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Original article - Biological control

## Natural biocontrol of fruit flies by parasitoids in indigenous hosts: a perspective for the control of populations within and outside the orchards.

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#### 13 Abstract

14 Fruit flies (Diptera Tephritidae) are a major pest to fruit production in Africa. Most efforts to control these pests are focused directly on the orchards where fruit damage has been recorded. However, 15 fruit flies are generally able to develop on alternative indigenous fruits from which they continuously 16 17 recolonize the orchards, challenging the ability to efficiently control these pests. In the natural and 18 semi-natural environments, parasitic Hymenoptera remain the primary means of keeping 19 populations of fruit flies at a reasonable level, but little is known about the diversity, the distribution 20 and the ability of these parasitoids to effectively control populations. In this study, we explored the 21 diversity and abundance of parasitoids of fruit fly pests in indigenous and exotic cultivated fruits of 22 two separate regions of South Africa: North-East (Limpopo and Mpumalanga provinces) and South-23 West (Western Cape Province). A total of 16 fruit species were collected and incubated to obtain 24 emergence of fruit flies and their associated parasitoids. Ceratitis capitata (Wiedemann), Ceratitis 25 rosa sensu lato Karsch, Ceratitis cosyra (Walker) and Bactrocera dorsalis (Hendel) were reared from the incubated fruit. In the Western Cape Province, only C. capitata and C. rosa sensu lato were 26 27 recorded. Our results show an important contrast in the distribution of fruit fly parasitoid species between regions and between indigenous fruit types. Fopius ceratitivorus Wharton and Psyttalia 28 29 humilis (Silvestri) (Hymenoptera: Braconidae) dominated parasitism in the north-eastern part of the 30 country, while fruit fly parasitoids were almost absent on fruit flies in the Western Cape Province. 31 Parasitism rate of fruit flies ranged from 0 to ca 50% depending on fruit species and locality within a region. The exact drivers of this variation in parasitism rate remain unclear, but smaller fruits generally seem to allow better control of infesting fruit flies by parasitoids than larger ones. The fruits of some indigenous trees (*Berchemia discolor* (Klotzsch) Hemsl.; *Syzygium cordatum* Hochst. ex Krauss and *Garcinia livingstonei* T. Anderson) are hosts of high densities of both fruit flies and their parasitoids. These species are good candidates for the application of augmentoria for the mass production and release of biological control agents.

#### 38 Key words

39 Natural biological control, Fruit flies, Tephritidae, Alternative hosts, Sub-Saharan Africa

#### 40 **1. Introduction**

41 Fruit-infesting fruit flies (Diptera, Tephritidae) are pests occurring worldwide that cause substantial damage to fruit production (Ekesi et al., 2016). In addition to the losses directly caused by the 42 43 development of the larval stages in the fruits, numerous fruit fly species have a quarantine status 44 and can strongly impact the export market of the country in which they occur (José et al., 2013). In 45 Sub-Saharan Africa, the horticultural sector is affected by serious losses caused by native species 46 (Ceratitis capitata (Wiedemann), Ceratitis cosyra (Walker), Ceratits rosa Karsch and Ceratits quilicii 47 De Meyer, Mwatawala & Virgilio), but also alien species (Bactrocera dorsalis (Hendel), Bactocera 48 zonata (Saunders)) that have invaded, established and spread rapidly through this region (De Meyer 49 et al., 2007; Khamis et al., 2009; De Villiers et al., 2016; Manrakhan, Venter & Hattingh, 2015). Across 50 many African countries, the total financial losses due to these pests are substantial and absence of 51 management can lead to the complete loss of production (Ekesi et al., 2016).

52

53 In Africa, the traditional management of fruit flies using pesticides is challenged by the strict residue 54 levels applied in export markets, in the larger context of the recognized detrimental effect of these 55 compounds on human and ecosystem health (Bourguet and Guillemaud, 2016). The management 56 practice has therefore evolved toward alternative methods such as bait application technique (BAT) 57 using bio-pesticides, sterile insect technique (SIT) or orchard sanitation methods (OS) (Klungness et 58 al., 2005; Ekesi and Billah, 2007; Manrakhan and Addison, 2014; Ekesi et al., 2016). Among OS 59 methods, the augmentoria consist in the collecting of infested fruits and their storage in a container 60 with a mesh retaining the fruit flies and allowing the biocontrol agents (parasitic hymenoptera) to emerge (Klungness et al., 2005). This simple approach contributes to control the population density 61 of pest fruit flies and is usually used in combination with other control methods. All these methods 62 63 are mostly deployed in the infested orchards or in the direct vicinity due to the cost and human 64 resources needed for their application. However, fruit-infesting Tephritidae are polyphagous and they are able to establish population reservoirs in neighbouring indigenous fruits (De Meyer et al., 2002; Copland et al., 2009; Aluja et al. 2014; Threon et al., 2017; Grové et al., 2017). Due to the dispersal ability of the adult stage (Moxley et al., 2017), these reservoir populations can spill over into orchards, resulting in limited efficiency of the above mentioned methods. Therefore, sustainable management of these pests also requires an understanding of the drivers affecting their abundance in natural and semi natural environments, within the framework of an area-wide integrated pest management (IPM) approach (Mau et al., 2007).

72 In natural and semi natural environments, fruit fly populations are naturally controlled by co-evolved 73 parasitic Hymenoptera mainly belonging to the subfamily Opiinae (Wharton and Gilstrap, 1983). The 74 Afrotropical region features a wide range of opiine species associated with tephritids, and an 75 important and sustained effort has been made to characterize this diversity for biocontrol purposes (Wharton and Gilstrap, 1983; Wharton, 1999; Wharton, 2009; Wharton & Yoder, 2018). In addition 76 77 to native species, several alien species were introduced in an attempt to improve the control of 78 populations of fruit fly in orchards and crops, sometimes with remarkable success (see Ekesi et al., 79 2016 for a review). These species are koinobiont endoparasitoids which lay their eggs in the flies' 80 eggs or first instar larvae and emerge as adults from the puparium, leading to the death of the host 81 fly (Rousse et al., 2005).

82 There is little information, however, on how efficiently the Opiinae and other parasitoids are 83 controlling the populations of fruit flies in natural and semi natural environments in Africa. Surveys 84 were conducted only on wild olives in southern Africa to estimate the natural control of populations 85 of Bactrocera oleae (Rossi) by parasitoids in non-crop habitat (Neuenschwander, 1982; Mkize et al., 2008). For most fruit-infesting flies, there is lack of data on how the parasitoids are controlling these 86 87 populations in alternative indigenous fruits. As a result, it is currently unclear if indigenous fruits are 88 reservoirs only for the fly population or for both the flies and parasitoids, and to what extent and for 89 what reason. This information is crucial because it will determine how habitats should be managed 90 to improve the control of fruit fly populations at a regional scale (Landi et al., 2000).

91 In this study, we (i) explored the diversity and distribution of parasitoids of fruit infesting flies in 92 South Africa, and we (ii) made a preliminary estimation of the ability of these parasitoids to control 93 fruit flies in wild indigenous or exotic ornamental and cultivated fruits. The potential use of 94 indigenous fruit trees as reservoirs of parasitoids for the application of augmentative techniques is 95 discussed.

- 96 2. Materials and Methods
- 97

#### 98 2.1. Study area and fruit sampling

99 Fruits were sampled between 2013 and 2018 in two separate and climatically different regions 100 located in the North-East (Mpumalanga and Limpopo Provinces) and the South-West (Western Cape 101 Province) of South Africa. The Western Cape province (WC) has a Mediterranean-type climate 102 characterized by winter rainfalls, with cold, wet winters and hot, dry summers (ARC, 2014) that is 103 suitable for the production of deciduous fruits. In contrast, the provinces of Mpumalanga and 104 Limpopo (M&L) are characterised by a subtropical climate with summer rainfall and hot, wet 105 summers and cold, dry winters (Government SA, 2018) which is more suitable for the production of 106 tropical fruits.

107 Fruits were collected in 18 localities, 5 in M&L and 13 in WC (Table 1). Exotic cultivated fruits were sampled in abandoned, organic orchards or home gardens where no chemicals, potentially affecting 108 109 wasp populations, were sprayed (including neurotoxic bio-pesticides such as Spinosad). Fruits were 110 collected on the trees at the appropriate time of maturation, and from the ground to maximize the 111 range of parasitoids recorded (Eitam and Vargas, 2007). Several collecting events (hereafter called 112 replicates) were conducted for each fruit type in different places and/or time of the year. Between 1 113 and 10 sampling replicates were carried out for each fruit type. A total of 16 fruit types were 114 sampled, with 7 being wild indigenous, 3 exotic ornamental, and 7 exotic cultivated on a commercial 115 scale (Table 1). In the WC Province, the natural vegetation surrounding orchards is of the Fynbos 116 type (characterised by proteoid, ericoid and restioid plants), which is a very dry and woody vegetation. Apart from wild olives, that are not focal hosts for fruit infesting Ceratitis spp., there was 117 118 no alternative wild hosts available for these species. Therefore, only exotic cultivated and 119 ornamental fruits (Mespilus sp.) could be collected in this province.

120 After collection, fruits were counted, weighed and placed in plastic boxes with sterile sand at the 121 bottom to allow the larvae to emerge and pupate. Only one layer of fruit was placed in each box to 122 limit excessive liquid accumulation that would be detrimental for the emergence of flies and their 123 parasitoids. Plastic boxes were placed in incubators consisting of a Perspex box of 1x1 meter. The 124 incubator was covered by black material except at the base of the collecting tube placed on top, in 125 order to allow emerging insects to go into it. Incubators were maintained in at 25°C in a climatic chamber for a period of 3-4 weeks (photoperiod 16:8, L:D). All emerging flies and parasitoids were 126 127 collected every two days, killed in a freezer and/or directly preserved in 96% ethanol before they 128 were identified and counted.

129 2.2. Species identification

Species identification of fruit flies based on morphology was made according to Virgilo et al. (2014) and De Meyer et al. (2016). *Ceratitis rosa* and *C. quilicii* are reported as *C. rosa sensu lato*, because some samples were collected and identified before the description of *C. quilicii* (De Meyer et al., 2016). The species of parasitoids were identified following Wharton & Yoder (2018), Wharton and Gilstrap (1983) and Wharton (1999).

135 Some species in the subfamily Opiinae comprise species complexes (Rugman-Jones et al. 2009), 136 therefore we also sequenced the standard barcode fragment of the mitochondrial cytochrome 137 oxydase I (COI, Hebert et al., 2003) in order to cross-validate morphological identifications. DNA was 138 extracted from a leg or a fragment of the abdomen of specimens using a DNeasy Blood & Tissue kit 139 (Qiagen, Hilden, Germany), according to the manufacturer's protocol. PCR amplification were 140 performed using the standard primers for barcoding (mitochondrial cytochrome c oxidase subunit I) 141 of invertebrates: LCO1490: 5'-GGTCAACAAATCATAAAGATATTGG-3' and HCO2198: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer et al., 1994). PCR reactions were carried out on a 142 143 Mastercycler<sup>®</sup> Nexus (Eppendorf, Hamburg, Germany) in a volume of 10 µL PCR mix containing 5 µl 144 of Multiplex Master Mix (Qiagen, Hilden, Germany), 0.8  $\mu$ l primers (Forward and Reverse at 2  $\mu$ M) 145 and 2  $\mu$ l of DNA. The PCR conditions were as follows: initial DNA denaturation at 94°C for 15 146 minutes, followed by 10 cycles of 30 s each at 94°C, 1 min at 60-50°C (touchdown of -1°C per cycle) 147 and 30 s at 70°C, followed by 30 cycles of 30 s at 94°C, 1 min at 55°C, and 1 min at 72°C with a final extension of 20 min at 72°C. The PCR products were sequenced by Eurofins Genomics 148 149 (http://www.eurofinsgenomics.eu/). Barcode sequences were aligned using CodonCode Aligner 150 V.3.7.1. (CodonCode Corporation, Centerville, MA, USA), and checked to identify the presence of 151 pseudogenes using standard detection methods (Haran et al., 2015). Each sequence was then 152 aligned with reference barcode sequences of parasitoids of Fruit fly (Rugman-Jones et al. 2009; 153 Haran et al. 2018). All voucher specimens were mounted on card or placed in 96% ethanol and were 154 deposited in the South African Museum collections (SAMC, Cape Town). Additional material was 155 deposited at CBGP, Montpellier, France (doi.org/10.15454/D6XAKL).

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#### 2.3. Fly infestation and parasitism rates

The fly infestation rate was considered as the mean number of fruit flies emerging from 1 kg of fruit across replicates. Parasitism rate of fruit flies for a specific fruit type was computed as the ratio of parasitoids over the total number of flies and parasitoids (each representing one parasitized fruit fly) emerging from this fruit across sites. Parasitism rates were estimated only for solitary parasitoids in which a single adult parasitoid emerged from a fly puparium, and for parasitoid taxa where we were confident that they were associated with Tephritidae. A reliable estimation of parasitism rate is usually conducted on a large number of replicates of fruit samples from a single locality over several years. This allows controlling the natural seasonal fluctuations of the parasitoid populations. Due to the exploratory nature of this study, and the limited number of spatial and temporal replicates, only an estimation of parasitism rate is provided. Therefore, the standard deviation of the mean parasitism rates were not computed, and only higher and lower values of parasitism rates from single replicates are reported.

#### 170 **3. Results**

171 A total of four fruit fly species were recorded on all incubated fruits: Ceratitis capitata, C. rosa sensu 172 lato, C. cosyra and B. dorsalis, with only the first two species found in the Western Cape province of South Africa. The infestation rates of fruit fly were higher in the M&L provinces than in the WC 173 province, with an average number of flies of 213.36 and 2.72 per kg of fruit, respectively. Five 174 175 species of parasitic Hymenoptera emerged from incubated fruits: two species of Opiinae (Braconidae): Fopius ceratitivorus Wharton, 1999 and Psyttalia humilis (Silvestri, 1913), one species 176 177 of Alysiinae (Braconidae): Asobara sp. Förster, 1862, one species of Aganaspis Lin, 1987 (Figitidae), and Tetrastichus giffardii Silvestri, 1913 (Eulophidae). The identification of P. humilis was confirmed 178 179 by the barcode sequences of specimens from South Africa that showed 99% similarity with a 180 Genbank sequence available for this species (accession number: EU761026.1).

181 The parasitoid Aganaspis sp. was the only species recorded in both WC and M&L provinces of South 182 Africa. The opiine species F. certitivorus and P. humilis and the Alysiine Asobara sp. were only 183 recorded in the M&L provinces, while T. giffardii was only found in the South-West. No 184 representatives of Opiinae were found in infested fruit samples of the Western Cape Province. 185 Within the North-Eastern sites, F. ceratitivorus was only collected around Nelspruit (Mpumalanga 186 province), while P. humilis was collected in both Mpumalanga and Limpopo provinces (Levubu, 187 Letsitele town, Nelspruit). Across all fruit samples, these two species never co-occurred in the same 188 batch of fruit. Mean parasitism rate of fruit flies by Opiinae ranged from 0% (Carissa spinarum L., 189 Psidium gujava L. and Sclerocarya birrea (A.Rich.) Hochst. ) to 38.5 % (Syzygium cordatum Hochst. ex Krauss) among fruit kinds (Table 2). Estimations of parasitism rate reached 54 % in a single replicate 190 191 of fruit incubation of Syzygium jambos (L.) Alston. Psyttalia humilis and F. certitivorus showed 192 variations in estimated parasitism rate, both sometimes not recovered or recorded at low level 193 (mean of 2.65% and 5.96%, respectively), or reaching higher rates (mean of 22.38% and 38.5 %, 194 respectively) among fruits collected.

Except for *Syzygium jambos* and *Carissa spinarum*, the smaller fruits (average weight of individual fruit below 10 g) allowed a higher parasitism rate than the larger ones (mean weight above 10 g), with an estimated mean parasitism rate of 21.46% and 8.42%, respectively. The two opiine *P. humilis*and *F. ceratitivorus* emerged together with all four species of fruit flies recorded in the study (Table
2).

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#### 201 4. Discussion

The environment surrounding an orchard is critical for the management of populations of polyphagous fruit flies. Indigenous hosts are known to be potential reservoirs of fly populations and their associated parasitoids in Central America (Ovruski et al. 2005, Aluja et al. 2014, Montoya et al. 2016). But, little quantitative investigation of parasitoids of fruit flies in indigenous hosts has been conducted in Africa in general (but see Copeland et al., 2009; Moxley et al., 2017). This study provides the first insights into the potential for wasp parasitoids to effectively control populations of fruit flies out of orchards in South Africa.

Among all the species of parasitoids that emerged from the fruits collected, only *Fopius ceratitivorus*, *Psyttalia humilis* and *Tetrastichus giffardii* are confirmed fruit fly parasitoids. Apart from a few exceptions (Ovruski et al. 2005; Tormos et al., 2013), the species belonging to the subfamily Alysiinae and the family Figitidae emerging from fruits are presently considered as parasitoids of Drosphilidae that are co-infesting the fruits (Wharton & Yoder, 2018). The two species belonging to these two groups (*Asobara* sp. and *Aganaspis* sp. respectively) will not be considered for further discussion.

215 The three parasitoid species we found on fruit flies contrast with the species assemblage obtained 216 by Manrakhan et al. (2010) on Ceratitis species attacking berries of Coffea species in South Africa 217 (Mpumalanga Province). In this study, we found a large representation of P. humilis. Psytallia 218 perproxima, Bracon celer and Tetrastichus giffardianus were not recovered in this study. In contrast, 219 F. ceratitivorus and T. giffardi were not reported on Ceratitis spp. attacking berries of Coffea species 220 while they were found, sometimes at a high rate, in the present study. This difference in species 221 composition might be due to differences in sampling localities, where parasitoid faunal assemblages 222 may vary at a local scale, or due to a difference in attraction of parasitoids between infested fruits 223 and berries of Coffea species.

224

#### 4.1. A contrasted distribution pattern of parasitism of fruit flies in South Africa

This study highlighted a remarkable difference of parasitism rate of fruit flies by their parasitoids among two climatically different regions of South Africa. The two major Tephritidae obtained on various fruits (*Ceratitis capitata* and *C. rosa* s. l.) are two native species widely distributed and abundant across South Africa (De Villiers et al., 2013; Karsten et al., 2015; De Meyer et al., 2016). While in the north-eastern areas, *C. capitata* and *C. rosa* s.l were parasitised by the dominant opiine parasitoïds (*F. ceratitivorus* and *P. humilis*), in the South-West regions these parasitoids were largely absent in the fruit sampled where these two fruit fly species were reared. Indeed, among the total of 3430 fruits belonging to 7 species infested by fruit flies collected in the WC province, not a single opiine specimen emerged. The eulophid *T. giffardi* was the only parasitoid emerging from *Ceratitis* spp. in this province and it was recorded only once on Medlar (*Mespilus* sp.).

Species of fruit flies, including *C. capitata* and *Bactrocera* sp. are known to have large climatic niches (Weldon et al., 2018) that may be wider than their parasitoids used in biocontrol (Lane et al., 2018) even at reduced scale (Etiam et al. 2004). It can be hypothesized, for *F. ceratitivorus* in particular, that the climatic conditions in the Western Cape are not appropriate for this species to develop on its host. Indeed, the genus *Fopius* is mainly distributed in the tropics (Wharton, 1999; Wharton and Yoder, 2018). The temperate winter-rainfall climatic conditions found in the Cape region are probably not suitable for the persistence of *Fopius* species in this area.

242 The case of *P. humilis* is different. This species is widely distributed in South Africa, from the North 243 Eastern part of the country, the southern coast (Jh, pers obs), to the WC province where it has been 244 mostly recorded from Bactrocera oleae attacking olives (Wharton and Yoder, 2018). Even though this species is present across the two sampled localities, it is found in much higher abundance on a 245 variety of fruit in the North East, whereas the WC populations attcking olive fly do not seem to be 246 247 able to shift effectively onto Ceratitis species attacking cultivated and ornamental fruit sampled in 248 this province. Further investigations are needed to explore whether populations of P. humilis are specialists on a specific host-fly or fruit type in South Africa. 249

250 Fopius ceratitivorus and P. humilis never co-occurred in the same batch of fruit, while being 251 distributed in the same regions. This result suggests a competitive exclusion of the two species, in 252 line with the study of Wang et al. (2008) that reported at individual level a systematic exclusion of 253 Psyttalia species by F. ceratitivorus when sharing the same host. It is therefore possible that at local 254 scale and for specific fruit types, the early acting species F. ceratitivorus (oviposition in the eggs of the host) can completely supress the population of a later attacking species such as P. humilis ( 255 256 oviposition in larvae of the host). More generally, the absence of co-occurrence of the two species in 257 a batch of fruit suggests contrasted performances of the two species that are commentary for the 258 control of fruit flies in indigenous hosts.

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#### 260

4.2. Fruit flies are unequally controlled by parasitoids in indigenous fruits

261 Fruit flies encountered in this study are using a large range of indigenous fruits to complete their life 262 cycle in tropical Africa (Copeland et al., 2009; Grové et al., 2017). Our results show a contrasting 263 control efficacy by their associated parasitoids across fruit type in South Africa. In fruit of some 264 families: Apocynaceae, Anacardiaceae and some Myrtaceae, opiine parasitoids seem unable to 265 control fruit flies, suggesting that some indigenous or ornamental trees can play a role of sole fruit 266 fly multiplier (Aluja et al. 2014). In contrast, these parasitoids were found attacking fruit flies at a 267 substantial rate in fruit of other families: Clusiaceae, Rhamnaceae and some Myrtaceae. The exact 268 drivers of this variation is difficult to determine as they may encompass a large range of parameters. 269 Parasitoids usually follow the phenology of their hosts, track the larvae using plant kairomones, or 270 oviposition marks of the flies. It is interesting to note that several fruit types that displayed either no 271 parasitism, or a rather high parasitism rate of fruit flies were collected in the same localities. 272 Therefore, these variations cannot be due to local absence of some parasitoids species. This observation rather suggests that some fruits might not be attractive for the opiine parasitoids, or 273 274 alternatively their physical structure may prevent the parasitoids from efficiently locating the 275 immature stages of fruit flies for oviposition.

276 Over all fruits sampled, the smaller fruits generally allowed a higher parasitism rate than the larger 277 ones. Other studies showed similar results in North America (Wang et al. 2009a, b) or tended to 278 confirm this trend in South Africa, with similar parasitism rates of fruit flies recorded from small 279 fruits such as Coffea berries and wild olives (Mkize et al., 2008; Manrakhan et al., 2010). This 280 observation is in line with the oviposition strategy of the genus Psyttalia that lays its eggs in the 281 larval stages of fruit flies. In this case host larvae might be difficult to reach with their ovipositor in 282 large fleshy fruits. However, this explanation does not apply to the genus *Fopius* that target the eggs 283 of fruit flies at the surface of the fruits directly after the oviposition of fruit flies. It can also be 284 hypothesized that opiine parasitoids are laying through oviposition marks on fruits, as has been documented in other braconid species (Stelinski et al., 2010). In this case, numerous small fruits 285 286 would allow more oviposition events than a few large ones for an equal amount of resource reward 287 for fruit fly larvae.

Three fruit tree species (*Berchemia discolor, Garcinia livingstonei* and *Syzygium cordatum*) showed a high infestation by fruit flies (about 800, 100 and 60 flies per kg of fruit respectively) that were themselves strongly parasitized by opiine species (about 22, 34 and 40 % of estimated parasitism rate respectively). The presence of these trees around orchards is notable, as they may play an attractant role for fruit flies, and hence for the parasitoids controlling them resulting in the development of a relatively high reservoir population of parasitoid wasps in an adjacent habitat. They would therefore contribute to the reduction of natural populations of fruit flies as described by 295 Aluja et al. (2014). In practice, however, the parasitism rate estimated still suggests that these trees 296 would release substantial volumes of non-controlled fruit flies near the orchards. Therefore, it seem 297 more appropriate to combine these trees with augmentative techniques, such as the harvesting of 298 fruits and their placement in augmentauria or simply the placement of appropriate nettings under 299 these in order to allow an important augmentative release of parasitoids together with a strong 300 reduction of fruit fly populations. As an illustration, our results show that in some localities, one kg 301 of the Brown Ivory fruits (Berchemia discolor) placed in an augmentoria can release about 300 302 parasitoid specimens while retaining about 800 fruit fly individuals. Other estimations reached 303 20,000 parasitoids per tree (Aluja et al. 2014). This approach for production of parasitoids may be 304 more cost effective than traditional laboratory mass rearing for field release. More generally, these trees can potentially be used as "decoy trees", attracting and retaining fruit flies out of the orchard, 305 306 killing them and releasing parasitoids using an augmentoria derived technique. This approach has 307 economic potential as it could be used to limit both orchard infestations and to reduce wild 308 populations of fruit flies.

309

#### **5.** Conclusion

This study showed a contrasting distribution of the natural biocontrol agents of fruit flies across two 311 climatically disparate regions in South Africa, with a higher diversity and higher efficacy of 312 313 parasitoids in the sub-tropical summer-rainfall part of the country in comparison to the area with a 314 temperate, winter-rainfall climate. This survey also suggests that some indigenous trees are host for 315 the flies and their parasitoids while some species seem to host only non-controlled populations of 316 fruit flies. This suggests that indigenous trees around orchards could be selected and potentially 317 developed to contribute to the reduction of fruit fly populations in natural and semi-natural 318 environment using augmentative methods. More investigation is needed across the rest of Africa in 319 order to determine the contributory role played by indigenous trees towards pest fruit fly control. 320 More generally, a better characterization of the underlying drivers affecting biocontrol efficiency of fruit flies by the opiine parasitoids is needed, such as adaptation or preference of the parasitoid 321 322 wasps for specific host flies, host plants, or climatic conditions.

323

#### 324 Table captions

Table 1. Details of fruits samples incubated from the Limpopo, Mpumalanga and Western-Cape
 provinces of South Africa. Dates: Months and Years of collecting of fruits; Repl.: number of sampling

327 replicates for each fruit kind in one locality; Avg fruit: mean number of fruit collected per replicate;
328 Avg weight: Mean total fruit weight (Kg); AVg flies: mean number of flies obtained; Avg flies/ kg:
329 mean number of flies per Kg of fruit incubated. Pres. Parasit: presence of confirmed parasitoids of
330 Fruit flies in the fruit sample. Fruits with a \* refer to exotic cultivated species and with a \*\* to exotic
331 ornamental species. Italic values indicates results obtained for simple replicates.

Table 2. Parasitism rate of fruit fly infesting indigenous fruits in South Africa. T: total number of fruit
 collected among replicates, W: total weight of fruit collected (g), Sz: average fruit weight (g), %:
 parasitism rate (%) among replicates, R- & R+: lower and higher parasitism rate obtain in single
 replicates. The fruit fly recorded from each fruit reared are reported.

336

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#### 344 **Competing interests**

345 Declarations of interest: none.

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Province of SA	locality	coordinates	fruit species	Dates	repl.	Avg. fruit	Avg. weight (kg)	Avg. flies	Avg. flies/kg	Pres. Parasit.
Limpopo	Letsitele	23°39'24.10''S 30°40'15.47''E	<i>Carissa spinarum</i> L. Simple spine num-num	February 2014-2015	2	81.5	0.189	122	645.50	
	Levubu	-	<i>Ekebergia capensis</i> Sparrm. Cape-ash	February 2014	1	328	0.42	125	297.62	х
		-	<i>Psidium guajava</i> L. Guava*	October 2013	1	40	3.43	111	32.36	
	Morebeng	-	<i>Psidium guajava</i> L. Guava*	May 2015	1	30	1.22	121	99.18	
	Thohoyandou	-	Sclerocarya birrea (A.Rich.) H Marula		2	52.5	1.07	14	13.08	Х
	Letsitele	23°39'24.10''S 30°40'15.47''E	Berchemia discolor (Klotzsch, Brown ivory		3	441.67	0.36	283.67	787.97	
Western Cape	Mbombela	25° 27'06.24''S	Psidium cattleianum Afzel. ez	February-March-April	5	63.6	0.23	61.4	266.96	Х
		30° 58'09.66''E 25° 27'06.24''S	Strawberry Guava** Syzygium jambos L.	2014-2016 December	3	40.33	1.32	53	40.15	х
		30° 58'09.66''E 25° 27'06.24''S	Rose apple** <i>Syzygium cordatum</i> Hochst.		2	125	0.2319	14	60.37	Х
		30° 58'09.66''E 25° 27'06.24''S	Water berry Sclerocarya birrea (A.Rich.) H	2014 February	1	50	1.13	129	114.16	
		30° 58'09.66''E 25° 27'06.24''S	Marula Garcinia livingstonei T.Ande	2015 November-December	2	55.5	0.44	44.5	101.14	Х
		30° 58'09.66''E 25° 27'06.24''S	African mangosteen Cordyla africana Lour.	2013-2014 February						
	Tulbagh	30° 58'09.66''E	Wild mango	2016	1	20	1.08	110	101.85	Х
	Tulbagh	33° 16'21.00''S 19° 10'08.40''E	<i>Prunus domestica</i> L. Plum*	January-April 2016-2017	2	11	0.5745	4.5	7.83	
	Stellenbosch	33° 55'19.68''S 18°48'4374''E		January-April 2016-2017	4	50	2.87	14.5	5.05	
	Ceres	_		January-April 2016-2017	2	55	6.4	0	0.00	
	Somerset West	34°02'56.58''S 18°50'25.72''E		February 2018	2	583	11.47	11	0.96	
	Tulbagh	33° 16'21.00''S 19° 10'08.40''E	<i>Prunus persica</i> L. Peach*	January-April 2016-2017	2	8.5	0.33	0.5	1.52	
	Ceres	_		January-April 2016-2017	2	51	6.055	1.5	0.25	
	Stellenbosch	33°56'21.63''S 18°51'00.79''E		February 2018	1	69	5.24	18	3.44	
	Robertson	33° 48'15.60''S 19° 53'00.60''E		March 2016-2017-2018	2	103	16.085	12	0.75	
	Stellenbosch	33°55'18.20''S 18°55'41.57''E	Malus domestica B. Apple*	January-April 2016-2017	2	52.5	5.6	1.5	0.27	
	Stellenbosch	33°56'51.84''S	Аррге	January-April	2	50	2.75	0	0.00	
	Stellenbosch	18°51'42.30''E 33°55'18.20''S	Pyrus communis L.	2016-2017 January-April	2	50	4.65	44	9.46	
	Stellenbosch	18°55'41.57''E 33°56'51.84''S	Pear*	2016-2017 January-April	2	75	5.35	22	4.11	
	Stellenbosch	18°51'42.30''E 33°58'11.23''S		2016-2017 February	1	300	24.18	128	5.29	
	Stellenbosch	18°47'37.35''E 33°55'24.82''S		2018 March	2	190	10.45	58	5.55	
	Tulbagh	18°52'22.36''E 33° 16'21.00''S		2018 January-April	2	35	5.18	3.5	0.68	
	Riebeeck Kasteel	19° 10'08.40''E 33°23'12.00''S	<i>Vitis</i> sp.	2016-2017 January-April						
		18°54'00.00''E	Table grape*	2016-2017	1	50	4	1	0.25	
	De Doorns	33°28'28.80''S 19°39'35.40''E		January-April 2016-2017	1	50	1.7	0	0.00	
	Stellenbosch	33°56'51.84''S 18°51'42.30''E	<i>Citrus limon</i> L. Citrus*	January-April 2016-2017	1	130	3.6	2	0.56	
	Stellenbosch	33°56'15.59''S 18°51'24.09''E	<i>Mespilus</i> sp. Medlar**	February 2018	1	103	2.11	12	5.69	

		_		- ( )					<sup>CQD</sup>	roso .	<sup>- 5.</sup>	dor.
Species	Species	Т	W(g)	Sz(g)	Parasitoid sp	%	R -	R+	C.	ୖ୰	C,	<i>\$</i> .
Berchemia discolor	Brown ivory	1325	1069.4	0.80	P. humilis	22.37	14.02	40.32	Х			
Carissa spinarum	Simple spine num-num	163	378.0	2.31		0	0	0	Х			
Cordyla africana	Wild mango	20	1079.1	53.95	P. humilis	2.65	na	na		Х	Х	Х
Ekebergia capensis	Cape-ash	328	421.0	1.28	P. humilis	6.02	na	na	Х			
Garcinia livingstonei	African mangosteen	111	873.5	7.87	F. ceratitivorus	34.41	18.82	50.00	Х	Х		
Psidium cattleianum	Strawberry Guava	318	1146.3	3.60	F. ceratitivorus	5.96	0	13.33	Х	Х	Х	Х
Psidium guajava	Guava	70	4649.8	66.42		0	0	0	Х	Х	Х	Х
Sclerocarya birrea	Marula	212	4523.3	21.33		0	0	0			Х	
Syzygium cordatum	Water berry	250	463.8	1.86	F. ceratitivorus	38.54	33.33	43.75	х	Х		
Syzygium jambos	Rose apple	121	3940.7	32.57	F. ceratitivorus	17.98	0	53.93		Х		