Perspective

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Overview and future research needs for development of effective biocontrol strategies for management of *Bactrocera dorsalis* Hendel (Diptera: Tephritidae) in sub-Saharan Africa

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Abstract

Infestation of fruits by native and invasive fruit flies causes significant economic losses. In most cases, incidence of 'regulated' dangerous fruit flies in orchards results in restrictions on export of fruits from such places to international markets. Unfortunately, use of insecticides applied on foliage and fruits does not kill the fruit-to-soil stages of fruit flies. However, diverse biological control agents (BCAs) do so. Thus, prevalence of native and invasive fruit flies in orchards will require that a combination of BCAs is included in integrated pest management (IPM) programmes. In the case of *Bactrocera dorsalis* Hendel and other economically important fruit flies found in sub-Saharan Africa (SSA), use of classical biocontrol approach involves concomitant releases of two exotic parasitoids (*Fopius arisanus* Sonan and *Diachasmimorpha longicaudata* Ashmead). These non-native wasps may have complemented the indigenous parasitoids in combination with application of entomopathogenic fungi (EPFs) and conservation of predatory ants (*Oecophylla longinoda* Latreille, with *O. smaragdina*) in fruit fly IPM plans. Consequently, some levels of decline in fruit infestation have been observed. Although interspecific interactions between BCAs against several insect pests have produced varying results, including threatening the survival of other BCAs, the prevalence of *B. dorsalis* in orchards across SSA requires further research to investigate effects of coalescing biocontrol approaches in IPM strategies. Therefore, future research into combining parasitoids, EPFs and entomopathogenic nematodes, in addition to conservation of predatory ants (*O. longinoda*, *O. smaragdina* and others) in IPM plans may improve the effectiveness of currently used strategies for the management of fruit-infesting tephritids.

Keywords: biological control; parasitoids; entomopathogenic fungi; predatory ants; entomopathogenic nematodes; native tephritid fruit flies; *Bactrocera dorsalis*; environmentally friendly pest control; sub-Saharan Africa

1 INTRODUCTION

The genus *Ceratitis* contains several economically-important species of fruit flies (Diptera: Tephritidae), e.g. *C. cosyra*, *C. rosa*, *C. fasciventris*, *C. anonae*, *C. ditissima* and *C. capitata*, among others, that are native to Africa.[1–3] These species are observed in orchards across sub-Saharan Africa (SSA),[4–6] but since the invasion of the African continent by the Oriental fruit fly, *Bactrocera dorsalis* Hendel, indigenous *Ceratitis* species have been suppressed and displaced.[2,7–15] Consequently, *B. dorsalis* has become the most economically important tephritid fruit fly pest in SSA.[9–12,14,15–18] Although *B. dorsalis* infests at least 30 different hosts in SSA,[9–12,14] the highest population densities are primarily observed in mango [*Mangifera indica* L. (Sapindales: Anacardiaceae)] orchards.[9–12,14,15] Sexually mature *B. dorsalis* females oviposit eggs into unripe mature green, partially ripe, and fully ripe mangoes.[15,19] As a result, export of mangoes from *B. dorsalis*-invaded countries and territories worldwide to international markets has been strictly regulated by many countries where *B. dorsalis* can likely establish.[10,11,14–16] Moreover, income from mango production to support livelihood or investments into production of several other food crops can be affected by the prevalence of *B. dorsalis* in orchards. Thus, the potential menace of *B. dorsalis* in many countries or territories can indirectly interfere with the strategic efforts aimed at achieving the United Nation Sustainable Development Goals (UN-SDGs) 1, 2, 3 and 8.[20]

Early detection of incipient populations of *B. dorsalis* in the United States (i.e. California and Florida), South Africa, Mauritius, Japan, Australia, Cook Islands, Guam and Nauru, among others, triggered successful eradication via strict interception programmes.[14,21–24] Continuous area-wide monitoring for

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subsequent emergence of *B. dorsalis* is required for timely eradication or successful prevention of fly establishment.[14,23] In Asia, some regional Pacific islands, Hawaii-USA and SSA, management of *B. dorsalis* rather than eradication is preferred, largely because the insect has already established in these parts of the world.[2,3,14,15,24]

In SSA, several management strategies are simultaneously applied to control *B. dorsalis* in orchards.[15,25–28] Among the fruit fly control tactics, well-studied macrobial and microbial biological control agents (BCAs)[29–35] have been used against *B. dorsalis* and other economically important fruit flies in orchards across SSA.[5,15,16,29–31] These BCAs could possibly be complementary to the use of low-to-moderately toxic insecticides (i.e. spinosad-based products, organophosphates and pyrethroids, among others), which are mainly applied to manage fruit flies and other insect pests in mango orchards.[15,27] Thus, the use of BCAs for control of tephritid fruit flies merits future studies to identify how to use them effectively against *B. dorsalis*.

Here, we considered the most studied BCAs that are commonly used against a wide range of tephritid fruit flies.[5,15,31–35] In the case of SSA, we considered the koinobiont and idiobiont parasitoids,[5] entomopathogenic fungi (EPFs)[15,32–35] and nematodes (EPNs)[35] largely because of their potential in suppressing a wide range of fruit flies.[32] In addition, we also considered predatory ants [*Oecophylla longinoda* Latreille (Formicidae: Formicinae), *O. smaragdina* and others] because they can be effective in controlling tephritid fruit flies in orchards.[26,30,36,37] Even though the persistent threats by *B. dorsalis* and other economically important fruit flies across SSA demand effective collaboration between research and commercial interests, our discussion does not include details on trade names or strains of formulated BCAs for biocontrol of tephritid fruit flies. Rather, our focus is on how recent research and future considerations may lead to development of more effective biological control strategies in fruit fly IPM programmes against the noxious *B. dorsalis*. Therefore, our main objective is to focus on biological control research and the fruit fly pest management efforts against *B. dorsalis* in orchards within SSA to identify knowledge gaps that can be filled with future research that will increase our understanding of all-inclusive biocontrol strategies in fruit fly IPM.

2 MAJOR TEPHRITID FRUIT FLIES AND *BACTROCERA DORSALIS*

At least four genera of tephritid fruit flies are major pests on fruits in terms of their wide-ranging geographical distributions to parts of the world. *Anastrepha*, *Ceratitis* and *Rhagoletis* fruit flies are largely native to Central and South Americas,[38] Africa[1,2] and temperate zones, respectively.[39–41] Nonetheless, *Bactrocera* spp. originated from Asia.[3,7,8,11,14] Thus, *B. dorsalis* is one of the Asian fruit flies.[7,8,13,14] It has distributed to the Pacific islands, Hawaii-USA and SSA.[14] In 2003, *B. dorsalis* was reported in Kenya in East Africa.[7] This fruit fly was very invasive in suppressing and displacing the native *Ceratitis* fruit flies as well as causing high fruit infestation in mango orchards across SSA.[2,7–12] Because of this, Drew *et al.*[8] described it as the Africa invader fruit fly (*B. invadens*). However, it was later confirmed (or synonymised) to be a species among the members of the *B. dorsalis* complex.[13,22,42] By 2012, *B. dorsalis* had invaded orchards in all the sub-Saharan African countries and territories.[11] Eradication of *B. dorsalis* was successful in Japan, the USA, the Cook Islands, Nauru, Guam, South Africa and Mauritius, among others, but the insect has established in 43 countries and three territories across SSA.[11,14,22,24] Regular emergence of *B. dorsalis* has been threatening many other countries and territories worldwide.[14,21–24] *B. dorsalis* has a high reproductive capability and a short life cycle of 2–3 weeks in SSA (authors' personal observations). An adult *B. dorsalis* female can achieve at least 12 generations of progeny in a year in SSA. They disperse quickly to invade distant orchards.[14] *B. dorsalis* infests a wide range of fruits and vegetables, including those in the wild, but mangoes in commercial orchards across SSA are more affected.[9–12,14,15,43] Thus, management of *B. dorsalis* across SSA requires research to develop innovative strategies.[15]

3 FRUIT FLY PEST MANAGEMENT PRACTICES ACROSS SSA

To the best of our knowledge, we here list the pest management practices applied in an integrated model to manage *B. dorsalis* across SSA. We excluded (i) regulatory and quarantine measures strictly implemented by South Africa and Mauritius, where eradication of *B. dorsalis* has successfully been achieved,[11,14,15,21] and (ii) the sterile insect technique (SIT), which is not applied across SSA. Rather, we considered how past and future studies may contribute to the use of the most widely studied BCAs in IPM programmes against fruit flies in orchards across SSA. We then identified knowledge gaps that should be the focus of future research.

3.1 Current overview of IPM for *Bactrocera dorsalis* in SSA

The IPM approaches applied against *B. dorsalis* and other economically important fruit flies in orchards across SSA involve (i) application of GF-120 (spinosad; Dow Chemical/Corteva Agriscience)[15,16] and/or different organophosphate insecticides,[27] (ii) release of parasitoids, (iii) conservation of predatory ants, (iv) application of dry spores of EPFs, (v) male-annihilation technique (MAT), which involves the use of methyl eugenol bait for monitoring and mass-trapping to kill large numbers of *B. dorsalis* males,[44] (vi) bait application techniques (BAT), which involves use of highly attractive protein food baits mixed with a small amount of killing agent (<1%) that will kill the flies upon ingestion of the bait[17,18] and (vii) the Global Good Agricultural Practices (i.e. GLOBAGAP-field sanitation which involves collecting fallen fruits on the ground and burying them to terminate the life cycle of fruit flies).[27] After harvest, cold or heat treatments are widely used to process mature green mangoes for local and international markets.[10,17] These treatments will kill any progeny of tephritid fruit flies in infested mature green fruits. However, bagging of mangoes on trees is rarely observed in growers' orchards in SSA, perhaps because of the high labour costs associated with this practice. Insecticide sprays in orchards do not kill fruit-borne (egg and larval) and soil-borne (pupal and eclosing adult) fruit fly stages, largely because these stages are generally protected in fruits and in the soil in infested orchards.[32] Conversely, BCAs have been effective in killing eggs, larvae, pupae and adults of fruit flies.[5,15] As a result, parasitoids, predatory ants, EPFs and EPNs have been studied to develop effective control of *B. dorsalis* and other fruit flies.[5,15,32]

3.2 The use of biological control agents against *Bactrocera dorsalis* in SSA

The BCAs that have so far contributed to the control of *B. dorsalis* and various *Ceratitis* species in orchards across SSA have largely been the introduced braconid wasps [*Fopius arisanus* Sonan and *Diachasmimorpha longicaudata* Ashmead (Hymenoptera: Braconidae)],[16,15] the native parasitoids [*F. caudatus* and *Psyttalia cosyrae* Wilkinson (Hymenoptera: Braconidae), among others],[6,28] numerous local idiobiont wasps,[5] EPFs,[16,21, 29] and the indigenous predatory African weaver ant *O. longinoda* along with *O. smaragdina*.[25,26,30,37] *P. cosyrae* has been very effective in parasitizing larvae of the mango fruit fly (*C. cosyra*) and the Mediterranean fruit fly (Medfly; *C. capitata*), but not the larvae of the Natal fruit fly (*C. rosa*), *C. fasciventris*, *C. anonae*, *Zeugodacus cucurbitae*-Coquillett (Diptera: Tephritidae) or *B. dorsalis,* among others, in infested fruits.[4–6,45] Even though there are no published data from Africa, it is likely that the numerous local predatory ant species of the genus *Solenopsis* are preying on the soil-borne pupal stage of fruit flies across SSA, similar to the way that *S. invicta* has been observed preying and feeding on *B. dorsalis* pupae under laboratory conditions.[36] Although the environmentally friendly soil-borne EPN species (native or exotic) have not yet been applied against fruit flies in the field across SSA, reports have shown that EPN augmentation can suppress the fruit-to-soil stages of *B. dorsalis*.[35,46,47]

3.2.1 *Parasitoids*

Diverse species of parasitoids reported across Africa are either idiobiont or koinobiont.[5] The former parasitize and kill larvae or pupae of fruit flies. Thus, idiobiont parasitoid-infected larvae or pupae do not develop to the next life cycle stage. On the other hand, koinobiont parasitoids are known for parasitizing eggs or larvae of fruit flies, which are killed only at the pupal stage.[5,15] In effect, koinobiont parasitoid-infected eggs or larvae of fruit flies develop to pupal stage for successful emergence of the parasitoid wasps from eclosing fruit fly pupae.

3.2.1.1. Koinobiont parasitoids. The widespread damage to mango and other fruits caused by *B. dorsalis* triggered a classical biological control approach for the concomitant release of *F. arisanus* and *D. longicaudata* within SSA.[15] The female *Fopius* parasitoid wasps oviposit eggs associated with release of polydnaviruses and nudiviruses into fruit fly eggs in fruits.[15,48] On the other hand, *D. longicaudata* wasps oviposit eggs associated with release of rhabdoviruses into fruit fly larvae in fruits.[49] These beneficial endosymbiotic viruses injected into the eggs or larvae of tephritid fruit flies protect the progeny of koinobiont braconid wasps (e.g. *Diachasmimorpha*, *Psyttalia* and *Fopius*, among others) to ensure their successful development inside the infected tephritid fruit flies in fruit-to-soil environments.[48–50] The *Fopius*-parasitized eggs or *Diachasmimorpha*-parasitized larvae of tephritid fruit flies are killed at the pupal stage following the emergence of parasitoid wasps from fruit fly puparia, consequently reducing the population densities of fruit flies in mango orchards.[15,28] Unfortunately, the progeny of *P. cosyrae* are mostly encapsulated by the induced immune system at the 'larval-to-pupal' stages of *C. rosa*, *C. fasciventris*, *C. anonae* and *B. dorsalis*.[4–6,45] In effect, the majority of the eggs of *P. cosyrae* do not successfully complete their life cycle through the resistant larval-to-pupal stages of these fruit flies as they do in *C. cosyra* and *C. capitata*. On the other hand, the exotic *D. longicaudata*, intentionally introduced to SSA, has developed very high parasitism preference for the larvae of *C. cosyra* more so than larvae of *B. dorsalis* in fruits.[4,6] Superparasitism by *D. longicaudata* prematurely kills its numerous progenies developing in an infected fruit fly larva.[51] These challenges associated with the use of koinobiont parasitoids can largely threaten biological control strategies against *B. dorsalis* in SSA. However, a recent report by Bokonon-Ganta *et al.*[28] shows that research is focusing on the deliberate release of the native parasitoid wasp *F. caudatus* against *B. dorsalis* across SSA in the future. In our view, combined releases of *F. caudatus*, *D. longicaudata*, *F. arisanus* and *P. cosyrae* will provide better control of *B. dorsalis*, *C. cosyra*, *C. capitata*, *C. fasciventris*, *C. rosa*, *C. anonae* and other fruit flies in orchards across SSA since a lack of negative interspecific interferences among diverse parasitoid wasps has been observed in orchards.[52] Moreover, the abilities of parasitoid wasps to discriminate between parasitized and unparasitized fruit fly larvae may possibly increase their efficiencies in fruit fly-infested orchards.[53]

3.2.1.2. Idiobiont parasitoids. Larva, pupa and 'larva-and-pupa' parasitizing idiobiont parasitoids are present in Africa.[5] The larval parasitoids are *Pteromalus semotus* Walker (Pteromalidae), *Halticoptera daci* Sivestri (Pteromalidae) and *Cyrtoptyx latipes* Rondani (Pteromalidae), among others.[5] Similar to the indigenous eulophids, *C. latipes* can parasitize both larvae and pupae of fruit flies.[5] *Dirhinus* spp. (Chalcididae), *Coptera* spp. (Diapriidae), *Trichopria* spp. (Diapriidae), *Meraporus graminicola* Walker (Pteromalidae) and *Pachycrepoideus vindemmiae* Rondani (Pteromalidae) are potential pupal parasitoids in Africa.[5] Native idiobiont parasitoids are known for parasitizing *B. olae*, *Ceratitis* spp. and *Dacus* spp. across Africa.[5] However, pteromalids, eulophids and many native koinobiont parasitoids have been retrieved from *B. dorsalis*-infested mangoes in Senegal.[5,54] In our view, research is needed to assess for augmentative releases of both idiobiont and koinobiont parasitoid wasps against *B. dorsalis*.

3.2.2 *Entomopathogenic fungi*

Bioefficacies of *Metarhizium anisopliae* (Metch.) Sorokin (Hypocreales: Clavicipitaceae), *Beauvaeria bassiana* Balsamo (Hypocreales: Cordycipitaceae) and other EPFs have been assessed in treatments against *B. dorsalis*.[9,29,31,55] However, EPFs do not search for their hosts as parasitoids, predatory formicids and EPNs do. Because of this challenge, EPFs are generally added to pheromone lure-traps or food bait-blocks and then used in the field to increase their efficiencies against *B. dorsalis* and other fruit flies.[29,56] This approach to attract, trap, and kill more *B. dorsalis* adults is similar to the way *B. pseudobassiana* was used in bait-traps against *C. capitata*.[57] Unlike the MATs, the pheromone lure-traps or the food bait-traps have an advantage to mass-trap and kill both male and female adult fruit flies. However, future research must assess whether adding EPFs to pheromone lure-traps or food bait-traps will negatively affect other arthropod fauna in the environment.

Dry spores of *M. anisopliae* have also been applied to cover mango trees from top to dripline in combination with spinosad bio-insecticide (i.e. GF-120) sprays in orchards in SSA.[16,55,56] The direct EPF treatment to entire trees and the ground in mango orchards significantly increased the amount of uninfested fruits, with no observed side-effects on emergence of parasitoid wasps from fruit fly pupae in the ground.[15,56] Martínez-Barrera *et al.*[33] observed no side-effects of *B. bassiana* on the parasitoid *Coptera haywardii* Ogloblin (Hymenoptera: Diapriidae) against *Anastrepha obliqua* Macquart (Diptera: Tephritidae) in the Americas. However, application of *B. bassiana* in combination with release of *C. haywardii* for management of *A. obliqua* was not effective.[33] Comparing the effectiveness of *B. bassiana* and *C. haywardii* combined in controlling *A. obliqua*[33] to the case of SSA, it can be concluded that the use of EPF species in IPM plans has been effective against *B. dorsalis* and lesser economically important fruit flies in SSA, where diverse parasitoids have established. However, it is not clear whether the practice of treating whole mango trees with dry spores of insect-killing EPF species against tephritid fruit flies would have negative side-effects on the performance of flying parasitoid wasps (exotic or native) and incidence of other arthropod communities in the canopies of EPF-treated trees.

3.2.3 Predatory formicids

Two genera of predatory ants are useful for biological control of tephritid fruit flies and other insect pests. The African weaver ant (*O. longinoda*) is native to SSA, whereas the predatory Asian weaver ant (*O. smaragdina*) is common in Australia and Asia.[37,58] Other tropical *Solenopsis* spp. are numerous across Africa,[59] including *S. globularia*, which is native to Ivory Coast, Congo, Senegal and Cape Verde,[60] and *S. geminata*, which is present in Gabon, Liberia, Mauritius and Réunion.[61]

3.2.3.1. African weaver ant, Oecophylla longinoda. According to Abdulla *et al.*,[26] augmentative biocontrol involving intentional releases of the native *O. longinoda* against fruit flies can be implemented across SSA. However, at this point only conservation biocontrol practices have improved predation of a significant number of *B. dorsalis* adults by *O. longinoda* in mango and citrus orchards.[26,30] Consequently, infestation of mango and citrus by *B. dorsalis* and other tephritid fruit flies in orchards significantly declined in SSA.[26,30] Unfortunately, the voracious predatory and foraging activities as well as the emission of semiochemicals by the aggressive *O. longinoda* against insects and other arthropods deter beneficial parasitoid wasps from successfully parasitizing fruit-borne life stages (i.e. eggs and larvae) of tephritid fruit flies in fruits on trees.[15,37] Perhaps this negative interspecific interference between predatory ants and parasitoids might have limited any plans for deliberate releases of large numbers of *O. longinoda* to the cultural conservation practices for these ants in fruit fly-infested orchards across SSA.

3.2.3.2. Asian weaver ant, Oecophylla smaragdina. As far back as 304 AD, *O. smaragdina* was used for biocontrol of a variety of insect pests in orchards and horticultural fields.[37,62] According to Vayssières *et al.*,[37] *O. longinoda* and *O. smaragdina* may co-occur in forests and agroforests across SSA. However, the effects of the combination of *O. smaragdina* and *O. longinoda* have not been measured and compared to those of either *O. smaragdina* alone or *O. longinoda* alone.

3.2.3.3. Predatory myrmicids. The genus *Solenopsis* is a predator of tephritid fruit fly pupae found in the soil.[36,63] The mortality of *B. dorsalis* pupae due to predation of *S. invicta* in sandy soils with soil moisture content of 0.4 or 0.8 $\mathrm{g\,g^{-1}}$ was highest (i.e. 55–100%) at soil depths ≤4 cm.[36] Unfortunately, some *Solenopsis* spp. are invasive and aggressive in cutting and harvesting plant leaves, buds and germinating seeds among others in agricultural, residential, forest and grassland environments.[60–64] Also, these ants sting, causing pain and discomfort in vertebrates, including humans.[65,66] Because of these major challenges, they are primarily managed wherever human activities are common.[60–64,66–68] Nonetheless, sugar solution sprays in maize [*Zea mays* L. (Angiosperms: Poaceae)] fields infested by the Fall armyworm [*Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae)] in Honduras attracted large numbers of *S. geminata*, *Lespesia* sp., *Doru* sp. and coccinellids.[69] Consequently, the population density of *S. frugiperda* and damage to maize crops were reduced by 35 and 18%, respectively.[69] No threat of *S. geminata* to humans in the *S. frugiperda*-infested maize fields was observed by Canas and O'Neil.[69] Therefore, similar conservation biocontrol practices to attract the indigenous *Solenopsis* spp. against *B. dorsalis* and lesser economically important fruit flies in SSA may merit research but caution should be exercised.

3.2.4 Entomopathogenic nematodes

Soil-borne EPNs are widely distributed across the world.[70,71] They can be retrieved through *in vivo* extraction technique from soils in agricultural, grassland and forest ecosystems, except in Arctic and Antarctic zones.[72] The most studied beneficial nematodes for biocontrol of insect pests belong to the families Heterorhabditidae and Steinernematidae.[70,71] Heterorhabditids and steinernematids are associated with environmentally friendly entomopathogenic endosymbiotic bacteria (EPEB) of the genera *Photorhabdus* and *Xenorhabdus* (Enterobacterales: Morganellaceae), respectively.[70,73–75] Additional genera of EPEB have recently been confirmed in some EPN species.[76] The nematode species in the *Insectivora* group of the genus *Oscheius* (Rhabditina: Rhabditidae) are considered EPNs.[75] *Oscheius* spp. have EPEB which belong to different genera.[77,78] They can also kill fruit flies and other insect pests,[73,74,79,80] even though *O. chongmingensis* is more attracted to feed on decomposing dead arthropods than being infectious to live insect pests.[81]

3.2.4.1. Isolates of entomopathogenic nematode species confirmed across Africa. In this study, we did not consider any reports on only baiting of unknown nematodes, which can be an EPN species alone, mixed EPN species or 'EPN species + soil-borne bacteria-feeding nematode competitors' from EPN-killed insect pests in soils.[82] We have determined that there have been in-depth EPN surveys involving morpho-molecular analytical procedures that actually confirmed the identity and distribution of EPN species from the rich agro-ecological zones in only 11 African countries (Table 1 and Fig. 1). We grouped these species of *Steinernema* (Rhabditida: Tylenchina), *Heterorhabditis* (Rhabditida: Rhabditina) and *Oscheius* as 'observed in and outside of Africa' or 'observed only in Africa' (Table 1). Moreover, we provided an overview of EPN species across Africa and discussed some basic principles used globally to screen EPN species for use against fruit flies.

3.2.4.2. Current overview of entomopathogenic nematode species in Africa. Among the EPN species that are observed both in and outside of Africa (Table 1), *H. bacteriophora* is the most widely distributed throughout the African continent (Fig. 1). Furthermore, some EPN isolates from different soil ecosystems in some parts of Nigeria in West Africa have been examined under microscopes and suspected to be either *H. bacteriophora* alone or *H. bacteriophora* with *S. weiseri*, *H. indica* and *S. karii*.[93,94] It may be necessary to confirm these species through molecular analyses. Most EPN species observed only in Africa (Table 1 and Fig. 1) are not widely distributed across African countries except *S. yirgalemense* (from Ehtiopia, Kenya and South Africa) and *H. taysearae* (from Kenya, Benin, South Africa and Egypt) (Fig. 1). However, Půža *et al.*[89] indicate that *S. pwaniensis* from Tanzania forms a well-supported monophyletic clade with *S. karii* from Kenya and *S. ethiopiense* from Ethiopia (Fig. 1). The native EPN isolate *H. egyptii* from Egypt has been considered an 'EPN species *inquirenda*' (see footnote of Table 1), requiring further detailed description to support an earlier report.[85] Moreover, Dhakal *et al.*[96] recently confirmed

Table 1. EPN species isolated from different African soils characterized, identified or described, according to the confirmatory morpho-molecular methods

	Isolates of the species have been observed		
EPN species validly reported across Africa[*]	In and outside of Africa	Only in Africa	Source(s) of information [†]
Heterorhabditis bacteriophora (Rhabditomorpha: Heterorhabditidae)[‡] [§]	True		83–85
H. amazonensis	True		85
H. baujardi	True		85, 86
H. indica[‡] [§]	True		46, 85
H. sonorensis[¶]	True		85
H. zealandica[§]	True		86
Steinernema abbasi (Panagrolaimomorpha: Steinernematidae)	True		85
S. arenarium	True		85
S. carpocapsae[§]	True		85
S. feltiae[§]	True		83–85
S. glaseri	True		85
S. kushidai[§]	True		85
S. weiseri[‡]	True		85
H. egyptii[‖]		True	85
H. noenieputensis		True	85, 86
H. safricana		True	85
H. taysearae		True	46, 85, 86
Heterorhabditis sp. (in Morocco)		True	84
Heterorhabditis sp. RW14-K-Ca (in Rwanda)		True	87
S. beitlechemi		True	85
S. biddulphi		True	85
S. cameroonense		True	85
S. citrae		True	85
S. ethiopiense[**]		True	85
S. fabii		True	85
S. feltiae-group (in Morocco)		True	84
S. innovationi		True	85
S. jeffreyense		True	85, 88
S. karii[‡] [**]		True	85
S. khoisanae		True	85
S. litchii		True	85, 86
S. nguyeni		True	85
S. nyetense		True	85
S. pwaniensis[**]		True	85, 89
Steinernema sp. RW14-M-C2a-3 (in Rwanda)		True	87
S. tophus		True	85
S. yirgalemense		True	85, 86
Steinernema sp. (in Benin)		True	90
S. sacchari		True	85
Steinernema sp. RW14-M-C2b-1 (in Rwanda)		True	87
S. bertusi		True	85
S. kandii		True	91
Oscheius safricana (Rhabditomorpha: Rhabditidae) in *Insectivora* group		True	73
O. basothovii in *Insectivora* group		True	74
S. scapterisci[§]	True		92
Total (i.e. at least)	**14**	**31**	

Distribution of isolate(s) of each confirmed EPN species across Africa is in Fig. 1.

[*] Not all undescribed new EPN species confirmed by DNA sequence and/or correct molecular phylogenetic analyses are presented here.[84,86,92]

[†] Using the references here, details of the DNA sequence(s) of each EPN species can be accessed from the GenBank.

[‡] EPN isolates from Nigeria that have been examined under microscopes and suspected to be the 'EPN species' aforementioned here may require confirmatory molecular analyses.[93,94]

[§] These EPN species have been commercialized worldwide,[75] but the report of Dunn *et al.*[95] suggests that some native South African EPN isolates (Fig. 1) are also likely commercially available.

[¶] Dhakal *et al.*[96] recently confirmed synonymisation of *H. sonorensis* with *H. taysearae*.

[‖] Proposed to be a 'species *inquirenda*', requiring further description.[85]

[**] These EPN species from East African countries (Fig. 1) form a well-supported monophyletic clade.[89]

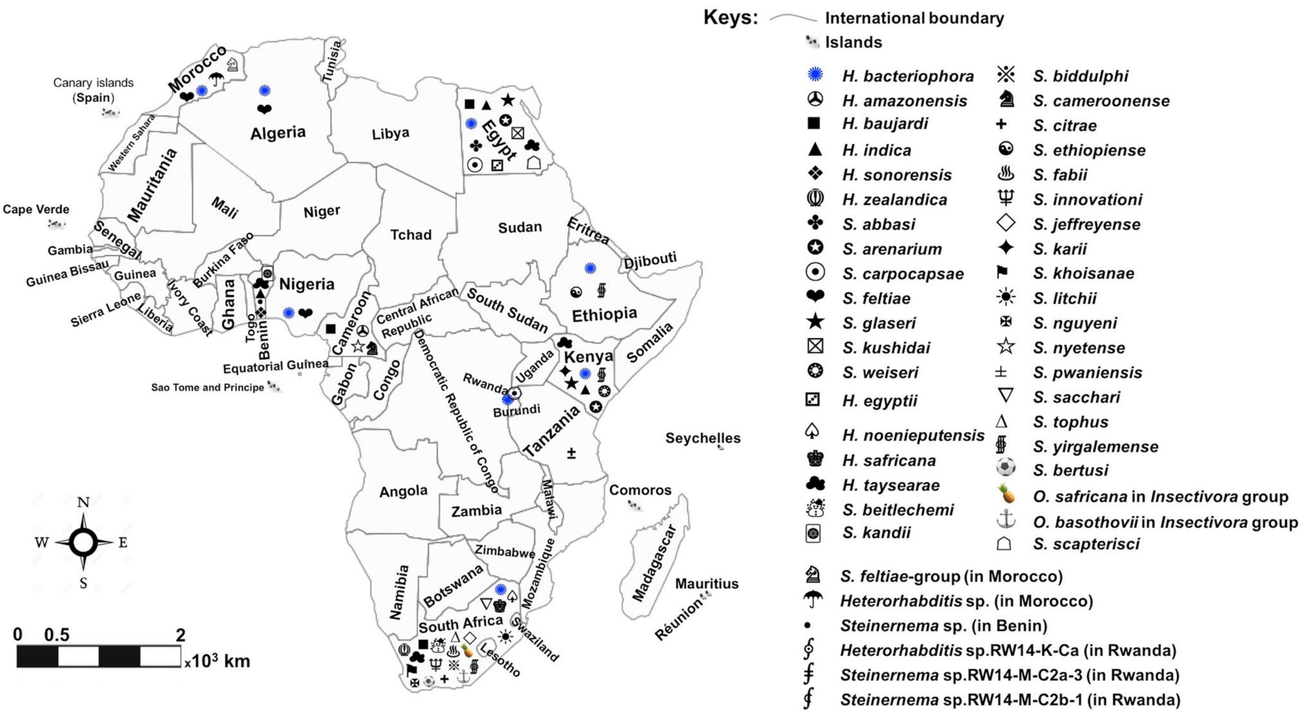

Figure 1. Distribution of isolates of *Heterorhabditis*, *Steinernema* and *Oscheius* species characterized, identified or described across Africa, according to the morphological and confirmatory molecular analytical methods. Details are presented in Table 1. Each pictograph, representing isolate(s) of each confirmed EPN species, on the African map is an approximation of the location (i.e. not the exact geographical coordinates of soil samples) where the EPN species was retrieved.

H. sonorensis [from the Mexican Sonora State, southern Benin (Fig. 1) and others] as a junior synonym of *H. taysearae* from African countries (Fig. 1). As a result, the total number of EPN species characterized and confirmed across Africa will reduce by one, although we could not present all undescribed new EPN species detected by DNA sequence analyses in Table 1. All the new EPN species, fully described or detected to be native only to Africa (Table 1 and Fig. 1), have been confirmed by analyses of ribosomal and/or mitochondrial DNA sequences deposited in the public repositories (e.g. the GenBank). The EPN species found only in a few African countries (Table 1) are diverse or phylogeographically different from those observed across Europe, the Americas, Asia, Oceania, the Pacific islands and other inhabited territories worldwide. Conceivably, extensive search or survey for beneficial soil-borne EPN species across other African countries (Fig. 1) may reveal a much greater EPN species diversity.

3.2.4.3. Principles of screening entomopathogenic nematode species against fruit fly pests. EPN species have exhibited a remarkable biological control potential against the subterranean life stages of numerous invasive insect pests, including tephritid fruit flies.[97–103] In trials, EPN species killed and successfully multiplied in larvae, pupae and adults of fruit flies.[46,99–101,104,105] Fortunately, isolates of some EPN species which are also present in Africa have already been commercialized worldwide (Tables 1 and 2). Moreover, several trials (in Table 2) have shown that commercially available or 'not yet commercialized' EPN species can outperform several other EPN species against any fruit-infesting tephritid fruit flies present across Africa. This evidence suggests that selection and use of EPN species in IPM plans against *B. dorsalis* may be less difficult than expected. However, any positive attributes (e.g. dessication tolerance and high efficacy) of EPNs which are native to Africa do not mean that non-native EPN species from other parts of the world cannot suppress *B. dorsalis* or produce comparable desired results. Usually, the effectiveness of an EPN species against an insect pest varies from field to field, and prediction has been improved using repeated laboratory and field trials.[71,99–101,116,121] In previous experiments, a number of EPN species which included exotic, native or both were randomly selected and tested against fruit flies.[46,47,98–112,117] Thus, selection of EPN species for screening against tephritid fruit flies in experimental trials has largely been guided by the availability of a considerable number of EPN species rather than principles of whether the selected EPN species are commercially available or are native. The most important research concerns have concentrated on the appropriateness of intended EPN screening methods to measure and compare bio-efficacies among several EPN species against the fruit fly pests.[105,122]

4 CONSIDERATIONS FOR FUTURE RESEARCH

The most studied practices for management of tephritid fruit flies worldwide have largely been the use of BCAs, when compared with SIT, application of insecticides and the approaches that manage behaviour of fruit flies.[32] The prevalence of *B. dorsalis* and lesser economically important fruit flies in orchards in SSA indicates that research needs to be done to ensure they are managed effectively and sustainably with a specific focus on biological control in fruit fly IPM programmes.[15] As a result, previous studies have largely resulted in the release of koinobiont parasitoids, application of EPFs and conservation of the predatory African weaver ants *O. longinoda* in orchards rather than research efforts to include EPN species in fruit fly IPM.[15] Even though studies on

Table 2. EPN species (commercially or not commercially available) identified in experimental trials across the world for management of economically important tephritid fruit fly pests present in Africa and other parts of the world

EPN species among the tested[*]	Status of EPN species in Africa	Place(s) where the species has been commercialized[†]	Target tephritid fruit fly pest(s) in Africa[‡] [§]	Reference(s)
H. bacteriophora	Native (Table 1, Fig. 1)	Europe, North America	*C. capitata*, *B. dorsalis*, *B. zonata*	47, 106–109
H. indica	Native (Table 1, Fig. 1)	North America	*C. capitata*, *B. dorsalis*	47, 110
H. taysearae	Native (Table 1, Fig. 1)	Not yet commercialized	*B. dorsalis*	46
S. feltiae	Native (Table 1, Fig. 1)	Europe, North America	*C. capitata*, *B. zonata*, *B. oleae*	103, 111–113
S. carpocapsae	Native (Table 1, Fig. 1)	Asia, Australia, Europe, North America, South America, Africa	*Dacus ciliatus* Loew (Diptera: Tephritidae), *C. capitata*, *B. zonata*, *B. dorsalis*	47, 109, 114, 115
H. noenieputensis	Native (Table 1, Fig. 1)	Not yet commercialized	*C. capitata*	98
H. baujardi	Native (Table 1, Fig. 1)	Not yet commercialized	*C. capitata*	116
H. zealandica	Native (Table 1, Fig. 1)	Australia, North America	*C. rosa*	106
H. asiaticum	Exotic	Not yet commercialized	*B. dorsalis*	47
S. riobrave	Non-native	North America	Pre-pupae of *C. capitata*	117

[*] Only the most efficacious EPN species are reported here.
[†] Details are in recent reports.[75,95]
[‡] *B. zonata* is commonly observed in the northern parts of Africa, whereas *B. oleae* is present in northern, eastern and southern parts of Africa including Réunion, Mauritius and Seychelles islands,[118, 119] but *D. ciliatus* is often observed in SSA.[120]
[§] In invaded parts of the world, including SSA, the most dangerous, damaging and invasive fruit fly has been the Oriental fruit fly, *B. dorsalis*.[21–26]

EPNs worldwide are almost a century old, including some recent investigations successfully carried out at the International Space Station (ISS-NASA),[123,124] exploration of EPN species is now slowly developing across Africa. Diverse EPN species have been isolated from soils and characterized in 11 African countries so far (Fig. 1). Also, studies have revealed that some native EPN species proved to be effective and promising against *B. dorsalis* and other fruit flies present across Africa (Table 2). However, future studies are required to examine the activities of the native and exotic EPN species in combination with other BCAs in *B. dorsalis* IPM programmes.

4.1 Entomopathogenic fungal species, predatory ants and parasitoids combined in fruit fly IPM in SSA

For the management of *B. dorsalis* and lesser economically important fruit flies in SSA, dry *M. anisopliae* spores and GF-120 spinosad bio-insecticides are applied to mango trees following release of parasitoids in orchards where *O. longinoda* colonies have established.[15,56] A decline in infestations of fruits has been observed.[56] In other studies, *O. longinoda* colonies in citrus and mango orchards were found to be effective against *B. dorsalis* and other economically important fruit flies.[26,30] Although *M. anisopliae* and *B. bassiana* have not had any significant side-effects on parasitoids,[15,33,56] their impacts on *O. longinoda*, which establishes its colonies on trees, have not been reported. Possibly, the entomopathogenic activities of fungal spores may interfere with predation of adult fruit flies by *O. longinoda* or may directly kill *O. longinoda* colonies on trees in orchards. These types of interactions need to be studied and documented to ensure sustainable conservation of the predatory formicid fauna in orchards.

4.2 Interspecific interactions between parasitoids and entomopathogenic nematode species

Several trials have shown that EPN species exert no significant side-effects on most parasitoids of insect pests.[125] For the case of the tephritid fruit fly, EPN treatments to *D. longicaudata* in *A. suspensa*-infested guava [*Psidium guajava* L. (Myrtales: Myrtaceae)] fruits on the soil surface did not prevent the emergence of the parasitoid wasps in some plots.[100–102] Other than that instance, however, potential effects of EPNs on progeny of parasitoids in other tephritid fruit flies remain unstudied. Perhaps assessments to determine any possible complementarity in the use of both parasitoids and EPN species against *B. dorsalis* in orchards across SSA may be useful for future decision-making. Parasitoids such as *P. cosyrae*, which cannot develop in the resistant larval-to-pupal stages of *B. dorsalis*, can be excluded from any studies unless its susceptible fruit fly hosts (e.g. *C. cosyra* and *C. capitata*) are the target fruit fly pests for the intended studies.[4–6]

4.3 Predatory ants and entomopathogenic nematode species in fruit fly IPM

Unlike *O. longinoda*, which will not interact with any EPN species in soils, the latter and *Solenopsis* spp. may have negative effects on each other in soils. *Solenopsis* spp. may prey on EPN-killed pupae of fruit flies to kill developing EPN-infective juveniles (IJs) in cadavers in soils. On the other hand, *Solenopsis* spp. may be susceptible to EPN species in soils even though previous reports have revealed that similar soil-borne predators of insect pests other than fruit flies were not vulnerable to many species of EPNs.[125] However, future research may be suggested with caution only to study these interspecific interactions towards conserving natural ecosystem services.

4.4 Entomopathogenic nematode species in combination with entomopathogenic fungal species in fruit fly IPM

In several previous trials, EPN species successfully infected and killed larvae, pupae and adults of tephritid fruit flies.[46,47,99,100,104,112,116,126] Similarly, EPF species have been effective in suppressing tephritid fruit flies.[9,33,55–57,127–129] However, combination of EPNs and EPFs in treatments to insect pests produced varying effects. Some treatments involving a mixture of EPN and EPF species against insect pests were mostly additive or synergistic in their effects,[130–133] whereas the effects of other EPN + EPF combinations against insect pests have been antagonistic.[134,135] The effects of *H. bacteriophora* in combination with either *M. anisopliae* or *B. bassiana* on the Diamondback moth [*Plutella xylostella* L. (Lepidoptera: Plutellidae)] or the Red palm weevil [*Rhynchophorus ferrugineus* Olivier (Coleoptera: Curculionidae)] were synergistic.[132,133] Also, application of *B. bassiana* in combination with *S. feltiae* and *S. carpocapsae* in species richness treatments to the Colorado potato beetle [*Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae)] caused synergistic effects.[131] In the case of fruit flies, the pupal stage has generally been resistant to treatments of single species of either EPN or EPF.[46,99,100,104,113,116,126,136] Nonetheless, application of *M. brunneum* or *Isaria javanica* (Friedrichs & Bally) Samson & Hywel-Jones (Hypocreales: Cordycipitaceae) in combination with virulent *S. riobrave* to the pupae of *Rhagoletis pomonella* Walsh (Diptera: Tephritidae) in sandy soil microcosms suppressed emergence of adult fruit flies better than their single species treatments did.[136] Similarly, application of *M. anisopliae* in combination with *H. bacteriophora* in treatments against the sugarcane borer [*Diatraea saccharalis* Fabricius (Lepidoptera: Crambidae)] was significantly more effective than treatments with *M. anisopliae* alone or *H. bacteriophora* alone achieved.[130] However, the combination of *M. anisopliae* and *H. bacteriophora* in the EPF + EPN treatments significantly decreased reproduction of IJs of *H. bacteriophora* in the co-infected *D. saccharalis*.[130] Moreover, Hummadi *et al.*[135] observed that toxic volatile organic compounds (i.e. 3-octanone and 1-octen-3-ol) of *M. brunneum* killed insects and IJs of EPN species but could not inhibit the endosymbiotic bacterium *P. kayaii* obtained from *H. bacteriophora* isolate. Consequently, the volatiles of *M. brunneum* suppressed penetration efficacies and reproductive capabilities of *S. feltiae*, *H. bacteriophora* and *S. carpocapsae*.[135] Thus, considering the varying effects of the mixture of EPN and EPF species on both insect pests and transmission of EPN species, studies are required to support future decisions on utilizing combinations of EPN and EPF for *B. dorsalis* management.

4.5 Effects of multiple entomopathogenic nematode species or mixed entomopathogenic fungi on fruit flies and parasitoids

Interspecific competition between multiple EPN species has often been antagonistic in their effects. Different EPN species are often involved in 'lethal fights' for resources or for defense.[137–140] EPN species use a multitude of toxins produced by their symbiotic bacterial strains to antagonise other EPN species inside EPN-killed hosts.[100,140–143] In effect, the presence of one EPN species in treatments often suppresses the reproductive capabilities of other EPN species in hosts following mixed infection.[100,137–142] Moreover, different EPN species often show different foraging tactics used to attack insect pests in soils.[144,145] As a result, combinations of different EPN species in treatments to insect pests often produce varying effects, i.e. synergism, additivity or antagonism.[99,131,137,146–148] In the case of the Caribbean fruit fly (Caribfly or *A. suspensa*) with the parasitoid *D. longicaudata* present in infested guava fruits, treatments of multiple EPN species were assessed in repeated laboratory and field trials.[100,101] The larval mortalities observed did not vary with increasing number of EPN species combined in treatments under laboratory conditions. However, similar treatments to Caribfly puparia in soil microcosms ostensibly caused fluctuating effects.[100,101] Consequently, the overall effects of mixed EPN species against Caribfly were antagonistic under field conditions.[100] Conversely, the emergence of *D. longicaudata* wasps from Caribfly-infested guavas on the ground did not vary significantly with the number of EPN species combined in treatments.[100,101] Varied effects of using mixed EPF species in orchards where parasitoids have deliberately been released against *B. dorsalis* have not been reported. In our view, these studies are crucial for identifying efficacious tactics that can be included in IPM programmes for *B. dorsalis*.

4.6 Manipulation of the orchard environment for biological control of fruit flies

The 'push-pull' techniques involving the use of 'edible coconut [*Cocos nucifera* L. (Arecaceae)] oil *vs* artificial fruits', 'protein bait sprays *vs* oil emulsion sprays' or 'pheromone sprays *vs* GF120™ sprays' modified field environments against tephritid fruit flies.[149–151] In effect, uninfested fruits were recovered. In a 'push' approach spraying of kaolin and limestone suspensions in orchards, or bagging fruits on trees significantly reduces fruit infestation by fruit flies.[152–154] These 'push-pull' strategies largely involve the use of nonlethal materials to conserve parasitoids and the weaver ant species (*Oecophylla* spp.) against fruit flies in fields.[149–155] On the other hand, zero tillage, including application of weedicides, will conserve EPNs in soils because EPNs are not generally affected by pesticides, except some nematicides.[156] Other 'push-pull' and orchard manipulation approaches suggested by Aluja *et al.*[157] can also be investigated to attract and conserve BCAs against *B. dorsalis* and other fruit flies in orchards across SSA.

4.7 Area-wide biocontrol strategies in fruit fly IPM plans across SSA

Some BCAs will control *B. dorsalis* on hosts in orchards and in the wild, whereas others will be economically effective when released in fruit fly-infested orchards. For example, predatory weaver ants (*Oecophylla* spp.) will prey on adult fruit flies in canopies of trees in orchards and those in the wild.[26,30,37] Similarly, parasitoid wasps will effectively parasitize fruit flies that infest fruits in orchards and other hosts in the wild.[43] Therefore, *O. longinoda*, *O. smaragdina* and parasitoids can be investigated to control *B. dorsalis* and other fruit flies inside and outside of orchards across SSA. However, an EPN augmentation method that targets only fruit fly-infested fruits fallen on the ground in orchards is effective and more economical to suppress emergence of adult fruit flies from soil.[102] This is primarily because EPNs are usually applied in fields where IJs can effectively perceive, locate and infect arthropod pests in soils.[70–72,75,80,103,112] Thus, screening different EPN species under different field conditions across SSA will provide better information for decision-making in terms of selecting the most efficacious EPN species against *B. dorsalis* in different ecozones of SSA.[82,100,127] Although EPF or EPN + EPF treatments to fruit-damaging flies in fruits on the soil surface have been efficient,[56,130,136] adding EPFs to multiple powerful bait-traps stationed inside and outside of orchards across SSA may effectively suppress *B. dorsalis*.[29,57,158,159]

Regular area-wide releases of diverse koinobiont and idiobiont parasitoids across SSA will be effective against *B. dorsalis* and lesser economically important fruit flies.[160] However, previous studies involving mass production and augmentative releases of exotic parasitoid wasps across SSA were funded by collaborations between organisations, institutions and agencies (third author's personal observations). In our opinion, sharing of responsibilities among stakeholders will be needed for research into effective use of parasitoids, predatory ants, EPNs, EPFs and manipulation of the orchard environment in combination with powerful adult baiting-and-annihilation stations, field sanitation practices and use of bio-insecticides against *B. dorsalis* and lesser economically important fruit flies across SSA.

Bagging fruits on trees reduces exposure of fruits to fruit flies and pathogens [e.g. anthracnose disease-causing *Colletotrichum gloeosporioides* Penzig & Saccardo (Glomerellales: Glomerellaceae)].[153,154,161] The latter is a destructive fungal pathogen that reduces fruit set, increases premature fruit drop and/or causes blemish to quality of fruits in many countries across SSA (authors' personal observations). In this case, research and education will change fruit growers' perception to bag fruits on trees so that the practice can conserve predatory weaver ants (*O. longinoda* with *O. smaragdina*) against *B. dorsalis* across SSA.

5 DISCUSSION

In the case of *B. dorsalis* and less abundant economically important fruit fly pests (i.e. *Ceratitis* spp.) across SSA, research has revealed that a single or multiple BCA approach involving parasitoids, EPF species and a local ant species (*O. longinoda*) in fruit fly IPM can significantly reduce infestation of fruit in orchards across SSA.[15,26,30] However, the persistence of *B. dorsalis* across SSA demands a need for identification of additional BCAs that can be included in fruit fly IPM to maximize control of these pests in orchards.

Although not yet applied in fruit fly IPM, the use of EPN species in combination with parasitoids, EPFs and *O. longinoda* may effectively improve control of fruit flies. As already outlined, however, it appears only a few studies have examined the effects of interspecific interactions between two or more groups of BCAs for management of tephritid fruit flies. Generally, multiple groups of BCAs have proved to be either complementary or antagonistic in their effects in the management of insect pests, which include tephritid fruit flies.[15,130–134,136] Moreover, the presence of some BCAs can threaten survival, abundance and/or prevalence of other BCAs in IPM.[15,130,135] In this regard, additional studies will be required before best management practice guidelines to focus on combining parasitoids, EPFs, predators (*O. longinoda*, *O. smaragdina* and others) and EPN species in an effort to achieve an environmentally friendly IPM programme for fruit flies while ensuring they are in line with the UN-SDGs.[20,162]

Considering the outcomes of laboratory and field trials,[156,163–166] the use of insecticides (WHO class I or II) in orchards will not affect the activities of soil-borne EPN species against the fruit-to-soil stages of fruit flies in orchards.[85,121] Moreover, adding EPFs to pheromone lure/bait traps sited on fruit trees for fruit fly adult annihilation in orchards will not interfere with EPN augmentation to soil to kill fruit-to-soil stages of fruit flies in the field. Conceivably, application of EPN species in orchards will complement insecticide sprays, the use of EPFs (added to lure/bait-traps on trees) and male annihilation methods in orchards.[121,156,163–166]

Several biotic and abiotic environmental factors can interfere with the host-searching and reproductive capabilities of virulent EPN species to *B. dorsalis* in the field.[75,78,82,167–171] Nonetheless, repeated assessments of field efficacies of diverse EPN species against *B. dorsalis* should result in better decisions in selecting the more promising EPN isolate(s) that will perform better in the field. Furthermore, future studies will be required to measure and compare the broad-spectrum virulence of EPN species (whether exotic or native) against *B. dorsalis* and many lesser economically important fruit flies often observed in orchards within SSA. Until research examines the underlining EPN augmentation principles to provide the necessary cost management guidelines, any EPN species selected cannot be included in any IPM plans against *B. dorsalis* and lesser economically important fruit flies in orchards.[102,126,172] Heve *et al.*[102] observed that a less costly EPN augmentation method must be identified to reduce the costs of including EPN species in fruit fly IPM programmes because combining many fruit fly management approaches increases the cost of producing fruits. Heve *et al.*[102] also presented a cost–benefit analysis that revealed a low-cost EPN spot-treatment of guava fruits in orchards within south Florida, USA. The method showed potential in significantly reducing and amortizing any incremental (or additional) costs after including *H. bacteriophora* in Carifly IPM. As a result, guava production in south Florida appeared to be insensitive to the negligible cost of the spot-treatment approach when compared to the field-wide broadcasting method.[102] Similar to the case of *B. dorsalis* and the lesser economically important fruit flies in orchards across SSA, mango production may be sensitive to high 'additional costs' if the field-wide EPN broadcasting method is used to apply any EPN species in fruit fly IPM. Possibly, the cost-effective EPN spot-treatment method suggested by Heve *et al.*[102] could be examined in terms of inclusion of EPN(s) in the current *B. dorsalis* IPM models.

EPN conservation practices following EPN augmentation may suppress fruit flies in the field to some extent, similar to the manner in which conservation of the native predatory weaver ant (*O. longinoda*) with other predatory ant species does.[15,30] However, future studies will be required to examine whether quality control policies to regulate quality requirements for commercially mass-produced EPN isolates are more important than regulatory import laws against environmentally friendly exotic EPN species.[173]

6 CONCLUSIONS

The release of multiple parasitoids and application of EPF species in combination with conservation of the predatory African weaver ant *O. longinoda* in IPM plans against *B. dorsalis* and lesser economically important fruit flies apparently caused a decline in infestation of fruits in SSA. However, prevalence of invasive *B. dorsalis* across SSA still demands research into the use of biocontrol approaches in IPM plans. Interspecific interactions between BCAs against fruit flies have been synergistic, additive or antagonistic in their effects. Moreover, the presence of some BCAs reduces the survival and reproductive potential of other BCAs in treatments where they are mixed together against insect pests. Therefore, considerations towards achieving all-inclusive biocontrol strategies in fruit fly IPM plans require future studies into the effects of combining parasitoids, EPFs and EPNs in addition to conservation of the predatory ants such as *O. longinoda* and *O. smaragdina* among others against *B. dorsalis*, the commonest fruit fly species across SSA.

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