher specimens of *C. rosa* s.l. were revisited for listing of hosts for *C. quilicii* (De Meyer *et al.*, 2016). In studies on distribution and host ranges of fruit flies in Reunion island, records of *C. quilicii* (the only species of FARQ complex known to occur in Reunion island) were obtained on several fruit types spanning several plant families (Charlery de la Masseliere *et al.*, 2017; Moquet *et al.*, 2021). It is to be noted that in these latter studies, the exact origin and condition of the fruit found to be infested were not provided in the results section and were not fully described in their methodology. Based on the raw data of Moquet *et al.* (2021), almost a quarter of fruit samples infested by *C. quilicii* were also infested by other fruit fly species (Moquet *et al.*, 2020). Infestation of *C. quilicii* on those fruit species could therefore have been opportunistic. Host records of *C. quilicii* obtained in Moquet *et al.* (2021) may therefore not be representative of the true natural host range of this species in the absence of other fruit flies.

It is clear that there are considerable gaps in the knowledge on the ecology of these two cryptic species in South Africa that would need to be filled in. Not only would complete information on the ecology of these pests be crucial in developing effective IPM practices against these pests but it would also help in providing a better baseline for determining pest risk. Models to predict the potential range expansion of *C. rosa* and *C. quilicii* based on life table parameters collected on laboratory reared flies were developed and predicted that *C. quilicii* could potentially establish over a wider range of climatic conditions than *C. rosa* (Tanga *et al.*, 2018). The model also predicted suitable areas in West and Central Africa where neither of these species have been recorded to date indicating that there are other factors at play in restricting the geographical distribution of the two species, factors such as natural geographical barriers and biotic factors such as the occurrence of competitors (Clarke and Measham, 2022).

The objective of this study was therefore to further define the geographical ranges of distribution and host ranges of *C. rosa* and *C. quilicii* in South Africa and to provide a first characterisation of their relative abundances and seasonal dynamics.

Materials and methods

Study sites

The study was conducted for two consecutive years between March 2020 and November 2021 in seven provinces of South

Africa where commercial fruit are mainly cultivated namely: Eastern Cape, Western Cape, Northern Cape, KwaZulu-Natal, North West, Limpopo, and Mpumalanga (fig. 1). Three to eight commercial fruit farms were selected in each province for this study. The number of and description of commercial fruit farms in each province are provided in table 1. In each year, the study periods were distributed over three austral seasons coinciding with ripening times of different fruit types: late summer (February, March, and April) for subtropical, deciduous and early ripening citrus, autumn-winter (May, June, and July) for citrus, and spring-early summer (September, October, and November) for deciduous fruit. In 2020, the study could only be conducted in two of the provinces during late summer due to COVID-19 related local travel restrictions at the time. Data on temperature, precipitation and relative humidity for the trapping sites during the survey periods were obtained from the closest weather stations of the Agricultural Research Council located between 2 and 102 km from each trapping site. Whenever available, climatic data were collected on daily basis. Fluctuations in temperatures, relative humidity and precipitation in each province across seasons over the two years are provided in the supplementary information (figs S1 and S2).

Trapping surveys

The distribution and abundance of *C. rosa* and *C. quilicii* were assessed by trapping. McPhail bucket traps (Insect Science [Pty] Ltd, Tzaneen, South Africa) were used, each baited with 2 ml polyethylene bulb of Enriched Ginger root Oil (EGO lure) (Insect Science [Pty] Ltd, Tzaneen, South Africa). EGO lure is a male-specific lure (Mwatawala *et al.*, 2013; Manrakhan *et al.*, 2017a, 2017b) and was found to be more effective than trimedlure and Capilure in trapping *Ceratitis* species, including *C. rosa* and *C. quilicii* during trials in South Africa and Tanzania (Mwatawala *et al.*, 2013; Manrakhan *et al.*, 2017a, 2017b). The lure was placed in a plastic mesh container fitted to the inside of the lid of the traps. Inside the trap, a 3 g strip of toxicant: 2,2-dichlorovinyl dimethyl phosphate (DDVP)-strip (Dichlorvos, 195 g kg⁻¹ active ingredient) (River Bioscience, Gqeberha, South Africa) was placed at the bottom to kill attracted flies. Three traps were placed in each commercial farm. Each trap was suspended on a tree branch at least 1.5 m above the ground. The distance between traps in a site was between 200 and 300 m. Traps were left in the sites for four to five weeks before collection. Trap catches were collected and placed in labelled vials and brought to the laboratory at Citrus Research International (CRI), Mbombela, South Africa for sorting, sexing, and identification. Fresh lures and toxicants were used for each trapping season during both years.

Fruit sampling surveys

Over the two years and across the seasons, mature ripe fruit were sampled from selected trapping sites in four of the provinces: Limpopo, Mpumalanga, North West, and Western Cape based on availability. In order to cover a wider range of fruit types, fruit were also sampled outside of but adjacent to the trapping sites in the same provinces referred above. These additional fruit sampling sites had fruit trees that were not used for commercial purposes. From all sampling sites, fruit were collected from the tree and ground, whenever available. Fruit that showed general external damage symptoms (not fruit fly specific) were preferably

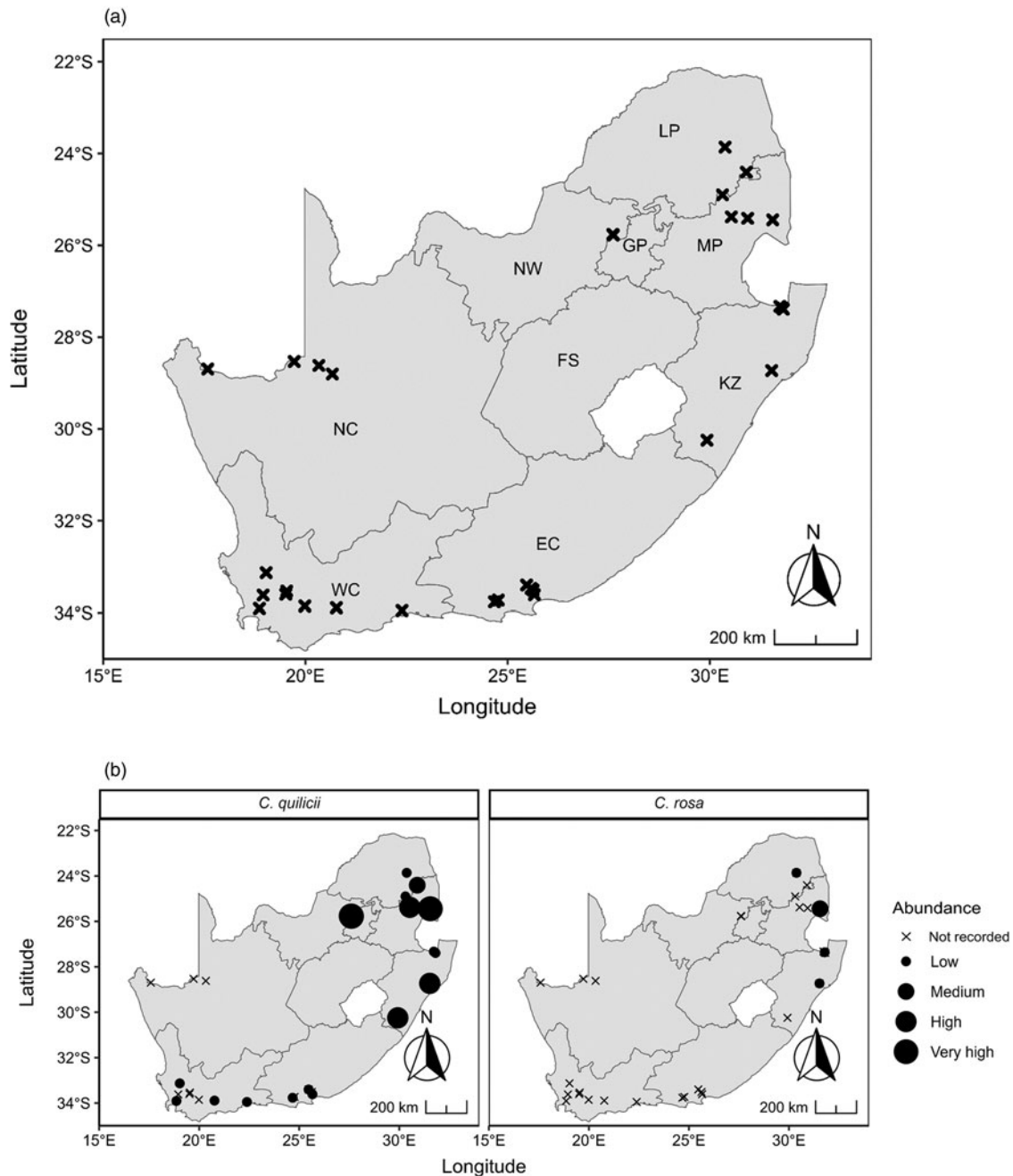


Figure 1. Map of South Africa showing (A) locations of study sites (indicated as crosses on the map) and (B) distribution and abundance of *Ceratit*s *quilicii* and *Ceratit*s *rosa* at the study sites during trapping surveys from March 2020 to November 2021. All sites were commercial fruit farms as described in table 1. The following were the classes of abundance used and represented average catches per trap per week averaged across the whole study period: not recorded, low, medium, high, and very high representing zero flies, 0.01–2 flies per trap per week, 2.01–10 flies per trap per week, 10.01–20 flies per trap per week and >20 flies per trap per week, respectively.

collected, but fruit that had no apparent damage symptoms were also collected. Sampled fruit from the tree and from the ground were kept separate after collection. Samples were brought back to the laboratory at the CRI for further processing. Sampled fruit were grouped according to species, date, site and origin and then as a group weighed and labelled. Each group was incubated separately. Fruit incubation was done following procedures outlined in Copeland *et al.* (2002) For some fruit sample groups, the origin of the fruit was not demarcated and those were marked as (both tree and ground). Fruit were incubated in transparent

plastic containers (length = 50 cm, width = 25 cm, height = 20 cm), each fitted on the lid with a fine mesh for aeration. Each container was filled with about 1 cm layer of sterilised sand. Sand in the container absorbed fluids from the fruit and served as a pupariation medium for jumping larvae. All containers were kept at 25 ± 2°C in the laboratory at the CRI. The sand was sieved at seven days after incubation and every 2–3 days thereafter for pupal collection. Fruit incubation period was between 30 and 60 days, depending on fruit type. Pupae collected were kept on sterilised sand under the same environmental conditions until adult emergence. Emerged

Table 1. Description of study sites (commercial fruit farms) in provinces of South Africa where fruit fly trapping surveys were carried out from March 2020 to November 2021

Province	Name of city/closest city of field location	Centroid GPS coordinates	Common name of fruit present/cultivated	Altitude (m.a.s.l)	Mean (±SE) average daily temperature (°C)	Mean (±SE) relative humidity (%)	Mean (±SE) precipitation (mm)
Eastern Cape	Andrieskraal	33°46'00.8"S 24°40'26.1"E	Citrus	100	15.61 ± 0.79	70.20 ± 1.56	25.39 ± 5.85
	Sunland	33°28'40.7"S 25°34'45.1"E	Citrus	60	18.15 ± 1.05	65.17 ± 0.69	20.21 ± 3.87
	Addo	33°36'43.4"S 25°39'39.1"E	Citrus	22	18.30 ± 0.84	66.40 ± 0.85	31.08 ± 4.13
	Kirkwood	33°30'35.9"S 25°37'44.6"E	Citrus	48	17.36 ± 1.11	66.53 ± 0.22	31.76 ± 4.47
	Kirkwood	33°24'06.0"S 25°28'06.2"E	Citrus	121	19.23 ± 0.86	62.07 ± 1.45	4.46 ± 2.03
	Patensie	33°43'43.3"S 24°46'07.8"E	Citrus	91	15.61 ± 0.79	70.20 ± 1.56	25.39 ± 5.85
KwaZulu-Natal	Ixopo	30°14'42.4"S 29°55'41.4"E	Citrus	732	15.38 ± 0.84	76.16 ± 2.93	85.41 ± 14.34
	Nkwalini	28°43'43.9"S 31°31'38.0"E	Citrus	143	18.69 ± 0.55	79.22 ± 1.73	129.34 ± 16.31
	Pongola	27°21'44.7"S 31°47'14.4"E	Citrus	176	16.52 ± 0.49	73.23 ± 1.31	85.69 ± 2.72
	Pongola	27°23'31.1"S 31°48'48.0"E	Mango	203			
	Pongola	27°19'49.3"S 31°43'51.6"E	Pecan/Macadamia	210			
Limpopo	Burgersfort	24°53'55.8"S 30°18'39.5"E	Citrus	807	20.15 ± 0.79	59.46 ± 0.96	19.09 ± 4.73
	Hoedspruit	24°24'18.9"S 30°54'02.8"E	Citrus	523	20.04 ± 0.96	60.68 ± 1.25	11.30 ± 3.38
	Letsitele	23°51'34.1"S 30°22'27.2"E	Citrus/Mango	525	19.84 ± 0.94	64.53 ± 1.17	43.57 ± 11.21
Mpumalanga	Mbombela	25°24'38.9"S 30°56'00.2"E	Citrus/Avocado/Litchi	793	19.30 ± 0.82	63.50 ± 1.21	49.17 ± 8.19
	Hectorspruit	25°26'40.4"S 31°33'08.1"E	Citrus/Mango	312	21.92 ± 0.82	68.45 ± 0.97	39.77 ± 14.50
	Schoemanskloof	25°22'45.6"S 30°31'52.5"E	Citrus	956	11.64 ± 0.90	61.47 ± 1.79	36.42 ± 7.03
Northern Cape	Augrabies	28°37'04.8"S 20°19'56.4"E	Grape	636	22.54 ± 0.67	35.06 ± 1.15	19.43 ± 4.26
	Kakamas	28°48'8.83"S 20°39'56.2"E	Citrus	694	23.03 ± 0.69	36.81 ± 1.32	5.07 ± 1.33
	Onseepkans	28°31'53.7"S 19°43'24.4"E	Grape	493	23.61 ± 0.64	32.26 ± 0.37	26.00 ± 6.48
	Volsdrif	28°41'44.3"S 17°35'03.6"E	Citrus	164	16.12 ± 1.39	48.53 ± 0.22	13.61 ± 2.51
North West	Mooinooi	25°45'37.2"S 27°36'01.5"E	Citrus	1248	17.57 ± 0.67	53.12 ± 1.16	16.00 ± 1.99
	Mooinooi	25°46'13.2"S 27°36'52.1"E	Citrus /Avocado	1289			
	Mooinooi	25°46'39.6"S 27°36'46.8"E	Peach	1329			
Western Cape	Barrydale	33°53'28.3"S 20°46'01.7"E	Nectarine/Peach	484	17.90 ± 0.47	71.71 ± 0.46	33.37 ± 5.94
	Porterville	33°07'56.5"S 19°01'45.7"E	Citrus	104	13.88 ± 0.72	73.08 ± 0.52	44.55 ± 13.82
	Worcester	33°31'57.2"S 19°32'15.1"E	Citrus	348	15.98 ± 0.94	62.04 ± 1.14	40.11 ± 9.43
	Worcester	33°36'08.5"S 19°30'49.8"E	Citrus	286			
	George	33°57'06.1"S 22°23'17.8"E	Fig/Blackberry	236	19.00 ± 0.26	61.70 ± 1.90	28.30 ± 5.87
	Ashton	33°51'21.7"S 19°59'05.9"E	Apricot/Plum	151	18.01 ± 0.27	64.48 ± 0.33	29.60 ± 0.67
	Stellenbosch	33°54'24.2"S 18°51'46.8"E	Pear/Nectarine	203	18.99 ± 0.00	66.28 ± 0.00	64.40 ± 0.00
	Wellington	33°37'04.2"S 18°57'13.0"E	Plum	139	17.74 ± 0.03	63.41 ± 0.23	28.95 ± 10.34

adult flies were fed with water and sugar *ad libitum* for four days for flies to fully develop and colour-up to aid identification of the species. After four days, flies were killed by freezing for identification.

Identification of target fly species

Flies collected in traps and during fruit incubation were sorted for identification using Zeiss Stemi 2000 – C microscope (Carl Zeiss (Pty) Ltd, Randburg, South Africa). A set of multi-entry electronic keys for African fruit fly species provided by Virgilio *et al.* (2014) was used for identification of all flies collected. Males of *C. rosa* and *C. quilicii* were identified using the shape and pattern of pubescence of the mid-tibia (De Meyer *et al.*, 2016). Females of *C. rosa* and *C. quilicii*, which were mostly reared from fruit, could not be differentiated using morphological characteristics and were considered as *C. rosa* s.l. (De Meyer *et al.*, 2016).

Statistical analysis

A generalised linear mixed model (GLMM) was used to assess how the abundances of *C. quilicii* and *C. rosa* varied between years, provinces, seasons, and prevailing climatic conditions at each site. The response variable was the number of each fly species collected per trap during each sampling event. Traps were exposed in the field for a variable number of days depending on site, year and province in which they were deployed (mean \pm SD = 36 \pm 16, range = 17–86 days). To account for this difference, we included the log of the number of days each trap was deployed as an offset variable in the GLMM, which allowed us to model the rate at which each fly species was caught in the traps, standardising for exposure time. We included four categorical fixed effect variables in the model, namely: (1) species (*C. quilicii*/*C. rosa*), (2) year (2020/2021), (3) province, and (4) season (autumn-winter, spring-summer, late summer). Prevailing climatic conditions (temperature ($^{\circ}$ C), relative humidity (%), and rainfall (mm)) were included as continuous variables in the model. For the effect of temperature on fly abundance, only minimum temperature was assessed since maximum temperatures and average daily temperatures were highly correlated with minimum temperatures ($r^2 > 0.7$). Minimum temperature was selected due to it being a more accurate predictor of insect distributions than maximum temperatures (Hill, 1987).

The province with zero counts for both *C. quilicii* and *C. rosa* – Northern Cape Province – was excluded in the model.

Five interaction terms were included in the final GLMM, namely: (1) species \times year, (2) species \times season, (3) species \times minimum temperature, (4) species \times relative humidity, and (5) species \times annual rainfall. These interaction terms were included to assess whether there were fly species-specific differences in trap counts due to the other fixed effect variables. One outlier site was detected in the North West Province (fig. S3) and excluded in the model when considering interaction terms. The trap data from the outlier site were inconsistent with the data from the other sites. Visual inspection of the relationships between climatic variables and fly trap counts indicated that assessment of the climatic variables on fruit fly abundances would be biased, should the outlier site be included.

The final GLMM model was run using the ‘glmmTMB’ R package (Brooks *et al.*, 2017). The model assumed a negative binomial error distribution and a log link function. Site was included as a random intercept term to account for the repeated sampling

events performed over time at each site (Bolker *et al.*, 2009). Model specification was checked by residual analysis using the ‘DHARMA’ R package (Hartig, 2022), which indicated no significant issues with the final model structure (fig. S3). Fixed effect parameter significance was assessed using a Likelihood Ratio Test using the ‘car’ R package ($P < 0.05$) (Fox and Weisberg, 2019). Marginal effects plots were produced to show the relationship between each fixed effect variable and fly trap counts using the ‘ggeffects’ R package (Ludecke, 2018).

Data on fruit fly rearing from fruit sampling surveys were calculated as percentage infestation (number of samples confirmed to be infested by fruit flies over total number of samples collected) and infestation rate which was the number of adult target fruit fly species and all other fruit fly species reared per kg of fruit sampled.

Results

Distribution and abundance of *C. quilicii* and *C. rosa* in commercial fruit farms in South Africa

Trapping records indicated a wider geographical distribution for *C. quilicii* than *C. rosa* in South Africa (fig. 1). The province variable was consistently identified as an important predictor of weekly fruit fly trap counts ($\chi^2 = 40.03$, $df = 4$, $P < 0.001$). *Ceratitidis quilicii* was recorded in all provinces sampled except the Northern Cape (fig. 1). *Ceratitidis quilicii* was most abundant in the North West Province with average catches (\pm SE) per trap per week being at 61.74 \pm 17.14 across seasons and years and least abundant in Eastern Cape and Western Cape provinces with average catches (across seasons and years) per trap per week varying from 0 to 0.16 and 0 to 0.44 respectively (fig. 1). In the provinces of Limpopo, Kwa-Zulu Natal, and Mpumalanga, average *C. quilicii* catches (across seasons and years) per trap per week varied from 0.19 to 2.63, 6.24 to 10.44, and 0.23 to 26.39 respectively. Despite the significantly higher abundances in the North West Province than the other provinces, trap counts of *C. quilicii* were extremely variable within that province, ranging from 0 to 747 flies trapped per week. *Ceratitidis rosa* was only recorded in the KwaZulu-Natal, Mpumalanga and Limpopo Provinces in low numbers with the highest abundance occurring in Mpumalanga Province with average catches (across seasons and years) per trap per week varying from 0 to 0.22 (fig. 1).

Trap counts were consistently higher for *C. quilicii* than *C. rosa* over the study period (fig. 2). On average, the number of *C. quilicii* captured per trap per week was 17.7 \pm 4.85, while the number of *C. rosa* captured per trap per week was 0.07 \pm 0.04. However, there was evidence for significantly higher overall trap counts between years for both species ($\chi^2 = 7.81$, $df = 1$, $P = 0.005$). Trap counts were 52% higher for *C. quilicii* in 2021 (4.92 \pm 0.34) than 2020 (2.39 \pm 0.38) (fig. 2), and 69% higher for *C. rosa* in 2021 (0.13 \pm 0.69) than 2020 (0.04 \pm 0.93) (fig. 2).

Seasonality of *C. quilicii* and *C. rosa* in commercial fruit farms in South Africa

There was statistical support for a significant species by season interaction term ($\chi^2 = 9.09$, $df = 2$, $P = 0.011$), indicating that differences in trap counts between seasons were species-specific. Trap counts were low and consistent between seasons for *C. rosa* (fig. 2). In contrast, trap counts for *C. quilicii* showed a

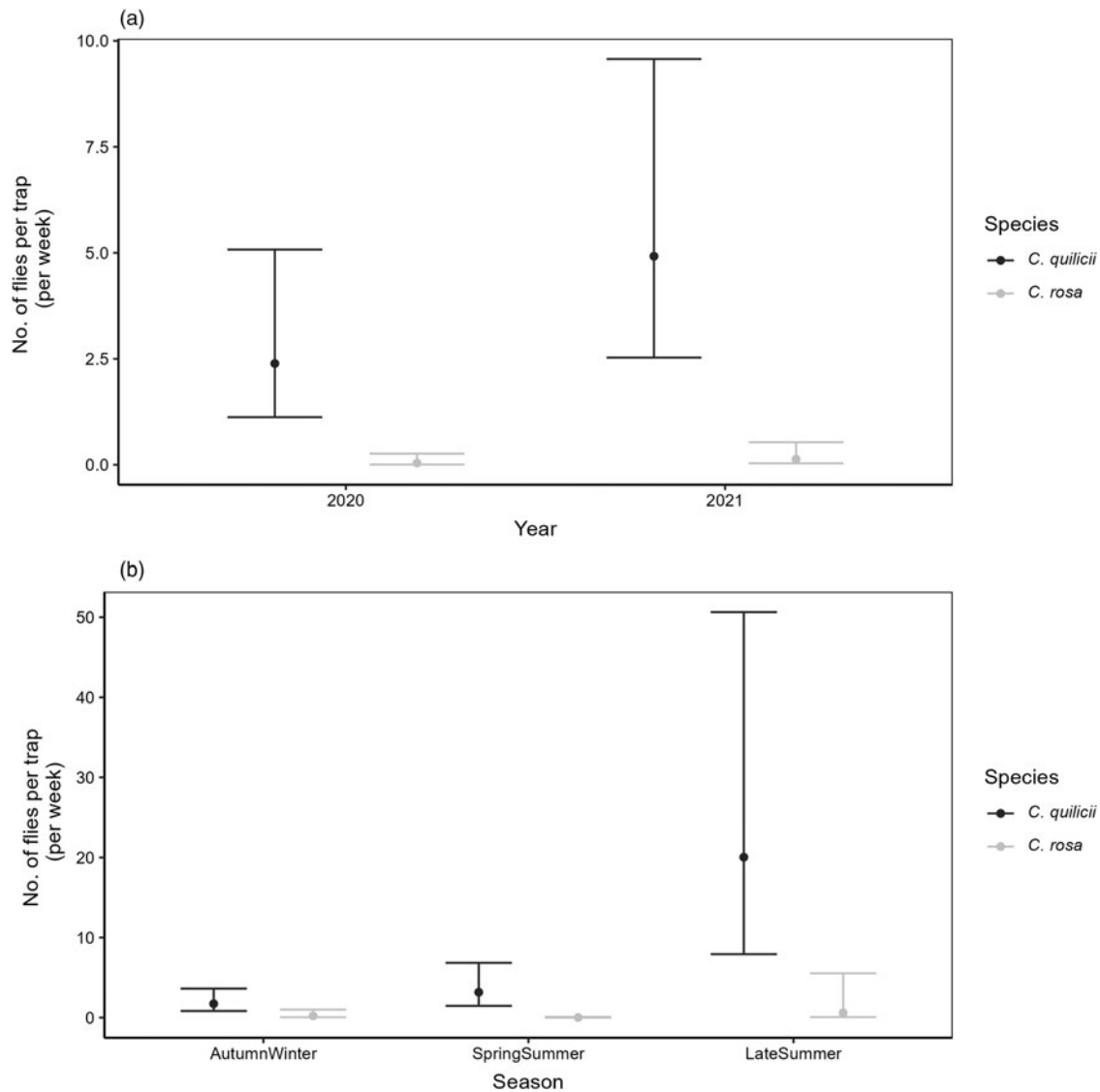


Figure 2. Estimated marginal mean weekly trap catches of *C. quilicii* and *C. rosa* ($\pm 95\%$ confidence interval of the mean) (A) in the two survey years: 2020 and 2021, averaged across provinces and sites and (B) over three seasons: autumn-winter, spring-summer and late summer (averaged across sites and year). Note the different scales of the y-axes for the trap counts between species.

strong seasonal pattern, with trap counts per week approximately 4 \times and 13 \times higher in late summer than either autumn/winter and spring/summer, respectively (fig. 2).

Effects of climatic factors on abundance of *C. quilicii* and *C. rosa* in commercial fruit farms in South Africa

The effects of climatic factors on fly abundance were evaluated for *C. quilicii* and *C. rosa*. However, because of the low trapping data records available for the latter species, any inferences made for *C. rosa* should be treated cautiously.

There was evidence for a significant interaction term between species \times minimum temperature ($\chi^2 = 5.56$, $df = 1$, $P = 0.018$), indicating that there were species-specific responses to minimum temperatures. Both *C. quilicii* and *C. rosa* showed a positive relationship between minimum temperature and trap counts, with higher trap counts at higher minimum temperatures (fig. 3), and an apparent inflection point at approximately 15°C for both species, whereby

trap counts increased sharply with increasing minimum temperatures above 15°C. In contrast, the two fly species showed different responses to minimum temperatures below 15°C with *C. quilicii* counts decreasing at lower rates than those of *C. rosa*. If altitude served as a proxy to minimum temperature in the northern regions of South Africa, it was clear that *C. quilicii* was present at higher altitudes than *C. rosa*. The highest altitude at which *C. quilicii* was captured was at 1329 m.a.s.l. in the North West Province while the highest altitude at which *C. rosa* was captured was at 525 m.a.s.l. in Limpopo (Letsitele) (table 1). Within Mpumalanga Province where both species were present, the highest altitudes at which *C. quilicii* and *C. rosa* were captured were 956 and 312 m.a.s.l. respectively (table 1). The effect of minimum temperature on *C. rosa* is however to be treated cautiously, due to low trap counts in provinces where it occurred and absence in three of the provinces considered in the model.

There was no evidence for either a species \times total annual rainfall interaction ($\chi^2 = 0.01$, $df = 1$, $P = 0.928$), or an additive effect

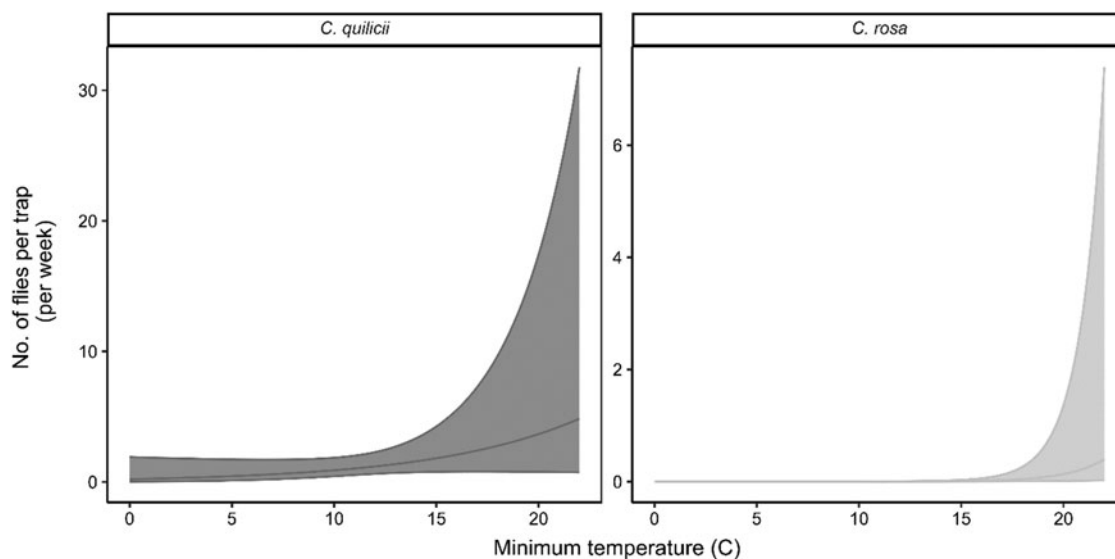


Figure 3. Estimated marginal mean weekly trap catches ($\pm 95\%$ confidence interval of the mean) of *C. quilicii* and *C. rosa* in relation to minimum temperature ($^{\circ}\text{C}$), averaged across provinces, sites and years. Note the different scales of the y-axes for the trap counts between species.

of total annual rainfall ($\chi^2 = 2.46$, $df = 1$, $P = 0.116$). Moreover, there was no evidence for either a species \times relative humidity interaction ($\chi^2 = 0.11$, $df = 1$, $P = 0.743$), or an additive effect of relative humidity ($\chi^2 = 0.62$, $df = 1$, $P = 0.431$). Taken together, these results indicate that where the two species occurred, rainfall and relative humidity did not have a substantial effect on trap counts. However, it is to be noted that both species were not recorded in Northern Cape which was co-incidentally the driest province (lowest rainfall and lowest relative humidity on average—see fig. S2).

Fruit sampling and infestation survey

A total of 12 plant species in eight families were sampled between March 2020 and November 2021 within the trapping sites (table 2). In these sites, *C. quilicii* was reared only from one plant species – *Psidium guajava* L. in one locality (Stellenbosch) in the Western Cape Province (table 2). *Ceratitris rosa* s.l. specimens (females only) were reared from *Mangifera indica* L. collected from the ground in one locality—Hoedspruit in Limpopo Province (table 2). Surveys were mostly conducted in commercial citrus orchards, hence the dominance of citrus fruit (61%) in the samples. Neither *C. quilicii* nor *C. rosa* was reared from any of the citrus sampled (*C. limon* (L.) Osbeck, *C. reticulata* Blanco and *C. sinensis* (L.) Osbeck) (table 2).

A total of 45 plant species in 23 families were sampled between March 2020 and November 2021 in sites that were outside of but adjacent to trapping sites (table 3 and table S1). In those sites, *C. quilicii* was reared from nine plant species in seven families (table 3) whilst *C. rosa* was reared from six plant species from six families (table 3). Five of the plant species infested by *C. rosa* were also infested by *C. quilicii*, with co-infestation recorded in the same samples. Highest infestation of *C. rosa* was recorded in *Syzygium jambos* (L.) Alston in Mpumalanga Province. On the other hand, highest infestation of *C. quilicii* was recorded in *Acca sellowiana* (O. Berg) Burret in Mpumalanga Province. *Ficus sycamorus* L. is a new host record for *C. quilicii* and *Casimiroa edulis* La Llave is a new host record for both *C. quilicii* and *C. rosa* (table 3).

Discussion

In this study, we defined the geographical distribution of *C. quilicii* and *C. rosa* in important fruit producing regions of South Africa. We showed for the first time a latitudinal limit for *C. rosa* in southern Africa (27°S). We found that both *C. quilicii* and *C. rosa* occurred in sympatry in the north and north eastern parts of the country. In provinces that are further south and central (Eastern Cape, Western Cape, and North West) in South Africa, only *C. quilicii* was recorded. The two species were absent in the Northern Cape Province and there were a few sites in the Western Cape Province where there were no records of *C. quilicii*. The distribution patterns found here are in line with previous findings by Virgilio *et al.* (2013) and De Meyer *et al.* (2015), which were based on either limited samples or historic collections from South Africa. The results also support previous findings by De Villiers *et al.* (2013) with regard to the absence of both *C. rosa* and *C. quilicii* (previously *C. rosa* s.l.) in the Northern Cape Province. The abundances of the two species varied in the provinces where they occurred. For *C. quilicii*, high prevalence of the pest was recorded in North West Province, while high prevalence of *C. rosa* was recorded in Mpumalanga Province. In provinces where both *C. quilicii* and *C. rosa* were recorded, *C. quilicii* outnumbered *C. rosa* in traps at all sampling times.

Abiotic conditions, principally temperature, may possibly be driving the distribution patterns of these two species, since we found that temperature and season were significant drivers of their abundances. For both species, warmer conditions increased their abundances. The two species were found to respond differently to minimum temperatures, with *C. quilicii* being less restricted from areas with temperatures below 15°C than *C. rosa*. However, these differences in responses are to be treated cautiously, due to (1) generally low counts of *C. rosa* in this study and (2) climatic parameters attached to the sampling sites being from stations at least 2 km away. In field studies done in Tanzania on *C. rosa* and *C. quilicii* (Mwatawala *et al.*, 2015), *C. rosa* was found to be predominant at lower altitude, whilst *C. quilicii* dominated at the higher altitude. It is to be noted that in the latter study *C. rosa* did occur at all altitudes and

Table 2. Records of *C. quilicii*, *C. rosa*, *C. rosa* s.l and other fruit fly species in mature ripe fruit sampled from the ground and tree in trapping sites located in four provinces in South Africa between March 2020 and November 2021

Province	Locality	Origin	Family	Plant species	Number of samples	Weight (kg)	Percentage fruit infestation	Fruit infestation rate (flies kg ⁻¹)	Count of emerged adult flies			
									<i>C. rosa</i>	<i>C. quilicii</i>	<i>C. rosa</i> sl (females)	Other Tephritidae ^a
Limpopo	Burgersfort	Ground	Moraceae	<i>Ficus sp</i>	1	0.17	0.00	0.00	0	0	0	0
			Rutaceae	<i>Citrus reticulata</i>	3	2.11	0.00	0.00	0	0	0	0
	Hoedspruit	Ground	Anacardiaceae	<i>Mangifera indica</i>	3	15.15	33.33	1.06	0	0	3	13
			Rutaceae	<i>Citrus sinensis</i>	2	1.90	0.00	0.00	0	0	0	0
	Letsitele	Ground	Rutaceae	<i>Citrus reticulata</i>	2	0.66	0.00	0.00	0	0	0	0
			Anacardiaceae	<i>Mangifera indica</i>	1	1.41	0.00	0.00	0	0	0	0
Mpumalanga	Halls	Ground	Lauraceae	<i>Persea americana</i>	1	1.25	0.00	0.00	0	0	0	0
	Riverside	Ground	Anacardiaceae	<i>Mangifera indica</i>	1	0.49	0.00	0.00	0	0	0	0
				<i>Sclerocarya birrea</i>	1	4.77	100.00	5.45	0	0	0	26
			Malvaceae	<i>Adansonia digitata</i>	1	0.16	0.00	0.00	0	0	0	0
			Moraceae	<i>Ficus sp</i>	1	0.72	0.00	0.00	0	0	0	0
			Rutaceae	<i>Citrus sinensis</i>	6	4.31	50.00	2.55	0	0	0	11
		Tree	Moraceae	<i>Ficus sp</i>	1	0.44	0.00	0.00	0	0	0	0
			Rutaceae	<i>Citrus reticulata</i>	3	1.59	0.00	0.00	0	0	0	0
				<i>Citrus sinensis</i>	3	1.72	33.33	0.58	0	0	0	1
		Sapindaceae	<i>Litchi chinensis</i>	1	0.09	0.00	0.00	0	0	0	0	
	Schoemanskloof	Ground	Rutaceae	<i>Citrus limon</i>	1	0.21	0.00	0.00	0	0	0	0
				<i>Citrus reticulata</i>	1	0.32	0.00	0.00	0	0	0	0
		Tree	Moraceae	<i>Morus alba</i>	1	0.07	0.00	0.00	0	0	0	0
North West	Mooiooi	Ground	Rutaceae	<i>Citrus reticulata</i>	1	0.75	0.00	0.00	0	0	0	0
				<i>Citrus sinensis</i>	1	0.85	0.00	0.00	0	0	0	0
Western Cape	Rheebokskraal	Ground	Rutaceae	<i>Citrus reticulata</i>	2	1.02	0.00	0.00	0	0	0	0
		Tree	Rutaceae	<i>Citrus reticulata</i>	2	1.21	0.00	0.00	0	0	0	0
	Denau	Ground	Rosaceae	<i>Prunus persica</i>	1	0.72	0.00	0.00	0	0	0	0
	Stellenbosch	Both ground and tree	Myrtaceae	<i>Psidium guajava</i>	1	1.32	100.00	273.69	0	120	81	160
		Ground	Myrtaceae	<i>Psidium guajava</i>	2	5.19	0.00	7.70	0	19	20	1

^aOther Tephritidae reared from samples referred to above were *Bactrocera dorsalis* (Hendel) (*Mangifera indica*, *Citrus sinensis*), *Ceratitis cosyra* (Walker) (*Sclerocarya birrea*) and *Ceratitis capitata* (Wiedemann) (*Sclerocarya birrea* and *Psidium guajava*).

Table 3. Fruit species infested by either *C. quilicii* or *C. rosa* or *C. rosa* s.l outside of trapping sites in the provinces of Limpopo

Province	GPS co-ordinate	Origin	Family	Species	Number of samples	Weight (kg)	Percentage fruit fly infestation	Fruit fly infestation rate (flies kg ⁻¹)	Count of emerged flies			
									<i>C. rosa</i>	<i>C. quilicii</i>	<i>C. rosa</i> s.l (females)	Other Tephritidae ^a
Limpopo	23°49'6.68" S 30°17'58.83" E	Ground	Anacardiaceae	<i>Mangifera indica</i>	3	58.04	66.67	5.48	0	4	3	318
Mpumalanga	25°27'8.12" S 30°58'16.91" E	Tree & Ground	Salicaceae	<i>Dovyalis caffra</i>	3	2.76	66.67	9.06	6	0	9	10
			Ground	Anacardiaceae	<i>Mangifera indica</i>	6	80.57	66.67	3.65	16	11	20
		Ground	Rubiaceae	<i>Coffea arabica</i>	2	16.74	100.00	25.51	0	1	2	424
			Rutaceae	<i>Casimiroa edulis</i>	1	1.80	100.00	16.11	12	5	11	1
	25°26'33.09" S 30°58'15.04" E	Ground	Moraceae	<i>Ficus sycomorus</i>	2	0.23	50.00	213.97	0	1	2	46
	24°41'1.63" S 30°49'50.50" E	Ground	Rosaceae	<i>Prunus persica</i>	3	69.29	100.00	25.52	37	839	874	18
			Sapotaceae	<i>Englerophytum magalismsontanum</i>	1	1.13	100.00	23.01	0	13	13	0
	25°28'47.26" S 30°59'26.57" E	Ground	Sapotaceae	<i>Englerophytum magalismsontanum</i>	1	1.37	100.00	28.45	20	2	17	0
	26°30'35.11" S 30° 0'1.37" E	Tree & Ground	Myrtaceae	<i>Acca sellowiana</i>	1	1.41	100.00	724.04	0	579	437	2
			Ground	Myrtaceae	<i>Acca sellowiana</i>	1	3.62	100.00	1164.92	0	2069	2148
25°26'44.21" S 31°40'19.10" E	Ground	Irvingiaceae	<i>Irvingia gabonensis</i>	2	1.67	100.00	34.17	0	0	1	56	
Western Cape	33°54'12.95" S 18°51'40.70" E	Ground	Rosaceae	<i>Eriobotrya japonica</i>	2	1.61	100.00	74.53	0	0	1	119
	33°54'7.92" S 18°51'35.90" E	Tree & Ground	Myrtaceae	<i>Psidium guajava</i>	1	3.35	100.00	0.30	0	1	0	0

Mpumalanga and Western Cape in South Africa. Fruit were sampled between March 2020 and November 2021.

^aSee supplementary table S1 for details on Other Tephritidae reared.

clear partitioning of the climatic niches of the two species could not be suggested by the authors (Mwatawala *et al.*, 2015). Differences in responses to constant temperature between *C. rosa* and *C. quilicii* were previously demonstrated in laboratory studies on populations of the two species sampled from two countries: Kenya and South Africa (Tanga *et al.*, 2015). *Ceratitis rosa* developed and survived better at higher temperatures than *C. quilicii* for both Kenyan and South African populations (Tanga *et al.*, 2015). Responses of the two species to lower temperatures were however dependent on their population origin (Tanga *et al.*, 2015). In populations sampled from Kenya, *C. quilicii* was found to tolerate lower temperature better than *C. rosa* (Tanga *et al.*, 2015). In populations sampled from South Africa, this was not the case (Tanga *et al.*, 2015). Subsequently, Tanga *et al.* (2018) used temperature-dependent development and survival data on *C. rosa* and *C. quilicii* originating from Kenyan populations in a life cycle simulation model and showed that *C. quilicii* can adapt to a wider range of temperatures than *C. rosa* and would therefore have a wider potential global distribution than the latter. The model of Tanga *et al.* (2018) was mostly accurate in depicting the distribution of *C. quilicii* and *C. rosa* in South Africa. However, our results did show the presence of *C. rosa* in some parts of Limpopo and KwaZulu Natal provinces in South Africa, which were classified as marginal for the species in the model (Tanga *et al.*, 2018). This shows that there is room for improved models to predict potential distribution of these two species. Ideally model parameters should be built on phenology of the two species across seasons within their entire range of geographical distribution.

We did not find that relative humidity and rainfall were important in driving populations of *C. rosa* and *C. quilicii*. However, the absence of the two species in the Northern Cape Province coincided with it being the driest (low rainfall and low relative humidity). The Northern Cape Province also had higher maximum temperatures during summer compared to the other provinces. *Ceratitis rosa* s.l. has been shown to have lower resistance to desiccation compared to one of its congeners – *Ceratitis capitata* (Wiedemann) (Duyck *et al.*, 2006; Weldon *et al.*, 2016). In this study, we could not detect differences between *C. quilicii* and *C. rosa* in their responses to relative humidity. Nonetheless this needs to be confirmed in controlled set ups where their desiccation tolerance and resistance are compared concurrently.

The fruit infestation survey results in this study showed that there are biotic factors such as presence of competitors, in the form of other polyphagous fruit fly species, as well as fruit type that may influence the abundances of both *C. quilicii* and *C. rosa* in regions where they occur in South Africa and elsewhere in southern and eastern Africa. Starting with the aspect on competition, we found that *B. dorsalis* outnumbered *Ceratitis* species including *C. rosa* and *C. quilicii* in infested mango samples. *Bactrocera dorsalis* is an invasive species that was declared established in the northern parts of South Africa in 2013 (Manrakhan *et al.*, 2015). *Bactrocera dorsalis* was found to be an important competitor for *Ceratitis* species and could, under optimal conditions such as lowland hot areas, even lead to displacement of these species in common hosts (Ekesi *et al.*, 2009; Moquet *et al.*, 2021). Under conditions which are less favourable for *B. dorsalis*, such as the high altitude areas of Morogoro in Eastern Central Tanzania, *C. rosa* s.l numbers were found to be unaffected by the presence of its competitor and were high in host fruit present in these areas (Geurts *et al.*, 2014). In this study, we also found that *C. quilicii* was outnumbered by *C. capitata*, an indigenous species, in loquat in the Western Cape Province. This

could possibly be explained by generally higher populations of *C. capitata* compared to *C. quilicii* in that province, as shown in traps and deciduous fruit (Manrakhan and Addison, 2014). The higher numbers of *C. capitata* would present a competitive advantage over *C. quilicii* in utilisation of common hosts. There were five fruit types that were infested by both *C. quilicii* and *C. rosa* and this may indicate possible larval and/or adult interactions between the two-sibling species on common hosts. Regarding fruit type, some were highly infested and were therefore preferentially utilised by *C. quilicii* and *C. rosa*. For *C. quilicii*, preferred hosts were *Acca sellowiana* (O.Berg) and *Psidium guajava* L. For *C. rosa*, high infestation rates were recorded on *Syzygium jambos* (L.) Alston. Infestation of these fruit species by both *C. quilicii* and *C. rosa* was previously recorded in the northern areas (Grove *et al.*, 2019). We support a previous suggestion by Grove *et al.* (2019) that fruit in the Myrtaceae family represent important breeding sites for *C. rosa* and *C. quilicii* and may need to be considered when planning a fruit fly control programme in an area. Control measures could include removal and proper disposal of the fruit of these species which are fallen on the ground, as well as placement of localised attract and kill products either on or near these preferred hosts. We found citrus sampled in commercial orchards to be resistant to infestation by *C. rosa* and *C. quilicii*. This was despite some citrus samples were from the ground (detached and therefore more susceptible) or were infested by other species such as *B. dorsalis*. This is in contrast to records of *C. quilicii* in citrus in Reunion island (Moquet *et al.*, 2021). It is to be noted that in this study (Moquet *et al.*, 2021), the origin and conditions of the citrus fruit found to be infested by *C. quilicii* were not provided. It could be that the infestation was opportunistic particularly if the fruit were damaged and, on the ground, and would therefore not be representative of the status of commercially produced citrus.

In conclusion, this study provided background information for establishment of pest free areas for both *C. quilicii* and *C. rosa* (such as Northern Cape Province for the two species; provinces other than Mpumalanga, Limpopo and KwaZulu Natal for *C. rosa*) as well as areas of low prevalence (such as Limpopo and KwaZulu Natal provinces for *C. rosa*; Western Cape and Eastern Cape provinces for *C. quilicii*). Pest free areas and areas of low pest prevalence should be established following international guidelines (IPPC, 2006, 2018) which would require continuous surveys for at least 12 consecutive months, appropriate buffer areas and contingency plans in case of detections that would imply a change of status. We also gained useful information in the seasonality of both *C. quilicii* and *C. rosa* in South Africa which would inform on the timing of management actions. Knowledge on utilisation of fruit by these two species is important in determining risk of these flies in different fruit types which would inform control and phytosanitary measures.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485324000294>.

Acknowledgements. Many thanks to the multiannual programme 2019–2023 of the framework agreement between the Royal Museum for Central Africa (RMCA) and the Directorate-general for Development Cooperation and Humanitarian Aid (DGD) for funding this study through the Project DISPEST: Redefining DISpersal potential for adequate fruit fly PEST management (Diptera: Tephritidae), under an agreement between Citrus Research International (CRI), South Africa and Royal Museum of Central Africa, Belgium; Sean Moore (CRI), Tim Grout (CRI) and Vaughan Hattingsh (CRI) for comments on earlier draft; Rooikie Beck for help in trapping and fruit

surveys; Agricultural research council for providing weather data, SANBI Lowveld botanical garden for permission to sample fruits from their sites.

Competing interests. None.

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