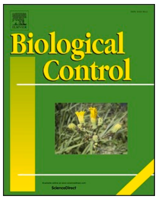
Biological Control 198 (2024) 105640

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon



Functional structure of the natural enemy community of the fall armyworm, *Spodoptera frugiperda* in the Americas

Kris A.G. Wyckhuys [a,b,c,d,*], Komivi S. Akutse [e,f], Divina M. Amalin [g], Salah-Eddin Araj [h], Gloria Barrera [i], Marie Joy B. Beltran [j], Ibtissem Ben Fekih [k], Paul-André Calatayud [e,l], Lizette Cicero [m], Marcellin C. Cokola [k], Yelitza C. Colmenarez [n], Kenza Dessauvages [k], Thomas Dubois [e], Léna Durocher-Granger [o], Carlos Espinel [i], José L. Fernández-Triana [p], Frederic Francis [k], Juliana Gómez [i], Khalid Haddi [q], Rhett D. Harrison [r], Muhammad Haseeb [s], Natasha S.A. Iwanicki [t], Lara R. Jaber [h], Fathiya M. Khamis [e], Jesusa C. Legaspi [u], Refugio J. Lomeli-Flores [v], Rogerio B. Lopes [w], Baoqian Lyu [x], James Montoya-Lerma [y], Tung D. Nguyen [z], Ihsan Nurkomar [aa], Jermaine D. Perier [bb], Gabor Pozsgai [cc], Ricardo Ramírez-Romero [dd], Annmarie S. Robinson-Baker [s], Francisco J. Sanchez-Garcia [ee], Luis C. Silveira [q], Larisner Simeon [s], Leellen F. Solter [ff], Oscar F. Santos-Amaya [gg], Wagner de Souza Tavares [hh], Rogelio Trabanino [ii], Carlos Vásquez [jj], Zhenying Wang [b], Ana P.G.S. Wengrat [t], Lian-Sheng Zang [kk], Wei Zhang [kk], Kennedy J. Zimba [ll], Kongming Wu [b], Maged Elkahky [d]

[a] *Chrysalis Consulting, Danang, Viet Nam*
[b] *State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China*
[c] *School of the Environment, University of Queensland, Saint Lucia, Australia*
[d] *Food and Agriculture Organization (FAO), Rome, Italy*
[e] *International Centre of Insect Physiology and Ecology (icipe), Nairobi, Kenya*
[f] *Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa*
[g] *De La Salle University, Taft Avenue, Manila, Philippines*
[h] *School of Agriculture, The University of Jordan, Amman, Jordan*
[i] *Centro de Investigación Tibaitatá, Corporación Colombiana de Investigación Agropecuaria - Agrosavia, Mosquera, Cundinamarca, Colombia*
[j] *National Crop Protection Center, University of the Philippines Los Baños, Laguna, Philippines*
[k] *Functional and Evolutionary Entomology, Gembloux Agro-Bio Tech, University of Liege, Gembloux, Belgium*
[l] *Institut Diversité Ecologie et Evolution du Vivant (IDEEV), Université Paris-Saclay, CNRS, IRD, UMR Evolution, Génomes, Comportement et Ecologie, Gif-sur-Yvette, France*
[m] *Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), Yucatán, Mexico*
[n] *CAB International Latin America, FEPAF-UNESp-FCA. Fazenda Exp. Lageado. Botucatu, São Paulo, Brazil*
[o] *CAB International, Kalundu, Lusaka, Zambia*
[p] *Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada*
[q] *Laboratory of Molecular Entomology and Ecotoxicology, Department of Entomology, Universidade Federal de Lavras, Brazil*
[r] *CIFOR-ICRAF, 12-14 St Eugene Office Park, Lake Road, Lusaka, Zambia*
[s] *Center for Biological Control, Florida A&M University, Tallahassee, FL, USA*
[t] *Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, São Paulo, Brazil*
[u] *United States Department of Agriculture-Agricultural Research Service (USDA-ARS), Center for Medical, Agricultural and Medical Entomology, Tallahassee, FL, USA*
[v] *Posgrado en Fitosanidad, Colegio de Postgraduados, Montecillo, Texcoco, México*
[w] *EMBRAPA Genetic Resources and Biotechnology, Brasília, Federal District, Brazil*
[x] *China Academy of Tropical Agricultural Sciences (CATAS), Haikou, China*
[y] *Department of Biology, Universidad del Valle, Cali, Colombia*
[z] *Vietnam National University of Agriculture, Hanoi, Viet Nam*
[aa] *Universitas Muhammadiyah Yogyakarta, Indonesia*
[bb] *Department of Entomology, University of Georgia, Tifton, GA, USA*

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* Corresponding author at: School of the Environment, University of Queensland, Saint Lucia, Australia.
E-mail addresses: kagwyckhuys@gmail.com, k.wyckhuys@uq.edu.au (K.A.G. Wyckhuys).

https://doi.org/10.1016/j.biocontrol.2024.105640
Received 6 August 2024; Received in revised form 17 October 2024; Accepted 18 October 2024

[cc] *cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, University of the Azores, Angra do Heroísmo, Portugal*
[dd] *Biological Control Laboratory (LabCB-AIFEN), University of Guadalajara, Guadalajara, Mexico*
[ee] *Instituto Murciano de Investigación y Desarrollo Agrario y Alimentario (IMIDA), Murcia, Spain*
[ff] *Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, IL, USA*
[gg] *Department of Agronomy, Universidad de Pamplona, Pamplona, Colombia*
[hh] *Riau Andalan Pulp and Paper (RAPP), Pangkalan Kerinci, Riau, Sumatra, Indonesia*
[ii] *Zamorano, Apartado Postal 93, Tegucigalpa, Honduras*
[jj] *Faculty of Agronomical Sciences, Technical University of Ambato, Campus Querochaca, Province of Tungurahua, Cevallos, Ecuador*
[kk] *National Key Laboratory of Green Pesticide, Key Laboratory of Green Pesticide and Agricultural Bioengineering, Guizhou University, Guiyang, China*
[ll] *School of Agricultural Sciences, University of Zambia, Lusaka, Zambia*

ARTICLE INFO

Keywords:
Biodiversity conservation
Agroecology
Ecological intensification
Functional ecology
Species richness
Biodiversity – ecosystem functioning

ABSTRACT

Ecosystem functions such as biological pest control are mediated by the richness and abundance of service providers i.e., biological control agents (BCAs), relative contributions of individual taxa and community structure. This is especially relevant in the native range of agricultural herbivores, where a speciose community of co-evolved BCAs can prevent them from attaining pest status. Here, we use a powerful graphical approach to assess the functional structure of BCA communities of the fall armyworm (FAW) *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on maize in the Neotropics. Drawing upon a curated database of all-time field and laboratory studies, we graphed patterns in the functional contribution, abundance and niche breadth for a respective 69, 53 and 3 taxa of resident parasitoids, predators and pathogens. Regardless of varying taxon coverage and rigor of the underlying studies, functional structure follows a saturating relationship in which the first three taxa account for 90–98% of aggregate biological control function. Abundance-functionality matrices prove critically incomplete, as more than 80% of invertebrate taxa miss empirically derived efficiency metrics while associated FAW infestation data are scarce. Despite its methodological shortfalls and data gaps, our work pinpoints *Chelonus insularis*, several taxa of egg parasitoids, *Doru* spp. and *Orius* spp. as taxa with outsized (average) functionality and conservation potential. This is also exemplified by the highly variable aggregate function across studies, with dispersion indices of 1.52 and 2.14 for invertebrate BCAs. Our work underlines the critical importance of functional ecology research, networked trials and standardized methodologies in advancing conservation biological control globally.

1. Introduction

Since 2016, the fall armyworm (FAW) *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) has invaded extensive areas of the global tropics and subtropics (Goergen et al., 2016; Wengrat et al., 2021; Kenis et al., 2023). This migratory noctuid native to the Neotropics has made its arrival in nearly 100 countries in Africa, the Middle East, Asia and the Pacific. By early 2022, *S. frugiperda* incursions had been reported as far as New Zealand. As a polyphagous herbivore, FAW feeds on globally important crops such as maize, rice, sorghum, cotton and forage grasses – with a notable preference for the former. Through their voracious feeding on vegetative and reproductive parts of plants and by acting as a cutworm, *S. frugiperda* larvae reduce primary productivity of the affected crops with onward impacts on food, feed or fiber output, agricultural efficiency, farmer income and food security. When left unmanaged, *S. frugiperda* populations reduce maize yields by an average of 17 % (Overton et al., 2021) though its impacts in invaded settings in Africa are not necessarily more severe (Baudron et al., 2019). In Africa alone, *S. frugiperda* is estimated to cause more than US $9 billion annual losses (Eschen et al., 2021). Among smallholder farmers in Africa and Asia alike, its invasion has routinely triggered the use of synthetic pesticides (Tambo et al., 2020; Yang et al., 2021b) and favored the diffusion of prophylactic seed treatment i.e., a practice that violates the core principles of integrated pest management, IPM (Tooker et al., 2017). As such, FAW has negatively impacted the economies of low-income countries, affected the livelihoods of millions of underprivileged farmers and food producers, and enlarged the environmental footprint of agriculture.

To sustainably manage *S. frugiperda* across its distributional range, biological control carries ample potential (Andrews, 1980; Gross & Pair, 1986; Kenis et al., 2023). In the presence of effective biological control agents (BCAs), the use of synthetic pesticides poses no comparative advantage (Janssen & van Rijn, 2021) and may even prove economically unattractive (Naranjo et al., 2015). Globally, at least 46, 304 and 215 taxa of entomopathogens, parasitoids and predators respectively are associated with different FAW life stages in maize (Wyckhuys et al., 2024a). While tens of BCAs have been successfully reared and mass-released (Figueiredo et al., 2015; Faria et al., 2022; Gu et al., 2023), a far larger number of naturally occurring on-farm biota can be manipulated to provide biological control at favorable economic returns. Indeed, maize fields harbor a speciose community of invertebrate and microbial BCAs and many of its constituent species exhibit variable abundance over space and time (Wyckhuys et al., 2024a). This inter-site variability underscores the potential of phased-down (pesticide) disturbance and targeted habitat management to promote these biota (Landis et al., 2000; Tooker et al., 2020). For instance, in Florida's maize crop, FAW parasitism levels average 28 % but reach 44 % in unsprayed fields and 92 % in unsprayed, diversified settings (Meagher et al., 2016). Similarly, parasitism averages 14 % in Mexico's maize crop but reaches levels up to 42 % under particular, unspecified conditions (Molina-Ochoa et al., 2004). To take biological control forward, critical insights into parasitoid-host or colonization dynamics are needed but these are largely absent in the tropics or subtropics (but see Wyckhuys & O'Neil, 2006). To complicate matters further, data on the in-field abundance, dynamics or biological control potential of predators or entomopathogens are rare. Given the scarcity of methodically collected data from various farm contexts, unguided 'trial-and-error' research and case-by-case empiricism abound in the exploration of conservation biological control (CBC) strategies for *S. frugiperda* and many other pests. In this regard, a newly-constructed database with BCA performance records and linked FAW infestation data (Wyckhuys et al., 2024a) can help to advance this valuable yet disregarded form of pest management.

CBC is inherently complex: as it involves myriad processes and functionally diverse plant, animal or microbial communities that act across spatio-temporal scales, its scientific understanding remains incomplete (Begg et al., 2017; Settele & Settle, 2018) and its functional ecology underpinnings stand weak (Perović et al., 2018). Often, experimental CBC interventions fail to direct biological control services, achieving few of their envisioned outcomes (Kleijn et al., 2019; González-Chang et al., 2020) and with their impacts critically obscured by landscape-level flows or processes (Karp et al., 2018). Evidently, to advance the implementation of CBC strategies, an in-depth understanding of BCA population levels and their ensuing ecosystem processes and functions is required (Luck et al., 2009; González-Chang et al., 2020). In light of the numerous CBC strategies that have been put forward or validated under restricted circumstances (Landis et al., 2000; Gurr et al., 2017; González-Chang et al., 2019; Albrecht et al., 2020), universal decision frameworks are imperative to methodically assess the effectiveness of particular BCAs and strategies for their on-farm conservation or augmentation. Graphic methods such as abundance-functionality (AF) species classifications (Balvanera et al., 2005) have proven invaluable to identify the exact determinants of ecosystem function at field or community scales and to assess the contributions of individual species. Though these approaches have become standard tools in fields such as pollination ecology, their usage in CBC is lagging. Yet, a delineation of the functional structure of *S. frugiperda* BCA communities can underpin trait-based approaches (Perović et al., 2018), weigh the relative contribution of landscape- versus field-level processes (Perez-Alvarez et al., 2021) and thereby inform CBC science and practice.

In this paper, we draw upon the database by Wyckhuys et al. (2024a) and standardized parasitoid censuses by Molina-Ochoa et al. (2004) to delineate the functional structure of *S. frugiperda* BCAs in its native range i.e., the Americas. Specifically, we use either laboratory-derived or inferred performance metrics (i.e., biological control ‘efficiency’; Balvanera et al., 2005) and field abundance data to estimate the functional contribution of each taxon within three main BCA guilds. In the absence of field-level performance data e.g., as derived from exclusion cage assays or life table and molecular gut content analyses, this functionality measure offers an imperfect proxy of a given species’ potential role in FAW biological control. Next, we assess the relative contribution of each BCA taxon at a field and supra-field or community level, link community and functional structures, and determine how aggregate function relates to FAW infestation pressure. Though hampered by data shortages and methodological failings, our work offers an initial, graphical interpretation of the contributions of hundreds of *S. frugiperda* BCAs in maize fields in the Americas. Exploratory in nature, it provides a valuable framework to further hone CBC science.

2. Materials & methods

To delineate the functional structure of the FAW natural enemy community in the Americas, we extracted field- and laboratory-level performance data for its regionally prevalent invertebrate and microbial BCAs. Given that field observations of certain BCAs (e.g., predators) were of low taxonomic resolution and often lacked species-level information, we refer to all BCAs as ‘taxa’. Specifically, from a comprehensive database composed by Wyckhuys et al. (2024a), we extracted field-level abundance records and laboratory-level performance data for BCA taxa that naturally occur in maize fields within Central America and the Caribbean, South America and the United States. The original database contained all-time data from a respective 127, 86 and 64 published laboratory studies and 35, 102 and 26 field studies for pathogens, parasitoids and predators across the FAW native and invasive ranges (Wyckhuys et al., 2024a). Out of the sub-set of data that pertained to the Americas, we then filtered all field-level abundance records that pertained to natural biological control by resident biota or to conservation biological control i.e., excluding any instances of augmentation or classical biological control (Bale et al., 2008). Further, an in-depth analysis was done of the larval parasitoid community as recorded through snapshot surveys in 64 maize fields across six states in Mexico (Molina-Ochoa et al., 2004), involving 5591 field-collected FAW larvae and 772 parasitoids pertaining to 13 species- and genus-level taxa.

2.1. Field abundance and laboratory performance

Per BCA taxon, field abundance data at one or more maize phenological stages were extracted from the original publications. For entomopathogens, parasitoids and predators, we collated information on the canopy-level occurrence and prevalence (%), parasitism rate (%) or absolute per-plant abundance as reported by the study authors. For predators, absolute abundance in area units was converted to a per-plant basis under the assumption that maize was planted at densities of seven plants per m^2 (Wyckhuys et al., 2024a). As such, field abundance data were collated for 69 parasitoids, 53 invertebrate predators and three entomopathogens out of a respective 304, 215 and 46 globally known taxa. For each BCA taxon, abundance data were either averaged across all sampling events or locations within a given study (i.e., obtaining one single average per study) or averages were computed separately for the vegetative and reproductive stages of maize i.e., VE-whorl and VT-R phenological stages (Ritchie et al., 1986). Associated FAW infestation data at any maize phenological stage –where reported- were converted to prevalence i.e., percentage of maize plants affected by FAW larvae or bearing at least one egg mass. As above, where multiple recordings were made of FAW infestation, these were either averaged across all maize developmental stages or assessed separately for vegetative and reproductive stages.

Out of the three to seven laboratory-level metrics that are routinely used to assess BCA performance (Wyckhuys et al., 2024), we solely considered per-capita attack rate i.e., total number of parasitized hosts or consumed prey items by one single BCA individual over its entire lifespan or the observation time window as adopted by the study authors, and inflicted mortality (%) of the exposed FAW development stage. Considering the overall lack of quantitative measures on the taxon-specific functional contribution to FAW biological control under field conditions, we relied upon laboratory-based measures. Specifically, we averaged the maximum performance values of a given BCA taxon across laboratory studies, FAW or BCA development stages, BCA strains and experimental conditions for further analyses. Given a general absence of standardized conditions and protocols for such laboratory assessments (Wyckhuys et al., 2024) and a current inability to infer in-field predation, parasitism or host mortality from laboratory data, the obtained values thus act as proxy measures of the actual performance of a given BCA against specific FAW developmental stages in field settings.

2.2. Community structure analysis

Once field- and laboratory-based data for each BCA were thus compiled, we followed a three-step approach as outlined by Balvanera et al. (2005). Specifically, we used community structure analysis to describe the functional structure of FAW natural enemy communities, relate community and functional structures, and examine how the abundance of a particular BCA taxon relates to its functional contribution. As per Balvanera et al. (2005) and Kremen (2005), we used the taxon-specific contribution of taxon j (c_j) for all resident natural enemies to characterize the overall aggregate function of biological control X. This contribution c_j was calculated by multiplying the per-capita efficiency of a particular BCA taxon j, e_{jx} with its field abundance n_j. Absolute values were used for the abundance of predators i.e., number of individuals per plant as recorded through field censuses. However, given that many studies failed to report actual FAW infestation data, we used relative abundance values for entomopathogens and parasitoids i.e., % prevalence of parasitism in field-collected FAW larvae. In a similar way as pollinator efficiency is defined by the number of pollen grains deposited per visit (Balvanera et al., 2005), we directly derived biological control efficiency of a given taxon from laboratory-based performance assays i.e., per-capita maximum attack rate for parasitoids and predators or FAW mortality for microbiota (over variable time periods and experimental conditions, as defined by the original study authors). Specifically, we averaged the above maxima that had been determined for each BCA across all of the exposed FAW life stages (i.e., eggs, larvae) in the originally published studies i.e., representing a 'best case' scenario. Taxon-specific efficiency was treated as a constant, effectively disregarding any species-species or species-environment interactions under the varying contexts of the published studies. For taxa with no empirically-derived data on biological control efficiency, these were imputed with median values. For taxa where field abundance was reported at the genus level, efficiency was derived from the actual attack rates or mortality level of species within the same genus that had been investigated under laboratory conditions. As such, the actual efficiency values for one species served as a proxy for those of other species within the same genus that had not been studied. For instance, the *Orius sauteri* (Poppius) (Hemiptera: Anthocoridae) attack rate against FAW larvae was used as a proxy for the *Orius* sp. biological control efficiency. At the level of individual fields, the aggregate function of biological control *X* was thus obtained by summing the empirically derived or imputed taxon-level contributions across all constituent members of the natural enemy community. In the absence of consistent reports of FAW infestation pressure in the original studies, function was expressed on a per-plant basis for predators and was unit-less for parasitoids and entomopathogens. Aggregate function was also computed at a supra-field or regional level by treating all known BCA taxa in the Americas as integral members of the natural enemy community.

At the supra-field level, individual BCA taxa were classified based upon their relative abundance and functional contribution (or functionality). Both metrics were computed in relation to a fictitious BCA community in which all constituent members of a given guild occurred at maximum abundance and functionality. This was to account for the (large share of) BCA censuses that were incomplete or geared towards one or few single taxa. In contrast, both metrics were calculated at a field level for the Mexican parasitoid community (Molina-Ochoa et al., 2004), given that field-level data were gathered through a standardized protocol, covering all parasitoid species that emerged from field-collected hosts and thus proved comparable. The resulting abundance-functionality (AF) species classification (Balvanera et al., 2005) allowed distinguishing taxa that are disproportionately more or less important to aggregate function across individual fields. For parasitoid and predator guilds, we further plotted absolute functionality against FAW infestation level across fields. Next, as per Perez-Alvarez et al (2021), we graphed the efficiency of individual parasitoid or predator taxa against average FAW infestation level (or niche position) and niche breadth i.e., (normalized) variance around the niche position as captured by SE. For parasitoids in particular, we also related efficiency with host breadth or degree – as determined by querying the open access interaction data repository GLoBI for each taxon individually (Poelen et al., 2014).

2.3. Cumulative magnitude of function vs. species richness

Lastly, we plotted aggregate function and the associated (or resulting) FAW infestation pressure against the richness of either parasitoid or predator BCA guilds at the field level, irrespective of the exact taxon coverage and underlying methodologies that were adopted by study authors. All studies, including those centered on one single taxon (i.e., singleton) or a sub-set of functionally important taxa within a given guild, were thus included in these graphics. Per BCA guild, we further graphed the relative functional contribution of individual taxa and the cumulative magnitude of the biological control function at the field level against the rank of functionality for each taxon i.e., taxa ranked as per their declining contribution to the aggregate function (Balvanera et al., 2005). Contrary to the above, given that this graphic method built upon data that were collected through a range of different methodologies and with varying organismal coverage, we excluded studies that covered BCA singletons. This graphic method in particular allowed clarifying whether functional contributions are evenly or unevenly distributed across species and visualizes the underlying processes of community assembly for either BCA guild.

3. Results

3.1. Field abundance and laboratory performance

Out of the initial database and associated literature corpus, we extracted field-level abundance data for a respective 69, 53 and 3 taxa of parasitoids, predators and pathogens from the Americas, out of which 22, 22 and 1 were reported at genus level. Out of these, a respective 35, 33 and 0 taxa had accompanying FAW infestation records and a mere 11, 8 and 3 taxa also counted with empirically-derived estimates of biological control efficiency. For the latter sub-set of taxa, efficiency of *Cotesia* sp., *Orius* sp., *Chrysoperla* sp. and *Chrysopa* sp. was inferred from laboratory-level maximum attack rates of *Cotesia ruficrus* (Haliday) (Hymenoptera: Braconidae), *O. sauteri, Chrysoperla sinica* (Tjeder) and *Chrysopa pallens* (Rambur) (Neuroptera: Chrysopidae), respectively.

For those BCAs that counted with concrete quantitative measures of efficiency, (averaged) maximum per-capita attack rates varied greatly, ranging from 14.2 FAW larvae for *O. sauteri* to 1385 FAW eggs for *Doru luteipes* Scudder (Dermaptera: Forficulidae) predators and from 2.4 FAW larvae for *Aleiodes laphygmae* Viereck (Hymenoptera: Braconidae) to 476 FAW eggs for *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) parasitoids (Fig. 1). For *Beauveria bassiana* (Bals.-Criv.) Vuill. (Hypocreales: Cordicypiticaeae) and *Metarhizium rileyi* (Farlow) Kepler (Hypocreales: Clavipitaceae) entomopathogens, efficiency was set to the maximum mortality of 100 % of exposed FAW eggs or larvae. At a niche position of low (i.e., less than 20 %) FAW infestation, *D. luteipes* exhibited the highest efficiency while *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), *Chetogena scutellaris* Wulp (Diptera: Tachinidae) or *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae) showed intermediate levels of efficiency (Fig. 1). At a niche position of high (i.e., more than 50 %) FAW infestation, the egg parasitoids *T. pretiosum* and *Trichogramma atopovirilia* Oatman & Platner (Hymenoptera: Trichogrammatidae) exhibited the highest efficiency among all studied taxa (Fig. 1). The majority of BCAs acted within a comparatively narrow niche, though parasitoids such as *A. laphygmae*, *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) and *Telenomus remus* Nixon (Hymenoptera: Scelionidae) (ranked by efficiency) acted across a broader range of FAW infestation levels. Lastly, for the four parasitoid species of which relevant data are available, host breadth (i.e., degree) and efficiency do not correlate (Spearman's rho = 0.200, p = 0.800).

3.2. Community structure analysis

How these initial patterns translate into (potential) biological control outcomes becomes clear when graphing the relative abundance (Table S1) and in turn absolute functional contribution or functionality of all BCAs against niche position (Fig. 2, S1). Within the FAW predator guild, *H. axyridis*, *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae), *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), *D. luteipes*, *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae), *Chrysoperla* sp. and *Solenopsis* sp. exhibited comparatively high absolute functionality – with the former three and latter two taxa of particular importance under low or high FAW infestation pressure, respectively. The relative contribution of some of these taxa is also evident when differentiating dynamics during vegetative and reproductive stages of maize (Fig. 2, S2). In early season, *D. luteipes* attains high relative abundance at low FAW infestation levels (Fig. S2). Meanwhile, *O. insidiosus* and *D. luteipes* are the most prominent predators at low-intermediate infestation pressure in late season (Fig. S2). Further, many of the taxa acting at intermediate FAW infestation levels (i.e., 20–30 %) exhibited comparatively broad niches. Within the parasitoid guild, *Meteorus* sp., *C. scutellaris*, *Eucelatoria* sp., *Ophion* sp., *Chelonus insularis* Cresson (Hymenoptera: Braconidae), *Campoletis grioti* Blanchard (Hymenoptera:

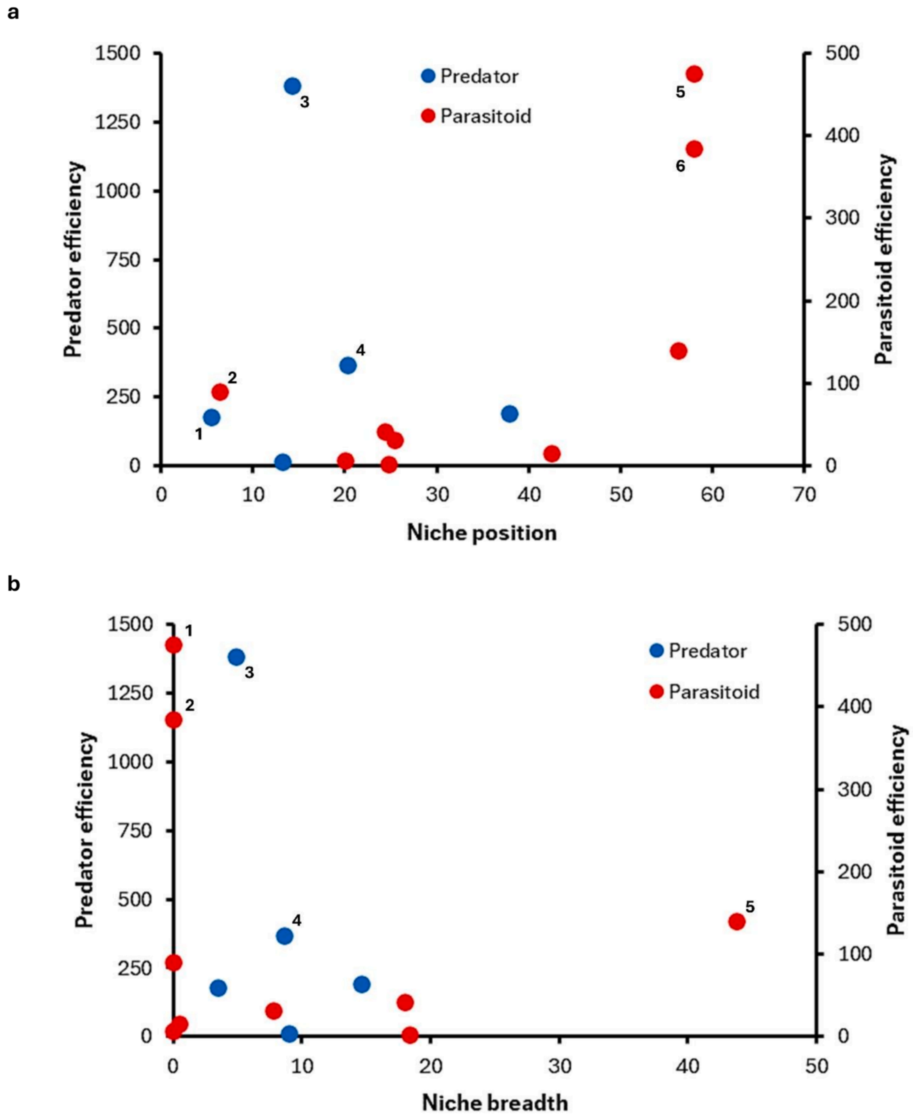

Fig. 1. Relationship between biological control efficiency, niche breadth and niche position of *S. frugiperda* parasitoids and predators in Neotropical maize. As per Perez-Alvarez et al. (2021), niche position (panel a) refers to average FAW infestation level, while niche breadth indicates variance (i.e., SE) around the niche position. Patterns are only depicted for taxa of which performance has been empirically assessed. In panel a, numbers refer to key taxa: *Harmonia axyridis* (1), *Chetogena scutellaris* (2), *Doru luteipes* (3), *Chrysoperla externa* (4), *Trichogramma pretiosum* (5) and *Trichogramma atopovirilia* (6), while in panel b, they refer to *Trichogramma pretiosum* (1), *Trichogramma atopovirilia* (2), *Doru luteipes* (3), *Chrysoperla externa* (4) and *Telenomus remus* (5). For *Orius* sp., *O. sauteri* is used as a proxy.

Ichneumonidae), *Te. remus*, *Tr. atoporilla* and *Tr. pretiosum* exhibited comparatively high functionality – with the former two taxa and the latter three taxa of particular importance under low or high FAW infestation pressure, respectively.

The AF classification of resident BCAs (Fig. 3) helped to characterize how specific taxa perform as FAW biological control agents within maize ecosystems. It equally showed the (functionally important) taxa for which empirical, laboratory-derived data on efficiency are lacking. Within the predator guild, taxa in or near the upper right quadrant (i.e., abundant, important biota) included *D. luteipes*, *Doru taeniatum* Dohrn and *Doru lineare* (Eschs.) (Dermaptera: Forficulidae), *O. insidiosus*, *C. externa* and *Chrysoperla* sp. The high per-capita attack of *D. luteipes* made this the most important biological control agent in Neotropical maize systems. Within the parasitoid guild, taxa in the upper right quadrant included *Te. remus*, *Tr. pretiosum*, *C. grioti*, *C. insularis*, *Meteorus* sp. and *Cryptus albitarsis* (Cresson), *Diapetimorpha introita* (Cresson) and *Temelucha difficilis* Dasch (Hymenoptera: Ichneumonidae). For most of these taxa, empirically derived efficiency data are not available. The egg parasitoid *T. atopovirilia* resorted in the upper left quadrant (i.e., rare, important biota). Despite a critical absence of data on entomopathogens, the AF classification revealed how *M. rileyi* was far more important than *B. bassiana* or *Entomopthora* sp. for FAW biological control in maize systems.

3.3. Cumulative magnitude of function vs. Species richness

Across all predator studies, aggregate biological control function ranged from 25.1 to 10,429.7 prey per plant (average 1,390.4; Fig. 4). Though the highest aggregate function was recorded in maize fields with 23 resident predator taxa (Zuim et al., 2023), aggregate function did not relate to (field-level) BCA richness. Similarly, FAW infestation levels varied greatly between studies ranging between 1.7 to 61.7 % and did not relate to the richness of in-field predator taxa. For instance, the natural enemy community with the lowest aggregate function was typified by low FAW infestation levels (i.e., 5.6 %) and composed of one single predator i.e., *Doru* sp. (Marenco & Saunders, 1993). Though other predator taxa were (likely) present, these were not reported by the study authors. Across all parasitoid studies, aggregate function ranged from

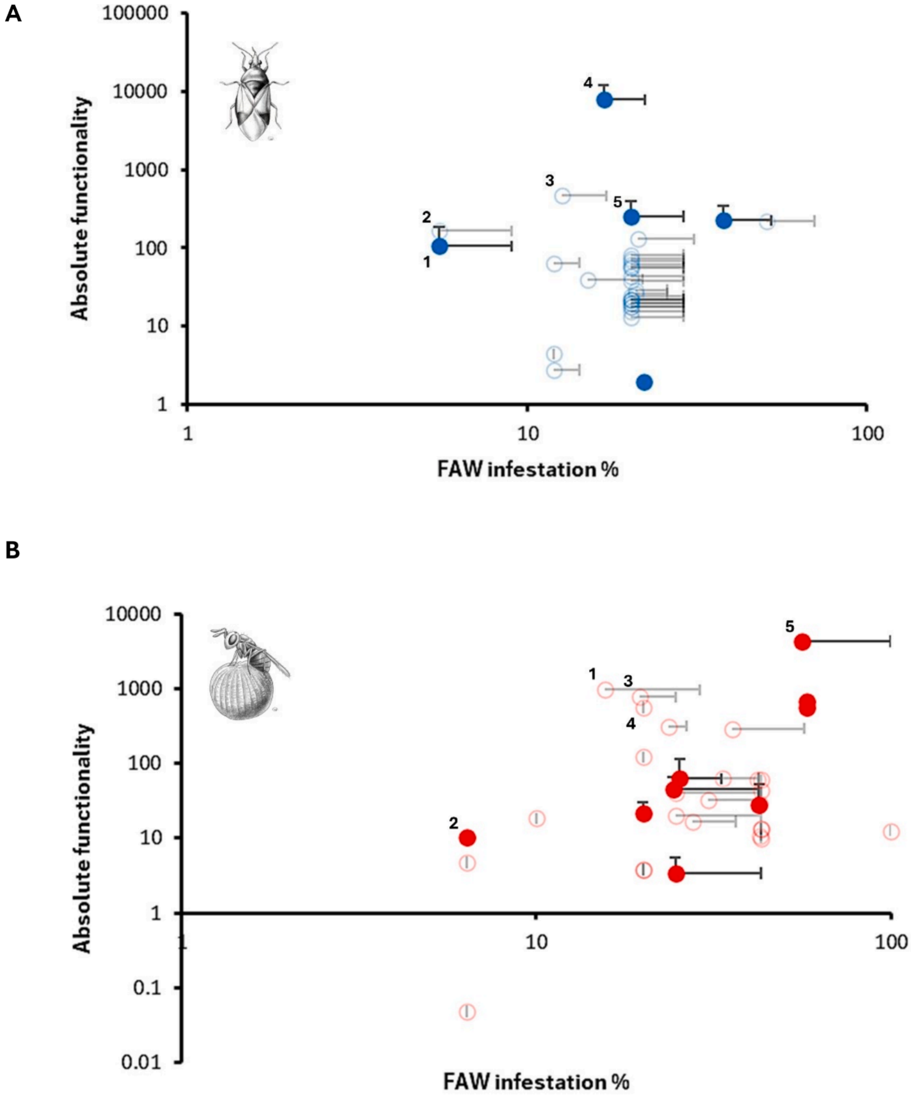

Fig. 2. Invertebrate predator and parasitoid functionality as related to FAW infestation pressure (% infested plants) throughout the maize growing season. Panels depict the absolute functionality (mean ± SE) of invertebrate predators (A) and parasitoids (B) and their associated FAW infestation levels. Empty dots indicate taxa for which empirically-derived efficiency data are lacking. In each panel, numbers refer to key taxa of predators: *Harmonia axyridis* (1), *Coleomegilla maculata* (2), *Orius insidiosus* (3), *Doru luteipes* (4), *Chrysoperla carnea* (5) and parasitoids: *Meteorus* sp. (1), *Chetogena scutellaris* (2), *Chelonus insularis* (3), *Campoletis grioti* (4), *Telenomus remus* (5). Each panel shows patterns for a respective 33 and 35 different taxa, drawn from 10 and 20 studies. Entomopathogen data are not plotted due to lacking FAW infestation data. In subplot B, the absolute functionality axis is truncated at 0.01.

19.5 to 33,682.54 (average 3,043.9). The highest aggregate function was recorded in fields with 3 taxa of egg parasitoids (Bezerra Dasilva et al., 2015), and – as above – function did not relate to field-level parasitoid richness. Similarly, FAW infestation levels ranged from 1.1 to 100.0 % and did not relate to parasitoid richness. In contrast with predator studies, highest FAW infestation level (1.2 larvae per plant) was recorded in settings where only one parasitoid species i.e., *Euplectrus furnicus* (Walker) (Hymenoptera: Eulophidae) was found or reported (Sturza et al., 2013).

Overall, we observed a strong hierarchy in taxon-level functionality that was most pronounced in predator studies. When removing all studies with BCA singletons (Fig. S3), more than 95 % of the cumulative function was provided by three predator taxa. Taxon-level contributions were highly uneven, with the first-ranked predator taxon accounting for 68.3 ± 8.3 % (average ± SE) of the aggregate functionality per field or study. After removal of the reports on parasitoid singletons (Fig. S3), more than 90 % of the cumulative function was provided by the first three parasitoid taxa. Equally, the first- and second-ranked parasitoid taxa accounted for a respective 59.8 ± 2.8 % and 21.9 ± 1.7 % of the aggregate functionality per field or study. While these patterns indicate how BCA community structure defines function, they are also partially defined by the high incidence of incomplete censuses especially for foliage-dwelling predators and a low share (i.e., 15.1 or 16.0 %) of predator or parasitoid taxa with non-imputed efficiency measures (Fig. 4).

3.4. Mexican FAW parasitoid community

As the former constraint did not apply in the Mexican parasitoid census (Molina-Ochoa et al., 2004), community-level contributions to function may reflect reality better. In this study, no less than seven larval or egg-larval parasitoid taxa occur in the upper right quadrant i.e., *Chelonus* sp., *Euplectrus plathypenae* Howard (Hymenoptera: Eulophidae), *Meteorus* sp., *C. flavicincta*, *Pristomerus spinator* (Fabricius), *Ophion flavidus* Brulle and *Eiphosoma vitticole* Cresson (Hymenoptera: Ichneumonidae), and *Glyptapanteles* sp. (in order of declining importance) (Fig. 5). Out of these, attack rates have only been quantitatively defined for *E. plathyphenae* and *C. flavicincta*. Across all 64 field sites, aggregate

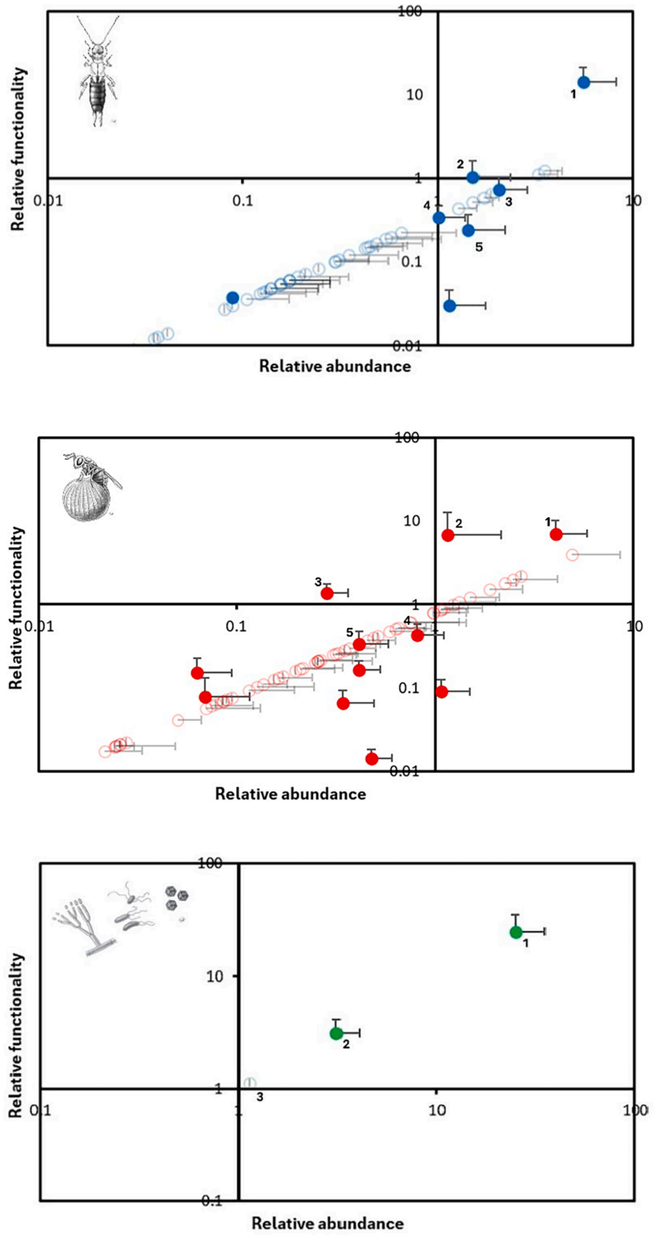

Fig. 3. Abundance-functionality species classification of *S. frugiperda* natural enemies in maize crops in the Americas. Panels depict the relative abundance (mean ± SE) of invertebrate predators (A), parasitoids (B) and pathogens (C), contrasted with their relative functional importance. Metrics are calculated at the supra-field level i.e., for an imaginary community composed of all taxa of a given guild. Solid dots refer to taxa for which efficiency has been empirically determined vs. imputed with median values. In each panel, numbers refer to key taxa of predators: *Doru luteipes* (1), *Chrysoperla externa* (2), *Chrysoperla* sp. (proxy *C. sinica*; 3), *Harmonia axyridis* (4), *Chrysopa* sp. (proxy *C. pallens*; 5); parasitoids: *Telenomus remus* (1), *Trichogramma pretiosum* (2), *Trichogramma atopovirilia* (3), *Campoletis sonorensis* (4), *Cotesia marginiventris* (5) and pathogens: *Metarhizium rileyi* (1), *Beauveria bassiana* (2) and *Entomophthora* sp. (3). Each panel shows patterns for a respective 53, 69 and 3 different taxa, drawn from 22, 61 and 9 studies. In certain panels, axes are truncated at 0.01.

function equals to 102.0 ± 14.4 (range 0 to 594.1). Field sites with the three highest levels of aggregate function harbored communities composed of 3–4 parasitoid taxa. The functional contribution of individual parasitoid taxa was highly uneven. Indeed, more than 98 % of the cumulative function was provided by the first three taxa of larval parasitoids. Across the 64 field sites, the first ranked taxon provided 73.0 ± 3.1 % of the aggregate function. Yet, parasitoid's functionality was distinctly more even in the two fields with the highest aggregate function. In those instances, the first- and second-ranked taxon provided a respective 48.1–52.6 % and 34.1–41.5 % of the aggregate function.

4. Discussion

Species-rich communities of biological control agents (BCAs) uphold crop yield in the face of herbivore attack (Cardinale et al., 2003; Dainese et al., 2019). As the relationship between biodiversity and the service of biological control is complex, highly variable and context-specific (Harrison et al., 2014; Karp et al., 2018) and mediated by community attributes besides species richness (Yang et al., 2021a), it is challenging to interpret patterns over space and time. In this regard, a delineation of the functional structure of BCA communities can help to estimate how BCAs individually and collectively contribute to biological control (Kremen, 2005; Balvanera et al., 2005). Here, we show that regardless of the rich body of data on (absolute or relative) abundance for *S. frugiperda* BCAs in Neotropical maize, merely 15.1 % and 16.0 % of parasitoids or predators though 100 % of entomopathogens count with laboratory-derived efficiency metrics. Egg parasitoids in particular have received further attention, with view towards their use in augmentative releases. These BCAs act across a spectrum of pest infestation levels (or niche positions) and comprise taxa with varying sensitivity or adaptability to farm contexts (or niche breadth). Yet, AF matrices prove gravely incomplete as they bear imputed data for more than 80 % of taxa within the two invertebrate BCA guilds. Also, accompanying FAW infestation are rarely available. Regardless of the above, parasitoids such as *Meteorus* sp., *Te. remus* and *Tr. pretiosum* or predators such as *D. luteipes*, *O. insidiosus* and *C. externa* may contribute disproportionately to FAW biological control function. Aggregate function varied greatly across parasitoid and predator studies with respective dispersion indices of 1.52 and 2.14, did not relate to organismal richness and exhibited a strong hierarchy in taxon-level functionality. Specifically, for either guild, the first three top-ranked taxa provided more than a respective 90 % and 95 % of the aggregate function in the continent-wide assessment and more than 98 % in Mexico's standardized parasitoid census. Despite the varying depth and taxon coverage of the original publications, this potentially could point towards a saturating function in which efforts that focus on one or few taxa could be most rewarding (Kremen, 2005). This is critical to the advancement of conservation biological control. Aside from exposing the (possible) functional role of resident BCAs, our work also underlines a pressing need for harmonized, standardized research in advancing biological control against *S. frugiperda* or other pests.

Our graphical approach identifies various taxa that are functionally important to *S. frugiperda* biological control in Neotropical maize systems. The earwig *D. luteipes* and related *D. taeniatum* potentially are two of the foremost predators, especially in manually harvested smallholder crops (Van Huis, 1981). Exhibiting the highest absolute functionality at low FAW densities –though with a narrow niche breadth, potentially due to their susceptibility to neonicotinoid and pyrethroid insecticides (Redoan et al., 2013) – and capable of maintaining viable populations through omnivory (Pacheco et al., 2021), earwigs may be instrumental in keeping FAW populations below economic thresholds. Yet, scant research has examined their biology, ecology or conservation modalities – possibly due to their nocturnal foraging habits (Naranjo-Guevara et al., 2017; Wyckhuys et al., 2024a). Anthocorids and lacewings such as *C. externa* also attain comparatively high abundance (Quispe et al., 2017; Zuim et al., 2023) and functionality, with the latter species consuming up to 250 or 368 *S. frugiperda* eggs or first-instar larvae in laboratory settings (Tavares et al., 2011). Pirate bugs such as *Orius* spp. likely play a central role as BCAs at low to intermediate FAW infestation or in early-season maize, but this is poorly captured by our assessment. The comparatively low efficiency of the Oriental *O. sauteri* (proxy for *Orius* sp.) does not mirror the true potential of members within this

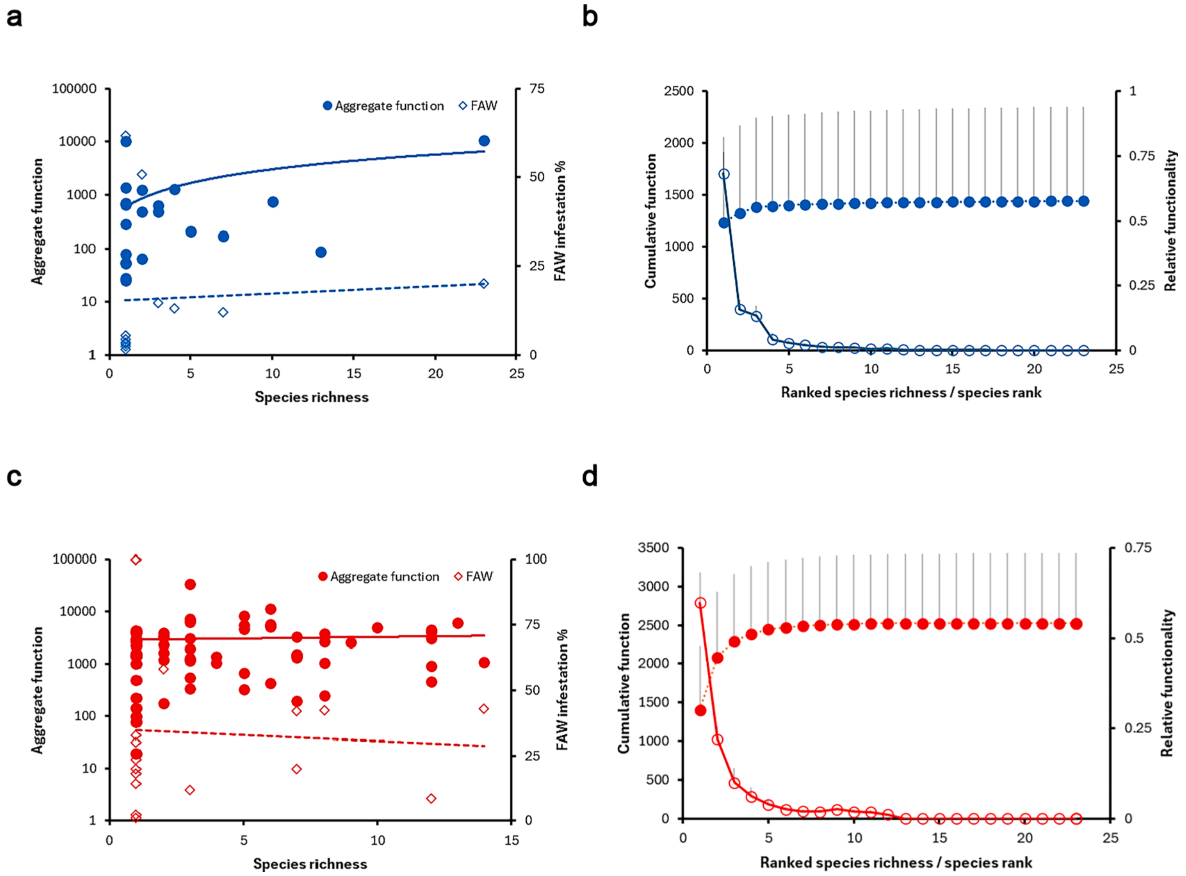

Fig. 4. Approximative biological control function provided by invertebrate natural enemy communities of varying species composition and richness in maize fields in the Neotropics. Patterns are shown for invertebrate predators (panels a,b) and parasitoids (c,d). Panels a and c depict the aggregate function and FAW infestation level in maize fields with varying natural enemy species richness. For data visualization purposes, linear trendlines with no statistical significance are shown. Panels b and d plot the cumulative function (± SE) by species richness, ranked by decreasing contribution to function, and the relative contribution to aggregate function of each species of the natural enemy community in a given field. All metrics are calculated at the field level. Patterns are shown for 53 predator taxa and 69 parasitoid taxa, drawn from a respective 21 and 60 studies. Panels 2 and 4 only show patterns for studies that report field-level abundance of more than 1 natural enemy species.

genus. While *O. sauteri* efficiency values firstly do not account for higher predation rates that were attained through *ad libitum* prey exposure (Di et al., 2021) in a study that does not feature in Wyckhuys et al., (2024a), its maximum attack rates are also six- to 20-fold lower than those of Neotropical species such as *Orius laevigatus* Fieber (Hemiptera: Anthocoridae) on the related *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) (Aragón-Sánchez et al., 2018). For parasitoids, several species figure in the top-right quadrant of the AF matrix though attack rates have only been defined for a fraction of these. Parasitoids such as *T. remus* and *T. pretiosum* already receive much-warranted attention in native and FAW-invaded settings alike (Kenis et al., 2019; Tepa-Yotto et al., 2021; Kenis, 2023) and this has borne effective biological control interventions (Figueiredo et al., 2015; Colmenarez et al., 2022). While either parasitoid is extensively used in classical and augmentation biological control (e.g., Cave, 2000; Colmenarez et al., 2022), its natural field populations have been reported by Bezerra Dasilva et al. (2015), Dequech et al. (2013), Varella et al. (2015) amongst others. Notably, the former authors report 100 % egg mass parasitism in Brazil by both species. Further, the braconid *Meteorus* sp. (most likely *Meteorus laphygmae* Viereck (Hymenoptera: Braconidae) as per Aguirre et al., 2011) reaches 40–42 % parasitism in weedy maize-bean fields at low FAW densities (Altieri, 1980) while species such as *Meteorus arizonensis* Muesebeck often attain high relative abundance (Ordóñez-García et al., 2015). Though its attack rate awaits empirical quantification, *C. grioti* also stands out in AF species classification and readily attains 50–95 % larval parasitism in areas where FAW is a seasonal migrant (Murúa et al., 2006). Parasitoids such as *C. insularis*, *T. difficilis* and *C. albitarsis* also feature in the upper right quadrant. Meanwhile, the full potential of common, widespread parasitoids such as *Eiphosoma laphygmae* Costa Lima (Hymenoptera: Ichneumonidae), *Archytas marmoratus* Townsend or *Lespesia archippivora* Riley (Diptera: Tachinidae) cannot be properly deduced from AF matrices due to a general absence of laboratory-derived performance metrics. While these data are available for other widespread parasitoids such as *C. sonorensis* (max. field parasitism 44.3 %), *C. flavicincta* (max. 47.0 %) and *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) (max. 28.5 %), their overall functionality is averaged out by highly variable abundance levels within and between geographically dispersed studies. Further, laboratory-based efficiency of most larval parasitoids is vastly inferior to that of comparatively well-studied egg parasitoids with e.g., *T. pretiosum* parasitizing up to 476 FAW eggs (Pratissoli et al., 2004), which translates into inferior functionality values regardless of their field abundance. Lastly, the relative functionality of FAW entomopathogens is unclear as in-field prevalence or related FAW infestation data are often lacking (Wyckhuys et al., 2024a) and there is a disconnect between laboratory- and field-level research for specific, promising strains. In addition to identifying key service providers, our approach helps to direct further research and associated expenditures towards filling critical data gaps and/or validating conservation biological control measures for prioritized taxa (Luck et al., 2009).

Exciting new research shows how biodiversity-function interactions could be captured by arithmetic relationships (O'Connor et al., 2017),

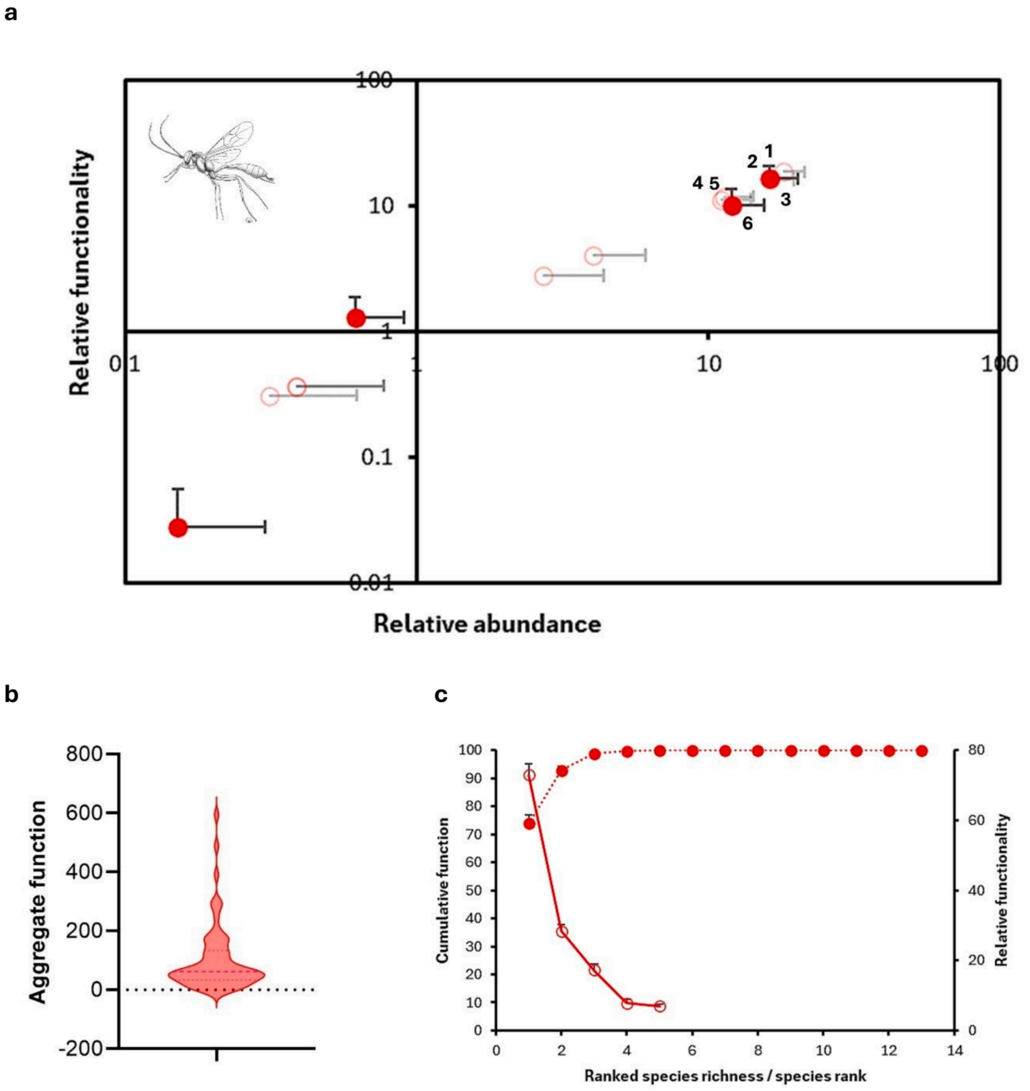

Fig. 5. Abundance-functionality species classification and species-level contributions of *S. frugiperda* larval parasitoids in Mexico's maize crop. In panel A, solid dots refer to taxa for which biological control efficiency has been empirically determined vs. imputed with average values. Numbers refer to key taxa: *Chelonus* sp. (1), *Meteorus* sp. (2), *Euplectrus plathypenae* (3), *Pristomerus spinator* (4), *Ophion flavidus* (5) and *Campoletis flavicincta* (6). Relative abundance and functionality of different parasitoid taxa was determined at the level of individual fields. Panels B and C show the distribution of aggregate function across fields and by species richness, ordered by rank of decreasing functional contribution. Patterns are shown for 13 parasitoid taxa and 64 maize fields distributed across six states as per Molina-Ochoa et al. (2004).

and a functional characterization of prevalent BCAs poses a critical step in attaining this goal for biological pest control. Counting natural enemies is easy, but BCA richness or diversity *per se* does not consistently explain biological control function (Straub & Snyder, 2006; Tylianakis & Romo, 2010; Griffin et al., 2013; Alhadidi et al., 2019) regardless of findings in (comparatively simple) North American maize ecosystems (Lundgren & Fausti, 2015). This relationship is distorted through intraguild predation, redundancy and complementarity, prey-mediated and non-consumptive effects or the unequal contributions of few effective taxa (Rosenheim et al., 1995; Wilby et al., 2005; Straub et al., 2008; Griffin et al., 2013; Mitchell et al., 2024). The latter transpires from our analyses: the three top-ranked invertebrate taxa generally account for up to 95 % of total function, which has also been reported by other authors (Denoth et al., 2002). Meanwhile, many confounding factors e.g., intraguild predation are not formally captured in our exercise as per Balvanera et al. (2005), but could be deduced by contrasting a taxon's computed functionality with actual recordings of biological control function or through life table analysis (Gardiner et al., 2009; Macfadyen et al., 2011; Naranjo et al., 2022). Further, it is worthwhile to closely examine the traits that drive the functional contribution of a given taxon e.g., body size, life history, dietary breadth (Sanders et al., 2015), dispersal capacities and/or adaptations to ephemeral habitats (Perović et al., 2018) or functional divergence in hunting strategy (Michalko and Pekár, 2016). In this regard, it may be valuable to closely examine the traits of *Doru* spp. or *Orius* spp., foliage-foraging ants and parasitoids such as *C. insularis*, *C. grioti* or *T. remus*. Eventually, this work may culminate in an identification and functional characterization of keystone biological control agents – a topic that has been largely ignored in the 55-year history of the keystone species concept (Power et al., 1996). Much is also to be gained from deciphering what drives aggregate function in maize fields of varying size, structure or management e.g., managerial aspects such as agroecological crop protection, habitat heterogeneity (Bellone et al., 2020) or plant functional diversity (Gardarin et al., 2021). In this regard, our graphical approach poses a stepping stone towards exciting new research at both the organismal, field and agro-landscape levels.

Yet, given its incipient nature, our work is hampered by multiple shortcomings. First and foremost, by solely relying upon laboratory-based estimates of attack rate, our approach imperfectly anticipates foraging efficiency, handling times and prey encounter rates under field conditions and myriad other species-environment interactions. Laboratory-based assessments might reliably reflect real-world conditions for BCAs that use effective (scout-and-recruit) strategies e.g., *Solenopsis* spp. (Diaz et al., 2004), but generate gross overestimates for ineffective foragers, poor competitors or those that exhibit pronounced omnivory e.g., *Doru* spp. (Rosenheim & Corbett, 2003; Frank et al., 2011; Pacheco et al., 2021). The same pertains to parasitoids: though *A. laphygmae* attacks 2.4 FAW larvae in the laboratory, its attack rate in the field is substantially higher and reaches levels up to 28 % (Van Huis, 1981; Kenis, 2023). Eventually, field-based performance measures should complement if not supplant laboratory-derived metrics in biological control functional assessments. Second, while the calculation of relative taxon-level contributions based upon a fictitious community with all taxa at maximum abundance circumvents the issue of varying taxon coverage (or completeness) of the original publications, it skews values from comparatively well-sampled geographies e.g., Mexico, Brazil or USA. Such could be resolved by weighting a species' abundance or functionality by publication output per geography. Third, total parasitism rate should be treated as the function (Rodriguez & Hawkins, 2000) and plant-level abundance data is then to be back-transformed from (often lacking) FAW infestation data. Otherwise, parasitoid abundance and parasitism rate can be recorded *in sync* through joint Malaise trapping and sentinel prey exposure (Letourneau et al., 2012, 2015) and disparities between these two metrics can then unveil species-species interactions or relative foraging efficiencies. Fourth, several important BCAs are conspicuously absent in our analyses and the underlying scientific publications. These include the ants *Solenopsis geminata* (Fabricius) or *Ectatomma ruidum* Roger (Hymenoptera: Formicidae) – (keystone) predators of *S. frugiperda* in Mexico and Central America (Risch & Carroll, 1982; Perfecto, 1990; Wyckhuys and O'Neil, 2006) – or multiple nocturnal and crepuscular predators (Wyckhuys et al., 2024a). Fifth, aggregate function as the simple sum of taxon-level functionalities, defined through unstandardized and often invalid methodologies (Wyckhuys et al., 2024a), currently offers our best, artefactual depiction of biological control in field settings. Given the above, we call for caution in interpreting our findings and related recommendations. Amongst others, field-based life table analyses, simulation modeling and cross-generational studies are vital to reliably compare the population-level impacts of common larval parasitoids with those of the comparatively rare egg parasitoids *Tr. pretiosum* or *Te. remus* (e.g., Wyckhuys et al., 2024a). The conservation potential of promising taxa will also become more apparent in pesticide-free, diversified settings as elegantly shown by Meagher et al. (2016). Evidently, if biological control scientists appreciate its value, this methodological approach will need to be upgraded and full-fledged functional inventories are to be performed to fill the most pressing knowledge gaps.

In the end, the calculation of aggregate (biological control) function across field or farm contexts poses a powerful analytical approach as it incorporates much of the complexity in biodiversity-function interactions and concurrently covers richness, abundance and trait-mediated effects (Kremen, 2005). Accounting for functional identity and community diversity can increase the predictive power of biodiversity-function research, and this has been well-recognized by ecologists (Mouillot et al., 2011). Yet, in the ~ 20 years since the toolkit was first presented, its potential has –to our knowledge- entirely been ignored by biological control scientists as they largely remain focused on single predator-pest interactions (Miller et al., 2021). Regardless of its methodological shortfalls, this approach can elucidate the field- and landscape-level processes that jointly define the biological control equation (Begg et al., 2017) e.g., through its integration with modeling efforts to forecast impacts of landscape composition (Perennes et al., 2023) or farm-level management (Delattre et al., 2023). As per Balvanera et al. (2005), it can help to assess how structural or managerial factors shape the abundance of functionally important biota and to pinpoint those features across scales that are central to aggregate function (Karp et al., 2018; Iuliano & Gratton, 2020; Tooker et al., 2020; Tamburini et al., 2020; Tscharntke et al., 2021). Abundance-functionality species classification further offers a simplified topological approach, exclusively centered on ecosystem providers, as a potentially low-cost, time-saving alternative to full-fledged bio-inventories (Lundgren & Fausti, 2015). The defined functional structure can be integrated with network approaches and open-access interaction data (Wyckhuys et al., 2024b) to identify key leverage points for more targeted and effective habitat management interventions. It could also be used to analyze BCA census data in other crop-pest systems or for particular taxa e.g., spiders (Young & Edwards, 1990), especially if efficiency metrics have been recorded for at least a share of these taxa. Lastly, for the subset of BCA species that count with (reliable) efficiency and functionality measures, carefully designed field research can unveil to what extent this is indicative of their relative role in FAW biological control in more real-world farm settings. To this end, networked multi-year, multi-location trials and standardized methodologies are imperative to illuminate the most important drivers of biological control across agroecological, socioeconomic and climatic contexts. In this regard, inspiration can be drawn from long-term ecological (LTER) or agroecological (LTAR) research networks (Spiegal et al., 2018; Jones & Driscoll, 2022) while funding has to be substantially increased (Moeller, 2020; Pavageau et al., 2020).

Irrespective of its shortcomings, our work carries implications for biological control science and practice. The (even approximative) position of taxa within AF matrices combined with their niche position and breadth (Perez-Alvarez et al., 2021) can help to prioritize specific BCAs for in-depth study including trait-based or landscape-level approaches. It can help target biological control research efforts, maximize the return on investment, dramatically raise the odds of success of BCA conservation strategies, and ultimately bolster farm-level uptake (González-Chang et al., 2020; Kleijn et al., 2021). Given the above, we call on biological control scientists to judiciously scrutinize this approach and to consider integrating functional approaches and graphical toolkits in their research. Doing so can help to firmly position biological control as a desirable, effective and tailor-made solution for the many ills of chemically-intensified agriculture worldwide.

CRediT authorship contribution statement

Kris A.G. Wyckhuys: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Komivi S. Akutse:** Writing – review & editing, Investigation. **Divina M. Amalin:** Writing – review & editing, Investigation. **Salah-Eddin Araj:** Writing – review & editing, Investigation. **Gloria Barrera:** Writing – review & editing, Investigation. **Marie Joy B. Beltran:** Writing – review & editing, Investigation. **Ibtissem Ben Fekih:** Writing – review & editing, Investigation. **Paul-André Calatayud:** Writing – review & editing, Investigation. **Lizette Cicero:** Writing – review & editing, Investigation. **Marcellin C. Cokola:** Writing – review & editing, Investigation. **Yelitza C. Colmenarez:** Writing – review & editing, Investigation. **Kenza Dessauvages:** Writing – review & editing, Investigation. **Thomas Dubois:** Writing – review & editing, Investigation. **Léna Durocher-Granger:** Writing – review & editing, Investigation. **Carlos Espinel:** Writing – review & editing, Investigation. **José L. Fernández-Triana:** Writing – review & editing, Investigation. **Frederic Francis:** Writing – review & editing, Investigation. **Juliana Gómez:** Writing – review & editing, Investigation. **Khalid Haddi:** Writing – review & editing, Investigation. **Rhett D. Harrison:** Writing – review & editing, Investigation. **Muhammad Haseeb:** Writing – review & editing, Investigation. **Natasha S.A. Iwanicki:** Writing – review & editing, Investigation. **Lara R. Jaber:** Writing – review & editing, Investigation. **Fathiya M. Khamis:** Writing – review & editing, Investigation. **Jesusa C. Legaspi:** Writing – review & editing, Investigation. **Refugio J. Lomeli-Flores:** Writing – review & editing, Investigation.

Rogerio B. Lopes: Writing – review & editing, Investigation. **Baoqian Lyu:** Writing – review & editing, Investigation. **James Montoya-Lerma:** Writing – review & editing, Investigation. **Tung D. Nguyen:** Writing – review & editing, Investigation. **Ihsan Nurkomar:** Writing – review & editing, Investigation. **Jermaine D. Perier:** Writing – review & editing, Investigation. **Gabor Pozsgai:** Writing – review & editing, Investigation. **Ricardo Ramírez-Romero:** Writing – review & editing, Investigation. **Annmarie S. Robinson-Baker:** Writing – review & editing, Investigation. **Francisco J. Sanchez-Garcia:** Writing – review & editing, Investigation. **Luis C. Silveira:** Writing – review & editing, Investigation. **Larisner Simeon:** Writing – review & editing, Investigation. **Leellen F. Solter:** Writing – review & editing, Investigation. **Oscar F. Santos-Amaya:** Writing – review & editing, Investigation. **Wagner de Souza Tavares:** Writing – review & editing, Investigation. **Rogelio Trabanino:** Writing – review & editing, Investigation. **Carlos Vásquez:** Writing – review & editing, Investigation. **Zhenying Wang:** Writing – review & editing, Investigation. **Ana P.G.S. Wengrat:** Writing – review & editing, Investigation. **Lian-Sheng Zang:** Writing – review & editing, Investigation. **Wei Zhang:** Writing – review & editing, Investigation. **Kennedy J. Zimba:** Writing – review & editing, Investigation. **Kongming Wu:** Writing – review & editing, Investigation. **Maged Elkahky:** Supervision, Funding.

Declaration of competing interest

KAGW own a private consulting firm that provides specialized backstopping to sustainable agriculture and biological control. The other 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.

Acknowledgements

This work was funded by the European Commission through project GCP/GLO/220/EC and executed by the United Nations Food and Agriculture Organization (FAO). Drawings of predators and parasitoids were produced by Visuals in Science LAB. We wish to thank two anonymous reviewers for their valuable comments and suggestions on an earlier draft.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2024.105640.

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