

## Review

## Global scientific progress and shortfalls in biological control of the fall armyworm *Spodoptera frugiperda*

Kris A.G. Wyckhuys<sup>a,b,c,\*</sup>, Komivi S. Akutse<sup>d,e</sup>, Divina M. Amalin<sup>f</sup>, Salah-Eddin Araj<sup>g</sup>, Gloria Barrera<sup>h</sup>, Marie Joy B. Beltran<sup>i</sup>, Ibtissem Ben Fekih<sup>j</sup>, Paul-André Calatayud<sup>d,k</sup>, Lizette Cicero<sup>l</sup>, Marcellin C. Cokola<sup>j</sup>, Yelitza C. Colmenarez<sup>m</sup>, Kenza Dessauvages<sup>j</sup>, Thomas Dubois<sup>d</sup>, Léna Durocher-Granger<sup>n</sup>, Carlos Espinel<sup>h</sup>, Patrick Fallet<sup>o</sup>, José L. Fernández-Triana<sup>p</sup>, Frederic Francis<sup>j</sup>, Juliana Gómez<sup>h</sup>, Khalid Haddi<sup>q</sup>, Rhett D. Harrison<sup>r</sup>, Muhammad Haseeb<sup>s</sup>, Natasha S.A. Iwanicki<sup>t</sup>, Lara R. Jaber<sup>g</sup>, Fathiya M. Khamis<sup>d</sup>, Jesusa C. Legaspi<sup>u</sup>, Refugio J. Lomeli-Flores<sup>v</sup>, Rogerio B. Lopes<sup>w</sup>, Baoqian Lyu<sup>x</sup>, James Montoya-Lerma<sup>y</sup>, Melissa P. Montecalvo<sup>i</sup>, Andrew Polaszek<sup>z</sup>, Tung D. Nguyen<sup>aa</sup>, Ihsan Nurkomar<sup>ab</sup>, James E. O'Hara<sup>p</sup>, Jermaine D. Perier<sup>ac</sup>, Ricardo Ramírez-Romero<sup>ad</sup>, Francisco J. Sánchez-García<sup>ae</sup>, Ann M. Robinson-Baker<sup>s</sup>, Luis C. Silveira<sup>q</sup>, Larisner Simeon<sup>s</sup>, Leellen F. Solter<sup>af</sup>, Oscar F. Santos-Amaya<sup>ag</sup>, Elijah J. Talamas<sup>ah</sup>, Wagner de Souza Tavares<sup>ai</sup>, Rogelio Trabanino<sup>aj</sup>, Ted C.J. Turlings<sup>o</sup>, Fernando H. Valicente<sup>ak</sup>, Carlos Vásquez<sup>al</sup>, Zhenying Wang<sup>b</sup>, Ana P.G.S. Wengrat<sup>t</sup>, Lian-Sheng Zang<sup>am</sup>, Wei Zhang<sup>am</sup>, Kennedy J. Zimba<sup>an</sup>, Kongming Wu<sup>b</sup>, Maged Elkahky<sup>ao</sup>, Buyung A.R. Hadi<sup>ao,ap,1</sup>

<sup>a</sup> Chrysalis Consulting, Danang, Viet Nam

<sup>b</sup> State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China

<sup>c</sup> School of Biological Sciences, University of Queensland, Saint Lucia, Australia

<sup>d</sup> International Centre of Insect Physiology and Ecology (icipe), Nairobi, Kenya

<sup>e</sup> Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa

<sup>f</sup> De La Salle University, Taft Avenue, Manila, Philippines

<sup>g</sup> School of Agriculture, The University of Jordan, Amman, Jordan

<sup>h</sup> Centro de Investigación Tibaitatá, Corporación Colombiana de Investigación Agropecuaria - Agrosavia, Mosquera, Cundinamarca, Colombia

<sup>i</sup> National Crop Protection Center, University of the Philippines Los Baños, Laguna, Philippines

<sup>j</sup> Functional and Evolutionary Entomology, Gembloux Agro-Bio Tech, University of Liege, Gembloux, Belgium

<sup>k</sup> Institut Diversité Ecologie et Evolution du Vivant (IDEEV), Université Paris-Saclay, CNRS, IRD, UMR Evolution, Génomes, Comportement et Ecologie, Gif-sur-Yvette, France

<sup>l</sup> Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), Yucatán, México

<sup>m</sup> CAB International Latin America, FEPAP-UNESP-FCA. Fazenda Exp. Lageado. Botucatu, São Paulo, Brazil

<sup>n</sup> CAB International, Kalundu, Lusaka, Zambia

<sup>o</sup> Laboratory for Fundamental and Applied Research in Chemical Ecology (FARCE), Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland

<sup>p</sup> Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada

<sup>q</sup> Laboratory of Molecular Entomology and Ecotoxicology, Department of Entomology, Universidade Federal de Lavras, Brazil

<sup>r</sup> CIFOR-ICRAF, 12-14 St Eugene Office Park, Lake Road, Lusaka, Zambia

<sup>s</sup> Center for Biological Control, Florida A&M University, Tallahassee, FL, USA

<sup>t</sup> Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, São Paulo, Brazil

<sup>u</sup> United States Department of Agriculture-Agricultural Research Service (USDA-ARS), Center for Medical, Agricultural and Medical Entomology, Tallahassee, FL, USA

<sup>v</sup> Posgrado en Fitosanidad, Colegio de Postgraduados, Montecillo, Texcoco, México

<sup>w</sup> EMBRAPA Genetic Resources and Biotechnology, Brasília, Federal District, Brazil

<sup>x</sup> China Academy of Tropical Agricultural Sciences (CATAS), Haikou, China

<sup>y</sup> Department of Biology, Universidad del Valle, Cali, Colombia

<sup>z</sup> Natural History Museum, Cromwell Road, London, Great Britain

<sup>aa</sup> Vietnam National University of Agriculture, Hanoi, Viet Nam

\* Corresponding author.

E-mail address: [kagwyckhuys@gmail.com](mailto:kagwyckhuys@gmail.com) (K.A.G. Wyckhuys).

<sup>ab</sup> Universitas Muhammadiyah Yogyakarta, Indonesia<sup>ac</sup> University of Georgia, Tifton, GA, USA<sup>ad</sup> Biological Control Laboratory (LabCB-AIFEN), University of Guadalajara, Guadalajara, Mexico<sup>ae</sup> Instituto Murciano de Investigación y Desarrollo Agrario y Alimentario (IMIDA), Murcia, Spain<sup>af</sup> Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, IL, USA<sup>ag</sup> Universidad of Pamplona, Pamplona, Colombia<sup>ah</sup> Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL, USA<sup>ai</sup> Riau Andalan Pulp and Paper (RAPP), Pangkalan Kerinci, Riau, Sumatra, Indonesia<sup>aj</sup> Zamorano, Apartado Postal 93, Tegucigalpa, Honduras<sup>ak</sup> EMBRAPA Maize and Sorghum Research Station, Sete Lagoas, Minas Gerais, Brazil<sup>al</sup> Faculty of Agronomical Sciences, Technical University of Ambato, Campus Querochaca, Province of Tungurahua, Cevallos, Ecuador<sup>am</sup> National Key Laboratory of Green Pesticide, Key Laboratory of Green Pesticide and Agricultural Bioengineering, Guizhou University, Guiyang, China<sup>an</sup> School of Agricultural Sciences, University of Zambia, Lusaka, Zambia<sup>ao</sup> Food and Agriculture Organization (FAO), Rome, Italy<sup>ap</sup> International Fund for Agricultural Development (IFAD), Bangkok, Thailand

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## HIGHLIGHTS

- In-depth information is absent for most invertebrate or microbial natural enemies.
  - Research progress is hampered by organismal, geographic and methodological biases.
  - ‘Snap-shot’ natural enemy censuses dominate over robust mortality assessments.
  - Egg and pupal predation, nocturnal taxa and conservation tactics are overlooked.
  - Standardized methodologies and metrics, and networked field trials are needed.
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## ABSTRACT

Since 2016, the fall armyworm (FAW) *Spodoptera frugiperda* has spread over extensive areas of the tropics and subtropics, imperiling food security, economic progress and the livelihoods of millions of cereal farmers. Although FAW has received long-standing scientific attention in its home range in the Americas, chemical inputs feature prominently in its mitigation and biological control uptake is globally lagging. Here, building upon a quantitative review of the global literature, we methodically dissect FAW biological control science. Of the known entomopathogens (46), parasitoids (304) and predators (215) of FAW, approx. 40% have been subject to laboratory- or field-level scrutiny. Laboratory-level performance has partially been assessed for 14–18% of the above invertebrate taxa. Yet, organismal, geographic, methodological and thematic biases hamper efforts to relate in-field biodiversity to actual ecosystem service delivery. Often, single-guild ‘snapshot’ surveys are preferred over comprehensive bio-inventories or population dynamics appraisals, trophic interactions are wrongly inferred from co-occurrence, standard pest infestation metrics are lacking and natural enemy censuses are performed arbitrarily. Diurnal biota receive inordinate attention, while egg and pupal predation - the main biotic sources of mortality - are routinely overlooked. Multiple microbial and invertebrate biota are investigated with a view towards mass-rearing and augmentative release, but the basis for agent selection is often unclear. Lastly, conservation biological control receives marginal attention and cross-disciplinary engagement with the agroecology domain is lagging. We lay out several steps, including standardized methodologies, smart use of biodemographic toolkits, networked field trials and a fortification of its ecological underpinnings, to sharpen the science of (FAW) biological control and urge further momentum in its global implementation.

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## 1. Introduction

The fall armyworm (FAW) *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is a highly mobile, migratory herbivorous moth native to the Americas (Luginbill, 1928; Andrews, 1980; Kenis et al., 2022), where it feeds on a range of plants, e.g., maize, rice and sorghum. FAW was first detected in West Africa in 2016, subsequently spread across the African continent and invaded extensive areas of the Middle East, Asia and the Pacific. Over a span of 6–7 years, *S. frugiperda* has reached more than 80 countries and poses an immediate threat to southern Europe’s farming sector. During the initial stages of its invasion, FAW reportedly inflicted yield losses of \$9.4 billion per year in Africa alone (Eschen et al., 2021). Aside from placing a major drag on national economies, the pest has impacted rural livelihoods in some of the world’s most underprivileged and food-insecure settings (Tambo et al., 2021). Further, its voracious feeding and highly visible foliar

damage have triggered the over-use of chemical pesticides, including highly hazardous and banned compounds (Tambo et al., 2020; Yang et al., 2021). For instance, in China’s Yunnan province, pesticide application rates have risen three-fold since the FAW invasion (Yang et al., 2021). In disregard of the founding principles of integrated pest management (IPM), insecticidal seed treatment has taken root as a ‘first line of defense’ against FAW in multiple countries. Though FAW sporadically acts as a cutworm, prophylactic seed treatment appears unwarranted to avert the minor (if not non-existent) yield implications of early-season defoliation (Tooker et al., 2017; Hruska, 2019; Blanco et al., 2022; Chisonga et al., 2023). In the meantime, its extensive usage generates environmental, socio-economic and health impacts (Abro et al., 2021) and drives a steady dismantlement of IPM programs in several developing countries (Thorburn, 2015; Shattuck et al., 2023).

Because many FAW host crops are staple foods, reducing losses from pests in an economically sound and environmentally responsible manner can ensure global food security, uphold human wellbeing and preserve nature. In this regard, a conscientious prioritization of agro-ecological and biodiversity based measures can bolster ecosystem resilience and reduce any need for chemical intervention (Deguine et al., 2023). Biodiversity is central to the sound functioning of natural and

<sup>1</sup> The views and opinions expressed in this paper are those of the authors and should not be attributed to IFAD, its Member States, or their representatives to its Executive Board.

man-made ecosystems alike. As the central pivot of biological pest control in agroecosystems, diverse communities of natural enemies keep pests at bay (Vidal and Murphy, 2018) and ensure a continuous flow of ecosystem benefits to human society (Dainese et al., 2019; Eisenhauer et al., 2019). Maize fields in temperate areas sustain complex ecological networks and harbor up to 600 arthropod species, many of which prey upon *S. frugiperda* (Pimentel et al., 1992; Lundgren and Fausti, 2015; Hu et al., 2023). Such numbers may be substantially higher in the tropics. In the presence of natural enemies, pesticide use does not provide any advantage for long-term pest management (Janssen and Van Rijn, 2021). Opportunities to harness this farm-level biodiversity appear limitless: different strategies are available to conserve resident natural enemies, augment their field populations with laboratory-reared individuals, or judiciously translocate biological control agents (BCAs) from the pest's region of origin (Bale et al., 2008; Van Lenteren et al., 2018). Their exact identity, community composition and overall effectiveness varies with farming context and geographical region, and exhibits dynamic changes over space and time. So far, FAW-associated BCAs have been covered in species inventories of varying taxonomic or geographic coverage and in qualitative reviews (Molina-Ochoa et al., 2003; Bahena et al., 2015; Ahissou et al., 2021; Abbas et al., 2022; Kenis et al., 2022). Yet, a globe-spanning quantitative review has not been performed.

Insect-killing viruses, bacteria, fungi, nematodes and microsporidia contribute to the natural regulation of herbivore populations and act as desirable alternatives to chemical pesticides (Lacey et al., 2015). Several entomopathogen taxa have proven highly effective against *S. frugiperda* under laboratory, screenhouse and field conditions. Some of these are commercially available as biopesticides (Bateman et al., 2018; Guo et al., 2020; Kenis et al., 2022) or cause natural epizootics (Guo et al., 2020). Furthermore, a diverse complex of egg, larval and pupal parasitoids is associated with *S. frugiperda* in its native range, especially in Latin America (Molina-Ochoa et al., 2003; Vírgen et al., 2013; Hruska, 2019), but also in southern parts of the USA (Pair et al., 1986; Meagher et al., 2016). In its invasive range, locally-occurring parasitoids have switched from local lepidopteran hosts to attack *S. frugiperda* (Fiaboe et al., 2017; Abang et al., 2021). In addition, researchers have listed a broad set of invertebrate predators which often inflict high levels of mortality (Pair and Gross, 1989; Varella et al., 2015; Wyckhuys et al., 2023b). Given that all the above natural enemy guilds contribute to agroecosystem functioning and societal wellbeing, they deserve far greater consideration and scientific study (Eisenhauer et al., 2019; Basset and Lamarre, 2019).

Through bold policy initiatives in Europe, China and the USA or the Kunming-Montreal Global Biodiversity Framework, biological control currently finds itself in the global limelight (Schebesta and Candel, 2020; Wang et al., 2022). Its scientific base has also been steadily firmed up in both affluent and developing nations (Wyckhuys et al., 2022). Yet, the global proliferation of chemical control underscores how biological control science struggles to translate into practice. As its farm-level uptake encounters various socio-technical obstacles (Lacey et al., 2015; Barratt et al., 2018; Van Lenteren et al., 2018), the scientific underpinnings and core knowledge domains of biological control need to be carefully reconsidered. To date, no critical, in-depth analysis of the biological control scientific enterprise has been performed for any particular pest or crop. Also, BCAs are routinely studied through monodisciplinary lenses and with restricted views on particular guilds or application modes (Brodeur et al., 2018), which puts a drag on biological control science and practice. Instead, an integrated, cross-disciplinary assessment of BCA abundance, diversity, ecology, and performance can clarify their contribution to sustainable crop protection. Such knowledge is critical to guide further scientific inquiry and investment.

Here, we present a quantitative review of biological control science concerning *S. frugiperda* in maize crops throughout its native and invasive range. Following a near-exhaustive screening of published

laboratory and field studies on microbial and invertebrate FAW biological control, we log the nature of scientific inquiry and prevailing organismal foci, and offer an inventory of potential natural enemies. We hereby consider FAW entomopathogens, their endotoxins or crystal proteins, and invertebrates. Because of a relative scarcity of research effort, vertebrate predators are excluded. Next, for each natural enemy guild, we rank biota in terms of research intensity, laboratory performance and field-level abundance or prevalence. For a subset of BCAs, we further relate species-level impact under natural or augmentative biological control arrangements to laboratory-derived performance metrics. Our work offers an unprecedented global, integrated view on FAW biological control science. This can help to steer future research and policy endeavors towards more desirable social-environmental outcomes.

## 2. Methodological approach

We used a systematic literature review to collect laboratory- and field-derived data on invertebrate and microbial biological control of FAW across its native and invaded range. Specifically, a stepwise process was followed for literature screening, data extraction and categorization, and statistical analysis (Suppl. Table 1).

First, we used Web of Science (WoS) to build an initial literature corpus. Literature searches were defined to access all publications that addressed FAW biological control and that covered entomopathogens, parasitoids or invertebrate predators. Topic searches were conducted using three different WoS search strings. For entomopathogens, the following search string was used: ALL=((*Spodoptera frugiperda*) OR (fall armyworm)) AND ((biological control) OR (biocontrol) OR (IPM) OR (management) OR (biopestic\*) OR (pest)) AND ((entomopathog\*) OR (virus\*) OR (fung\*) OR (nematod\*) OR (bacteri\*) OR (microbia\*)). Meanwhile, we adopted the following strings for parasitoids and predators respectively: TS=((*Spodoptera frugiperda*) OR (fall armyworm)) AND ((biological control) OR (biocontrol) OR (IPM) OR (management) OR (pest)) AND ((parasitoid) OR (parasitic) OR (parasit\*)); and TS=((*Spodoptera frugiperda*) OR (fall armyworm)) AND ((biological control) OR (biocontrol) OR (IPM) OR (management) OR (pest)) AND ((predator) OR (prey\*) OR (predat\*)). In the above process, the WoS Core Collection database (1900–2022) was queried using a University of Queensland staff subscription on March 3, 2023. All publications, from across the global distributional range of FAW, were taken into consideration. The initial literature corpus thus consisted of 710, 320 and 215 publications for entomopathogens, parasitoids and predators respectively. We further expanded the search by adding relevant citations in the original publications.

For each organismal guild (entomopathogens, parasitoids, predators), publications within the initial literature corpus were categorized as field or laboratory studies and individually screened for relevance. Publications were only retained when reporting one or more performance metrics (laboratory studies) or plant-level abundance (field studies) for the biological control organisms subject to study. For field studies, only entomopathogens isolated from FAW larvae or eggs and canopy-foraging arthropods on maize were taken into consideration, omitting publications that surveyed predators using soil-deployed baits (e.g., ants), pitfall traps (e.g., ground beetles) or trap nests (e.g., social wasps). Publications that provided detailed abundance or prevalence data for foliage-level biological control on other FAW host crops e.g., sorghum, rice or cotton were not considered. Lastly, any duplicate publications were removed. This process yielded a smaller final literature corpus i.e., a respective total of 127, 86 and 64 publications addressing laboratory studies and 35, 102 and 26 publications covering field studies of the natural enemies, which were then subject to further data extraction and statistical analysis (Suppl. Fig. 1).

Following an in-depth screening of each publication, a number of observations were extracted. The scientific name of the investigated biological control agents (BCA) was recorded at the finest taxonomic

resolution. As BCAs were regularly listed at the genus level, especially for field studies, we refer to them as ‘taxa’. For field studies, we recorded the study country, maize variety and field characteristics such as field or plot size, presence and type of inter- or cover crops, tillage regime, chemical or organic fertilizer usage, presence of ecological infrastructures e.g., flower strips (Landis et al., 2000) and extent and type of pesticide use. Further, we logged whether the published work pertained to natural control by resident biota or to any of the three prevailing forms of biological control i.e., conservation, augmentation or classical biological control (Bale et al., 2008). Next, we logged canopy-level occurrence and prevalence (%; entomopathogens), absolute per-plant abundance (predators) or parasitism rate (%; parasitoids) as recorded by the study authors during one or more maize phenological stages. Predator counts were converted to a per plant basis, assuming optimum planting densities of seven maize plants per m<sup>2</sup>. Further, we recorded the associated FAW infestation level either as prevalence (%) or plant-level abundance of particular developmental stages i.e., eggs or larvae. Lastly, when pathogen-induced FAW mortality was not separately recorded but successive recordings were made of FAW larval infestation level, we inferred larval mortality by calculating the % reduction in infestation pressure over time. Findings from field studies were interpreted separately for the FAW native range and invasive ranges. For laboratory studies, we consistently recorded the exposed FAW developmental stage and experimental conditions. For entomopathogens, data were extracted regarding the source of isolation (soil, plant or insect cadaver), isolate feature (toxin, conidia or formulation), isolate status (lab-cultured, endemic or introduced), type of bio-assay (contact, immersion or indirect), and three distinct performance metrics: mortality (%) of the exposed FAW stage, lethal concentration (LC50) and lethal time (LT50). Per study and exposed FAW developmental stage, we exclusively listed the best metrics e.g., highest mortality % or shortest LT50, across pathogen strains, formulation types, delivery modes or other experimental conditions. Irrespective of its eventual shortcomings, we thus solely considered best-case scenarios. For parasitoids, we recorded any of the following seven performance metrics: functional response type (Holling, 1966), attack rate (lifetime or daily number of parasitized hosts or parasitism %), sex ratio (i.e., female/male ratio), longevity, fecundity, handling time and emergence

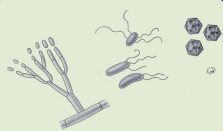


rate. For predators, we logged any of eight performance metrics: functional response type, fecundity, attack rate (i.e., lifetime, stage-specific or daily number of prey items consumed), handling time, adult longevity, development time, emergence rate and sex ratio. Because a given study often compared BCA performance for different life stages (e.g., adult, immature) between one or more FAW larval stages, or under varying climatic conditions, we exclusively listed the best performance metrics, e.g., highest attack rate or shortest development time across BCA developmental stages and experimental conditions. As above, we thus only addressed best-case scenarios. Given that one single field or laboratory study often covered multiple microbial or arthropod BCA taxa, research effort and BCA performance was analyzed per taxon-level record rather than per scientific study.

### 3. Entomopathogens

#### 3.1. Global patterns

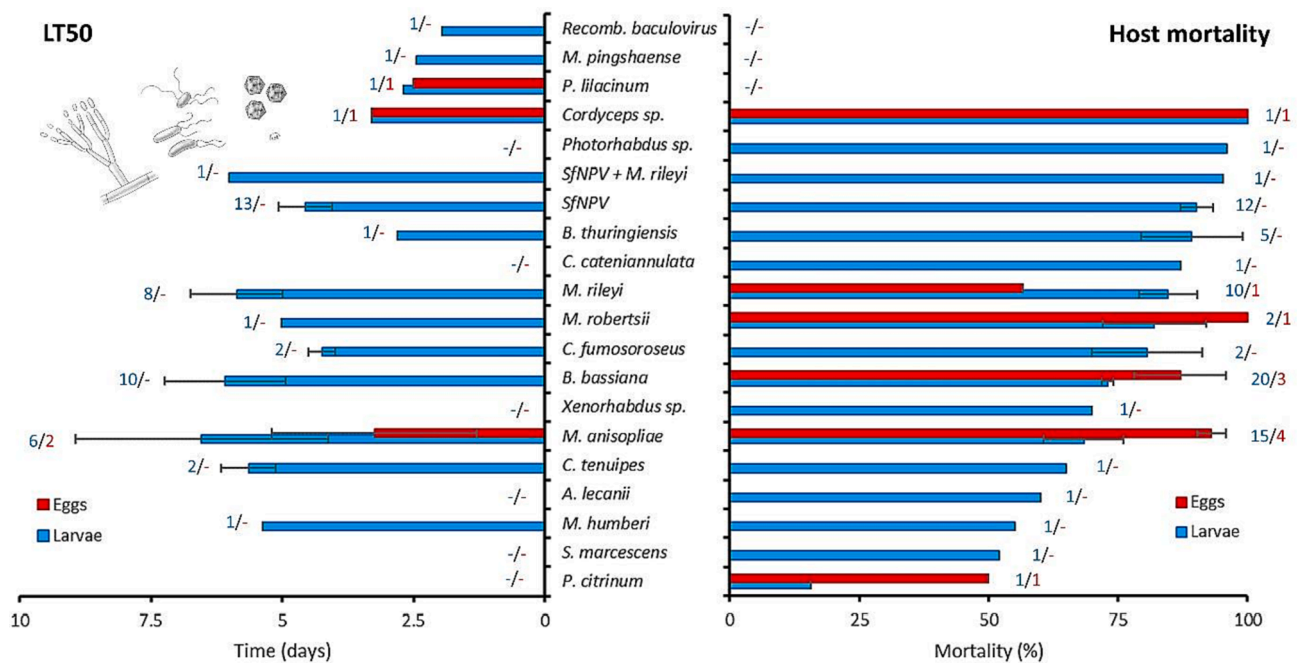
Field or laboratory based performance was determined for 34 FAW entomopathogen species or genera, ~72 % of known taxa associated with this herbivore globally (Figs. 1, 2; Suppl. Table 1). Specifically, 33 of these taxa were addressed in 127 laboratory studies (159 taxon-level records), and nine taxa (19.6 %) were evaluated under field conditions in 35 publications or 49 taxon-level records. Field studies primarily were conducted in the FAW native range (71.4 %) compared to Africa (12.2 %) and Asia (16.3 %). Laboratory research has primarily focused on a small complement of known pathogens (Fig. 1; Supplementary Fig. 2), with five taxa accounting for 79.9 % of all records; *Beauveria bassiana* (Balsamo) Vuillemin, *Bacillus thuringiensis* Berliner, *Metarhizium anisopliae* (Metschnikoff), *Metarhizium rileyi* (Farlow), and *S. frugiperda* multicausid or multiple nucleopolyhedrovirus (SfMNPV). For several pathogens e.g., *Nosema* spp. or *Vairormorpha* spp. (Suppl. Table 1), performance has not been evaluated either under field or laboratory conditions.

Two laboratory studies investigated the possible combination of two entomopathogens, SfMNPV + *M. rileyi* and SfMNPV + *Anticarsia gemmatalis* multiple nucleopolyhedrovirus (AgMNPV). Field research has covered a more restricted set of pathogens: out of the 33 pathogen taxa

			
<b>Globally known FAW-associated BCAs</b>	<b>46 taxa</b>	<b>304 taxa / 229 species</b>	<b>215 taxa / 155 species</b>
<b>BCAs with field-level performance metrics</b>	<b>9 taxa</b>	<b>119 taxa</b>	<b>56 taxa</b>
<b>BCAs with laboratory-level performance metrics</b>	<b>33 taxa</b>	<b>44 taxa</b>	<b>39 taxa</b>
<b>BCAs with critical research attention</b>	<b>Field: 5 taxa Laboratory: 8 taxa</b>	<b>Field: 58 taxa Laboratory: 18 taxa</b>	<b>Field: 14 taxa Laboratory: 16 taxa</b>

**Fig. 1.** Comparative scientific attention to the three main natural enemy guilds across the FAW global distributional range. Per guild of biological control agents (BCAs), we contrast the share of known taxa for which field- or laboratory-level performance has been assessed. We equally list the number of taxa that have received critical research attention i.e., for which its performance is reported in more than one single peer-reviewed scientific publication.





**Fig. 2.** Laboratory-based performance of entomopathogenic fungi, bacteria and viruses against FAW eggs or larvae. Performance metrics include host mortality (right panel; %) or lethal time LT50 (left panel; days) of exposed individuals. Per pathogen and exposed FAW developmental stage, maximum host mortality and minimum LT50 are averaged across studies. Data are shown for the 20 best performing organisms, out of a respective 25 and 17 taxa for which mortality or LT50 was assessed. Data are drawn from a total of 127 published laboratory studies from the FAW native and invasive range. Organisms are ranked by decreasing host mortality. In both panels, values on top of each bar represent sample size i.e., the number of studies across which given metrics are averaged. Full species names are provided in [Suppl. Table 1](#).

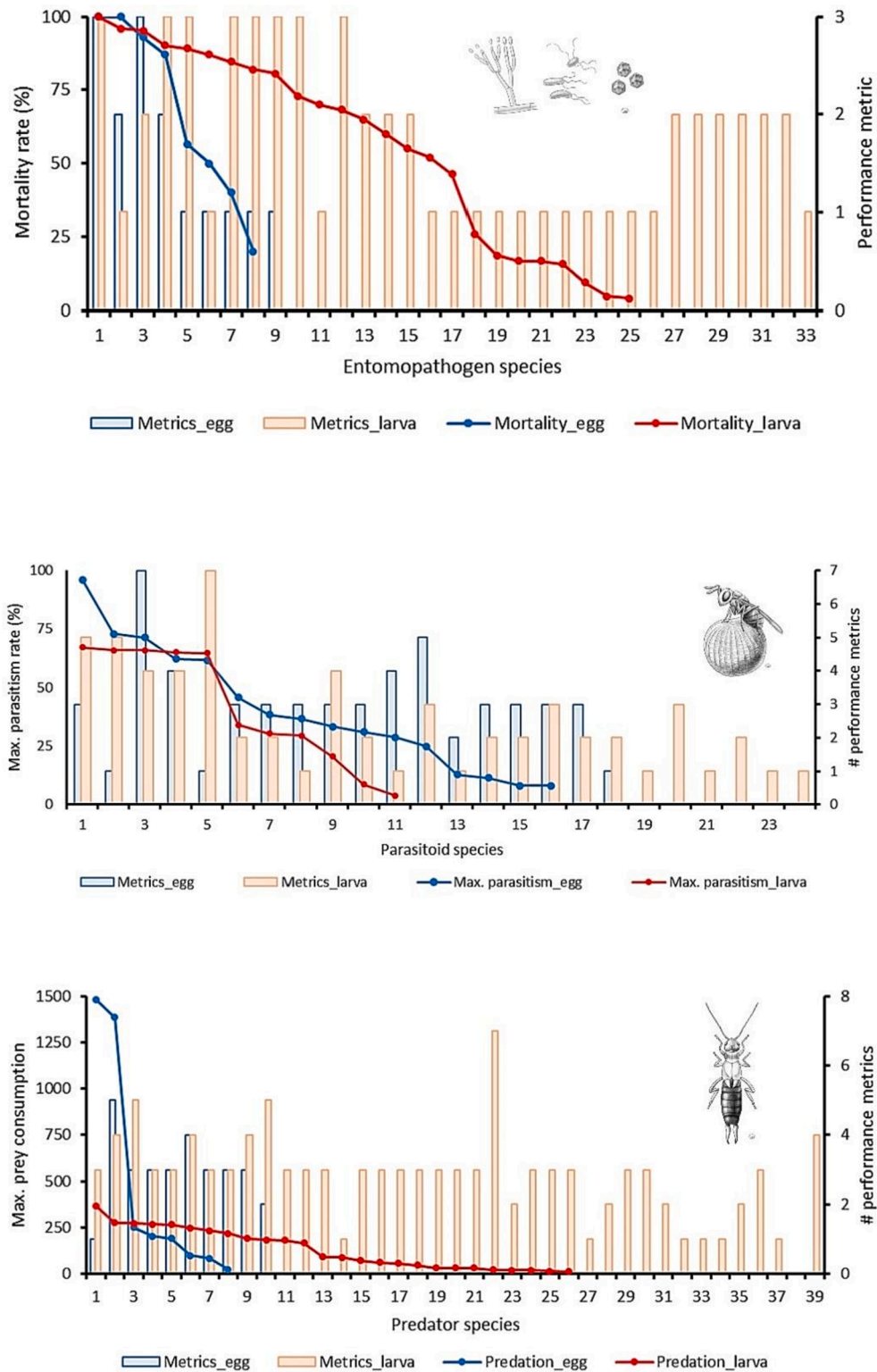
screened in laboratory set-ups, only *B. bassiana*, *M. rileyi* and SfNPV featured in more than five field studies. Field studies covered an equal share of natural control (49.0 %) and augmentation biological control (51.0 %), but omitting other forms of biological control. Further, two of the 35 field studies explicitly evaluated FAW entomopathogen performance under no-till arrangements ([Barros et al., 2021](#); [Faria et al., 2022](#)) and one study assessed augmentative applications of *B. bassiana* in push-pull systems and maize-cowpea intercroops in Tanzania ([Ngangambe and Mwatawala, 2020](#)), but no studies covered maize fields with organic matter addition or ecological infrastructures e.g., hedgerows or grass barriers.

Laboratory assays were performed with isolates that were either sourced from insect cadavers (62.3 % of records), soil (18.0 %), plant parts (1.6 %), or that were commercially available (9.8 %). Research primarily focused on the evaluation of conidial suspensions (56.7 % of records), viral or polyhedral occlusions (20.6 %), and spores, crystal proteins or endotoxins (18.4 %). Trials were run either with the commercial isolates directly (4.5 %) or with isolates that were cultured (94.6 %) or engineered (0.9 %) under laboratory conditions. Where reported, isolates either comprised endemic (82.6 %) or introduced biota (17.4 %). Lastly, contact applications e.g., spray (39.7 %), droplet, leaf or artificial diet feeding (33.1 %) and immersion (19.9 %) bioassays were most common. Experimental conditions were variable across studies, with pathogen performance evaluated at an average  $26.4 \pm 0.3$  °C ( $n = 113$  taxon-level records; mean  $\pm$  SE) and  $67.3 \pm 11.4$  % RH ( $n = 65$ ).

Pathogen performance was predominantly assessed against FAW larvae and eggs. Only one published study evaluated fungal pathogens against FAW adult stages ([Gutierrez-Cardenas et al., 2019](#); but see [Akutse et al., 2020](#)), whereby *M. anisopliae* and *B. bassiana* caused 95.8 % and 100.0 % mortality. Two studies in the FAW invasive range evaluated the effect of *B. bassiana*, *M. rileyi* and *M. anisopliae* on prepupae and pupae ([Montecalvo and Navasero, 2021](#); [Montecalvo et al., 2022](#)), finding low levels of pupal mortality but that the fungi hampered pupation rates,

adult emergence and/or development. Nine pathogen taxa were evaluated against eggs and 33 against larvae ([Fig. 3](#)). For eggs, pathogen performance was expressed as LC50 (4 taxa), LT50 (3) and host mortality (8). Meanwhile, for larvae, the above performance metrics were tested for 16, 17 and 25 taxa, respectively. When assessed against FAW eggs, a total of four pathogen taxa attained 100 % embryo mortality in at least one study; *B. bassiana* (1 of 3 studies reporting this metric), *Cordyceps (Isaria) sp.* (1/1), *M. anisopliae* (1/4) and *Metarhizium robertsii* J.F. Bisch., S.A. Rehner & Humber (1/1) ([Lezama-Gutiérrez et al., 1996](#); [Cruz-Avalos et al., 2019](#)). When assessed against FAW larvae of varying developmental stage, seven pathogen taxa caused 100 % mortality in at least one study; *B. thuringiensis* (3/15 studies), *B. bassiana* (3/20), *Cordyceps sp.* (1/1), *M. anisopliae* (3/15), *M. rileyi* (2/10), *M. robertsii* (1/2) and SfMNPV (3/12). The fastest speed of kill against FAW eggs or (neonate) larvae was reported for specific strains of *M. anisopliae*, an LT50 of 1.3 days for both developmental stages at  $9.8 \times 10^5$  conidia/mL and  $1.5 \times 10^4$  conidia/mL, respectively ([Lezama-Gutiérrez et al., 1996](#)). For several other pathogens that cause high rates of FAW egg or larval mortality, key performance metrics await determination ([Fig. 3](#)).

Field assays have assessed the prevalence of four naturally-occurring pathogen taxa in the FAW native range and three in the invasive range ([Table 1](#)). In both geographies, *M. rileyi* attains the highest prevalence levels, up to 92 % in Brazil ([Tigano-Milani et al., 1995](#)) and 42.0 % in India ([Firake and Behere, 2020](#)). Undoubtedly, this fungus stands as the primary naturally occurring pathogen of FAW in maize. In addition, 13 studies have examined augmentative applications of entomopathogens in the FAW native range and four in its invasive range. Among a set of five taxa, *B. thuringiensis* and SfMNPV exhibit the best performance under field conditions in the native range, with the former causing 100 % larval mortality over 25 days at 3–5 g/L at unknown application rates in Ecuador ([Ezeta-Leon et al., 2018](#)). Meanwhile, SfMNPV causes 100 % larval mortality with repeated applications of  $1.235 \times 10^{13}$  occlusion bodies per ha over a span of three weeks, as assessed in whorl-stage maize in South Carolina, USA ([Farrar et al., 2009](#)). Additionally,



**Fig. 3.** Relative completeness of laboratory-based performance assessments for FAW biological control agents globally. Patterns are shown for all entomopathogens (n = 33), parasitoids (n = 24) and predators (n = 39) for which performance has been evaluated under laboratory conditions against FAW eggs or larvae. Lethality is expressed as the laboratory-derived maximum mortality rate (%), parasitism rate (%) or life-time predation rate as averaged across studies. Per guild, organisms are ranked by declining lethality. Performance is regularly expressed by either of three, seven or eight performance metrics (listed in the main text) for the respective guilds. Per BCA taxon, the number of known performance metrics (length of bar) is contrasted with its lethality (line), where available.

different isolates of SfMNPV have been evaluated in the field using application doses between  $8 \times 10^{11}$  and  $1.5 \times 10^{12}$  OB/ha, which keep FAW below a 30 % economic loss threshold (Gómez et al., 2013; Barrera et al., 2017). Multiple pathogens are occasionally combined, taking

advantage of their different modes of action. By combining *M. rileyi* and SfMNPV, one obtains an additive effect at half the recommended dose (Gómez et al., 2022). Strategies for mixtures of two virus genera, including nucleopolyhedroviruses and granuloviruses, have been

**Table 1**

Field-level prevalence and (inferred) larval mortality by naturally-occurring or released entomopathogens across the global FAW distributional range. Prevalence data are shown for naturally occurring pathogens, while mortality rates exclusively refer to experimental evaluations of augmentative spray applications of biopesticides. Averages (mean  $\pm$  SE) and maxima are provided for each species and geography i.e., FAW native or invasive range. Per entomopathogen species or genus, maximum prevalence or mortality rates are averaged across studies and sub-species or strains. The number of original studies is reported between brackets.

Species	Prevalence (natural BC; %)		Mortality (augmentation BC; %)	
	Native range	Invasive range	Native range	Invasive range
<i>Akanthomyces lecanii</i>	–	–	–	82.2 $\pm$ 0.0 (1)
<i>Bacillus thuringiensis</i>	–	16.4 $\pm$ 0.0 (1)	61.9 $\pm$ 20.3 (3) Max: 100.0	–
<i>Beauveria bassiana</i>	3.0 $\pm$ 0.9 (3) Max: 4.2	–	77.6 $\pm$ 0.0 (1)	78.4 $\pm$ 6.9 (2) Max: 85.2
<i>Cordyceps fumosoroseus</i>	–	–	–	80.3 $\pm$ 0.0 (1)
<i>Entomophthora</i> sp.	1.1 $\pm$ 0.0 (1)	–	–	–
<i>Hirsutella</i> sp.	0.6 $\pm$ 0.0 (1)	–	–	–
<i>Metarhizium anisopliae</i>	–	–	91.8 $\pm$ 0.0 (1)	82.6 $\pm$ 1.0 (2) Max: 83.6
<i>Metarhizium rileyi</i>	24.3 $\pm$ 10.0 (9) Max: 92.0	32.0 $\pm$ 5.2 (5) Max: 42.0	–	62.9 $\pm$ 0.0 (1)
<i>Metarhizium robertsii</i>	–	–	92.0 $\pm$ 0.0 (1)	–
SfNPV	–	23.6 $\pm$ 0.6 (2) Max: 24.0	68.2 $\pm$ 8.6 (10) Max: 100.0	–

reported, whereby SfGV acts as an enhancer for SfMNPV. A low GV:NPV ratio (97.5 % of SfMNPV and 2.5 % of SfGV) produces the maximum enhancer potential by increasing the pathogenicity nearly 10-fold (Cuartas et al., 2019).

Among a set of five taxa, *B. bassiana* and *M. anisopliae* exhibit the best field performance in the invasive range. The former causes larval mortality rates of up to 85.2 % over 7 days, when applied at  $5 \times 10^9$  spores/L, though at unreported application rates in Egypt (Mansy et al., 2023). Meanwhile, field applications of an oil-based formulation of *M. anisopliae* at  $1 \times 10^8$  conidia/mL result in 83.6 % larval mortality at 7 days post-treatment in Kenya (Munywoki et al., 2022).

Overall, detailed information on FAW dynamics throughout the

**Table 2**

Comparative extent to which FAW infestation data are reported in biological control field studies globally. Per natural enemy guild, the percentage of studies is shown that either report FAW infestation data based upon a single ‘snapshot’ survey restricted to a given maize growth stage i.e., pre-whorl, whorl or reproductive stage from tasseling onwards, multiple successive surveys across growth stages or those that present no infestation data.

Natural enemy guild	Attention to in-field FAW dynamics (% studies)		
	Snapshot survey	Season-long dynamics	FAW infestation data not reported
Entomopathogen (N = 35)	28.6	5.7	65.7
Parasitoid (N = 102)	23.5	2.9	73.5
Predator (N = 26)	34.6	38.5	26.9

maize growing cycle is routinely lacking in field studies (Table 2). Globally, 94.2 % of field studies that cover natural control or pathogen augmentation do not present data on season-long FAW dynamics. Further, FAW infestation is often expressed using different currencies, such as foliar damage, larval incidence, plant-level larval abundance or egg mass density. This thwarts further efforts to quantitatively relate field-level prevalence of (natural, applied) entomopathogens to subsequent FAW population suppression across BCA taxa, geographies or years.

### 3.2. Overlooked taxa

Entomopathogenic nematodes (EPN) are user-friendly, effective and environmentally-sound pathogens to manage soil-dwelling biota and above-ground pests such as caterpillars, leaf miners, thrips and beetle larvae (Tomar et al., 2022; Wakil et al., 2023). EPN applications prove as effective as chemical insecticides against the tomato leaf miner *Tuta absoluta* (Meyrick) and the lesser peachtree borer *Synanthedon pictipes* (Grote & Robinson). In these cases, the EPN are applied by foliar sprays or directly onto bark wounds (Shapiro-Ilan et al., 2016; El Aïmani et al., 2021). As soil organisms, EPN are sensitive to environmental exposure, including desiccation, heat and UV radiation (Kaya and Gaugler, 1993). By overcoming those challenges via anti-desiccant and UV protectant formulations, the range of target pests could be broadened.

Several EPN strains are effective against FAW larvae (Fuxa et al., 1988; Andaló et al., 2010; Acharya et al., 2020; Fallet et al., 2022b). Philippine isolates of *Heterorhabditis indica* Poinar, Karunakar & David and *Steinernema abbasi* Elawad, Ahmad & Reid were pathogenic to FAW larvae in laboratory tests (Duza et al., 2023). Additionally, the compatibility of EPN with other biological control agents (Imperiali et al., 2017; Sáenz-Aponte et al., 2020) and many synthetic insecticides presents opportunities for synergistic pest management (Li et al., 2021). First attempts to use EPN against FAW explored the possibility of spraying EPN with water, or in combination with adjuvants, onto the leaves of maize plants. These trials resulted in inconsistent or low efficacy, mainly due to rapid desiccation of the nematodes, their incapacity to establish on the plants or the absence of substrate allowing them to move towards the caterpillars (Richter and Fuxa, 1990; Garcia et al., 2008; Negrisoli et al., 2010; Fallet et al., 2022a; Patil et al., 2022). To overcome these limitations, a cellulose-based gel was recently tested and has yielded promising results (Fallet et al., 2022a). Applied in the whorl, the cellulose gel ensured that nematodes remained on the plants and hydrated, and facilitated FAW larval infection. In preliminary field trials in Rwanda, the EPN-gel formulation was as effective as the chemical insecticide cypermethrin in preventing plant damage and reducing FAW infestation (Fallet et al., 2022a). Follow-up trials with repeated applications have also shown positive yield effects. Costs of an EPN-based strategy may be lower than commonly assumed because of the high vulnerability of FAW larvae to EPN (Acharya et al., 2020; Fallet et al., 2022b). Precise and targeted application further allows the use of dosages that are far lower than those commonly used against belowground pests and provides opportunities for a cost-effective use of EPN.

### 3.3. Next steps

By making effective use of locally occurring or laboratory-grown entomopathogens, conservation and augmentation biological control (CBC; ABC) carry ample promise. CBC offers a powerful and cost-effective FAW mitigation strategy, especially in diversified smallholder systems (Pell et al., 2012; Naranjo et al., 2015). Still, even though several pathogen taxa attain high prevalence in maize fields and exert significant epizootic activity against FAW (Fronza et al., 2017; Devi and Prasad, 2000), little research effort is specifically geared towards CBC. One of these agents, *M. rileyi*, contributes notably to the natural control of lepidopteran pests in soybean in the Americas (Moscardi and Sosa-Gómez, 2007; Sosa-Gómez, 2017). When advancing entomopathogen

CBC, *M. rileyi* could thus be a suitable first control agent. It could prove rewarding to advance CBC along the following five avenues. 1) Reduce fungicide applications that are directed towards plant pathogenic fungi and are often used prophylactically. These treatments can reduce germination rates and delay infection by beneficial fungi by at least 2–3 weeks (Johnson et al., 1976; Horton et al., 1980; Mietkiewski et al., 1997; Sosa-Gómez et al., 2003; Fronza et al., 2017). Equally, chemical insecticide use interferes with SfMNPV propagation by killing FAW parasitoids and predators that disseminate or transmit the virus in a standing crop (Castillejos et al., 2001; Abbas, 2020; Zhang et al., 2020). Future research can examine how biological alternatives, selective compounds or improved agronomy can bolster CBC. 2) Deploy commercial honeybee hives to disseminate conidia of beneficial fungi. Up to 14 % of honeybees that forage within spring-time crops collect sugar-rich guttation fluids (Schmolke et al., 2018) and can raise fungal incidence rates. A similar strategy could be followed with augmentatively released parasitic wasps or mites (Gonzalez et al., 2016). 3) Assess soil type, organic matter addition, altered plant nutrition or (cover) crop sequence to determine variable effects on fungal inoculum quantity and viability (Quesada-Moraga et al., 2007; St. Leger and Wang, 2020). Because the soil constitutes the main repository for fungi such as *M. rileyi*, holistic assessments of how soil- and crop management variables affect fungal incidence, FAW infestation and ultimately crop yield are sorely needed. 4) Gauge the spatio-temporal interactions with susceptible (pest, non-pest) hosts and communities of co-occurring pathogens through a farming systems lens. Though the host range of *M. rileyi* is more restricted than for *B. bassiana* or *M. anisopliae*, it infects at least 60 (lepidopterous) host species including several major crop pests (Fronza et al., 2017). Novel ways to induce epizootics, such as through banker plant systems (Pijnakker et al., 2020) wait to be identified. 5) Unravel the environmental determinants of fungal epizootics that in the case of *M. rileyi* can affect up to 92 % of FAW larvae. Climate-based prediction systems can be developed, allowing farmers to delay fungicide or insecticide spray applications and take full advantage of natural epizootics for pest control (Steinkraus, 2007; Pell et al., 2010).

Over the past 20 years, biopesticides based on fungi, virus, bacteria and EPN have been developed in several FAW-affected countries. Indeed, major biological control programs are in place and numerous products are commercially available in the Americas, Africa, and Asia (Faria and Wraight, 2007; Williams et al., 2013; Haase et al., 2015; Bateman et al., 2018; van Lenteren et al., 2018; Mascarin et al., 2019; Arthurs and Dara, 2019; Fisher et al., 2023). More recently, on-farm production of microbials has been operational in Brazil (Faria et al., 2023). Our study shows that multiple FAW pathogens have been studied under laboratory conditions, mostly focusing on pathogenicity towards the target host, but only a subset of these pathogens have been evaluated in the field. Commercial biopesticides are not only defined by pathogenicity but also by other technical aspects, such as shelf-life, product stability, sporulation rate and/or microbe adhesion rate, and these elements should all be properly tested *in vitro*, *in vivo* and *in eco*. For example, *M. rileyi* possesses a major advantage in epizootic ability but unstable virulence limits the number of products for field application. Ideally, the underlying biological and technical aspects to be studied include composition of the cultivation medium, formulation, fungus-virus interactions and host-pathogen immune interactions. Also, product cost can be a limiting factor especially for low-value commodities such as maize that are routinely grown by cash-strapped smallholders. However, next-generation bioreactors produce biopesticides at prices that are competitive with chemical pesticides (Mascarin and Jaronski, 2016; Reid et al., 2023).

For successful use of microbial control against FAW, research and development (R&D) should focus on the following considerations. The cryptic feeding behavior of FAW larvae within maize whorls (Pannuti et al., 2016) poses an obstacle for several biopesticides because viral occlusion bodies, Bt spore-crystals and other infective propagules must either be directly ingested or come into contact with the larval cuticle to

initiate the infection process. Timing of biopesticide application is also important; early-instar larvae typically are more susceptible to microbial infection. Novel application technologies can circumvent several of these obstacles e.g., with drones delivering microorganisms directly into the whorls. Innovative, user-friendly delivery strategies such as microbial seed coating reduce FAW survival and improve plant growth (De Lira et al., 2020). Spores of *Beauveria* and *Metarhizium* spp. are horizontally transferred among FAW adults and could be delivered at low volumes inside pheromone traps using ‘lure-and-infect’ approaches (Akutse et al., 2020). Parasitic wasps and the highly-abundant earwig *D. taeniatum* vector entomopathogens (Patel and Habib, 1984 in Andrews, 1988; Castillejos et al., 2001), and augmentatively-released parasitoids such as *Trichogramma* spp. could serve as vehicles for microbial biological control (Zang et al., 2021). Overhead EPN spray applications are often constrained by environmental factors but can be countered, at least partially, through subsequent crop irrigation (Ebssa et al., 2004). In addition, EPN delivery through drip irrigation, gelatin capsules or cellulose gel offer innovative ways forward (Fallet et al., 2022a; Ulu and Erdoğan, 2023). Research in the FAW native and invasive ranges has revealed how several beneficial fungi can colonize maize plants and impact FAW larval development as endophytes (Ramos et al., 2020; Herlinda et al., 2021). Though endophytic control carries advantages over standard spray application (Akello et al., 2007), much remains unknown about colonization mechanisms, plant responses and the ensuing impacts on (co-occurring) crop antagonists (Vega, 2018). Further, the often complex interplay with abiotic factors and downstream effects, such as lowered EPN virulence or parasitoid recruitment to endophyte-exposed larvae needs to be considered (Richmond et al., 2004; Miranda-Fuentes et al., 2021).

When evaluating pathogens, virulence is a key defining parameter but subtle effects should also be considered (Polanczyk and Alves, 2005). It is crucial to identify agents that are tolerant to prevailing agroclimatic conditions – which requires extensive laboratory and field-level screening and testing. Entomophthorales, a group of pathogenic fungi that has not been extensively explored for FAW (as compared to gypsy moth), definitely deserves more attention. If and where possible, local strains should be prioritized to avoid introduction of non-native organisms and associated regulatory procedures while providing advantages in terms of adaptability to local environmental conditions. Where one single agent proves to be inadequate, agents with different modes of action can be combined e.g., SfMNPV and *M. rileyi* (Gomez-Valderrama et al., 2022). Lastly, biotechnological tools and genomic approaches could improve entomopathogen performance; for example increasing virulence could lower application rates and enhance economic sustainability (Leung et al., 2020).

To ensure ease of use and optimum field performance, the development of effective, practicable formulations is essential. Formulations protect fungal conidia from abiotic stress, including interference from chemical pesticides (Moore et al., 1993; Lopes et al., 2011; Oliveira et al., 2018), and increase shelf life and field-level persistence and efficacy (Brar et al., 2006; Haase et al., 2015). For example, microencapsulating purified NPV occlusion bodies with a methacrylic acid polymer provided UV protection, and the formulated product achieved 100 % laboratory-level mortality and held FAW infestation pressure below a 30 % economic threshold in field trials (Villamizar et al., 2010; Gómez et al., 2013). Recently tested gel-based formulations keep EPN on the plants post-application and provide sufficient humidity to ensure motility and effective larval host infection by infective juveniles (Fallet et al., 2022a). Antidesiccants or adjuvants could further be added to enhance EPN survival and persistence on sun-exposed leaves especially in tropical or subtropical settings. In this regard, recent advances using titanium dioxide or silica nanoparticles hold great promise (Kotliarevski et al., 2022; Ramakrishnan et al., 2023). Once proper microbial solutions have been formulated and commercialized, the recycling of field-applied virus inoculum would constitute a cost-saving solution for resource-poor smallholders (Mweke et al., 2023).



## 4. Parasitoids

### 4.1. Global patterns

Globally, field or laboratory-based performance has been assessed for a total of 129 parasitoid taxa including 93 different species. This represents 42.4 % of the 304 known genus- and species-level taxa (40.6 % of the 229 individual parasitoid species) associated with this herbivore globally (Fig. 1; Supplementary Fig. 2; Suppl. Table 2). Specifically, 44 taxa (14.5 %) were evaluated through 86 laboratory studies accounting for 126 taxon-level records. Meanwhile, 119 taxa (39.1 %) were evaluated in the field, reported in 102 publications, representing 429 taxon-level records as many field studies reported multiple species. Field studies primarily originated in the FAW native range (67.6 % of records) as compared to Africa (20.0 %) and Asia (12.4 %). Many species of the sacrophagid, chalcid or ichneumonid complex have not been investigated (Suppl. Table 2) but braconids and trichogrammatids have received much laboratory research attention. Laboratory research has

emphasized a relatively small set of species, with *Telenomus remus* Nixon, *Trichogramma pretiosum* Riley, *Cotesia marginiventris* (Cresson) and *Trichogramma dendrolimi* Matsumura accounting for 24.6 %, 8.7 %, 6.3 % and 6.3 % of records, respectively. Few (or no) laboratory studies have addressed the remaining taxa. Field research also has been geared towards a small subset of species (Fig. 1; Supplementary Fig. 2); only nine taxa featuring in more than 10 studies. These include *Chelonus insularis* Cresson, *Co. marginiventris*, *Archytas marmoratus* (Townsend), *Te. remus*, *Ophion flavidus* Brullé, *Pristomerus spinator* (Fabricius), *Campoletis sonorensis* (Cameron), *Aleiodes laphygmae* (Viereck) and *Cotesia icipe* (Wilkinson) (ranked by greatest to least research coverage). Field performance of these taxa, except for *Te. remus* and *Co. icipe*, has been assessed solely in the FAW native range. Field studies primarily addressed natural control (82.4 % of studies) and augmentation biological control (12.7 %), while only 2.9 % of studies addressed CBC. CBC studies included an experimental evaluation of FAW parasitism in maize-bean intercrops and natural weed complexes in Colombia and Florida, USA (Altieri, 1980), maize-bean intercrops in Nicaragua (Van

**Table 3**

Laboratory-based performance of egg, larval and pupal parasitoids as assessed across the global distribution range of fall armyworm. For the five most commonly recorded performance metrics, we average the highest values across studies and experimental regimes i.e., study temperature. Averages are shown as means  $\pm$  SE. For studies in which the (life-time) number of exposed host individuals is specified, parasitism percentage data are converted to absolute numbers. Per taxon, performance metrics are those assessed under the specific experimental conditions as in the published work. Per FAW host stage, parasitoid species are ranked by declining parasitism rate.

FAW stage	Species	Performance metric					
		Max. parasitism (%)	Max. number of hosts attacked	Max. sex ratio <sup>§</sup>	Max. emergence rate (%)	Max. longevity (days)	
Egg	<i>Chelonus bifoveolatus</i>	96.0 $\pm$ 0.0	–	0.9 $\pm$ 0.0	86.0 $\pm$ 0.0	–	
	<i>Trichogramma confusum</i>	73.0 $\pm$ 0.0	–	–	–	–	
	<i>Telenomus remus</i> *	71.3 $\pm$ 7.4	72.7 $\pm$ 9.0	3.5 $\pm$ 0.4	79.6 $\pm$ 5.3	10.8 $\pm$ 1.4	
	<i>Trichogramma pretiosum</i>	62.3 $\pm$ 10.9	65.3 $\pm$ 38.3	11.4 $\pm$ 9.7	96.5 $\pm$ 1.3	8.9 $\pm$ 1.9	
	<i>Trichogramma embryophagum</i>	61.7 $\pm$ 0.0	–	–	–	–	
	<i>Trichogramma chilonis</i>	45.7 $\pm$ 29.9	–	3.2 $\pm$ 1.9	56.3 $\pm$ 43.3	–	
	<i>Trichogramma ostriniae</i>	38.4 $\pm$ 36.1	4.4 $\pm$ 2.7	4.2 $\pm$ 0.0	98.3 $\pm$ 0.0	–	
	<i>Trichogramma dendrolimi</i>	36.7 $\pm$ 7.0	73.4 $\pm$ 53.3	7.1 $\pm$ 1.0	97.7 $\pm$ 0.3	–	
	<i>Chelonus formosanus</i>	33.4 $\pm$ 0.0	–	–	57.5 $\pm$ 0.0	7.0 $\pm$ 0.0	
	<i>Trichogramma japonicum</i>	31.1 $\pm$ 26.5	3.4 $\pm$ 1.6	1.5 $\pm$ 0.3	95.1 $\pm$ 3.9	–	
	<i>Trichogramma atopovirilia</i>	28.8 $\pm$ 0.0	137.2 $\pm$ 123.7	4.3 $\pm$ 0.0	82.7 $\pm$ 12.6	8.0 $\pm$ 0.0	
	<i>Trichogrammatoidea</i> sp.	25.0 $\pm$ 0.0	25.0 $\pm$ 0.0	2.0 $\pm$ 0.0	25.0 $\pm$ 0.0	11.3 $\pm$ 0.0	
	<i>Trichogramma exiguum</i>	12.8 $\pm$ 0.0	49.2 $\pm$ 46.0	–	95.9 $\pm$ 0.0	–	
	<i>Trichogramma mwanzai</i>	11.4 $\pm$ 0.0	12.5 $\pm$ 0.0	5.7 $\pm$ 0.0	98.0 $\pm$ 0.0	–	
	<i>Trichogramma leucaniae</i>	8.2 $\pm$ 0.0	7.4 $\pm$ 1.6	3.9 $\pm$ 0.8	96.3 $\pm$ 0.7	–	
	<i>Trichogrammatoidea lutea</i>	8.2 $\pm$ 0.0	16.5 $\pm$ 0.0	8.1 $\pm$ 1.1	99.2 $\pm$ 0.6	–	
	<i>Chelonus insularis</i>	–	–	1.6 $\pm$ 0.4	59.0 $\pm$ 15.0	39.0 $\pm$ 9.0	
	<i>Trichogramma bilingensis</i>	–	9.6 $\pm$ 0.0	–	–	–	
	Larva	<i>Campoletis flavicincta</i> *	67.1 $\pm$ 0.0	67.1 $\pm$ 0.0	–	–	13.9 $\pm$ 0.0
		<i>Campoletis sonorensis</i> *	66.0 $\pm$ 13.2	23.3 $\pm$ 6.7	–	–	11.2 $\pm$ 0.0
<i>Cotesia icipe</i>		66.0 $\pm$ 10.1	–	2.2 $\pm$ 0.0	60.0 $\pm$ 0.0	16.1 $\pm$ 0.0	
<i>Lespesia aletiae</i>		65.0 $\pm$ 0.0	65.0 $\pm$ 0.0	1.1 $\pm$ 0.0	81 $\pm$ 0.0	–	
<i>Cotesia marginiventris</i> *		64.7 $\pm$ 11.3	15.1 $\pm$ 4.8	2.2 $\pm$ 0.0	76.2 $\pm$ 17.7	7.7 $\pm$ 0.0	
<i>Cotesia ruficrus</i>		34.0 $\pm$ 0.0	190.4 $\pm$ 0.0	–	–	20.0 $\pm$ 0.0	
<i>Coccygidium luteum</i>		30.3 $\pm$ 0.0	–	–	–	7.5 $\pm$ 0.0	
<i>Chetogena scutellaris</i>		29.5 $\pm$ 0.0	90.0 $\pm$ 0.0	–	–	–	
<i>Euplectrus plathypenae</i> *		20.5 $\pm$ 17.5	8.1 $\pm$ 7.1	–	90.0 $\pm$ 0.0	–	
<i>Charops</i> sp.		8.7 $\pm$ 0.0	–	–	–	13.0 $\pm$ 0.0	
<i>Aleiodes laphygmae</i>		4.0 $\pm$ 0.0	2.4 $\pm$ 0.0	–	–	–	
<i>Archytas marmoratus</i>		–	–	–	60.8 $\pm$ 0.0	61.4 $\pm$ 11.4	
<i>Campoletis chloridae</i>		–	–	3.2 $\pm$ 0.0	–	–	
<i>Cotesia flavipes</i>		–	–	–	0.0 $\pm$ 0.0	–	
<i>Cotesia sesamiae</i>		–	–	–	0.0 $\pm$ 0.0	–	
<i>Habrobracon hebetor</i>		–	–	–	70.0 $\pm$ 0.0	24.0 $\pm$ 0.0	
<i>Hyposoter</i> sp.		–	–	–	70.0 $\pm$ 0.0	–	
<i>Megaselia scalaris</i>		–	–	–	–	7.0 $\pm$ 0.0	
<i>Megaselia</i> sp.		–	–	–	–	–	
<i>Meteorus laphygmae</i>		–	–	10.0 $\pm$ 0.0	98.0 $\pm$ 0.0	–	
<i>Meteorus pulchricornis</i>		–	–	–	100.0 $\pm$ 0.0	20.0 $\pm$ 0.0	
<i>Microplitis manilae</i>		–	–	–	93.0 $\pm$ 0.0	–	
<i>Ophion flavidus</i>		–	–	2.0 $\pm$ 0.0	–	7.0 $\pm$ 0.0	
<i>Ophion flavidus</i>	–	–	–	84.7 $\pm$ 0.0	–		
Pupa	<i>Brachymeria ovata</i>	–	–	6.4 $\pm$ 0.0	67.0 $\pm$ 0.0	–	
	<i>Diapetimorpha introita</i>	–	–	–	–	30.2 $\pm$ 0.0	

\* Functional response type defined.

§ Female/male ratio.

Huis, 1981), and Tanzanian push–pull systems and maize-cowpea intercroppings (Ngangambe and Mwatawala, 2020). One study investigated parasitoid augmentation in Brazilian organic maize systems (Figueiredo et al., 2015).

Under laboratory conditions, a total of 18, 23 and 2 parasitoid taxa were evaluated against FAW eggs, larvae and pupae, respectively (Table 3). Most taxa were identified at the species level, except for *Trichogrammatoidea* sp. (egg), *Charops* sp., *Hyposoter* sp. and *Megaselia* sp. (larva). Overall, per study, an average of  $1.8 \pm 0.1$ ,  $1.8 \pm 0.2$  and  $1.5 \pm 0.5$  metrics were reported for egg, larval and pupal parasitoids, respectively. Out of seven performance metrics, attack rate, emergence rate, sex ratio and longevity are commonly assessed for egg parasitoids and were determined for a respective 17, 15, 13 and 6 taxa (Table 3; Fig. 3). For parasitoids of FAW larvae, emergence rate, longevity, attack rate and fecundity prove the most popular metrics and were assessed for a respective 13, 12, 11 and 8 taxa. Lastly, for the two pupal parasitoids, one single study recorded longevity of *Diapetimorpha introita* (Cresson) while a second one determined the emergence rate and sex ratio for *Brachymeria ovata* (Say). Per taxon of egg, larval or pupal parasitoid, an average of  $3.1 \pm 0.3$ ,  $2.5 \pm 0.3$ , and  $1.5 \pm 0.5$  performance metrics were recorded. Further, only two species, *Te. remus* and *Co. marginiventris*, were evaluated using a complete set of seven metrics. For top-performing species such as *Trichogramma confusum* Viggiani or *Tr. embryophagum* (Hartig), only attack rate was determined and other metrics remained unspecified (Fig. 3). In the studies, egg, larval or pupal parasitoid performance was evaluated under variable temperature and relative humidity regimes: a respective  $25.5 \pm 0.3$  °C,  $25.9 \pm 0.3$  °C and  $23.5 \pm 3.5$  °C, and  $71.6 \pm 15.1$  %,  $68.2 \pm 2.5$  and  $40.0 \pm 30.0$  % RH across studies ( $n = 101$ , 34 and 2 taxon-level records). Given the fragmentary evaluation of a myriad of performance metrics under wide-ranging experimental conditions, a more targeted, systematic approach may be warranted to gauge the potential of individual BCAs and to pinpoint the most promising species for ABC or CBC.

In laboratory studies, a Zambian strain of the egg-larval parasitoid *Ch. bifoveolatus* Szepligeti and a Brazilian strain of the larval parasitoid *Campoplex flavicincta* (Ashmead) attained the highest relative parasitism rate within their respective guilds, respectively 96.0 % and 67.1 % (Table 3; Shen et al., 2023; Zanuncio et al., 2013). For egg parasitoids, the greatest absolute attack rate, sex ratio, emergence rate and longevity were recorded for *Tr. atopovirilia* Oatman & Platner, *Tr. pretiosum*, *Trichogrammatoidea lutea* Girault and *Ch. insularis*, respectively. For the same metrics, the larval parasitoids, *Co. ruficrus* (Haliday), *Meteorus laphygmae* Viereck, *Megaselia* sp., and *A. marmoratus* performed best. For pupal parasitoids, research effort has been insufficient to reliably rank taxa in terms of performance.

Field assays covered both natural and augmentative biological control throughout the FAW native and invasive range. In terms of natural control, field-level performance (i.e., maximum or average parasitism rates) were determined for 70 taxa in the native range and 52 taxa in the invasive range. In the native range, *Te. remus*, *Ca. grioti* (Blanchard), *Tr. pretiosum* and *Ch. insularis* reach the highest maximum parasitism rates at 98–100 % across sites (Fig. 4). Of these, 13 parasitoid taxa surpass local thresholds for effective biological control, producing 32 % maximum parasitism (Hawkins and Cornell, 1994). Meanwhile, in the invasive range, *Te. remus*, *Tr. chilonis* Ishii and *Ch. bifoveolatus* attain the highest maximum parasitism rates ranging from 87.3 to 100 % (Fig. 4). Nine taxa surpass the 33–36 % parasitism threshold for effective biological control, including *Te. remus* and *Tr. chilonis* in Cameroon (100 %), *Telenomus* sp. in Niger (87.3 %), *Ch. bifoveolatus* and *Coccygidium luteum* Brullé in Ghana (87.3 %; 49.4 %), *Co. icipe* and *Drino imberbis* (Wiedemann) in Ethiopia (45.3 %; 35 %), and *Chelonus* sp. and *Ch. formosanus* Sonan in India (70.9 %; 33.3 %) (Amadou et al., 2018; Sisay et al., 2019; Abang et al., 2021; Sagar et al., 2022; Agboyi et al., 2023). In addition to natural control, augmentative releases have been conducted for four parasitoid species in the native range and six in the invasive range (Table 4). In the native range, highest parasitism maxima

were recorded for the egg parasitoids *Te. remus* and *Tr. pretiosum* in Brazil (Figueiredo et al., 2002, 2015) and the larval parasitoid *O. flavidus* under screen-cage conditions in the USA (Gross & Pair, 1991).

Though the number of laboratory studies per taxon related to maximum field parasitism rate (Spearman Rank,  $\rho = 0.315$ ,  $p < 0.001$ ,  $n = 123$ ), logistic regression only provided a weak fit between the field parasitism rate of a given taxon and its actual inclusion in laboratory studies (Fig. 5). Well-performing parasitoids are thus not systematically evaluated under laboratory conditions. For example, taxa that attained high field parasitism, such as *Telenomus* sp. in Niger (87.3 %; Amadou et al., 2018) and *Euplectrus* sp. in Mexico (84.6 %; Avila-Rodriguez et al., 2023) still await laboratory-level scrutiny. Conversely, parasitoids such as *Hyposoter* sp., *Co. flavipes* (Cameron), *Megaselia* sp. and *Co. sesamiae* Cameron were assessed under laboratory conditions even though they merely reach 0.1–0.5 % parasitism maxima in the field. Also, it remains unclear whether and how field abundance relates to laboratory-derived performance metrics. Under natural control, maximum field parasitism rate of a given taxon did not significantly correlate with laboratory-derived maxima for parasitism rate (Spearman Rank,  $\rho = 0.399$ ,  $p = 0.09$ ), number of hosts attacked ( $\rho = -0.430$ ,  $p = 0.10$ ), sex ratio ( $\rho = -0.039$ ,  $p = 0.89$ ) or emergence rate ( $\rho = 0.270$ ,  $p = 0.25$ ). However, field parasitism rate for studied taxa showed positive regression against laboratory-level maximum longevity (ANOVA;  $F_{1,17} = 10.687$ ,  $p = 0.005$ ,  $R^2 = 0.380$ ). As with entomopathogens, detailed information on FAW dynamics throughout the maize growing cycle was routinely lacking in field studies (Table 2). Indeed, 97.1 % of field studies on FAW parasitoids globally did not present data on season-long FAW dynamics. This, again, thwarts further efforts to link parasitism levels to FAW population suppression across studies, years or geographies.

#### 4.2. Overlooked taxa

Pupal parasitoids are critically overlooked in the FAW native and invasive ranges alike. This is a potentially serious oversight, as *D. introita* and *Cryptus albitarsis* (Cresson) jointly cause pupal parasitism rates up to 44.4 % in Georgia, USA (Pair and Gross, 1989). Life history parameters of *D. introita* have been assessed in the laboratory with a primary aim towards mass-rearing (Pair, 1995) and artificial diets have even been developed (Carpenter and Greany, 1998; Ferkovich et al., 1999). Further, *D. introita* populations have been effectively monitored in the field using wing traps baited with live females (Jewett and Carpenter, 2001), which could progress to attract-and-reward approaches with synthetic lures. For other species, such as *B. ovata*, laboratory-level performance on freeze-killed pupae has been assessed with a view to mass-rearing (Grant and Shepard, 1987), but field-level abundance is unknown. Notwithstanding the exciting progress with *D. introita* in the USA, pupal parasitoids have been neglected in other parts of the Americas. Equally, though larval-pupal parasitoids such as *Meteoridae* sp., *Meteorus* sp. or *Metopius discolor* Tosquinet have been reported in the invasive range in Ghana, Benin, Uganda or Zambia (Agboyi et al., 2020; Durocher-Granger et al., 2021; Otim et al., 2021) and *Exorista xanthaspis* (Wiedemann) in India (Navik et al., 2020), pupal parasitoids *sensu stricto* remain virtually un-investigated.

#### 4.3. Next steps

Parasitoid-mediated biological control of FAW can be promoted through both conservation and augmentation tactics. Though naturally-occurring egg and larval parasitoids sporadically attain (aggregate) parasitism levels of 80–90 %, their on-farm conservation has largely been overlooked. To move CBC forward, an essential first step is to identify the species of parasitic wasps that exert the greatest impact on FAW populations and to then study their field ecology. Nearly all studies in our review report parasitoid species richness and numerical abundance based on one or few ‘snapshot’ surveys. Though this information is valuable (Heraty, 2017), such metrics do not reveal the extent to

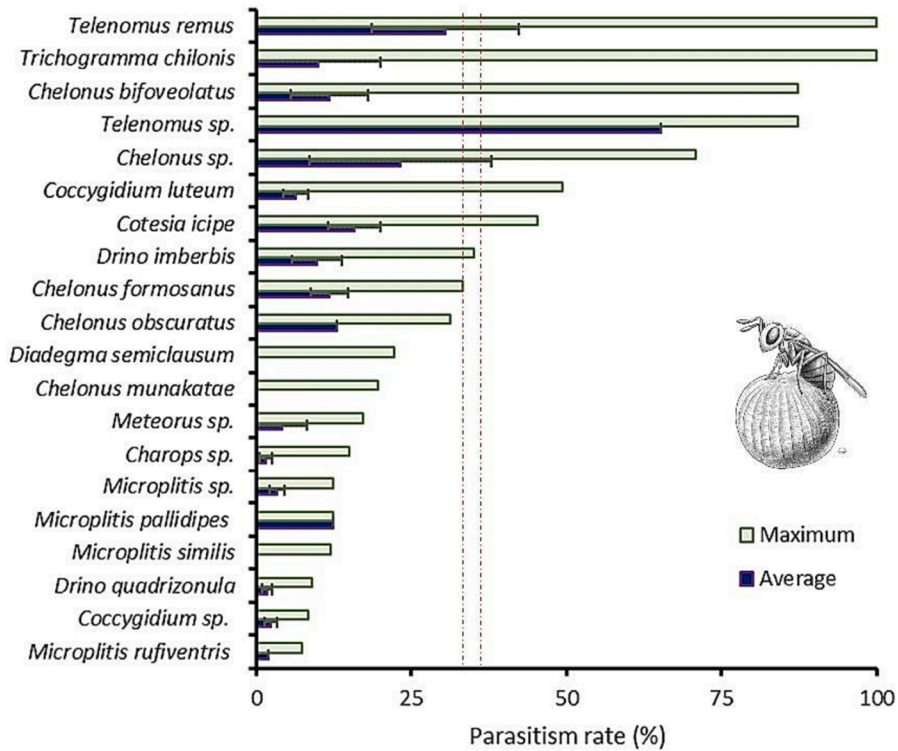
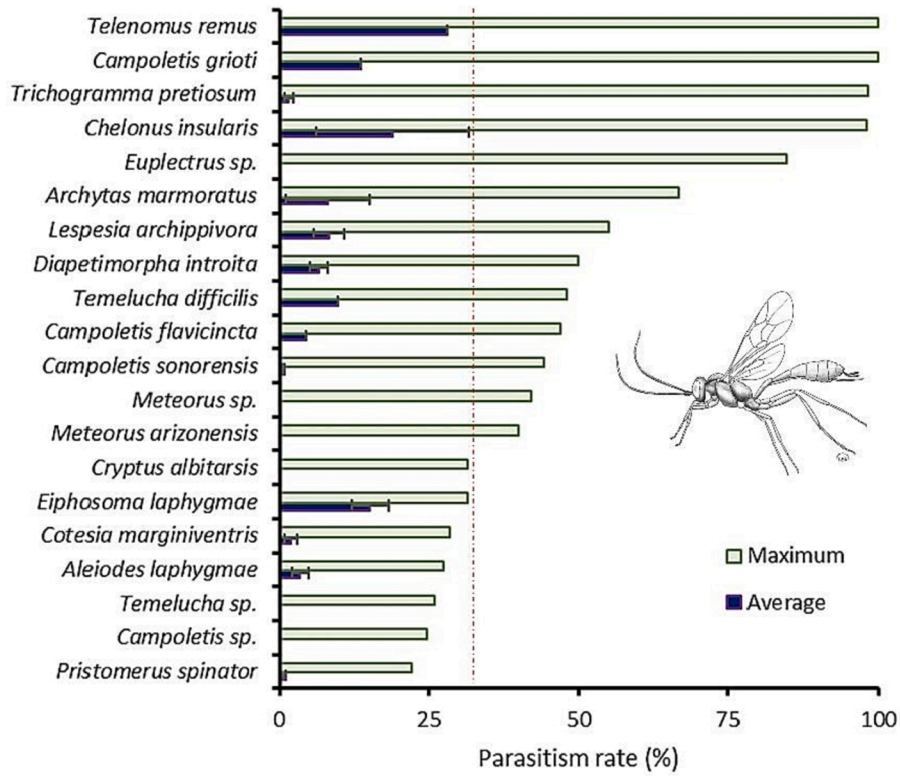


Fig. 4. Field-level parasitism rates (%) of the 20 best performing parasitoids in the FAW native (top) and invasive (bottom) range. Maximum and average (mean  $\pm$  SE) parasitism levels are plotted for each species based upon the actual availability of the respective metrics in the original studies. FAW parasitism rates are either assessed during one single ‘snap shot’ census or at multiple instances during the maize cropping cycle. Threshold values for effective biological control are indicated by the vertical dotted line and refer to 32 % or 33–36 % maximum parasitism in the native or invasive range, respectively (Hawkins and Cornell, 1994).

**Table 4**

Average and maximum parasitism rates (%) achieved through augmentative releases of different parasitoid species in the native or invasive range of fall armyworm. Mean values ( $\pm$ SE) are computed by averaging data from multiple studies. In the original studies, FAW parasitism rates are either assessed during one single 'snap shot' census or at multiple instances during the maize cropping cycle, with the latter often restricted to the whorl stage. Reported values i.e., averages or maxima depend upon those that were logged during the data extraction phase. Parasitoid species are listed alphabetically. Literature references are provided in full in [Suppl. Table 5](#).

Parasitoid species	Native range		Invasive range		Literature refs. <sup>5</sup>
	Average	Maximum	Average	Maximum	
<i>Archytas marmoratus</i>	35.6 $\pm$ 15.2	76.4	–	–	1–4
<i>Habrobracon hebetor</i>	–	–	16.0 $\pm$ 0.0	22.0	5
<i>Ophion flavidus</i>	–	88.9	–	–	4
<i>Telenomus remus</i>	31.7 $\pm$ 4.2	88.3	15.9 $\pm$ 4.9	100.0	6–10
<i>Trichogramma chilonis</i>	–	–	–	75.0	11,12
<i>Trichogramma confusum</i>	–	–	–	61.5	12
<i>Trichogramma dendrolimi</i>	–	–	–	31.4	11
<i>Trichogramma ostrinae</i>	–	–	–	87.5	12
<i>Trichogramma pretiosum</i>	56.6 $\pm$ 11.9	79.2	–	76.9	10–13

- No data available in original studies.

<sup>5</sup> Gross et al., 1985 [1]; Gross, 1988 [2]; Gross & Young, 1984 [3]; Gross & Pair, 1991 [4]; Ghosh et al., 2022 [5]; Pomari-Fernandes et al., 2018 [6]; Figueiredo et al., 2002 [7]; Agboyi et al., 2021 [8]; Zhao et al., 2020 [9]; Zhu et al., 2020 [10]; Yang et al., 2022 [11]; Jin et al., 2021 [12]; Figueiredo et al., 2015 [13].

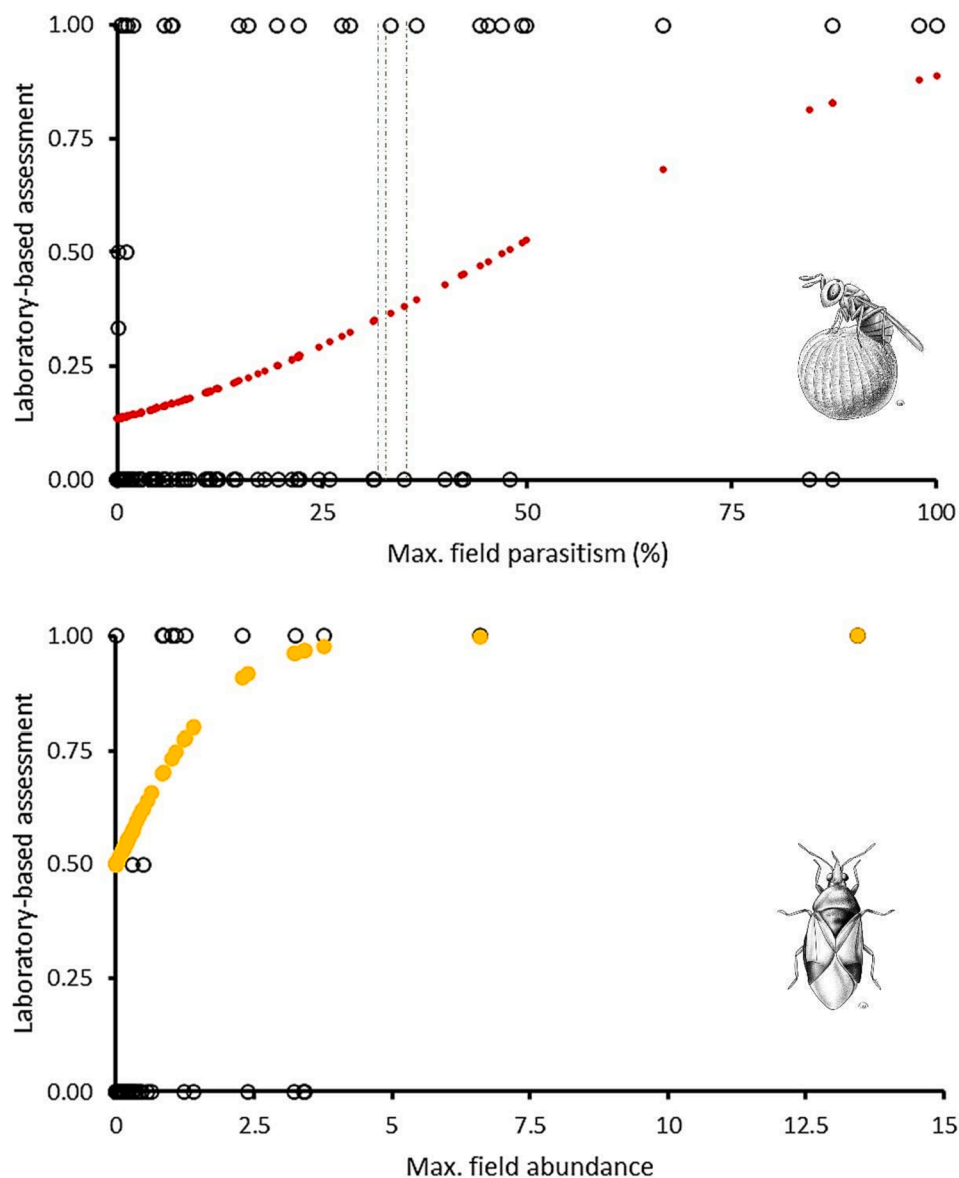
which one or more species contribute to FAW mortality. [van Driesche et al. \(1991\)](#) compare this to attempting to assess the total inflow of water (recruitment) into a sink (a population) by measuring the volume of water within this sink at a given point in time. Indeed, in many parasitoid-host systems, parasitoids are under 'donor control' and have minimal effects on their hosts ([Hawkins, 1992](#)) or face skewed trophic structures, such as in low-diversity systems that reduce their top-down influence ([Rosenheim, 1998](#); [Duffy, 2002](#)). Also, timing and consistency of parasitoid-inflicted mortality between seasons is often more important than its absolute magnitude ([Macfadyen et al., 2015](#)). As a result, r-selected species attaining 90 % attack rates can still be ineffective biological control agents ([Barrat et al., 2018](#)) even while they surpass thresholds for successful biological control on a particular host ([Hawkins and Cornell, 1994](#)). To estimate their role as regulators of FAW populations, one should determine whether they act in a positive density-dependent manner and exhibit spatial heterogeneity in parasitism rate, abiding by the  $CV^2 > 1$  rule ([Pacala et al., 1990](#); [Hawkins, 1992](#)). Other ways to quantitatively assess how a given species contributes to FAW mortality include stage-frequency analysis, direct measurement of recruitment or death rate analysis ([Van Driesche et al., 1991](#)), in which observational and manipulative studies (e.g., field cages, barriers, sentinel prey or chemical exclusion assays) all play a role ([Macfadyen et al., 2015](#); [Thancharoen et al., 2018](#); [Jervis et al., 2023](#)). Season-long assessments, like those conducted for egg parasitoids in Brazil ([De Sá and Parra, 1994](#); [Dequech et al., 2013](#)), are rare, but provide critical insights.

For none of 229 FAW parasitoid species listed in this review have we learned to effectively increase numerical abundance, colonization rates or biological control impact through on- or off-farm habitat management ([Landis et al., 2000](#)). Even for prominent species, such as *Ch. insularis* or *Te. remus*, laboratory and field trials have not been performed to assess whether certain habitats or companion plants provide shelter, nectar, alternative prey/hosts, and pollen (SNAP) ([Landis et al., 2000](#); [Gurr et al., 2003](#)). Only recently has preliminary information been generated in Florida, USA and Peru on parasitoids associated with flowering plants or weeds ([Johanowicz et al., 2002](#); [Meagher et al., 2016](#); [Quispe et al., 2017](#)). Exploratory research shows how marigold flower strips bordering maize fields raise the abundance of various egg or larval parasitoids and lower FAW infestation pressure ([Mendez, 2017](#)). Yet, we remain far from identifying traits that relate to parasitoid performance or from using such insights to guide CBC strategies ([Fiedler and Landis, 2007](#); [Perovic et al., 2018](#)). This does not only apply to the comparatively well-studied scelionids or ichneumonids, but also to dipterans such as *A. marmoratus* - species that use floral food rewards and visual or chemical cues to guide foraging ([Woodcock et al., 2014](#)) and that relies upon the presence of alternative hosts for early-season

colonization ([Gross et al., 1985a](#)). Yet, on a positive note, the floral host plants of tachinids such as *Lespesia archippivora* (Riley) have been identified in the midwestern USA ([Tooker et al., 2006](#)). As *L. archippivora* is the primary FAW parasitoid in Central America ([Cave, 1993](#)), such floristic survey should be replicated in this part of the host range. Similarly, though species, such as *Ch. insularis*, were already observed feeding on extra-floral nectaries in the early 1900s ([Luginbill, 1928](#)), nutritional requirements of parasitoids have primarily been investigated with a view towards laboratory mass-rearing ([Su et al., 2021](#)) and not in-field conservation. However, innovative field research has shown how spray applications of table sugar raise abundance of BCAs such as *L. archippivora* by 70 % in Honduras and double parasitism by *Ca. flavicincta* and two tachinids in Brazil ([Canas and O'Neil, 1998](#); [Bortolotto et al., 2014](#)). Similar results were achieved with more costly maltodextrin in Africa ([Babendreier et al., 2020](#)). However, adult food alone is not sufficient to raise parasitoid performance ([Gillespie et al., 2016](#)).

Parasitoid colonization dynamics are determined by the local abundance of suitable, alternative hosts especially in areas where FAW varies seasonally e.g., in its migratory range. In these areas, it is unwise to count on the (often) arbitrary influx of BCAs from outside a focal agro-ecosystem, but to improve such through habitat management. Baseline knowledge needs to be generated on the use of alternative hosts for parasitoids that are active in early-season, such as *A. marmoratus* and *D. introita* in the USA ([Gross et al., 1985b](#); [Jewett and Carpenter, 2001](#)) or *Co. icipe*, *Parapanteles* sp., *Euplectrus laphygmae* and *M. curvimauculatus* in Zambia ([Durocher-Granger et al., 2021](#)). These hosts should be identified in local agro-ecosystems and evaluated under laboratory conditions. However, laboratory-level evaluations of alternative host suitability are routinely geared towards mass-rearing such as screening *Corcyra cephalonica* (Stainton) eggs for *Te. remus* ([Queiroz et al., 2017](#); [Li et al., 2023a](#)). For a subset of parasitoids, for example, *Ch. insularis*, the role of plant and host volatiles in foraging has been determined and these insights possibly can guide CBC interventions ([Roque-Romero et al., 2020](#)). Parasitoids often co-migrate with their host, either through active or phoretic means ([Huigens et al., 2009](#); [Furey et al., 2018](#); [Zhou et al., 2023](#)) and an improved understanding of their seasonal biology, dynamics and dispersal capabilities can help to replicate successful biological control along the migration front. Insecticide spray applications -even directed towards other pests- impact FAW parasitoids to a substantial extent. Sprays of high-risk compounds such as chlorpyrifos reduce *Ca. grioti* parasitism ten-fold ([Berta et al., 2000](#)) and the 'low-risk' flubendiamide nullifies the contribution of *Ch. bifoveolatus* or *C. luteum* ([Ngangambe and Mwatawala, 2020](#)). Insecticide usage intensity, in addition to timing of sampling, crop management and landscape context, thus likely explains the large variability in species-level parasitism rates between locations ([Molina-Ochoa et al., 2004](#)). Clearly, to





**Fig. 5.** Likelihood that arthropod natural enemies are evaluated under laboratory conditions based upon their field-level abundance across the FAW global distribution range. Data are shown for parasitoids (top) and predators (bottom). For either dataset, a logistic regression curve is plotted offering a moderate fit (Cox & Snelling  $R^2 = 0.152$  and  $0.180$ , respectively). For parasitoids, threshold values for effective biological control in the native and invasive range are indicated by vertical dotted lines (Hawkins and Cornell, 1994). Patterns are plotted for 123 (species- or genus-level) parasitoids and 57 predators.

gauge true parasitoid contribution to CBC, research should be carried out in fields (or plots) where even low-risk insecticide usage is suspended.

Our exercise found few studies that assessed parasitoid performance under intercrop arrangements. Though these studies provide pointers for CBC, this kind of research has not progressed beyond case-by-case empiricism. Crop diversification often leads to higher parasitism and lower FAW damage compared to monocropping (Ngangambe and Mwatawala, 2020), although impacts were species-specific. For example, *Meteorus* sp. and *Ch. insularis* attain a respective 40 % higher and 91 % lower parasitism in weedy maize-bean systems compared to maize monocrops (Altieri, 1980; Penagos et al., 2010). The role of nectary-bearing legume intercrops or borders in meeting parasitoid nutritional needs and bolstering FAW biological control is a field that remains wide open (Wyckhuys et al., 2023a). The elevated tachinid parasitism levels in maize-bean intercrops, as compared to those of braconids (Van Huis, 1981), can either be ascribed to foraging efficiency or the availability of nectar resources, but this needs to be tested more

broadly. To create further momentum for ecological intensification (Kleijn et al., 2019), parasitoid-mediated biological control evidently should be studied more extensively under polyculture arrangements (Altieri et al., 1978; Risch, 1981; Jaworski et al., 2019).

In addition to the above, lepidopteran pests such as *S. frugiperda* are common targets of parasitoid augmentation programs (Stiling and Cornelissen, 2005). ABC indeed poses a lucrative option, as scheduled releases of parasitic wasps not only mitigate FAW infestation pressure but also raise maize yields by 19.4 % (Figueiredo et al., 2015). In ABC, the type of parasitoids, often r-selected egg parasitoids, differs markedly from those that lend themselves to CBC. Simple criteria such as population growth rate or climatic adaptability can help eliminate inefficient species (Van Lenteren et al., 2018). Also, as parasitoid augmentation is often a profit-oriented undertaking, its success not only depends on proper agent selection (see above; Li et al., 2023a), but also on cost-effectiveness and commercial viability of mass-rearing operations. Ideally, ABC should be economically competitive with the prevailing pesticide-based approaches.

For top-performing parasitoids in the native range e.g., *Ch. insularis*, *Euplectrus plathypenae* Howard, *A. marmoratus* and *C. sonorensis*, basic biology, alternative host or artificial diet suitability and related fitness parameters have been recorded in the laboratory (Gross, 1994; Hu and Vinson, 1998; Hay-Roe et al., 2013; Barreto-Barriga et al., 2017; Padilla-Cortes and Martínez-Martínez, 2022), but those studies only culminated in full-fledged ABC programs in a few countries. This ‘translational gap’ is not necessarily due to poor performance of ABC programs but to socio-political conditions (Wyckhuys et al., 2022). For example, in the USA, innovative *A. marmoratus* rearing and release systems involved mechanical extraction of maggots from gravid females and their delivery through overhead irrigation systems (Gross, 1994; Pyrah, 1985). However, this ABC program failed to take root due to its labor-intensive nature and farmers’ preference of Bt corn. Nonetheless, it may prove suitable in other farming contexts in the tropics. Meanwhile, parasitoids that regularly occur at background levels such as *Tr. pretiosum* have received extensive research and are successfully used for fall armyworm ABC in Brazil (Parra and Zucchi, 2004). A broader suite of trichogrammatids is under study in China (Tao et al., 2021; Yang et al., 2022; Li et al., 2023a). Other egg parasitoids (e.g. *Te. remus*) are effectively reared on eggs of the rice moth *C. cephalonica* in several countries (Li et al., 2023a; Queiroz et al., 2017), but not in China, where the more expensive *Spodoptera* spp. eggs are chosen as factitious hosts (Chen et al., 2021; Li et al., 2023b). Larval parasitoids, such as *Habrobracon hebetor* (Say), have also been deployed effectively in India (Ghosh et al., 2022) and *Co. icipe* shows promise in East Africa (Mohamed et al., 2021). ABC programs also can incorporate other locally abundant species e.g., *Chelonus* spp. in Africa or South Asia, though production costs may pose a constraint for *Ch. bifoveolatus* (Shen et al., 2023). Drawing on dynamics in North America, we argue that targeted augmentation (or conservation) in overwintering areas in Asia may be particularly worthwhile. In overwintering areas of south Texas and Mexico, *Ch. insularis* and *A. marmoratus* parasitize up to 61.7 % of small larvae and 66.7 % and medium-size larvae (Pair et al., 1986). Without accounting for the added impact of resident entomopathogens, pupal or egg parasitoids and predators, ABC programs can raise the degree of FAW suppression even further and permit non-chemical pest control.

Once suitable species and strains are identified for use in ABC programs, laboratory and field studies are needed to improve biological control efficacy (Parra and Zucchi, 2004; Li et al., 2023a). In addition to research on host acceptance or in vitro rearing for *Te. remus* and other species (Colmenarez et al., 2022; Li et al., 2023a), reproductive biology studies can resolve issues such as skewed sex ratios or loss of host-finding ability that result from mass-rearing. Work is required on insecticide sensitivity, foraging behavior, release systems and interspecific competition or complementarity. The last can resolve the long-standing issue of low *Trichogramma* sp. parasitism on multi-layered FAW egg masses (De Sa and Parra, 1994). FAW females deposit their eggs in multiple layers and cover these with scales, which act as a physical barrier to some parasitoid species (e.g., *Tr. dendrolimi* or *Tr. pretiosum* but not *Te. remus*) (Beserra and Parra, 2005; Dong et al., 2021). Hence, though *Trichogramma* spp. offer clear advantages in terms of inexpensive mass-rearing, long-term storage, and release, they only act effectively against *S. frugiperda* eggs of low or medium scale cover. Tactically integrating them with *Telenomus* or *Chelonus* spp. constitutes the next frontier in egg parasitoid augmentation (Li et al., 2023b).

## 5. Predators

### 5.1. Global patterns

A total of 82 canopy-foraging predator taxa, 21 of which were only identified at the genus level, have been studied under field and/or laboratory conditions. This represents 38.1 % of the 215 known genus- and species-level taxa or 38.7 % of the 155 individual predator species associated with this herbivore globally (Fig. 1; Supplementary Fig. 2;

Suppl. Table 3). A small subset of 39 taxa (18.2 %) featured in 64 laboratory studies, accounting for 70 taxon-level records. Meanwhile, 56 taxa (36.7 %) were evaluated under field conditions and reported in 26 publications, representing 93 taxon-level records. Field research in the FAW native range addressed 51 taxa and accounted for 90.3 % of records, while just seven taxa (two of which were cosmopolitan i.e., *Geocoris* sp. and *Doru* sp.) were studied in the invasive range. The role of most ants, vespids or soft-winged flower beetles in FAW biological control has not been studied (Suppl. Table 3). On the other hand, lady beetles, predatory stink bugs, earwigs and minute pirate bugs have received comparatively more field and/or laboratory research attention. The bulk of laboratory research was conducted on few taxa; only 3 out of 215 taxa were covered in more than three studies, the stink bugs *Podisus nigrispinus* (Dallas) and *Eocanthecona furcellata* (Wolff), and the lady beetle *Harmonia axyridis* (Pallas). Although field studies did cover a broader range of taxa (Fig. 1; Supplementary Fig. 2), taxon-level research attention proved equally limited. Only the pirate bug *Orius insidiosus* (Say), the earwigs *Doru taeniatum* (Dohrm) and *D. luteipes* (Scudder), the big-eyed bug *Geocoris* sp. and the lacewing *Chrysoperla* sp. featured in more than three studies. Field research on these predators was solely conducted in the FAW native range. Out of all field studies, 84.6 % addressed natural control, while the remaining four studies evaluated CBC. These entailed an evaluation of weediness and pumpkin, sesame, bean, or sunflower intercropping in Mexico (Penagos et al., 2002; Garcia et al., 2013), maize-sorghum bicultures in Honduras (Jones et al., 1989) or intercropping with groundnut, bean or soybean in India (Udayakumar et al., 2021). Although other studies also assessed the effects of weediness or polycultures, these centered on soil-dwelling ants in Nicaragua or Benin (Perfecto and Sediles, 1992; Dassou et al., 2021) or failed to report species-level impacts (Altieri, 1980). One Peruvian study assessed FAW predators associated with a set of 15 flowering plants (Quispe et al., 2017), with a view to defining habitat management strategies. No studies specifically investigated the impacts of no-till arrangements or organic matter addition on foliage-dwelling predator communities.

Under laboratory conditions, a respective ten and 39 predator taxa were evaluated against FAW eggs and larvae (Table 5) but no pupal predators were studied. Per predator species,  $3.0 \pm 0.3$  metrics were reported for egg predators and  $2.9 \pm 0.2$  metrics for larval predators. Although other predators, such as the stink bug *Supputius cincticeps* (Stål), were also studied (Silva et al., 2012), predation performance was not assessed. Out of eight performance metrics, attack rate, handling time and functional response type were routinely assessed for both egg and larval predators (Table 5; Fig. 3). Specifically, attack rate was assessed for 9 egg and 32 larval predators; handling time for 5 egg and 25 larval predators; and functional response type for 5 egg and 20 larval predators. Across studies and FAW host stages, there are no predators for which the full set of eight metrics have been reported. Species for which the most complete repertoire of performance metrics is in place include *P. nigrispinus* (7 metrics; larvae), *D. luteipes* (5; eggs, larvae) and the assassin bug *Rhynocoris marginatus* (Fabricius) (5; larvae). Surprisingly, only one metric was recorded for the egg predator with the highest attack rate i.e., the earwig *Euborellia annulipes* (Lucas) (Fig. 3; da Silva et al., 2009). Though unevenly logged or reported, experimental conditions proved more consistent than for other BCA guilds at  $25.3 \pm 0.3$  °C and  $61.3 \pm 1.3$  % for egg predators, or  $25.8 \pm 0.4$  °C and  $67.0 \pm 1.0$  % RH for larval predators across studies ( $n = 4$  and 31 taxon-level records). Nevertheless, a near-arbitrary selection of different performance metrics likely precludes proper agent selection for ABC or CBC endeavors.

Across laboratory studies, Brazilian strains of *E. annulipes* and *D. luteipes* exhibited the highest lifetime predation of FAW eggs (da Silva et al., 2009; 2022), while Brazilian strains of the lacewing *Chrysoperla externa* (Hagen) and lady beetle *Eriopis connexa* (Germar) consume most FAW larvae (Tavares et al., 2011; Silva et al., 2013; Table 5). Though not included in our analyses, Romero-Sueldo and Virla (2009) showed how

**Table 5**

Laboratory-based performance of egg and larval predators as assessed across the FAW global distribution range. For five performance metrics, we average the highest values across studies and experimental regimes i.e., study temperature. Immature development time refers to the duration between egg eclosion and adult emergence. Per exposed FAW development stage, predators are ranked by declining life-time predation rate i.e., maximum number of prey consumed. Holling's functional response type is indicated by Roman numerals. For larval predators, the range of exposed FAW developmental instars is indicated between brackets.

FAW stage	Species	Performance metric				
		Lifetime predation	Functional response type	Min. handling time (h)	Max. longevity (d)	Min. development time (d)
Egg	<i>Euborellia annulipes</i>	1,481.2 ± 0.0	–	–	–	–
	<i>Doru luteipes</i>	1,385.0 ± 0.0	–	–	29.8 ± 14.8	24.5 ± 6.4
	<i>Chrysoperla externa</i>	250.2 ± 0.0	–	–	–	19.3 ± 0.0
	<i>Propylaea japonica</i>	204.6 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Chrysoperla sinica</i>	192.3 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Eriopis connexa</i>	100.0 ± 0.0	–	–	–	16.3 ± 1.4
	<i>Mallada basalis</i>	85.1 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Harmonia axyridis</i>	25.6 ± 0.0	II	0.9 ± 0.0	–	–
	<i>Chrysoperla carnea</i>	–	II	0.3 ± 0.2	–	–
	<i>Orius insidiosus</i>	–	–	–	–	15.4 ± 0.0
Larva	<i>Chrysoperla externa</i> (1)	367.7 ± 0.0	–	–	–	18.0 ± 0.0
	<i>Eriopis connexa</i> (1)	275.9 ± 0.0	–	–	–	16.9 ± 0.0
	<i>Doru luteipes</i> *	272.6 ± 0.0	–	–	46.0 ± 0.0	14.1 ± 0.0
	<i>Hippodamia variegata</i> (1–2)	269.1 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Propylaea japonica</i> (1–2)	265.5 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Chlaenius bioculatus</i> (1–6)	248.4 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Coccinella septempunctata</i> (1–2)	233.1 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Cheilomenes sexmaculata</i> (1–2)	217.4 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Eocanthecona furcellata</i> (1–6)	190.1 ± 81.3	II, III	0.3 ± 0.1	20.0 ± 0.0	–
	<i>Rhynocoris marginatus</i> (2–6)	184.9 ± 0.0	–	1.9 ± 0.0	–	–
	<i>Harmonia axyridis</i> (1–2)	180.1 ± 101.5	II	0.3 ± 0.2	–	–
	<i>Chrysoperla sinica</i> (1–2)	166.7 ± 0.0	II	0.1 ± 0.0	–	–
	<i>Chrysopa pallens</i> (1–3)	90.5 ± 76.2	II	0.9 ± 0.8	–	–
	<i>Euborellia annulipes</i> (1–2)	89.2 ± 0.0	–	–	–	–
	<i>Mallada basalis</i> (1–2)	72.1 ± 0.0	II	0.3 ± 0.0	–	–
	<i>Euborellia pallipes</i> (2)	62.5 ± 0.0	II	0.4 ± 0.0	–	–
	<i>Sphedanolestes impressicollis</i> (1–3)	55.9 ± 0.0	II	0.4 ± 0.0	–	–
	<i>Sycanus fallen</i> (3–5)	47.6 ± 0.0	II	0.5 ± 0.0	–	–
	<i>Picromerus lewisi</i> (3–6)	32.8 ± 28.2	II	2.8 ± 2.4	–	–
	<i>Labidura riparia</i> (1)	31.5 ± 0.0	–	–	17.3 ± 0.0	–
	<i>Arma chinensis</i> (3–6)	31.5 ± 28.2	II	4.0 ± 3.6	–	–
	<i>Podisus nigrispinus</i> (3)	21.0 ± 8.9	II, III	0.9 ± 0.2	35.7 ± 7.2	18.2 ± 0.0
	<i>Zelus longipes</i> *	20.0 ± 0.0	–	2.4 ± 0.0	–	–
	<i>Sycanus croceouittatus</i> (3–5)	19.9 ± 15.9	II	7.1 ± 0.0	–	–
	<i>Orius sauteri</i> (1–2)	14.2 ± 4.4	II	0.5 ± 0.3	–	–
	<i>Andralus spinidens</i> (3–5)	12.2 ± 0.0	II	2.0 ± 0.0	–	–
	<i>Calosoma granulatum</i> *	–	–	–	5.0 ± 0.0	–
	<i>Chrysoperla rufilabris</i> (2)	–	–	0.9 ± 0.0	–	24.0 ± 0.0
	<i>Coleomegilla maculata</i> *	–	–	–	–	17.4 ± 0.0
	<i>Doru lineare</i> *	–	II	0.0 ± 0.0	–	–
	<i>Doru taeniatum</i> *	–	–	0.1 ± 0.0	–	30.0 ± 0.0
	<i>Euthyrhynchus floridanus</i> (3–4)	–	–	–	–	–
	<i>Geocoris punctipes</i> (1)	–	–	–	–	–
	<i>Geocoris uliginosus</i> (1)	–	–	–	–	–
<i>Orius insidiosus</i> (1)	–	–	–	–	–	
<i>Podisus maculiventris</i> (3–4)	–	–	0.1 ± 0.0	–	–	
<i>Pyemotes zhonghuajia</i> (2)	–	–	2.0 ± 0.0	–	–	
<i>Suppitiatus cincticeps</i> *	–	–	–	–	–	
<i>Zelus renardii</i> (1)	–	–	–	34.5 ± 0.0	34.3 ± 0.0	

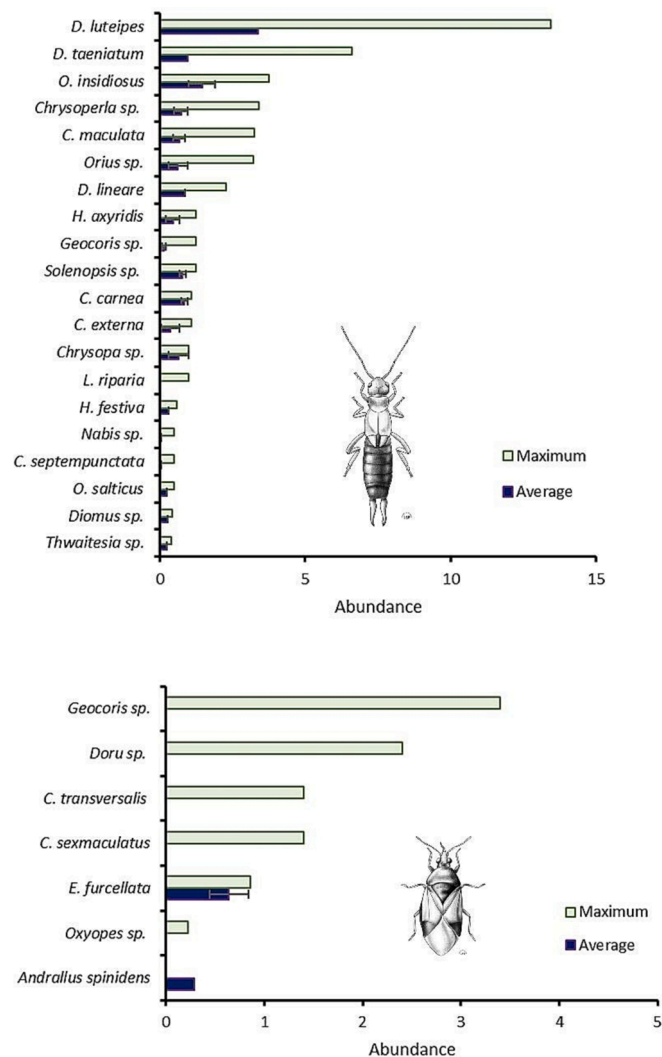
\* No information on the larval instar (or instar range) exposed to predation

*D. lineare* (Eschscholz) nymphs consume an average of 438.6 FAW eggs until adult molting. Other predator species, however, performed better on different metrics. For egg predators, Chinese strains of the lacewing *Mallada basalis* (Walker) exhibit the shortest handling time while Brazilian strains of *E. connexa* develop most quickly (Shi et al., 2022; Silva et al., 2013). For larval predators, an Argentinian strain of the earwig *D. lineare* exhibits the shortest handling time and a Brazilian strain of *D. luteipes* has the greatest longevity and shortest development time (Sueldo et al., 2010; da Silva et al., 2022).

Field-level performance (maximum or average abundance) has been determined for 52 canopy-dwelling taxa in the native range and seven taxa in the invasive range (Fig. 6). In the native range, the earwigs *D. taeniatum* and *D. luteipes* attain by far the highest abundance across sites. Specifically, up to 13.4 *D. luteipes* were recorded per maize plant in Brazil (Zuim et al., 2023), while *D. taeniatum* adults and nymphs reach

abundance maxima of 6.6 individuals per plant in Honduran maize crops (Jones et al., 1989). Further, the pirate bug *O. insidiosus* reaches the second-highest average abundance (1.4 ± 0.5 individuals per plant) across sites. Notably, highly abundant soil-dwellers, such as the fire ant *Solenopsis geminata* (Fabricius), are only sporadically sighted at abundance levels up to 0.3 individuals per plant (n = 2 studies). Data from the invasive range are more limited, only covering seven different taxa. Of these, *Geocoris* sp. (India) and *Doru* sp. (Indonesia) reach the highest abundance levels of 3.4 and 2.4 individuals per plant, respectively (Udayakumar et al., 2021; Tarigan et al., 2023).

Similar to FAW parasitoids, laboratory-based research attention to canopy-dwelling predators was not entirely in accordance with their field abundance. The number of laboratory studies per taxon did not relate to its maximum field abundance (Spearman Rank,  $\rho = 0.373$ ,  $p = 0.210$ ,  $n = 13$ ), and logistic regression provided a moderate fit between



**Fig. 6.** Population levels of the 20 most abundant foliage-foraging arthropod predators in maize fields within the FAW native (top) and invasive (bottom) range. Maximum and average (mean  $\pm$  SE) abundance are plotted for each species based upon the actual availability of the respective metrics in the original studies. Predator abundance is either assessed during one single ‘snap shot’ census or at multiple instances during the maize cropping cycle. Abundance is expressed as the number of individuals per plant, combining all developmental stages of a given species. In the invasive range, abundance data are only available for seven canopy-dwelling predators. Full species names are provided in [Suppl. Table 3](#).

the field abundance of a given taxon and its actual coverage in laboratory studies (Fig. 5). Hence, highly-abundant taxa do not necessarily receive laboratory-level scrutiny and vice versa. For example, highly abundant predators such as *Chrysoperla* sp. in southern Mexico (3.4 individuals/plant; [Penagos et al., 2003](#)), *Orius* sp. in Brazil (3.2; [Bortolotto et al., 2014](#)) and *Doru* sp. in Indonesia (2.4; [Tarigan et al., 2023](#)) have yet to be studied in the laboratory. Conversely, predators that attain relatively low field abundance such as *Geocoris punctipes* (Say) (one individual per 114 plants in Peru) ([Quispe et al., 2017](#)) have been subject to laboratory-based research. At the species level, these patterns are exacerbated. Out of 24 predator species with known maximum field-level abundance, per-capita FAW larval or egg predation has only been determined for a respective seven (29.2 %) and three (12.5 %) species ([Table 5](#)). Amongst the ten most abundant predator species, egg predation has been recorded for three species, *D. luteipes*, *Harmonia axyridis*, *C. externa*, and larval predation has been assessed for two

species, *Eocanthecona furcellata* (Wolff) and *Labidura riparia* (Pallas). For highly abundant species such as *D. taeniatum*, *O. insidiosus* or *Coleomegilla maculata* (DeGeer), predation rates have not been assessed. Hence, whether or how field abundance and FAW biological control efficacy relates to one or more laboratory-derived performance metrics is difficult to assess.

In contrast with other BCA guilds, insights into FAW population dynamics throughout the maize growing cycle were reported in 38.5 % of field studies and only a fraction of these studies did not present FAW infestation data ([Table 2](#)). Yet, as FAW infestation pressure is expressed using variable currencies, further efforts to quantitatively relate predator abundance to FAW population dynamics may be obstructed.

## 5.2. Overlooked taxa

Ants prey upon multiple pests in temperate and tropical crops ([Perfecto and Snelling, 1995](#); [Armbrecht and Perfecto, 2003](#)) and are viewed as efficient biological control agents because of their voracity, effective scout-and-recruit foraging and omnivorous feeding habits ([Risch and Carroll, 1982b](#); [Drummond and Choate, 2011](#); [Anjos et al., 2022](#)). Yet, while ants are likely the most abundant and voracious invertebrate predators in (sub-)tropical agro-ecosystems, their role as BCAs is critically overlooked. Even in the FAW native range, less than a handful of studies cover ant predation. A sequence of groundbreaking studies during the 1970 s-80 s however emphasized how ant conservation should be a core component of FAW management especially in small-holder maize systems ([van Huis, 1981](#); [Risch and Carroll, 1982b](#); [Castiñeiras et al., 1982](#); [Castiñeiras and Castellanos, 1983](#); [Carroll and Risch, 1983](#)). Our review, however, does not do fully cover these studies given that they examined soil-foraging ants as compared to canopy-dwelling ones.

In the early 1900s, US scientists recorded high levels of FAW egg and/or larval predation by *Iridomyrmex humilis* (Mayr), *Pogonomyrmex barbatus* (Smith) and the fire ant *Solenopsis geminata* ([Luginbill, 1928](#)). In Mesoamerica, pioneering work by [van Huis \(1981\)](#) and [Perfecto \(1991\)](#) pointed at the role of *Ectatomma ruidum* (Roger), *Pheidole radowszkoskii* Mayr and *S. geminata* in suppressing FAW populations. Equally, 55 different ant morpho-species were recorded in Honduran maize fields, with *S. geminata* the most abundant on tuna fish bait ([Wyckhuys and O’Neil, 2007](#)). Due to its extensive foraging, role as pioneer species and omnivorous feeding habits including weed seed granivory, *S. geminata* acts as a keystone predator in tropical maize agroecosystems, where it preys upon FAW, shapes community structure ([Risch and Carroll, 1982b](#)) and ultimately underpins ecological resilience ([Cabell and Oelofse, 2012](#)). Equally, ants act as prominent predators of FAW in the Caribbean ([Wilson, 1923](#); [Vázquez et al., 2005](#); [Alfonso-Simonetti, 2017](#)). In those settings, *S. geminata* routinely attains the highest abundance or activity-density followed by species such as *Wasmannia auropunctata* (Roger) or *Paratrechina longicornis* (Latreille). In other countries such as Brazil, Colombia or Argentina, there are no observational or experimental studies on the role of ants in FAW biological control. The lack of information from Mexico, the primary center of origin of maize and where ants are widely studied ([Dattilo et al., 2020](#)) and FAW is a long-standing issue ([Blanco et al., 2014](#)), is paradoxical.

In addition to predaceous ants, erythraeid mites (*Balaustium* sp.) feature as the most abundant FAW egg predators in traditionally-managed, weedy maize fields in Mexico ([Jaraleño-Teniente et al., 2020](#)). Aside from one single anecdotal report of larval predation ([Luginbill, 1928](#)), this constitutes the first observation of FAW x mite associations and suggests that their occurrence and potential role in FAW biological control has been systematically overlooked. In contrast, in the FAW invasive range, predatory mites have received more attention. In China, researchers have explored the potential of *Pyemotes zhonghuajia* Yu, Zhang & He (Acari: Pyemotidae) as a FAW biological control agent ([Liu et al., 2020](#)). One single *P. zhonghuajia* female induces mortality of young larvae, while a density of 40 mites/individual yields



complete mortality of all FAW larval instars and prepupae. Aside from inflicting direct mortality, mite inoculation negatively affect FAW fitness, immune response and other life-history traits (Song et al., 2023). Short periods of starvation (24 h) substantially improve efficacy (Tian et al., 2020) and potentially can be used to precondition mites in augmentative release programs. Experimental releases of *P. zhonghuajia* in sorghum confirm its role as an efficacious FAW predator (Feng et al., 2022), although its cost effectiveness needs to be scrutinized. In Nigeria, the parasitic mite *Trombidium* sp. has been found infesting young larvae in the field (Ogunfunmilayo et al., 2021). Ectoparasitic stages of *Trombidium* sp. reduce larval feeding, development and movement while mobile stages directly prey upon early-instar larvae. As mites are widely used for biological control and can easily be mass-produced on inexpensive food sources (Vangansbeke et al., 2023), newly-recorded species such as *Balaustium* sp., *Trombidium* sp. and *P. zhonghuajia* might soon find a place in augmentative biological control programs targeting FAW.

### 5.3. Next steps

Exophytic herbivores tend to suffer substantially higher mortality by predators (and pathogens) than endophytic ones especially in tropical settings (Hawkins et al., 1997). As only late-instar larvae are protected inside the maize whorl, invertebrate predators often act as the main mortality factor of FAW eggs, larvae and pupae (Pair and Gross, 1989; Varella et al., 2015; Jaraleno-Teniente et al., 2020). Predation features notably in the 90–100 % mortality of early FAW developmental stages in Brazil (Varella et al., 2015) and Colombia (Murillo, 2014) and causes an average 95.8 % pupal mortality in Georgia, USA (Pair and Gross, 1989), thus slowing inter-generational population build-up. Even in biodiversity-poor settings in the invasive range, ground-dwelling predators cause up to 100 % mortality of late-instar larvae and pupae (Wyckhuys et al., 2023b), which could be ascribed to the ineffectiveness of evolved FAW anti-predator responses (Culshaw-Maurer et al., 2020). Further, prominent omnivores such as *Diabrotica speciosa* (Germar) or cockroaches also engage in FAW control (Menezes-Netto et al., 2012; Omoregie et al., 2023). However, nearly all published studies erroneously infer functional interactions i.e., predation from co-occurrence (Blanchet et al., 2020). As all FAW predators are polyphagous and likely either obligate or facultative omnivores, they tend to represent 'lying-in-wait' instead of 'search-and-destroy' agents (Murdoch et al., 1985) and their efficacy can be modulated by altering prey/non-prey resources, prey richness or competition (Katano et al., 2015; Capinera, 2017; Perier et al., 2022; Saha et al., 2023). If this is done effectively, maize could be grown without any insecticide use (Carrillo-Sánchez, 1993).

Opportunities to expand predation may be limitless (Gross and Pair, 1986), but the potential of predator CBC remains critically underexplored and untapped. Overall, it seems rational to start exploring CBC options for the most abundant and voracious predators (e.g., *D. luteipes* and *D. taeniatum*), the latter attaining absolute maxima of 100 individuals per plant in late-season maize (Van Huis, 1981). Yet, beyond baseline insights into their biology, foraging decisions, insecticide sensitivity or behavioral ecology (Naranjo-Guevara et al., 2017; Pacheco et al., 2021; Moreira et al., 2023), practical strategies to conserve or enhance their field populations have yet to be devised. The ability of *D. taeniatum* to develop and reproduce on pollen (Jones et al., 1988) offers the prospect of (natural, artificial) pollen supplementation. Equally, grass strips or residue retention in manually harvested systems (Fonteyne et al., 2023) could carry earwig populations over between cropping cycles, but this has not been investigated. Hence, except for small-scale fields bordered by tall grasses (Wyckhuys and O'Neil, 2007), the biological control capital that accrues over a cropping cycle is lost due to combine harvesting or residue burning. The same lack of CBC progress applies to the lady beetles, syrphids and erythraeid mites that prey upon eggs (Menezes-Netto et al., 2012; Murillo, 2014; Varella et al., 2015; Jiron-Pablo et al., 2018) or the carabids, staphylinids and ants that

attack pupae (Pair and Gross, 1989; Wyckhuys et al., 2023b). For other abundant taxa such as lacewings, minute pirate bugs or geocorids, in-field dynamics and predation rates have yet to be assessed, and basic ecological information is absent. There may however be myriad strategies to enhance the resident populations of all these predators. Inventive work in the 1980 s showed how foliar sprays of aqueous FAW larval homogenates raise *C. maculata* and *G. punctipes* recruitment 11.4-fold (Gross et al., 1985a), but this research has since not advanced. Research intensity also differs markedly between countries in the native range, with recent studies almost exclusively performed in Brazil and Mexico. Context-specific research however is essential, as universal CBC solutions are nearly impossible due to large spatio-temporal variation in predator community composition in different environments. Meanwhile, in the invasive range, even rudimentary knowledge about FAW predator identity, numerical abundance and seasonal dynamics is lacking.

Many studies count with restricted sampling, are geared towards few taxa and are not replicated over time; they therefore offer an incomplete understanding of FAW predation. Direct observation, although time-consuming, may clarify the contribution of certain taxa but can also be misleading. Strikingly, all studies from the native range record foliage-foraging predators through day-time censuses or direct observation (e.g., Hoballah et al., 2004; Wyckhuys and O'Neil, 2007) even though the prevailing actors, such as earwigs and ants are mostly nocturnal (Norasmah et al., 2006). As a result, social wasps are seen as key predators in Mesoamerica (Gonzalez, 1993), while their role in FAW biological control is likely marginal. Infra-red videography or molecular gut content analysis can help to gauge the impact of nocturnal FAW predation (Santos-Neto et al., 2010; Maggio et al., 2022). Lastly, surveys routinely comprise one-time sampling 'snapshots' (Shylesha et al., 2018; Sharanabasappa et al., 2019; Keerthi et al., 2020b), and thus preclude a reliable assessment of the contribution of early-season predation by agents such as ants, ballooning spiders or pirate bugs.

Crop diversification, conservation agriculture and landscape-level heterogeneity raise predator abundance, but the evidence base is weak. For example, weediness favors the two main ground-dwelling predators in Nicaraguan maize fields, the carabid *Galerita* sp. and the gelastocorid *Nerthra fuscipes* (Guérin-Méneville) (Van Huis, 1981), but whether this translates into enhanced biological control is unknown. Natural or semi-natural habitats provide nesting sites, shade, shelter and other resources for predators, such as ants (Tscharntke et al., 2007; Sobek et al., 2009) and facilitate their spillover into neighboring annual crops (Tscharntke et al., 2005; Holzschuh et al., 2009). Proper crop management is equally important; no-till systems favor soil-dwelling predators (Pineda et al., 2012), residue retention enhances early-season biological control (Rivers et al., 2016) and weediness favors predator abundance (Penagos et al., 2003). Pioneering work in the 1980 s showed how maize x bean intercropping raises ant-mediated FAW biological control (Perfecto and Sedilles, 1992), but follow-up studies are needed. Indeed, legume integration carries ample potential (Wyckhuys et al., 2023a) as their constitutive secretion of extra-floral nectar fuels carnivores, such as lady beetles or *S. geminata* (Lanza et al., 1993; Lundgren, 2009; Heil, 2015), but these interactions are seldom assessed. Also, the potential of artificial nectaries to enable predator recruitment in disturbed settings should be explored (Schifani et al., 2020). Lastly, pesticide phasedown may promote FAW biological control more effectively than crop diversification for predators, such as ants or carabids (Perfecto, 1990; Perfecto and Sedilles, 1992; Armenta et al., 2003; Dassou et al., 2021).

Almost 40 different larval predators have been evaluated under laboratory conditions, with more than half of these studied in China or India over the past 3–4 years. In the native range, laboratory-based performance has routinely been investigated in the frame of non-target impact assessments of insecticides (Tavares et al., 2010; Hernández-Juárez et al., 2016; Soares et al., 2019) or genetically-modified GM crops (e.g., Dutra et al., 2012; Tian et al., 2012; Su

et al., 2015), or geared towards laboratory mass-rearing without considering in-field conservation. Thus, while per-capita predation rates are known for multiple lacewings, stink bugs or lady beetles, their in-field population dynamics and ecological interactions are unknown. Hence, these data are of limited use to inform CBC. Additional insights into foraging or nutritional ecology, climatic adaptability or insecticide sensitivity have only been gained for a subset of taxa (Naranjo-Guevara et al., 2017; Zeng et al., 2021; Xu et al., 2023; Zhu et al., 2023). Meanwhile, ground-foraging predators such as ants, staphylinids or ground beetles consistently attain high abundance or activity-density (Fernandes et al., 2007), but laboratory studies that examine their biology or feeding ecology are rare (but see Young, 2008 for the carabid *Calosoma sayi* Dejean).

Compared to parasitoids or microbials, predators have received minor attention from an ABC angle. In recent years however, laboratory-based predation capacity and fitness parameters have been recorded for at least 22 predator species in China or India, with a view to future augmentative releases. These include stink bugs, assassin bugs, earwigs, lady beetles, lacewings and the predatory mite *P. zhonghuajia*. Though this work is praiseworthy, underlying criteria for organismal selection are often unclear and the suitability of individual taxa for *S. frugiperda* ABC likely varies: charismatic species such as *E. fuscicornis* and *M. basalis* receive disproportionate degrees of research attention (Nyunt, 2008; Sattayawong et al., 2016), but are may not necessarily be the best BCAs. So far, most ABC work has been restricted to the laboratory, with only limited (published) field-level evaluation of augmentative releases of *E. fuscicornis* in India and China (Keerthi et al., 2020a; Kenis et al., 2022) and *P. zhonghuajia* in China on sorghum (Feng et al., 2022). Although augmentative releases of large-bodied predators may bolster ecological illiteracy of farmers and promote societal awareness of biological control (Wyckhuys et al., 2019), practicality and cost-effectiveness of these endeavors needs to be scrutinized. In the end, these parameters will determine whether predator-based ABC will prosper.

## 6. Overcoming the taxonomy challenge

Biological control science initiates from the foundational principle of biodiversity (González-Chang et al., 2020), and sound taxonomic description is thus of fundamental importance to its overall success. Yet, natural history work has been systematically geared towards temperate regions and vertebrates, and a ‘full’ picture of insect biodiversity has merely been gained for 0.5 % of the terrestrial surface (García-Rosello et al., 2023). While the megadiverse biomes of the tropics may harbor large shares of the 4.5–7.5 million insect species and the one trillion ( $10^{12}$ ) microbiota on Earth (Locey and Lennon, 2016; Finn et al., 2023; Srivathasan et al., 2023), most of it remains unknown to science. Invertebrate biological control may be disproportionately more important in the tropics (Roslin et al., 2017), yet only 43 % of tropical biodiversity studies cover invertebrates (Titley et al., 2017) and taxonomic neglect inversely correlates to organismal body size (Gaston, 1991). This is also evident in our analyses. Our listing of 46, 304 and 215 genus- and species-level taxa of FAW-associated entomopathogens, parasitoids and foliage-foraging predators (Suppl. Table 1,2,3) likely constitutes a small slice of the BCAs that operate in the world’s ~200 million ha maize crop. Hence, much ground still needs to be covered in terms of BCA discovery and description.

Invertebrate and microbial taxonomy involves dedicated, painstaking work by (often under-funded) experts. The road towards attaining accurate and reliable species-level identification of BCAs thus tends to be long and circuitous. We illustrate this by clarifying the taxonomic status of the scelionid wasp, *Te. remus*. The state of species-level taxonomy in Scelionidae is highly variable, and detailed studies are restricted to species that affect high-profile invasive pests. The “deep clean” that occurs with a well-executed taxonomic initiative often involves examination of historical type specimens. In turn, this reveals long-standing taxonomic issues, names that have languished in

obscurity and a proliferation of confusing or misleading names and synonyms. These issues could soon be resolved through fast-evolving taxonomic intelligence services (Upham et al., 2021).

Taxonomic uncertainties are apparent in the FAW-associated species of the genus *Telenomus* Haliday (Scelionidae): *Telenomus heliothidis* Ashmead, *Telenomus minutissimus* Ashmead, *Telenomus remus*, and *Telenomus solitus* Johnson (Arredondo-Bernal and Perales-Gutiérrez, 1998). The authors also report *Te. hawaii*, which likely is a misspelling of *Telenomus nawai* Ashmead that was recorded from *Spodoptera litura* Fab. eggs (Fukuda et al., 2007) and has in turn been misspelled as *Te. hawaii* (Bahena and Cortez, 2016). As *Te. heliothidis* and *Te. minutissimus* have not been treated taxonomically since their original descriptions, we limit our discussion to *Te. remus*: an effective FAW parasitoid that has been identified by comparing the holotype to reared specimens (Liao et al., 2019). It has been properly described from specimens reared from *Spodoptera* egg masses near Kuala Lumpur, Malaysia (Nixon, 1937), is morphologically inseparable from *Te. nawai* from Gifu, Japan, and *Telenomus soudanensis* (Risbec) from West Africa (Polaszek, 1998), and widely distributed. Specifically, the H1 haplotype is shared by *Te. remus* specimens from South and Central America, South Asia, southern China and Africa (Wengrat et al., 2021). Such expansive geographical range is also evident amongst other scelionids e.g., *Psix striaticiceps* (Dodd) and *Gryon aetherium* Talamas (Johnson and Masner, 1985; Talamas et al., 2021), and likely relates to polyphagy and the broad distribution of its spodopteran hosts including *S. frugiperda* (Wojcik et al., 1976). Moreover, prior to the FAW invasion, *Te. remus* already existed in Africa as a possible conspecific of *Te. soudanensis* (Kenis et al., 2019).

A proper delineation of species is pivotal to biological control science. Species or conspecifics have traditionally been separated based upon morphological characters e.g., size, shape or position of setae and sensilla. Yet, taxonomic uncertainties can now be resolved by cross-breeding presumed species in the laboratory (Kenis et al., 2019; Tortorici et al., 2019; Hogg et al., 2021), examining host records, DNA-barcoding or tactical use of simple molecular tools. Thus, images of the holotype specimen of *Te. remus* and *Te. nawai* (Talamas et al., 2017; Liao et al., 2019) must be interpreted through pluralistic, integrative taxonomy thrusts.

In the superfamily Ichneumonoidea, the state of species-level taxonomy is also very variable. Several genera of Braconidae and Ichneumonidae are highly diverse and currently poorly understood. Taxonomic keys are either lacking or outdated, and presence of cryptic species complicates species-level identification. Braconid genera such as *Aleiodes*, *Chelonus* and the related *Microchelonus*, *Cotesia*, *Meteorus*, and *Microplitis* and Ichneumonidae genera such as *Campoplex*, *Charops*, *Diadegma*, *Eiphosoma*, *Enicospilus*, *Netelia*, *Ophion* and *Temelucha* are probably the most difficult. Any of them could potentially contain large errors, and a tactical use of molecular tools can resolve those uncertainties.

## 7. Rebooting biological control science

Without a doubt, considerable effort has gone into characterizing FAW-associated natural enemies globally. More than 100 agents have been evaluated under controlled laboratory settings and the global knowledge of FAW biological control has, thus, been advanced. Fruit of the painstaking work of countless scientists can only be applauded. Yet, in light of the rapid proliferation of chemical control for FAW and myriad other pests (Kenis et al., 2022; Shattuck et al., 2023; Tapa-Yotto, 2023), we fail to effectively harness what nature has provided (Gross and Pair, 1986). First and foremost, we only possess rudimentary knowledge of the full complement of BCAs in any particular setting (Gross, 1987), especially, although not exclusively, in its invasive range. Given that over 1,000 predator species exist in soybean fields in Florida, USA (Whitcomb, 1974), the known BCAs are most certainly a tiny proportion of the entire FAW natural enemy complex in the global maize crop. Brazil, USA, Mexico, China and India are prime contributors to this

knowledge stockpile, while scant progress is made in other geographies. Serendipity features notably in our status of knowledge. For instance, foundational knowledge on natural enemy biodiversity has often been acquired through the mandatory bio-inventories within GM maize risk assessments. The biodiversity discovery phase however cannot be skipped and clear priorities need to be set (Soulé, 1990), especially at the current pace of biodiversity loss (Eisenhauer et al., 2019). Next, as field or laboratory performance has only been measured for approx. 40 % of known BCAs, there is a critical void of information on countless biota. Despite decennia of FAW research, it remains difficult to determine whether and how certain biota actually contribute to FAW biological control. All too often, critical research shortfalls leave us ill-informed about their role as BCAs and how such is mediated by (biotic, abiotic) aspects of the farming system. With a near-total inertia on CBC i.e., arguably the preferred option for open-field agriculture (Lewis et al., 1997; Michaud, 2018), ecological intensification becomes a distant if not unattainable goal (Vanbergen et al., 2020). Hence, to fully tap the ecosystem service of biological control, a step-change is needed (Kremen, 2005) in which the following five elements can remediate critical shortcomings.

*Move beyond stamp collecting.* Ernest Rutherford, ‘father’ of nuclear physics, dismissed most scientific disciplines as mere ‘stamp collecting’. Evidently, the science of biological control does not compare to Victorian-era postage stamp collecting. But laymen may perceive it as such and the most assiduous scientists suffer from such stigma. As multiple studies solely offer single-guild ‘snap-shot’ surveys or incidental parasitoid censuses without the accompanying pest incidence records, they also feed this perception. Counting species or individuals is easy, but understanding how these figure into FAW population dynamics in real-world ecosystems is no small chore and hence regularly ignored (Balvanera et al., 2014). The mere cataloging of biodiversity is still warranted to remediate the taxonomic neglect on BCAs in multiple countries (Srivathsan et al., 2023). Once biodiversity has been documented, this knowledge also needs to be properly synthesized. For example, range modeling and machine learning could yield high-resolution BCA distribution maps, as has been done for ants (Kass et al., 2022). Meanwhile, the functional role of individual taxa or species richness urgently needs to be ascertained (Rodríguez and Hawkins, 2000). We need to comprehend biostructure i.e., the network of inter-organismal interactions and the ecological processes (and functions) that sprout from them (McCann, 2007). This could be achieved by systematically gathering evidence through standardized methodologies i.e., appropriate timing, sampling frequency and uniform abundance metrics (Kenis et al., 2022) or manipulative assays. Comprehensive bio-inventories (Lundgren and Fausti, 2015), eventually paired with network analyses, fit seamlessly into such exercises. Also, proper follow-up needs to be given to ‘loose’ functional ecology ends, such as the asserted role of *S. geminata* and possibly *Doru* spp. as keystone species or the critical importance of early-season (egg) predation.

*Draw upon the biodemographic toolbox.* Our understanding of the ecological underpinnings of FAW biological control is inordinately weak. Quantitative metrics of taxonomic specificity, robust ecological theories or advanced modeling all underpin classical and augmentative biological control (Knipling, 1977; Van Driesche et al., 2004; Plouvier and Wajnberg, 2018; Abram et al., 2021). Yet, for FAW CBC, a mere ‘divining rod’ steers research effort towards the most promising agents. In-field organismal abundance irregularly informs laboratory-level scrutiny, where up to eight metrics may (or may not) shine light on their actual efficacy. This decision-making process has to be sharpened and trait-based approaches are often touted as a game-changer (Perović et al., 2018). While such tools are being developed, demographic analyses can clarify the impact of individual BCAs or gauge their (collective) contribution to pest population regulation (Bellows et al., 1992; Carey, 2001). Life table analyses constitute the ‘gold standard’ in biological control studies, yet are critically underused in FAW research (but see Varella et al., 2015). Instead, to judge the respective role of predators or

parasitoids, researchers tend to resort to direct observation (DO) or the rearing of parasitoids from field-collected larvae and sentinel egg masses. However, DO is impeded by species-specific activity patterns (DeBach, 1964) and day-time recordings do not clarify the role of crepuscular or nocturnal predators. These issues can be resolved partly by employing other tactics such as Malaise trapping, sweep-netting, time-laps or infrared videography, pitfall traps or leaf-litter sampling. Pairing DO with exclusion cages or recordings of feeding duration and patterns can help to quantify per capita consumption rates (Latham and Mills, 2009) while serological analyses and molecular gut content assays can complement or even supplant life table techniques (Furlong, 2015). These tools should be used far more extensively across geographies and farm contexts.

*Head back to the field.* FAW pest management programs need to be anchored in pesticide-free diversified smallholder fields (Van Huis, 1981), such as Mesoamerican maize polycultures or ‘milpas’ and maize-legume intercrops in Asia and Africa. In these systems, BCA communities are consistently more abundant, speciose and afford superior levels of FAW biological control (Perfecto and Sedilles, 1992; Dassou and Tixier, 2016; Meagher et al., 2016; Ngangambe and Mwatawala, 2020; Fonteyne et al., 2023). By examining how BCA numbers and biological control service indices (*sensu* Gardiner et al., 2009) vary along an intensification gradient (Duffy, 2002), effective CBC options could be identified. In such endeavor, an ecological ‘systems perspective’ i.e., looking beyond single taxa or guilds and accounting for spatial and temporal heterogeneity (Tylianakis et al., 2008) helps to comprehend biodiversity-ecosystem function relationships. Field trials ideally are replicated across sites and years, as to capture the environmental determinants and spatio-temporal response scales of individual organisms and overall FAW biological control (Kremen, 2005). Agro-climatic, edaphic, crop management and landscape parameters all shape FAW biological control outcomes (Noma et al., 2010; Karp et al., 2018; Moya-Raygoza and Figueroa-Bautista, 2021), and their respective roles need to be carefully disentangled. In the end, such multivariate assessments will be instrumental in amending the prevailing belief that one single ‘silver bullet’ BCA, instead of a complex of interacting invertebrate and microbial agents, provides effective biological control. Lastly, field work with realistic controls and decision-relevant endpoints (i.e., yield, profit) is indispensable -though rarely performed- when evaluating augmentatively released or naturally occurring BCAs.

*Integrate or perish.* Disciplinary fragmentation constitutes a formidable hurdle for biological control science and practice (Brodeur et al., 2018). Scientists that cover particular BCA guilds often act in isolation and irregularly engage with other agriculture-related disciplines, such as plant breeding, soil science or agronomy. Silo attitudes are both counterproductive and counterintuitive. Through enhanced functional or response diversity and regardless of eventual intraguild predation (Polis and Holt, 1992; Rosenheim et al., 1995), diverse natural enemy communities indeed provide improved, temporally stable pest control (Letourneau et al., 2009; Northfield et al., 2014; Dainese et al., 2019; Sánchez-Hernández et al., 2021). Further, entomopathogen applications often have no or ephemeral adverse impacts on invertebrate BCAs (Escribano et al., 2000; Barros et al., 2020; Avery et al., 2022; Faria et al., 2022), and the latter routinely vector beneficial microbiota. Under cross-guild biological control, the modes of action and lethal and sublethal effects on specific FAW developmental stages of naturally-occurring and released BCAs are matched in order to enhance their aggregate biological control impact. For example, resident parasitoids and anthocorid or coccinellid predators can reduce egg hatchability while entomopathogens kill FAW neonates that emerge from the remaining eggs. Equally, CBC or ABC approaches need to be methodically integrated with behavior-modifying chemicals or defense priming, agroecological practices such as spatial/temporal crop diversification, manuring or mulching and crop varietal resistance or tolerance (Peterson et al., 2018; Harrison et al., 2019; Kenis et al., 2022). Using the ‘tritrophic defense’ concept (Stenberg et al., 2015; Wyckhuys et al.,



2022), biological control scientists can team up with plant breeders, soil microbiologists and landscape ecologists to jointly put in place ecologically sustainable FAW management.

**Muster broad stakeholder support.** Deficient stakeholder engagement, scant financial support and an overall lack of enabling policies constitute key obstacles in the global diffusion of biological control (Barratt et al., 2018). All these issues directly relate to the way biological control science is performed. Biological control carries resounding societal benefits, but scientists routinely fail to properly measure or communicate them to decision makers, farmers and myriad other stakeholders including consumers. Broad societal awareness is essential to leverage financial support, especially in developing countries where governments routinely invest a very small sliver of GDP in (agricultural) research (Ciocca and Delgado, 2017; Galina et al., 2023). In addition, global funding for biological control research represents less than 1 % of the budgetary resources that are allotted to chemical control (Van Lenteren, 2012). Steadfast public support can generate critical momentum for biological control, as evidenced by the decade-long Farmer Field School (FFS) program in Asia and Latin America (Waddington et al., 2014). Yet, since the 1990 s, financial shortfalls have caused an erosion of core technoscientific capacity for biological control in many countries (Warner et al., 2011; Thorburn, 2015; Arredondo-Bernal and González-Cabrera, 2020). Clearly, without revived support for nature-friendly farming, meeting the ambitious goals of the Kunming-Montreal Global Biodiversity Framework may become a difficult predicament. A major funding boost, coupled with a phase-out of harmful subsidies, can reconstitute critical capacity and put (FAW) biological control back on the rails.

## 8. Final considerations

Throughout the tropics and subtropics, the fall armyworm is impacting food security, jeopardizing farmer livelihoods and triggering pesticide overuse. Agroecological and biodiversity-based measures such as biological control constitute safe, cost-effective and environmentally-sound alternatives to pesticidal control and offer ‘best-bet’ solutions for millions of (smallholder) cereal growers. Our review shows a robust, fast-expanding scientific foundation for FAW biological control. Hundreds of BCAs have been discovered, described and subject to laboratory- or field-level scrutiny. Across the FAW native and invasive range, tens of predator and parasitoid species occur at elevated field abundance while entomopathogens inflict high rates of egg or larval mortality. Given this vast knowledge stockpile and the mere existence of numerous high-performing BCAs, biological control scientists find themselves at the brink of exciting new opportunities and solutions. However, to effectively harness this biodiversity for sustainable FAW management, the scientific enterprise faces several shortcomings: 1) Organismal discovery and description, the very foundation of biological control, encounters critical geographic and taxonomic biases; 2) Simple BCA inventories or abundance ‘snapshots’ far outweigh the number of methodical assessments of population dynamics; 3) BCA numerical abundance is irregularly recorded in concert with (standard) pest infestation metrics; 4) Large-bodied, day-active BCAs receive uneven attention, while nocturnal or pupal predators are disregarded; 5) A critical mismatch exists between laboratory and field research attention with field- or laboratory-level evaluations pending for numerous top-performing BCAs; 6) While many biota are evaluated for augmentation purposes, conservation biological control receives insufficient attention. In addition to remediating these deficiencies, it is crucial to fortify the ecological underpinnings of FAW biological control and to methodically link species abundance to ecosystem-service provision. We are hopeful that our guidelines can improve the measurement, analysis and management of the ecosystem service of biological control and put it into practice for FAW mitigation globally.

## CRedit authorship contribution statement

**Kris A.G. Wyckhuys:** . **Komivi S. Akutse:** Writing – review & editing, Data curation. **Divina M. Amalin:** Writing – review & editing, Data curation. **Salah-Eddin Araj:** Writing – review & editing, Data curation. **Gloria Barrera:** Writing – review & editing, Data curation. **Marie Joy B. Beltran:** . **Ibtissem Ben Fekih:** Writing – review & editing, Data curation. **Paul-André Calatayud:** Writing – review & editing, Data curation. **Lizette Cicero:** Writing – review & editing, Data curation. **Marcellin C. Cokola:** Data curation. **Yelitza C. Colmenarez:** Writing – review & editing, Data curation. **Kenza Dessauvages:** Writing – review & editing, Data curation. **Thomas Dubois:** Writing – review & editing, Data curation. **Léna Durocher-Granger:** Writing – review & editing, Data curation. **Carlos Espinel:** Writing – review & editing, Data curation. **Patrick Fallet:** Writing – review & editing, Data curation. **José L. Fernández-Triana:** . **Frederic Francis:** Writing – review & editing, Data curation. **Juliana Gómez:** Writing – review & editing, Data curation. **Khalid Haddi:** Writing – review & editing, Data curation. **Rhett D. Harrison:** Writing – review & editing, Data curation. **Muhammad Haseeb:** Writing – review & editing, Data curation. **Natasha S.A. Iwanicki:** Writing – review & editing, Data curation. **Lara R. Jaber:** Writing – review & editing, Data curation. **Fathiya M. Khamis:** Writing – review & editing, Data curation. **Jesusa C. Legaspi:** Writing – review & editing, Data curation. **Refugio J. Lomeli-Flores:** Writing – review & editing, Data curation. **Rogério B. Lopes:** Writing – review & editing, Data curation. **Baoqian Lyu:** Writing – review & editing, Data curation. **James Montoya-Lerma:** Writing – review & editing, Data curation. **Melissa P. Montecalvo:** Writing – review & editing, Data curation. **Andrew Polaszek:** Writing – review & editing, Data curation. **Tung D. Nguyen:** Writing – review & editing, Data curation. **Ihsan Nurkomar:** Writing – review & editing, Data curation. **James E. O’Hara:** Writing – review & editing, Data curation. **Jermaine D. Perier:** Writing – review & editing, Data curation. **Ricardo Ramírez-Romero:** Writing – review & editing, Data curation. **Francisco J. Sánchez-García:** Writing – review & editing, Data curation. **Ann M. Robinson-Baker:** Data curation. **Luis C. Silveira:** Writing – review & editing. **Larisner Simeon:** Data curation. **Leellen F. Solter:** Writing – review & editing, Data curation. **Oscar F. Santos-Amaya:** Writing – review & editing, Data curation. **Elijah J. Talamas:** Writing – review & editing, Data curation. **Wagner de Souza Tavares:** Writing – review & editing, Data curation. **Rogelio Trabanino:** Writing – review & editing, Data curation. **Ted C.J. Turlings:** . **Fernando H. Valicente:** Writing – review & editing, Data curation. **Carlos Vásquez:** Writing – review & editing, Data curation. **Zhenying Wang:** Writing – review & editing, Data curation. **Ana P.G.S. Wengrat:** Writing – review & editing. **Lian-Sheng Zang:** Writing – review & editing, Data curation. **Wei Zhang:** Writing – review & editing, Data curation. **Kennedy J. Zimba:** Writing – review & editing, Data curation. **Kongming Wu:** Writing – review & editing. **Maged Elkahky:** Writing – review & editing. **Buyung A.R. Hadi:** Supervision, Funding acquisition.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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