



Biodiversity loss impacts top-down regulation of insect herbivores across ecosystem boundaries

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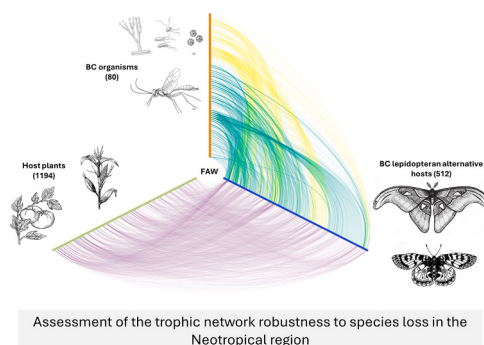
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HIGHLIGHTS

- Eighty FAW parasitoids or entomopathogens are indirectly linked to 1194 genera of plants.
- On-farm biological control is inherently tied to off-farm plant and animal biodiversity.
- Agriculturally-subsidized natural enemies shape off-farm restoration outcomes.
- Herbivore loss disproportionately impacts top-down regulation across habitat boundaries.
- Conservation biology, restoration ecology and biological control domains are to be entwined.

GRAPHICAL ABSTRACT



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ABSTRACT

Biodiversity loss, as driven by anthropogenic global change, imperils biosphere intactness and integrity. Ecosystem services such as top-down regulation (or biological control; BC) are susceptible to loss of extinction-prone taxa at upper trophic levels and secondary 'support' species e.g., herbivores. Here, drawing upon curated open-access interaction data, we structurally analyze trophic networks centered on the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and assess their robustness to species loss. Tri-partite networks link 80 BC organisms (invertebrate or microbial), 512 lepidopteran hosts and 1194 plants (including 147 cultivated crops) in the Neotropics. These comprise threatened herbaceous or woody plants and conservation flagships such as saturniid moths. Treating all interaction partners functionally equivalent, random herbivore loss exerts a respective 26 % or 108 % higher impact on top-down regulation in crop and non-crop settings than that of BC

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organisms (at 50 % loss). Equally, random loss of BC organisms affects herbivore regulation to a greater extent (13.8 % at 50 % loss) than herbivore loss mediates their preservation (11.4 %). Yet, under moderate biodiversity loss, (non-pest) herbivores prove highly susceptible to loss of BC organisms. Our topological approach spotlights how agriculturally-subsidized BC agents benefit vegetation restoration, while non-pest herbivores uphold biological control in on- and off-farm settings alike. Our work underlines how the on-farm usage of endemic biological control organisms can advance conservation, restoration, and agricultural sustainability imperatives. We discuss how integrative approaches and close interdisciplinary cooperation can spawn desirable outcomes for science, policy and practice.

1. Introduction

The integrity of the Earth system, as underpinned by genetic, species and landscape biodiversity, is increasingly uncertain. Across the globe, ecosystems are ever more subject to biotic homogenization (McKinney and Lockwood, 1999; Seebens et al., 2017) and biodiversity is under precipitous decline (Díaz et al., 2019). Defaunation is driven by habitat loss, farmland intensification and global warming (Jauregui et al., 2022), with rates of species decline exacerbated for invertebrate and microbial biota (Sánchez-Bayo and Wyckhuys, 2019; Averill et al., 2022), upper trophic levels such as parasitoids (Estes et al., 2011; Hu et al., 2023) and agriculture-dominated landscapes (Seibold et al., 2019). These phenomena impact anthropogenic and natural habitats alike (Hallmann et al., 2017; Brühl et al., 2021), affecting ecosystem functioning and resilience (Oliver et al., 2015), the services that humanity derives from them (Cardinale et al., 2012), and ultimately human well-being (Burra et al., 2021).

Biodiversity loss is prone to disrupt invertebrate- or microbe-mediated services such as biological control. By keeping herbivore populations within bounds, this service ensures restoration success (Hairston et al., 1960; Xu et al., 2023) and acts as a core constituent of pest management or ecological intensification (Bommarco et al., 2013; Deguine et al., 2023). Its outcomes in terms of pest suppression or crop yield recovery are mediated by the richness of biological control agents (BCAs) or so-called natural enemies and their (trophic) interactions (Dainese et al., 2019; Yang et al., 2021a). Thus, global change drivers such as habitat loss can affect biological control by upsetting either BCA richness or inter-species interactions (Kruess and Tscharnke, 1994; Tylianakis et al., 2007), in which interaction networks pose especially fragile (Janzen, 1974; Valiente-Banuet et al., 2015). Further, as herbivore regulation is performed by biota within upper trophic levels, though upheld by lower-rank ‘secondary’ species (Petermann et al., 2010), it may pose vulnerable to species loss (Keyes et al., 2021). This is especially important in ephemeral agroecosystems, where strength and stability of biological control is shaped by the dietary breadth of BCAs. Generalist BCAs contribute greatly to herbivore regulation in those settings (Symondson et al., 2002; Snyder, 2019; Mata et al., 2021), and their on-farm occurrence and performance is closely tied to the spatio-temporal abundance (and plant associations) of their alternative hosts. Hence, biological control outcomes will be impacted by the loss of BCAs themselves and ‘secondary’ support organisms. In a similar way as vulnerability scales from individual mutualist species to seed dispersal services (Fricke et al., 2022), defaunation can thus release herbivores from top-down regulation, trigger pest outbreaks and reduce primary productivity. What fraction of species loss may be tolerated prior to service collapse can be established by computing network fragility and the associated service robustness (Ma et al., 2019; Ross et al., 2021). Robustness of pollination, seed dispersal or disease regulation to species loss has been quantified (Ostfeld and LoGiudice, 2003; Ross et al., 2021; Keyes et al., 2021; Fricke et al., 2022), but this remains to be performed for biological control. Similarly, the extent to which (vegetation) restoration outcomes are vulnerable to loss of BCAs is unclear.

Biological control plays a central role in the sustainable management of the fall armyworm (FAW) *Spodoptera frugiperda* (Lepidoptera: Noctuidae) (Kenis et al., 2022; Wyckhuys et al., 2024). This neotropical

herbivore has recently spread across most of the global (sub-)tropics, jeopardizing food and livelihood security while triggering pesticide abuse (Tambo et al., 2020; Yang et al., 2021b). In its native range, a suite of microbiota and invertebrate parasitoids or predators provide top-down forcing and keep its populations below economically damaging levels (Lezama-Gutiérrez et al., 2001; Molina-Ochoa et al., 2003). Yet, the robustness of FAW biological control to loss of ecosystem service providers i.e., BCAs or ‘secondary’ support species remains to be clarified. So far, this has been obstructed by the prevailing pest- or crop-centric vs. system-level research foci (Ma et al., 2019; Wyckhuys et al., 2023). This in particular is impeded by scant data on non-pest reservoirs of FAW entomopathogens (EP; Hochberg, 1989; Lacey et al., 2015) or parasitoids (Miller et al., 2021), and interaction networks that are either not properly delineated or restricted to single ecosystem compartments (Stireman III et al., 2017; Alfaro-Tapia et al., 2022). By looking beyond the boundaries of those compartments, meta-ecosystem approaches as per Harvey et al. (2023) transcend such impediments and aid the prediction of biological control robustness at a macro-scale.

In this study, we assess whether species loss differentially affects top-down regulation of herbivorous insects with the (semi-)natural and man-made habitats that compose farming landscapes. Further, viewing inter-species interactions from a holistic systems perspective, we aim to compare how loss of service providers vs. secondary support organisms impacts those ecological processes in landscape matrices. Drawing upon network theory (Dee et al., 2017), we extract and curate interaction linkages between *S. frugiperda*, its BCA associates and their subsequent (lepidopteran, plant) reservoir hosts from the open-access GloBI data repository (Poelen et al., 2014). Following the construction of interaction networks, we quantitatively assess how biodiversity loss impacts biological control at a species or crop level under various ‘extinction’ scenarios. Given the absence of sufficient empirically-derived functional trait data for all organismal nodes in the network (Wyckhuys et al., 2024), we treat the strength of all BCA-FAW, BCA-host and host-plant interactions as equivalent and all interaction partners as essential i.e., non-substitutable (Ross et al., 2021) for biological control. As such, our unweighted topological approach only permits coarse-grained robustness predictions at the ecosystem process (vs. service) level. Despite these shortcomings, our work offers unique vistas onto the structural fragilities of biological control at an area-wide scale and clarifies its intrinsic dependency upon lepidopteran conservation in natural habitats.

2. Materials & methods

We used published data on FAW (microbial, invertebrate) BCAs, their alternative hosts, and the host plants of the latter to generate two multilevel trophic networks. In these networks, FAW BCAs are situated at the origin and their alternative hosts and their associated host plants in consecutive levels.

First, a comprehensive list of 350 FAW associated entomopathogens and parasitoids was drawn from Wyckhuys et al. (2024). This list of BCAs was complemented by querying the Global Biotic Interaction (GloBI) database for any pathogenic and parasitoid interactions between FAW and other BCA species. GloBI is a curated collection of databases for biotic interactions which hosts 700,000 species interactions across about

50,000 taxa which are systematically organized around interaction ontologies and can either be queried directly through the website or an application programming interface (API) (Poelen et al., 2014). We queried GloBi using the *rglobi* R package, first parametrizing the obtained *interactions_by_taxa()* function with “*Spodoptera frugiperda*” as source taxon and either with “hasParasite” or with “hasPathogen” as interaction type. We both programmatically and manually curated the results and the alternative hosts of FAW’s BCAs were identified through a second GloBi query in which BCAs were listed as target taxa and interaction types were set to either “parasiteOf”, “parasitoidOf”, “eat” or “pathogenOf”. In order to include all interactions of interest, we consciously used broader interaction categories (such as “parasiteOf” and “eats”) to find parasitoids in both queries. Non-parasitoid interactions were manually filtered off.

The host plants of lepidopteran alternative hosts were queried from Database of the World’s Lepidopteran Hostplants (Robinson et al., 2023). Host plants were recorded at the genus level. The taxonomy of all species was updated to the currently accepted scientific names based on the Taxonomy Backbone of the Global Biotic Information System (GBIF, www.gbif.org) and duplicated species and interactions were removed. When automated taxon match attempts failed, the authors confirmed species identity by reviewing published literature. All interactions containing unresolved species names ($n = 9$) and those based solely on genus-level identifications were removed. Higher taxa, such as kingdom, phylum, class, order, and family, were assigned to all parasitoid species and kingdom, phylum and class to pathogens (except for the viruses where only kingdom information was reliably available).

GBIF identifiers (GBIFIDs) were assigned to each species and used for querying the occurrences of parasitoids, alternative hosts, and plant genera on GBIF, with the help of the *rgbif* R package (Chamberlain et al., 2024). Of parasitoids, alternative host species, and host plants, only species with documented occurrences from the Americas (i.e. North, South, and Central America, including the Caribbean region) were included. Since the geographic distribution of most pathogens is highly data deficient, and pathogens are tightly linked to their hosts, all reported FAW pathogens were included in the analysis. Host plant genera were cross-referenced with the crop list of FAO (<https://www.fao.org/3/a0135e/A0135E00.htm>, accessed 19/01/2024) to highlight crop genera in our database.

The first of the two networks consisted of two separate levels, the first showing interactions between FAW and its BCAs, including pathogens and parasitoids, but excluding predators, and the second showing interactions between the BCAs of FAW and their alternative host species. Predators were excluded because of the paucity of records on GloBi and our inability to confirm their functional importance (Wyckhuys et al., 2024). The second network consisted of three levels, the first showing interactions between FAW and its BCAs as in the previous case, the second listing interactions of FAW’s BCAs with Lepidoptera alternative hosts only, and the third showing the host plant associations of these lepidopteran species. We generated the networks, adjusted network structure, calculated network properties and subsetting networks using the *igraph* (Csárdi and Nepusz, 2006) and bipartite packages (Dormann et al., 2008).

In order to investigate the controlling effect of FAW’s BCAs on alternative host herbivores that feed on crop plants, we linked the BCA species directly to crop genera when they had a herbivore species in common (i.e., attacked by the BCA and fed on the plant). Interaction strength between a BCA species and a crop genus was defined as the number of herbivores fed on the crop genus and were also infected/parasitized by the BCA. To explore similarities in linking preferences and indirect interactions between taxa within the same trophic levels, we converted the BCA – alternative host, alternative host – host plant, and the BCA – crop networks to bipartite networks (i.e. removed hyper-parasitoid interactions and those between pathogens and parasitoid hosts) and generated the monopartite projections of each. Monopartite projections link nodes (in this case animal species or plant genera) from

one group of the bipartite network to each other when they have common links to the other group. The adjacency matrices of each of the projections were converted into Bray-Curtis distances and fed into a hierarchical cluster analysis and were visualized as dendrograms. Densely connected groups of taxa (modules) were detected using Beckett’s algorithm (Beckett, 2016).

To assess how biodiversity decline impacts on biological pest control, we simulated the loss of BCAs and recorded the number of controlled herbivores, the number of crops, and non-crop plant genera protected by BCAs from all associated alternative hosts (protected plants or crops henceforth). We considered two distinct scenarios: a random removal of BCAs and one in which the enemies were selectively removed based on how many links to herbivores they had (i.e., degree), starting from the most linked species and gradually reaching the least connected ones. When a species was removed from the network, all links which it had to other species were deleted as well and all species with no links to other nodes in the network were removed. Since the presence of BCAs depends on their shared hosts (Keyes et al., 2021), we also simulated how the removal of herbivore hosts affects the number of BCAs and the crops they protect remaining in the network. In this case, we separately simulated the targeted removal of the herbivore species most connected to BCAs (in degree) and their host plants (out degree). All random processes were simulated in 1000 iterations.

We employed a Generalized Additive Model (GAM) to analyze how species losses affected the number of protected crops and non-crop plants. The GAM was fitted with a Poisson family and an identity link function. For smoothing we specified a shrinkage version of cubic spline regression (‘cs’) with 20 knots. We modelled the number of crop and non-crop species as a function of the loss of BCAs, as well as that of the secondary hosts. We repeated the process for both the raw species numbers and the percentage of maximum species richness remaining in the networks. Models were fit using the *mgcv* R package (Wood, 2017).

All data gathering and clean-up, data analysis and simulations were conducted using R (R Core Team, 2012).

3. Results

Altogether we collected 146 BCAs of FAW including 96 parasitoids and 51 pathogens (Fig. 1). BCAs interacted with 1110 alternative hosts through 2216 interaction links. Out of these BCAs, 80 were linked to 512 species of Lepidoptera through 1375 interactions (Suppl. Table 1 for network properties). Of the 146 BCAs, GloBi did not find any alternative hosts besides *S. frugiperda* for 59 species. The BCA – secondary host network could be divided into two modules (M1 & M2), the first encompassing insect parasitoids, viruses and microsporidia attacking mostly Lepidoptera and Psocodea, whilst in the second entomopathogenic fungi, bacteria and nematodes were linked to mites and a wide variety of insect taxa. The most numerous interactions in this network were between (parasitoid) Hymenoptera and Lepidoptera, Diptera and Lepidoptera in M1 and between hypocrealean fungi and beetles (Fig. 2). Fungi within the Hypocreales infected the most higher taxa ($n = 14$) but parasitic hymenopterans attacked more species ($n = 1028$, 497, respectively). Indeed, Hypocreales, Hymenoptera, and Diptera were often linked to similar herbivore taxa (Supplementary Fig. 1). Lepidoptera were the most often infected or parasitized by BCAs, with 1375 species in 12 higher taxa. Coleoptera was the second most important alternative host taxon with 295 recorded BCAs, albeit only in 8 taxa. The most commonly parasitized or infected orders belong to modern winged insects (e.g. Lepidoptera, Diptera, Hymenoptera) and they also were attacked by similar BCAs (Suppl. Fig. 1).

For 484 out of the 512 lepidopteran alternative host species, we logged trophic linkages to 1194 genera of plants, out of which 147 are crops. The 11 most linked lepidopteran species fed on a total of 470 plant genera (Fig. 3). Noctuidae consumed the most plant orders, with a particular preference for Fabales, Poales and Asterales. Tortricidae, Geometridae and Erebidae mostly favored Rosales (Suppl. Fig. 2).

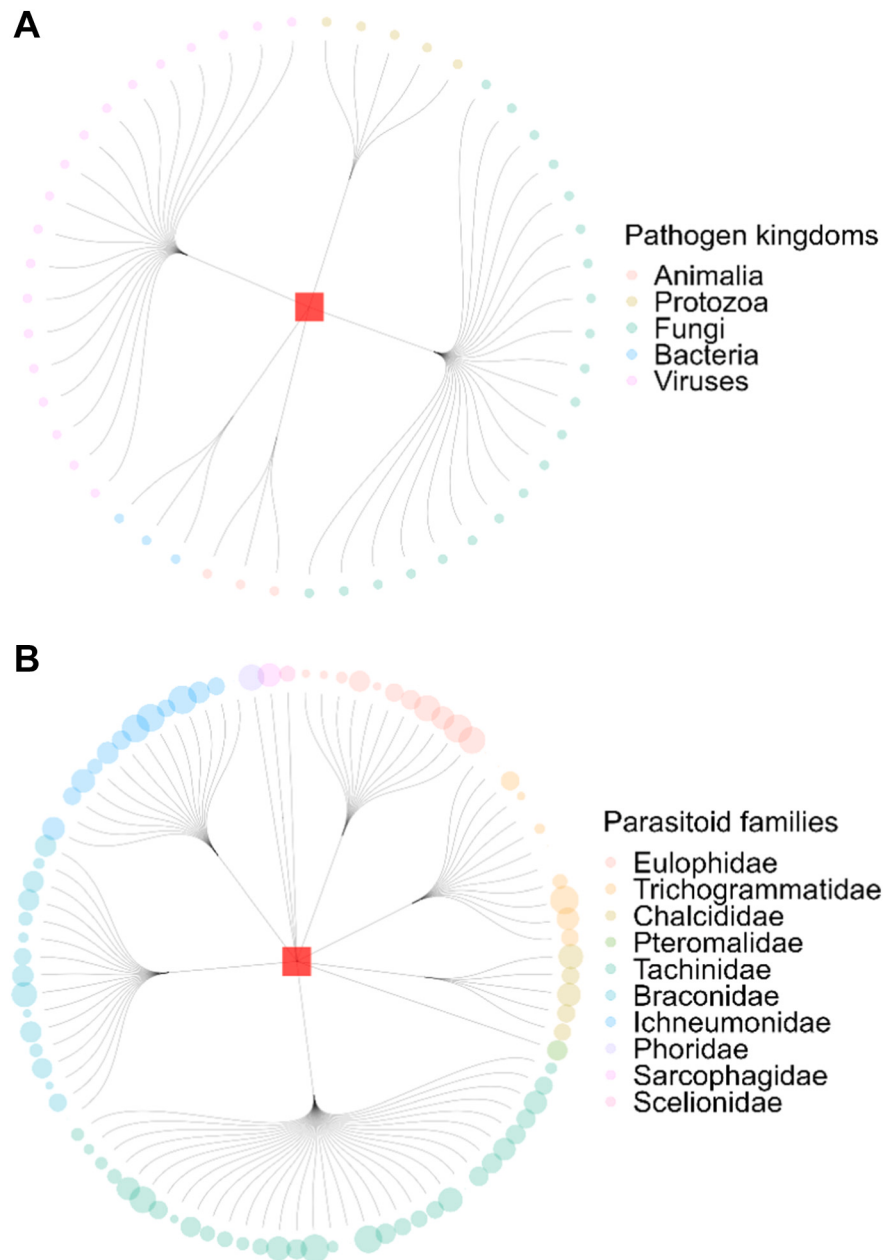


Fig. 1. Pathogens (A) and parasitoids (B) linked to *Spodoptera frugiperda* in its region of origin. Each circle represents one species and the central square represents FAW. Colour codes of circles represent kingdoms and families of pathogens and parasitoids, respectively. For parasitoids, node size is proportional to the number of Latin American and the Caribbean (LAC) countries from which a given species is reported in GBIF. For pathogens, geographical distribution was not assessed and node size is kept uniform.

Noctuidae, Tortricidae, and Erebidae were, however, grouped together based on their host-plant associations in the hierarchical cluster analysis (Suppl. Fig. 3).

Of the 146 BCA species 68 (25 pathogens and 43 parasitoids) were indirectly linked to (protected) 1194 plant genera, of those 146 were crops (Fig. 4). *Zea*, *Solanum*, and *Brassica* were the most protected crop genera, with 59, 56, and 55 BCAs linked to them, respectively, whilst *Trichogramma minutum*, *T. pretiosum*, and *Beauveria bassiana* protected the most plants (706, 552, and 500 genera, respectively) and *T. minutum*, *T. pretiosum*, and *Metarhizium rileyi* the most crops (128, 127, and 115 genera, respectively). The higher-taxon grouping showed three modules: i) fungi and tachinid flies linked to several plant orders, ii) hymenopteran parasitoids and nematodes linked to economically important orders like Cucurbitales, Fabales, and Poales, and iii) viruses, bacteria, microsporidian Protozoa and smaller insect families linked to

Brassicales and Solanales (Fig. 5). The analysis of the projected network of the indirect interactions between NEs and plant revealed distinct clustering of NE groups according to the plant species they defend. Groupings included Bacteria, nematodes, and various smaller insect families in one cluster, while Tachinidae, Trichogrammatidae, Eulophidae, and Fungi formed another cluster. Additionally, Protozoa (specifically Microsporidia), Chalcididae, and viruses were associated with another unique set of plants (Suppl. Fig. 4).

The degree distribution of parasitoids is heavily right-skewed, suggesting a comparatively narrow dietary breadth. Meanwhile, entomopathogens are comparatively more generalist. Both groups have numerous indirect links to plants, but the degree distribution for pathogens is more uniform and they cover more plant genera (Suppl. Fig. 5).

GAM-smoothed curves of the simulated species removals were highly significant ($p < 0.001$) and explained over 90 % of the deviance. The

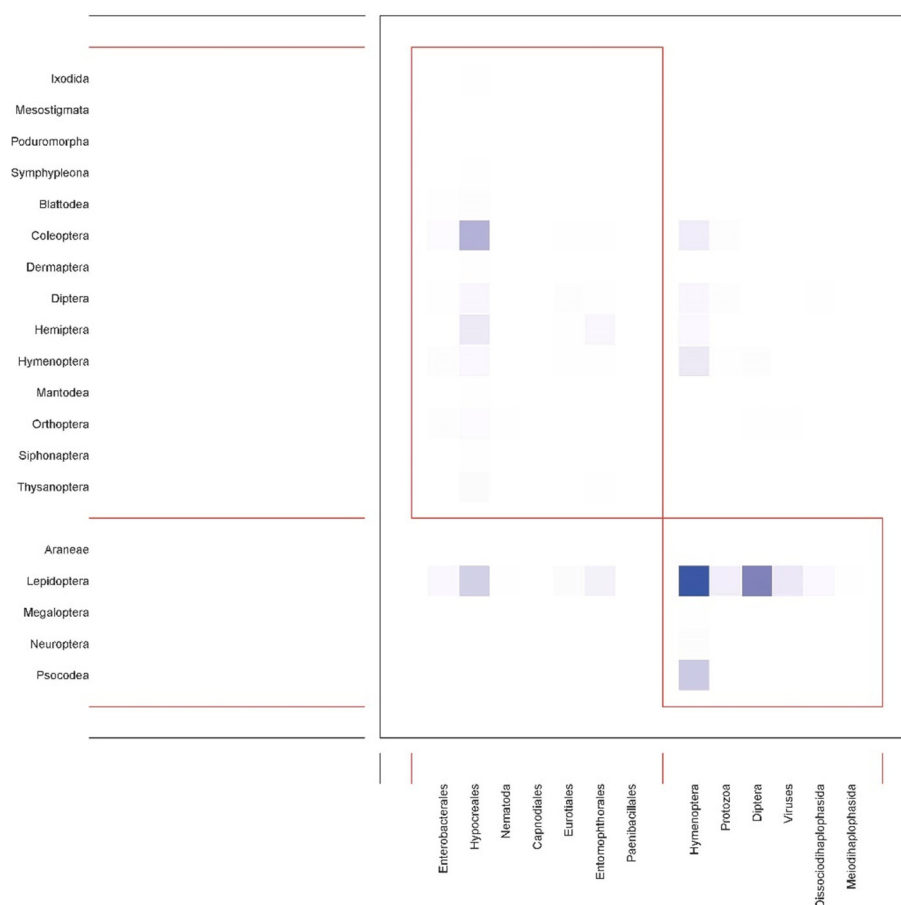


Fig. 2. Logged interactions between FAW natural enemies and their alternative hosts. Inter-specific interactions are grouped by kingdom and insect order for the natural enemies (columns) and insect order for alternative hosts (rows). Coloured cells indicate an association between the taxa listed within a given row and column, and colour intensity indicates the number of species-level associations between these groups. Red lines and rectangles indicate communities (modules) detected using Beckett's algorithm.

gradual removal of alternative host species resulted in cascading 'extinction' of both BCAs and herbivores in the tripartite BCA - secondary host - plant networks (Fig. 6), with the random removals consistently causing a slower decay in network structure than those prioritizing highly linked species. Indeed, when species were removed in a random order, both BCAs and crops showed considerable resilience for the removal of the first half of secondary hosts but declined rapidly after that. Conversely, with the elimination of BCAs, secondary hosts gradually disappeared from the network in a nearly linear fashion. However, the majority of crops remained protected even after the removal of two-thirds of these BCAs (Fig. 7).

4. Discussion

Much of the world's farmland lacks a critical influx of biodiversity benefits from the adjoining landscape matrix (Garibaldi et al., 2021). To uphold services such as biological control in the face of unrelenting biodiversity loss, one needs to ascertain the role of inter-specific interactions and associated ecological processes (Abdala-Roberts et al., 2019). Here, we demonstrate how 80 FAW-associated microbial or invertebrate natural enemies are trophically linked with at least 512 lepidopteran herbivores and almost 1200 plant species at a continental scale. This inclusive listing of BCA host (plant) reservoirs guides future efforts to harness biodiversity for sustainable pest control (Landis et al., 2000; Lacey et al., 2015; Quesada-Moraga et al., 2022). In addition, our work gauges the repercussions of a progressive loss of such biodiversity. Specifically, plant-herbivore-BCA networks prove far more vulnerable to moderate loss of service providers i.e., BCAs than of secondary 'support'

organisms. At 50 % species loss however, top-down regulation in non-crop settings poses less resilient to the loss of herbivores than of BCAs. Meanwhile, a preservation of BCAs in farm settings is crucial to herbivore regulation at a landscape scale. Further claims about downstream service delivery however are impeded by a scarcity of functional data layers or fine-resolution network structure. Overall, by unveiling how agriculturally subsidized biota benefit top-down regulation or vegetation restoration across the boundaries of single (natural, man-made) ecosystems, we provide invaluable guidance for science, policy and practice in sustainable agriculture, restoration ecology and conservation domains.

Our topological analyses unveil how BCAs that act in agricultural realms engage in two-way interactions with non-pest herbivores including conservation flagships such as the saturniid moths and a diverse set of plant species of varying conservation status. These secondary biota are highly susceptible to environmental change: many lepidopterans have undergone rapid declines with implications for insectivores and native vegetation (Sánchez-Bayo and Wyckhuys, 2019). While it is well established that non-pest lepidopterans contribute to biological control, as secondary hosts for natural enemies of pests, and pollination in farm settings (Marino et al., 2006; Cusser et al., 2021; Requier et al., 2023), the benefits of on-farm biological control for conservation practice have received far less attention. Instead, conservation science has centered on the risks that a small sub-set of poorly selected or accidentally introduced exotic BCAs pose to native biota (Boettner et al., 2000; but see Heimpel and Cock, 2018). Yet, endemic parasitoids and pathogens link ecosystem compartments in a similar way as plants or generalist predators (Scheu, 2001), and the strong

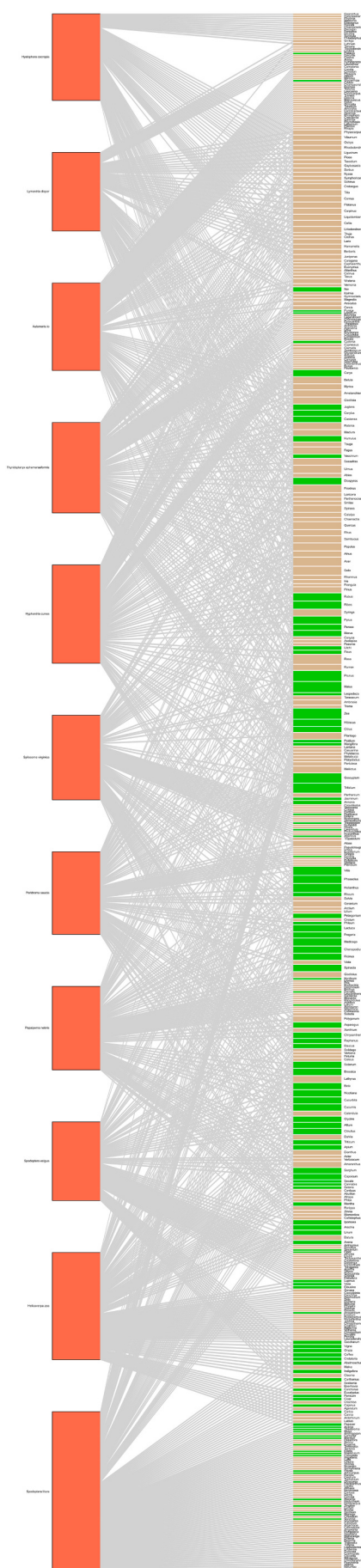


Fig. 3. The eleven most common alternative lepidopteran hosts of FAW natural enemies and their associated host plant genera. For each lepidopteran (left) or plant (right) species, box size indicates the number of interactions with other taxa. Plant genera that are cultivated (i.e., crops) are highlighted in green. From top to bottom, lepidopteran hosts include *Hyalophora cecropia*, *Lymantria dispar*, *Automeris io*, *Thyridopteryx ephemeraeformis*, *Hyphantria cunea*, *Spilosoma virginica*, *Peridroma saucia*, *Papaipema nebris*, *Spodoptera exigua*, *Helicoverpa zea* and *Spodoptera litura*.

habitat specificity of even polyphagous taxa largely restricts their impacts to crop habitats (Romeis et al., 2005). Hence, aside from its role in alleviating pesticide use, the on-farm conservation or augmentation of naturally-occurring taxa can secure the trophic structure and ecological regulation of native butterflies and moths, regenerate natural vegetation, and advance restoration outcomes (Hairston et al., 1960; Villar, 2023). Closer cooperation between conservation biology and biological control disciplines may thus prove mutually beneficial (Van Driesche et al., 2010; Heimpel and Wyckhuys, 2021) and the conservation of area-wide interactions or biostructure -instead of individual taxa- poses a suitable focus of collaborative thrusts (Memmott et al., 2007; Heinen et al., 2020).

Natural enemies exert strong top-down selection pressure on (lepidopteran) herbivores in both natural and man-made habitats (Vidal and Murphy, 2018), yet the implications of biodiversity loss are variable, context-dependent and difficult to anticipate. Loss of ecosystem service providers and their support species differentially impacts the processes that underpin service delivery and this is mediated by extinction sequence (Ostfeld and LoGiudice, 2003; Bruno and Cardinale, 2008; Keyes et al., 2021). Such is imperfectly mirrored in the speed at which (crop, herbivore, BCA) interaction partners disappear under progressive loss of herbivores or BCAs (Turchin et al., 1999; Abdala-Roberts et al., 2019). Though our analyses do not account for species' functional role as in Pocock et al. (2021) and Fricke et al. (2022), curve steepness notably differs between organismal groups and extinction scenarios. Thus, random loss of herbivores exerts stronger impacts on the number of trophic links for crop protection (137.7 ± 0.1 crop genera or 94.3 ± 0.8 % of the original diversity remaining in the network at 50 % loss of secondary herbivore hosts) or vegetation restoration (746.9 ± 0.2 non-crop genera or 71.3 ± 0.7 %) than BCA loss (i.e., 98.5 ± 2.0 %, 86.2 ± 1.9 %). Herbivore loss thus exerts 26–108 % higher impacts on top-down regulation in crop or non-crop settings. The comparatively lower vulnerability of both ecosystem processes to BCA loss may hint at their heightened resilience, but can also accentuate how the interaction linkages between BCAs and non-crop host plants largely remain to be uncovered or digitized. For instance, it is difficult to assess the exact dietary breadth of generalist parasitoids that attack hosts in various habitats (Raymond et al., 2016). Regardless of this plausible knowledge gap, on-farm biological control may be especially vulnerable to landscape-level loss of primary consumers such butterflies or moths, although extinctions are biased towards upper trophic levels (Duffy, 2002; Estes et al., 2011).

Further, random BCA loss might impact herbivore regulation to greater extent (902.7 ± 0.6 species, that is 86.2 ± 1.9 % at 50 % loss) than herbivore loss mediates their preservation (70.9 ± 0.1 or 88.6 ± 0.8 % remaining in the system). Moreover, the loss of secondary herbivore hosts would indirectly release 2- to 12-fold more plant genera from BCA-mediated herbivore (or pest) regulation than BCA loss directly. Hence, if richness loss indeed relates to functionality loss, the 75 % decline of *Trichogramma* sp. parasitoid species in China's maize agro-landscapes over the past 4 decades (Hu et al., 2023) may have severe repercussions for plant diversity and abundance (Xu et al., 2023). This however does not necessarily hold when BCAs and their lepidopteran hosts experience declines of similar magnitude. Lastly, as extinction sequences affect the number of interaction partners 3- to 6-fold, species identity likely has marked effects as in other predator-prey or

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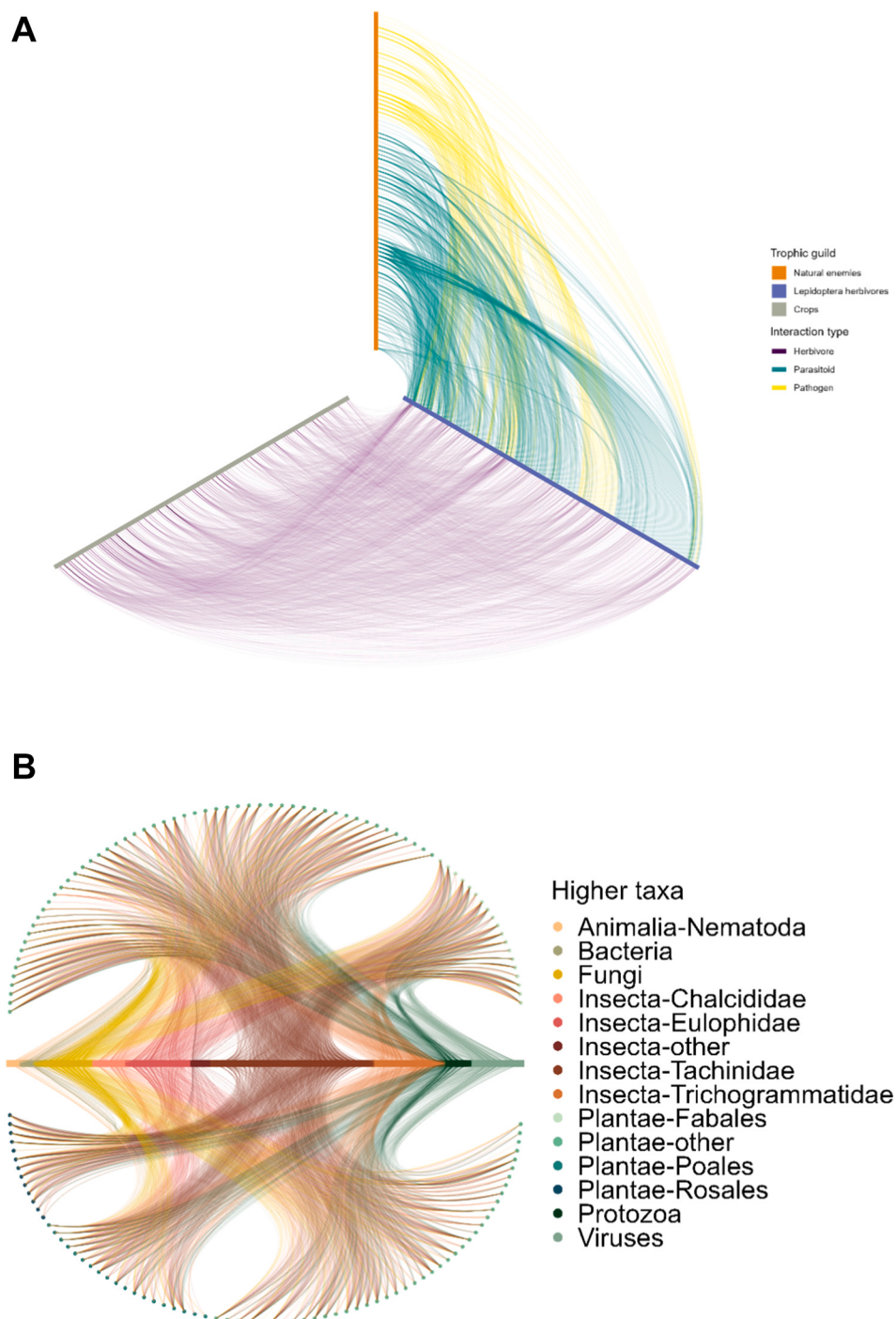


Fig. 4. Interaction networks between FAW natural enemies and the crop genera that they indirectly protect by feeding upon alternative hosts. In panel A, all constituents in the tri-partite plant-herbivore-natural enemy network are shown. In panel B, natural enemy taxa are listed on the horizontal axis, while plant taxa are plotted along the circumference of the enclosing circle. The main plant and animal taxa are colour-coded. In both panels, non-crop plant species are excluded for data visualization purposes.

pollinator-plant networks (Straub and Snyder, 2006; Winfree et al., 2015; Mei et al., 2024). Yet, as all species are treated functionally equivalent, identity effects solely relate to host breadth or degree while discounting rare species contributions (Leitão et al., 2016) and the role of functional redundancy or complementarity (Dee et al., 2019; Snyder, 2019). As such, broader implications for ecosystem service delivery are hard to predict. Though ecological regulation may scale with species richness (Felipe-Lucia et al., 2020; Ross et al., 2021), its functional outcomes go far beyond our simple biodiversity and interaction metrics

(Fricke et al., 2022).

A restricted coverage of FAW natural enemies, absence of a functional (trait) layer and omissions of BCA's plant-based food resources limit the applicability of our structural approach. Data within interaction repositories such as GloBi are biased, fragmented and noisy (Poisot et al., 2021) and this severely restricts our analysis: the 80 digitized BCAs only pose a small slice of FAW-associated taxa in the Neotropics and notably disregard invertebrate predators (Wyckhuys et al., 2024). Further, our approach disregards tri-trophic interactions such as plants'

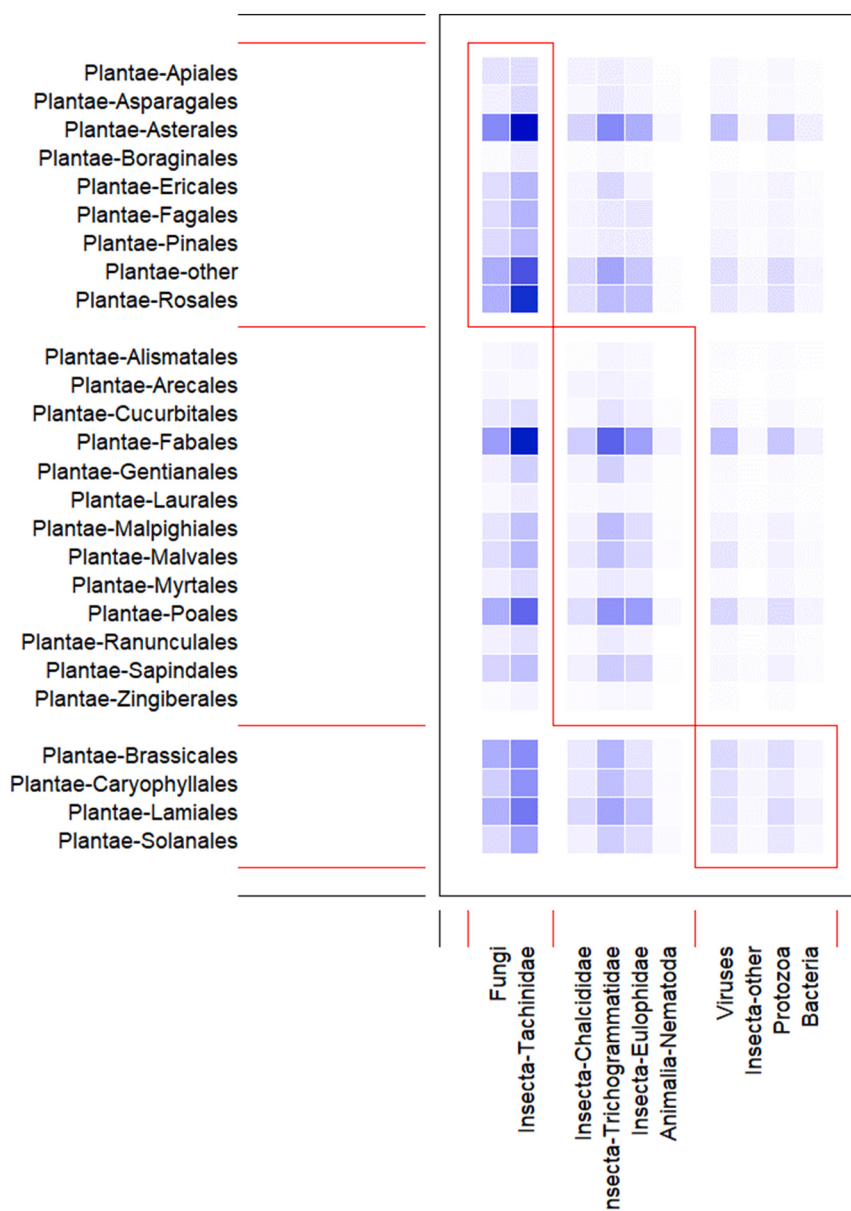


Fig. 5. Logged interactions between FAW natural enemies and the cultivated plants i.e., crops they indirectly protect by feeding upon alternative hosts. Interspecific interactions are grouped by higher taxa for the natural enemies (columns) and by plant order for the crops (rows). Coloured cells indicate an association between the taxa listed within a given row and column, and colour intensity indicates the number of species-level associations between these groups. Red lines and rectangles indicate communities (modules), detected by using Beckett's algorithm.

central role in nectar or pollen provisioning for foraging parasitoids (Zemenick et al., 2019) but also the contribution of shelter of refuge habitats (Gillespie et al., 2016). The above shortfalls likely also apply to the non-crop herbivore-plant interactions in the network, and need to be fixed. A consideration of these broader (trophic, non-trophic) interactions between plants, invertebrates and microbiota is imperative to operationalize tri-trophic defense concepts (Wyckhuys et al., 2022). As a logical next step, our analysis also needs to raise experimental realism through an added functional layer e.g., by incorporating plant, herbivore and BCA trait data. To reliably predict outcomes in terms of top-down regulation, one needs to include BCA performance variables such as parasitism rate and the traits underpinning redundancy, intra-guild predation and niche complementarity (Straub et al., 2008). Some of these might be inferred through proxies such as biomass (Ostandie et al., 2021) or abundance (Winfree et al., 2015; but see Barry et al., 2019). Meanwhile, traits that capture response diversity or extinction proneness may be especially important in highly disturbed (farm)

settings (Redhead et al., 2018; Walker et al., 2023). While extensive trait databases exist for plants, invertebrate or microbial trait data tend to be scarce, uncurated and scattered across the literature (Perović et al., 2018; Segoli et al., 2023). Trait-based approaches however are imperative to reliably pinpoint tipping points for network collapse (Bascompte and Scheffer, 2023) e.g., in which the respective loss of endemic macro-moth or parasitoids may either trigger farm-level pest outbreaks or lower restoration success (Villar, 2023). They are equally instrumental in pinpointing those taxa that can switch (plant) partners adaptively following species loss or act as landscape-level connectors (Hackett et al., 2019; Grass et al., 2018) and thereby help to outline trajectories towards enhanced resilience (Winfree and Kremen, 2009). Metrics such as modularity feature in structure-stability relationships and can be valuable yardsticks to assess biological control or vegetation restoration outcomes under biodiversity loss (Grass et al., 2018; Robinson and Strauss, 2020; Valverde et al., 2020; Yang et al., 2021a).

Our work reiterates a need for holistic food-web research and

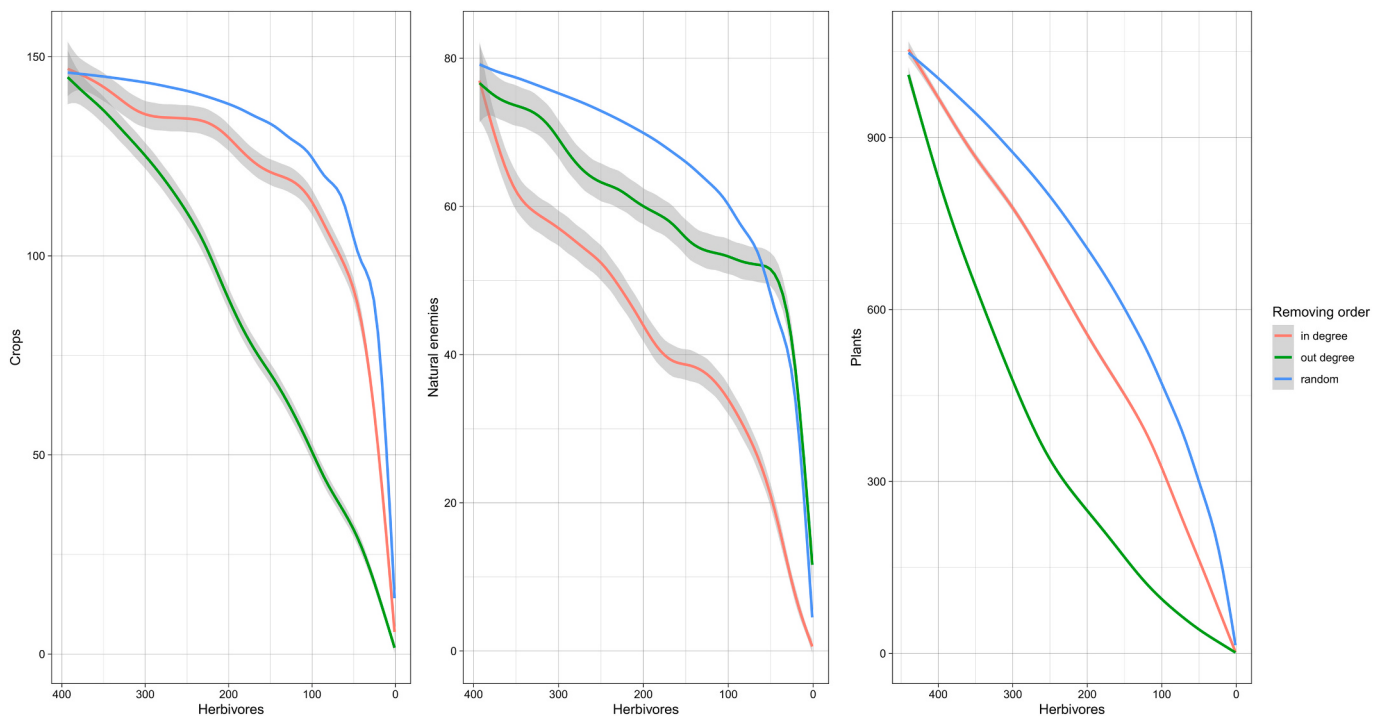


Fig. 6. Effect of alternative host loss on the number of FAW natural enemies (left), protected crops (centre) or non-crop host plants (right) that remain within the tripartite network. The tripartite network is composed of FAW natural enemies or BCAs, alternative hosts and their cultivated host plants i.e., crops. Alternative hosts are either removed by declining number of associated natural enemies (in degree, red line) or cultivated plant hosts i.e., crops in the initial network (out degree, green line), or removed in a random fashion (blue line).

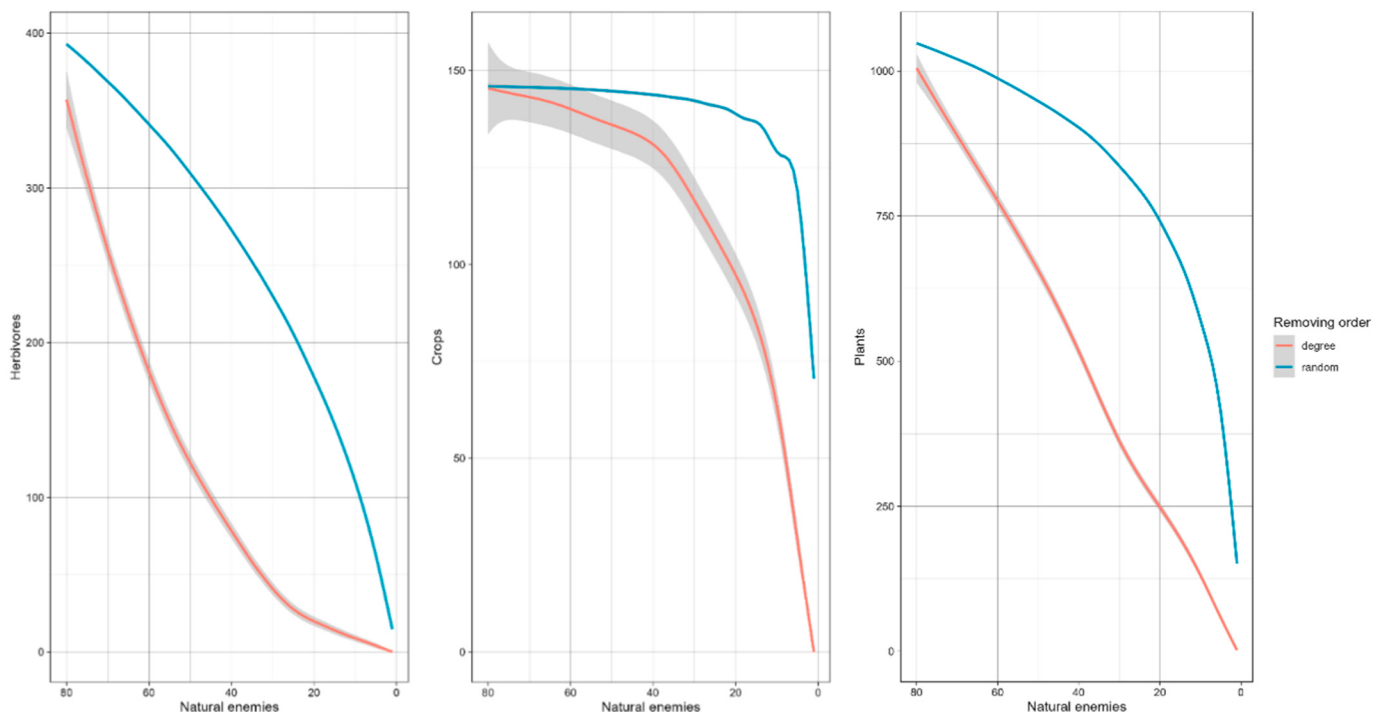


Fig. 7. Effect of FAW natural enemy loss on the number of impacted alternative hosts (left), protected crops (centre) or non-crop host plants (right) in the tripartite network. The tripartite network is composed of FAW natural enemies or BCAs, alternative hosts and their cultivated host plants i.e., crops. Natural enemies are either removed by declining number of associated alternative hosts in the initial network i.e., by declining degree (red line) or randomly (turquoise line).

network perspectives that go much beyond logging bi-trophic interactions for individual pests or conservation priority targets (Dee et al., 2017; Ma et al., 2019; Wyckhuys et al., 2021; Allen et al., 2022). Indeed, by viewing the tri-trophic interactions between BCAs, lepidopteran

hosts and host plants comprehensively, ecological concepts based on various hypothesis including natural enemy, resource concentration, insurance, and aggregation can be put into practice (Root, 1973; Hopper and Roush, 1993; Shanafelt et al., 2015; Blubaugh et al., 2021; Loreau

et al., 2021) and the imperatives of biodiversity conservation and on-farm pest resilience can be made mutually enforcing (Tscharnkte et al., 2021; Wyckhuys et al., 2022). The examination of the strength of the reported interactions with the various biological theories (hypotheses) are also important to investigate the impact of species decline on FAW biological control practice. Network approaches are a powerful tool as they permit partitioning biodiversity effects on vegetation restoration or biological control across scales and ecosystem compartments. Network approaches such as ours can thus help to refine diversification tactics for sustainable pest control (Ditzler et al., 2021) by adding in a ‘fourth’ off-farm dimension, or adapt conservation strategies to taxon-specific response scales (Gonthier et al., 2014). They also help to account for those biodiversity effects on vegetation restoration that amplify or attenuate over time (Reich et al., 2012; Grass et al., 2018). Our exploratory study further underlines the value of network approaches in pinpointing the overlooked complementary or secondary supporting species that underpin top-down regulation in crop and non-crop habitats (Cusser et al., 2021; Keyes et al., 2021), be it the non-pest herbivores in off-farm settings or the agriculturally-subsidized natural enemies. Once properly delineated, these networks can be interwoven with social ones to put ecology at the heart of ecosystem service science e.g., in shaping stakeholders’ payment for or recognition of off-farm biodiversity conservation (Quintessence Consortium, 2016; Dee et al., 2017) and to effectively inform science, policy and practice (Kleijn et al., 2019).

Irrespective of its methodological shortfalls, our structural delineation of FAW food webs reveals how ‘best-bet’ restoration and crop protection solutions are to be found beyond the confines of single ecosystem compartments i.e., at the landscape level. In particular, on- and off-farm conservation of consumer organisms (or BCAs) can simultaneously enhance restoration success (Villar, 2023) and curb pest-induced crop losses in a preventative, non-chemical manner (Dainese et al., 2019). Under (plausible) scenarios of moderate biodiversity loss, lepidopteran and plant species in natural habitats can be effectively conserved by protecting BCAs in farmland e.g., through pesticide phasedown, crop diversification and agroecological measures. As such, farmland intensification and species conservation need not be mutually exclusive goals. When aiming to establish self-sustaining, pest-suppressive landscapes (Heinen et al., 2020; Tscharnkte et al., 2021; Wyckhuys et al., 2022) and to turn the tide on biodiversity loss (Johnson et al., 2017), bold, integrative and interdisciplinary action is key to harness this top-down forcing by BCAs. Top-down regulation finds itself at the core of conservation biology, restoration ecology and biological control; like-minded disciplines disjointed by the grand agriculture-conservation divide. In the pursuit of a more biodiverse planet, this divide needs urgent mending. Network approaches point the way.

CRedit authorship contribution statement

Kris A.G. Wyckhuys: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization. **Gabor Pozsgai:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Ibtissem Ben Fekih:** Writing – review & editing, Data curation. **Francisco J. Sanchez-Garcia:** Data curation. **Maged Elkahky:** Writing – review & editing, Resources, Project administration.

Declaration of competing interest

Kris A.G. Wyckhuys reports financial support was provided by European Commission. Gabor Pozsgai reports financial support and administrative support were provided by Center for Ecology, Evolution and Environmental Changes (CE3c). Ibtissem Ben Fekih reports financial support was provided by National Fund for Scientific Research F.R.S.-FNRS. KAGW is the chief executive officer of Chrysalis Consulting, a firm that provides tailored support to nature-friendly farming and

biological control. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All scripts and data used for the analysis will be made openly available upon publication on G.P.’s GitHub page.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.172807>.

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