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Review

Restoring functional integrity of the global production ecosystem through biological control

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ABSTRACT

Human society is anchored in the global agroecosystem. For millennia, this system has provided humans with copious supplies of nutrient-rich food. Yet, through chemical intensification and simplification, vast shares of present-day farmland derive insufficient benefits from biodiversity and prove highly vulnerable to biotic stressors. Here, we argue that on-farm action centered on biological control can effectively defuse pest risk by bolstering foundational ecosystem services. By harnessing plant, animal and microbial biodiversity, biological control offers safe, efficacious and economically-sound plant health solutions and coevolved options for invasive species mitigation. In recent years, its scientific foundation has been fortified and solutions have been refined for myriad ecologically brittle systems. Yet, for biological control to be mainstreamed, it needs to be rebooted, intertwined with (on- and off-farm) agroecological tactics and refurbished - from research, policy and regulation, public-private partnerships up to modes of implementation. Misaligned incentives (for chemical pesticides) and adoption barriers further need to be removed, while its scientific underpinnings should become more interdisciplinary, policy-relevant, solution-oriented and linked with market demand. Thus, biological control could ensure human wellbeing in a nature-friendly manner and retain farmland ecological functioning under global change.

1. Introduction

Food is a formidable imperative for human and societal existence. Ancient Sumerians' pursuit of stable food supplies prompted plant domestication and a lasting shift away from hunter-gatherer lifestyles. By becoming a food producer, *man made himself* (Childe, 1936) and agriculture became the foundation stone of modern human civilization. Under bountiful biodiversity, healthy ecosystems and stable climates, agriculture gave rise to the development of complex societies. Aside from its vital role in ensuring food security, agriculture contributes to multiple other ecosystem services and 11 (out of 17) sustainable development goals (SDGs) (Viana et al., 2022).

Yet, since its earliest origins, farming has changed radically. Today's agri-food production model poses a threat to humanity and partially explains why SDGs are off-track (Sachs et al., 2023). In its pursuit to feed more than 8 billion people, agriculture is pushing the Earth system

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beyond its safe operating space, with food production transgressing several interlinked planetary boundaries (Richardson et al., 2023). Modern-day agriculture has become "techno-centric", focused on enhancing input use efficiencies to maximize crop output with little regard for the environment (Durr et al., 2015). As such, agriculture currently accounts for 34% of global greenhouse gas emissions, drives land use change and biodiversity loss, and degrades both natural and man-made ecosystems (Crippa et al., 2021; Peñuelas and Sardans, 2022). Its often-hidden externalities are estimated at US $22.4 trillion (inflation-adjusted), far surpassing the actual market value of its aggregate outputs (Hendriks et al., 2021). System-level solutions are needed to address these deeply interconnected challenges, calling for a transformation of global agri-food systems (Willett et al., 2019).

The recent food system report (Schneider et al., 2023) underlines how a critical loss in ecological functioning (or functional integrity) jeopardizes sustainable food production on at least 12% of global farmland. Meanwhile, two thirds of human-modified lands (including farmland) lack a sufficient influx of biodiversity benefits from surrounding off-farm habitats (Mohamed et al., 2024). This carries severe societal repercussions. Indeed, the food system - and society as a whole - is anchored in local to global agroecosystems. Local production ecosystems have become progressively simplified, chemically intensified and interconnected through myriad layers (Nyström et al., 2019) replacing nature's supporting or regulating services. Currently, external and anthropogenic inputs dictate the overall structure, function, and outputs of agro-ecosystems (Rist et al., 2014). Under an industrial agriculture paradigm, a one-size-fits-all farming model has developed in which (plant) genetic resources are narrowed, input dependencies created, and critical natural variation eliminated (Rist et al., 2014; Moore and Schindler, 2022; Walker et al., 2023). Though the double-yielding cereal germplasm of the Green Revolution lessened famine and spurred economic growth, the diffusion of single cereal varieties through 'seed x chemical' technology packages raised vulnerabilities and reduced resilience of the agroecosystem (Pingali, 2012). Crop improvement programs largely focused on yield gain, neglecting crops' innate characteristics to resist pest damage or disease (Stenberg et al., 2015; Bernal and Medina, 2018). Intricate pest outbreak avoidance tactics are regularly replaced by simplified strategies to control pests before or after their emergence, or even on a scheduled basis in the absence of target pests. Thus, dynamic, adaptive, and self-regulating systems gave way to simplified, inflexible ones (DeFries and Nagendra, 2017) that necessitate constant intervention to maintain desirable conditions (Rist et al., 2014). Though today's agroecosystem yields predictable flows of biomass in the short run, it suffers from heightened vulnerabilities to chronic or acute disturbance - raising the odds of crop failure and thus, food production shortfalls, while contributing to climate change, resistance development and biodiversity loss. The ensuing volatility and impacts are prone to proliferate across supply chains, posing systemic risks for global food security (Savary et al., 2020) and raising societal susceptibility to full-blown crisis (Holling and Meffe, 1996; Gould et al., 2018).

Proactive stewardship is therefore crucial to restore internal feedbacks and enhance adaptability (Moore and Schindler, 2022), in which our goals are ideally set on building long-term resilience (Nystrom et al., 2019) and improving the transformative capacity of the production system and its coupled social-ecological system rather than maximizing short-term delivery of provisioning ecosystem services (Oliver et al., 2015; Meuwissen et al., 2019; Rosenzweig et al., 2020; Turner et al., 2022). To achieve such, transforming farm-level practice constitutes a powerful lever (Springmann et al., 2018) and is crucial to take full advantage of landscape-level flows and impacts of beneficial organisms (Larsen et al., 2024).

From a biophysical perspective, agroecosystem resilience is the system's ability to continuously supply ample nutritious food in the face of environmental adversities (Meuwissen et al., 2019). A proxy measure of ecological complexity estimated from the number of biodiversity components (e.g., species, habitat types) and their biostructure i.e., the underlying architecture and ecological interactions, is used to gauge resilience to environmental stressors (Bullock et al., 2022; McCann, 2007; Oliver et al., 2015). Ecological complexity contains core resilience principles such as functional redundancy, that is the capacity of one species to functionally replace another, and response diversity i.e., variety of responses to disruptions (Naeem, 1998; Walker et al., 2023). Thus, by achieving multi-scale ecological complexity in a particular system, one effectively builds or retains broad ecological functionality under global change (Bullock et al., 2022). Critical analysis of risks is beneficial to optimally interpret the long-term consequences of farm-level adaptations or (preventative, responsive) management action (Logan et al., 2022). Risk analysis tools such as bow-tie diagrams (Fig. 1) are valuable for anticipating the actual risk of agroecosystems reaching a degraded state and for restoring resilience-enhancing features through input substitution or a wholesale system redesign (Tittonell, 2014). Such diagrams exemplify how agroecological and biodiversity-driven solutions can lower pest-related risks, suspend a need for pesticide-based interventions and ultimately unlock opportunities for transformative change of the entire agroecosystem. Along these lines, the reduction of pesticide use risks has become an essential policy goal e.g., in the EUs Farm to Fork strategy and the Global Biodiversity Framework (Candel et al., 2023). Yet, while pesticide phasedown is essential to restore the functional integrity of farmland and bolster agroecosystem resilience, the exact *modus operandi* of achieving such end goal and the relative potential of non-chemical strategies such as biological control tends to remain elusive. As a core ecosystem service, biological control underpins agroecosystem resilience (Barrios et al., 2018) while its human-mediated manipulation can help to curb or suspend pesticide usage. Given that agroecology is increasingly viewed as the principal pathway towards upholding food security under today's climate change crisis (De Schutter, 2011), biological control may thus be pivotal to restoring on-farm ecological functionalities and making this approach feasible. Intuitively, biological control presents a best-bet approach, but the actual biodiversity and resilience outcomes of its on-farm adoption are not often empirically assessed, its science irregularly transcends case-by-case empiricism and its true potential is seldom described in a comprehensive fashion e.g., due to disciplinary fragmentation (Barratt et al., 2018; but see Bale et al., 2008).

Here, we try to remediate this pressing knowledge gap by discussing how biodiversity-driven solutions centered on biological control can raise the pace of sustainability progress while bolstering transformative capacity and resilience. We define biological control as the reliance upon (naturally-occurring) living organisms to manage pest populations (Heimpel and Mills, 2017; IPPC, 2024), integrated as appropriate with other compatible tactics including non-toxic semiochemicals, botanicals, microbial metabolites or toxins (FAO and WHO, 2017) and more broadly ecologically-underpinned farming practice. These measures are ultimately aimed at reconstituting or strengthening the core ecosystem service of (on-farm) biological control. First, we summarize how chemical pesticides are now the default tool to suppress arthropod and other pests of crops, weeds, and diseases (or 'pests'; IPPC, 2024), and have become entrenched, self-reinforcing measures that drive agri-food production to inefficient outcomes. These include a critical loss of functional integrity (Schneider et al., 2023), a globe-spanning pesticide resistance crisis (Gould et al., 2018) and deepening poverty vulnerability through smallholders overreliance upon external (agrochemical) inputs. Second, we outline how biological control strategies have achieved critical scientific progress in recent years. These measures now smartly draw upon (plant, animal, microbial) biodiversity and its potential to restore the functional integrity of ecosystems, and are intended to lower pest risk in a safe, efficacious and environmentally-responsible manner. Specifically, biological control strategies have been devised and refined to fortify the ecosystem service of biological control through different modalities i.e., importation, augmentation, and conservation of ecosystem service providers or so-called biological control agents.

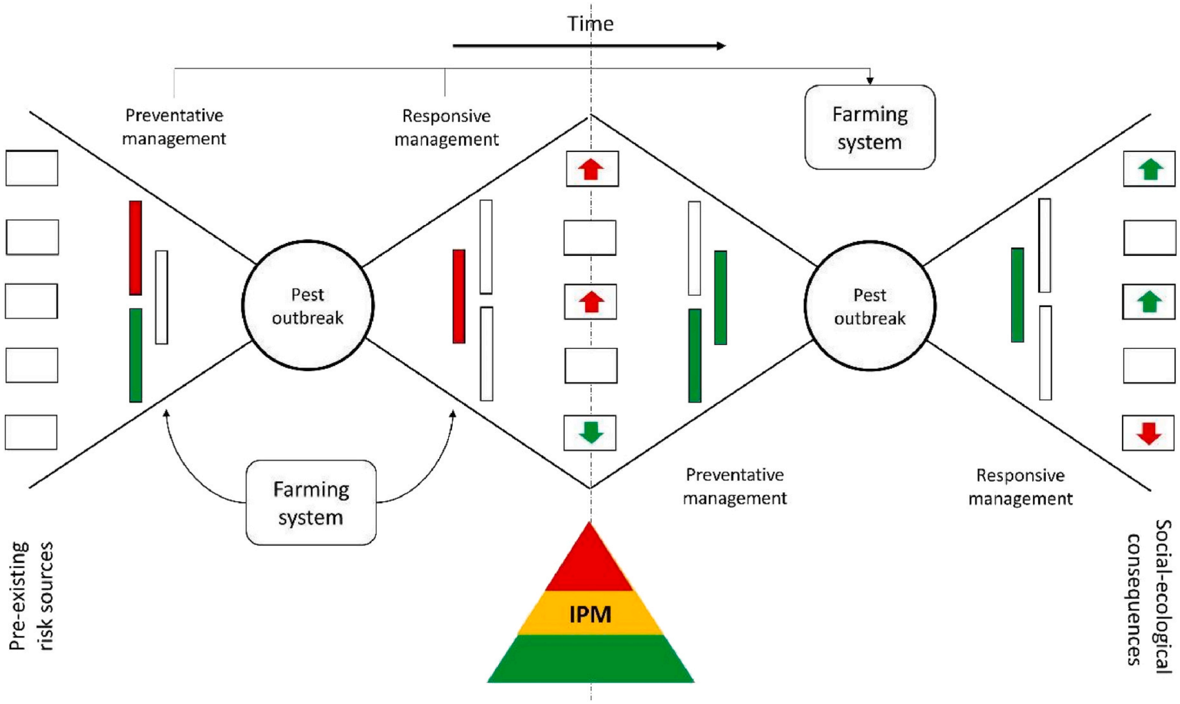

Fig. 1. Visual illustration of how biological control dampens pest outbreak risk and bolsters functional integrity over time. A chain of bow-tie diagrams shows how pre-existing risk sources affect pest outbreak incidence (Logan et al., 2022) in which pest management success is modulated by resilience-enhancing features of a farming system. Responsive treatments aimed at system recovery e.g., augmentative biological control enable adaptation and transformation. Equally, preventive measures such as conservation biological control or agroecological tactics reduce outbreak incidence. The IPM solution package is depicted as a pyramid in which non-chemical avoidance strategies (e.g., biological control; green) constitute a solid foundation and curative chemical control (red) a 'measure of last resort' (Deguine et al., 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Third, using a holistic systems approach, we outline how biological control knowledge, science and technology can be adapted and broadened to become more policy-relevant, solution-oriented and adopted at scale. Some sections of this paper are supported by systematic literature searches that were performed through Web of Science, using search strings that were specifically designed to capture all-time scientific output on particular aspects of biological weed, plant disease and pest control. Overall, this review argues that agroecosystems in which biodiversity is aptly harnessed and tactically integrated with other on- and off-farm measures secure the delivery of ecosystem service 'bundles' over the long run, bolster functional integrity, prove more resilient to environmental perturbation, and constitute a cornerstone of sustainable food systems. To improve Earth's resilience, biodiversity-rich, diversified and resilient agroecosystems are not a "nice-to-have" but a must.

2. Pesticide-centered control: an increasingly defunct strategy

Weeds, plant diseases and animal herbivores are fundamental constituents of the global agroecosystem. When not effectively managed, they cause respective crop losses of 34%, 16% and 18% (Oerke, 2006) which are often exacerbated in food-deficit regions (Savary et al., 2019). Despite a continuous intensification of agriculture, the extent of those losses has not declined over the past decades (Oerke, 2006). Today's agri-food production model, in which global food output is largely secured under a pesticide umbrella, obstructs progress towards SDG targets (Sachs et al., 2023). For instance, in intensified European potato or grapevine systems, where 10–16 fungicide spray applications are made per season, pathogens such as *Phytophthora infestans* or *Plasmopara viticola* still lower yields substantially (e.g., Haverkort et al., 2008). Global warming is bound to deepen these impacts, as pest-inflicted losses are anticipated to rise by 10–25% per degree warming (Deutsch et al., 2018). Climatic anomalies will further broaden the distribution of pests, alter their phenology, shorten their generation cycles, disengage existing natural and anthropogenic biological control and hasten resistance development, thus jeopardizing their (conventional) management. Also, international trade and passenger transport facilitate the proliferation of non-endemic biota and lead to a continuing spread of new invasive pest threats (Seebens et al., 2017; Ristaino et al., 2021), which presently inflict US$ 0.5–1.4 trillion in agricultural losses (Turbelin et al., 2023). Those burgeoning costs hinder sustainable development, accentuating a need for improved management. Hence, effective crop protection is pivotal to safeguarding global food security, rural livelihoods and societal wellbeing.

Since the late 1940s, synthetic chemical pesticides have become the default pest control tool in most systems. While synthetic pesticides boosted food output, they also became hallmark features of a new political economy typified by lowered labor inputs or knowledge needs, and economies of scale (Shattuck, 2021). Over the past 75 years, pesticide usage rates and toxicity loading have risen unremittingly (DiBartolomeis et al., 2019) – with a 153% increase in low-income countries over the past decade (Shattuck et al., 2023). Selling pesticides has become a lucrative business. Four transnational corporations presently control 84% of the world's US$ 73.4 billion pesticide market (Marrone, 2019). As new product development becomes costly and less successful, companies regularly turn toward old chemistries, down-priced off-patent or generic compounds and stacked herbicide tolerance traits (Shattuck, 2021; McDougall, 2016), with associated risks for resistance development, product abuse and environmental impact.

To face mobile, diverse and fast-evolving crop antagonists, farmers in many parts of the globe often resort to few tools and habitually treat synthetic pesticides as a 'go-to solution'. For disease control, most farmers either rely on resistant varieties or single target-site fungicides (Corkley et al., 2022), while chemical control (i.e., insecticides, herbicides) dominates treatments for pests and weeds (MacLaren et al., 2020). Several of those present limitations or have proven defunct.

Indeed, pests often readily evolve to overcome simple add-on constitutive defenses and pesticides, i.e., the main tools in farmers' arsenal. For instance, insecticidal or fungicidal seed treatments (aimless 'blanket' applications at crop establishment) hasten resistance development and undermine ecological regulation – often with negligible or negative economic benefits for growers (Mourtzinis et al., 2019; Lamichhane et al., 2020). Pesticide efficacy is becoming increasingly ephemeral (Jørgensen et al., 2018): where ecological safeguards are debilitated, pesticide resistance can emerge within one year after a new compound is commercialized (Grimmer et al., 2015). Natural, bred or engineered plant-based defenses are also increasingly circumvented by pests e.g., as evident in the continual emergence of resistant strains of wheat stem rust and soybean rot pathogens or the cross-resistance of the maize-feeding caterpillar *Spodoptera frugiperda* to transgenic insecticidal crops (Machado et al., 2020; Mapuranga et al., 2022; McCoy et al., 2023). The socio-economic implications of such resistance breakdown are often immense.

The efficacy of farmers' chosen tools is further constrained by conventional farming practice in which genetically uniform monocultures, chemical fertilizer use, intensive soil disturbance and simplified landscapes 'sow' pests (Rashid et al., 2017; Bernal and Medina, 2018; Dainese et al., 2019). Pesticides or monogenic varietal resistance are swiftly defused by evolution under this strong unidirectional selection, calling for improved, informed stewardship of remaining effective tactics (Fisher et al., 2022) and a more extensive, conscious leveraging of ecological complexity. By resorting to recurrent pesticide applications in simplified farm settings, farmers construct niches under which less susceptible organisms proliferate (Jørgensen et al., 2018), fail to address systemic challenges, and instead delay, relocate and progressively aggravate existing pest issues.

2.1. Social-environmental externalities of chemical pest control

Notwithstanding its beneficial impacts on food security and human nutrition, pesticide-intensive crop protection leads to many social-environmental externalities. Pesticide misuse is linked to declining total factor productivity (Savary et al., 2020) and profitability, with carry-over implications for agricultural efficiency, household purchasing power and wellbeing. Backward linkages can be substantial: pesticide expenditure exceeds the economic optimum by up to US $391/ha per cropping cycle in certain smallholder systems (Schreinemachers et al., 2020). Synthetic and other harmful pesticides regularly pollute terrestrial and aquatic ecosystems (Tang et al., 2021), where they degrade soil health, drive biodiversity loss and harm pollinators and natural enemies. The carbon footprint of their synthesis, distribution and field-level use is substantial, amounting to the annual equivalent of more than 18 coal-fired power station (Wyckhuys et al., 2022). For chemical control of one single pest in US soybean, 17.4 million kg CO2 equivalent is emitted which requires nearly 6000 ha of US forests to be offset through sequestration (Heimpel et al., 2013). Chemical control further directly and indirectly harms human health i.e., causing 385 million cases per year of acute unintentional poisoning (Boedeker et al., 2020), compromising food safety (Wyckhuys et al., 2020a), increasing infant mortality, adverse birth outcomes, infertility or neurodevelopmental impairment (Larsen et al., 2017; Landrigan et al., 2019; Vasseur et al., 2024; Frank, 2024) and causing pollination deficits that translate into suboptimal nutrition (Smith et al., 2015). As disease vectors or infectious organisms also evolve resistance to agricultural pesticides (Nkya et al., 2013), pesticide-intensive practice imperils human and animal health (Gould et al., 2018). Pesticide-induced impacts on the interlinked health of humans, animals and the environment or 'One Health' (Falkenberg et al., 2022) can be readily defused by substituting chemical toxins with ecological or biodiversity-driven (or so-called nature-based) alternatives (Schaffner et al., 2024). The global advancement of biological control could nurture the agroecosystem back to resilience (Lewis et al., 1997; Gould et al., 2018; MacLaren et al., 2020) and science *in principle* can lead the way in such endeavor.

3. Pest management science poorly calibrated

In the 1930s, scientists already foresaw that pesticides' broad-spectrum action might render them “distinctly harmful if not valueless” (Clausen, 1936) – as empirically proven a century later (Janssen and van Rijn, 2021). Once their adverse side-effects became apparent (Carson, 1962), scientists advocated a phasedown of chemical measures and their closer integration with ecologically-based measures under integrated pest management (IPM; van den Bosch and Stern, 1962). As IPM is founded upon agroecological principles and treats chemical pesticides as 'a measure of last resort', this universal decision framework was originally geared towards building resilience (e.g. Barzman et al., 2015). Yet, as IPM rules have been continuously twisted, emerging paradigms such as agroecological crop protection better reflect its genuine foundational principles (Deguine et al., 2023). IPM adoption is highly context specific and is often hard to monitor and assess, and adopting only some IPM measures may not necessarily reduce pesticide risks (e.g. Finger et al., 2024). 'Ticking a box' on a single or few IPM measures, as routinely preferred by farmers and academics alike (Dentzman, 2022), is thus misleading and ineffective. Scientists equally underscored the value of a systems approach in which production ecosystems are seen as dynamic, intricate and self-regulating and in which IPM-compatible technologies are to be smartly bundled across spatio-temporal scales and organizational layers (Altieri, 1984; Lewis et al., 1997; Stenberg, 2017; Wyckhuys et al., 2023b). As such, IPM is to be systematically treated as the tactical integration and deliberate prioritization of all available strategies to keep pest populations below economically damaging levels and to achieve such with minimal, if any, use of synthetic pesticides. IPM draws extensively upon ecosystem-based strategies and preventative, non-chemical solutions that discourage pest population build-up, slow or prevent pesticide resistance development and diminish the environmental footprint of agriculture. Indeed, biological control and agroecological measures are to be consciously treated as a 'first line of defense' while pesticide-based prophylactics such as insecticidal seed treatment are to be discouraged because their use violates core IPM principles (Tooker et al., 2017). The extent to which synergistic combinations of IPM strategies conserve or reconstitute biodiversity and ecosystem functionalities, while resolving pest issues in an economically sound and safe manner (i.e., actual on-the-ground impacts; Finger et al., 2024), is to be given far greater attention during the implementation stage. In this regard, multi-dimensional impact criteria that touch upon all the facets of One Health and which include social as well as ecological perspectives carry inordinate value. Overall, this kind of 'paradigm shift' of vision, goals, values and evaluation parameters in pest management is imperative to achieve the envisioned transformation of farming systems (Tittonell, 2014; Deguine et al., 2023).

However, IPM has encountered numerous obstacles, faces a plethora of alternate definitions, and its degree of sound implementation is highly variable (Deguine et al., 2021). In spite of some notable success stories in western industrialized countries (Kogan, 1998; Lamichhane, 2017) and emerging economies in Africa (Nwilene et al., 2008) or those emanating from the Farmer Field Schools in the 1980–90s (Van den Berg and Jiggins, 2007; Waddington et al., 2014), IPM “has lost its way” (Peterson et al., 2018). Although the scientific enterprise conforms to the IPM framework, it is marked by reductionism instead of holism (Wyckhuys et al., 2023b): hampered by disciplinary specialization or 'silo' approaches, science is often conducted in simplified observational contexts e.g., laboratories, *in vitro*. Contrary to IPM's founding principles, individual component technologies are routinely studied in isolation – even if *in vivo*, they are not *in ecolo*, that is, considered as interacting with the larger ecosystem, much less in an evolutionary context. In fact, the actual impact of adjusted pest management on pesticide risks, biodiversity and ecosystems is largely unknown (Finger et al., 2024), which impedes efforts to promote more environmentally compatible tactics (Bruhl and Zaller, 2019). For instance, preemptive broad-spectrum seed treatments and scheduled or reactive controls receive a disproportionate share of attention as compared to the IPM-compatible tactics such as ecologically-based prevention and suppression (Tooker et al., 2017). The current scientific enterprise tends to disregard farming system complexities (Wyckhuys et al., 2023b), omitting below-ground realms, non-pest companion biota, farm- or landscape-level variables or social strata. Particularly, pest management science has failed to put people and social or political institutions in a central place (Kleijn et al., 2019; Chaplin-Kramer et al., 2019; Mansfield et al., 2023) and numerous barriers obstruct a transformative impact of science on crop protection practice (Hofmann et al., 2023). Though social science is instrumental in understanding such obstacles and in unveiling mechanisms for incentivizing adoption or defining pathways for technology adoption and behavioral change at scale (Norton et al., 1999; Magarey et al., 2019), its actual contribution should be strengthened (Wyckhuys et al., 2023b; Mansfield et al., 2023). Such transformation also requires a fundamental change of the current economic accounting system which fails to capture production externalities i.e., real costs on nature, human wellbeing, and sustainability. Economic approaches such as True Cost Accounting (TCA) aim to identify and manage the hidden environmental, social, health and economic costs and benefits as well as the associated risks of economic activities, thus enabling better decision-making for multiple stakeholders (Shah et al., 2023). A small body of literature (e.g., Gress et al., 2024; Huang et al., 2018; Zhang and Swinton, 2012) has combined ecological field experiments and farm-level bioeconomic analysis to demonstrate the economic value of alternative forms of pest management. However, applying evidence from these studies to inform actual decision-making appears to be a long way to go. Not only is interdisciplinary research like this costly but its results also tend to be highly context-specific with low degree of direct transferability of knowledge. Nevertheless, economic valuation studies or TCA analysis to evaluate the performance of biodiversity-driven crop protection (and redesigned farming systems) must be integrated into national and international policy frameworks.

Further, there is a lack of "actionable" information and concrete experiences that consider an integrated social-ecological approach to food and agriculture. Nonetheless, various agroecological approaches are continually trialed and the science of biological control has gained critical momentum over the past decade. The time is now to strategically wed both social and natural science disciplines and to smartly integrate biological control and biodiversity-driven alternatives and agroecological approaches (Deguine et al., 2023).

4. A fast-expanding toolkit of biological control strategies

In natural and man-made ecosystems, consumer organisms keep fluctuating populations of herbivores, plants or pathogens within bounds (Murdoch, 1994). This 'population regulation' process underlies many ecological phenomena, is viewed as one of Earth's prime regulating services (Hairston et al., 1960; Estes et al., 2011) and is a core constituent of preventative pest management. As such, in efforts to restore degraded (farmland) ecosystems, consumer organisms such as parasitic wasps or predators assume a critical role (Xu et al., 2023). In cropland alone, natural population regulation or 'biological control' is valued at US$ 50–196 billion per year (Pimentel et al., 1997; Costanza et al., 2014), with Nature's cost-free control of native insect pests in the USA annually worth US$ 20.7 billion, as adjusted for inflation (Losey and Vaughan, 2006). Its monetary value is four times that of insect pollination across biomes and 50% higher in cropland settings (Costanza et al., 2014). In addition to microbiota and arthropods, free-living insectivorous birds, mammals and bats sustain crop yields in the face of pest attack - the latter annually prevent 3000 tons of rice losses in Thailand alone (Wanger et al., 2014). Bat-mediated biological control is valued at US$ 109 per ha of Brazilian maize (Aguiar et al., 2021) and contributes notably to economical pest control in myriad other systems (Tunue-Corral et al., 2023). Off-farm predation of the soybean pest *Euschistus heros* by native marsupials within Brazil's savannah is annually worth US$ 33 per hectare of native forest (de Camargo et al., 2022). Aside from being prominent pests in certain production systems, birds also provide valuable biological control services; their skillful management has the potential to substantially enhance pest suppression (Garcia et al., 2020; Díaz-Siefer et al., 2022).

No pests are without foes. Arable weeds, for instance, face plant competitors, pathogens, folivores, stem-borers or seed-feeders; granivorous ants and rodents that consume up to 91% of weed seeds post-dispersal, constituting potent 'little hammers' for sustainable weed management (Liebman and Gallandt, 1997). Naturally occurring predators, parasitoids and pathogens feature prominently among the mortality factors of the cosmopolitan silverleaf whitefly *Bemisia tabaci* (Togni et al., 2019b; Naranjo et al., 2022), and their abundance, seasonal dynamics and pest control action is affected by farm management intensity (Togni et al., 2019b). Over time, humans have implemented diverse biological control strategies using beneficial arthropods, nematodes, vertebrates and microbiota in myriad agroecosystems (Heimpel and Mills, 2017; Mason, 2021). Based on Eilenberg et al. (2001), biological control strategies can be grouped as 1) classical biological control (scientifically guided introduction of non-native biota targeting invasive pests, also known as importation biological control (Heimpel and Mills, 2017), 2) inoculation biological control (focused on the intentional release of biological control agents or BCAs with the expectation for long-term perpetuation after multiplication), 3) inundation biological control (focused on mass multiplication and release of natural enemies; perpetuation of the natural enemy in the environment is not a key focus in such strategies) and 4) conservation biological control (focused on modifying the environment and/or agricultural practices to protect and support the multiplication and efficiency of resident natural enemies). Despite attempts to unify the terminology in biological control (Eilenberg et al., 2001), inoculation and inundation strategies are often treated under a common denominator of 'augmentation biological control'. The richness and diversity of (resident and released) BCAs directly relates to the strength of the resulting ecosystem service (Dainese et al., 2019). Biological control can be geared towards a long-term management of pests, diseases and weeds, and is arguably the best solution to simultaneously meet farmers' crop protection needs and curb chemical pesticide use. In the presence of effective BCAs, weed biomass or seed load can be reduced by 82–89% and pest mortality increases by 159% as compared to control groups unexposed to BCAs (Stiling and Cornelissen, 2005). More so, under those conditions, pest mortality regularly reaches up to 100% (Hawkins and Cornell, 1994; Hawkins et al., 1997). Thus, in terms of long-term pest control efficacy, synthetic pesticides do not necessarily present a comparative advantage over natural enemies (Janssen and van Rijn, 2021). Further, in the developing economies of Africa, where pesticide use is still comparably low due to their non-availability and affordability for smallholder farmers (Srinivasan et al., 2022), biological control has contributed markedly to the sustainable management of invasive pests such as cassava mealybug, *Phenacoccus manihoti* (Hemiptera: Pseudococcidae; Zeddies et al., 2001), Asian maize stemborer, *Chilo partellus* (Lepidoptera: Crambidae; Soul-Kifouly et al., 2016), diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae; Macharia et al., 2005) and Oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae; Agboka et al., 2024a,b). Similarly, biological control has generated sizable economic benefits in the Asia-Pacific (Wyckhuys et al., 2020b) and India (Ballal, 2022), with the former amply surpassing those of Green Revolution improved rice germplasm.

However, to efficiently and effectively harness biodiversity and biostructure for the wholesale 'redesign' of farming systems and the advancement of biological control, a robust scientific foundation is sine qua non. At present, its use has been investigated in all main crop categories (Fig. 2), with major progress in arthropod pest control for cereal

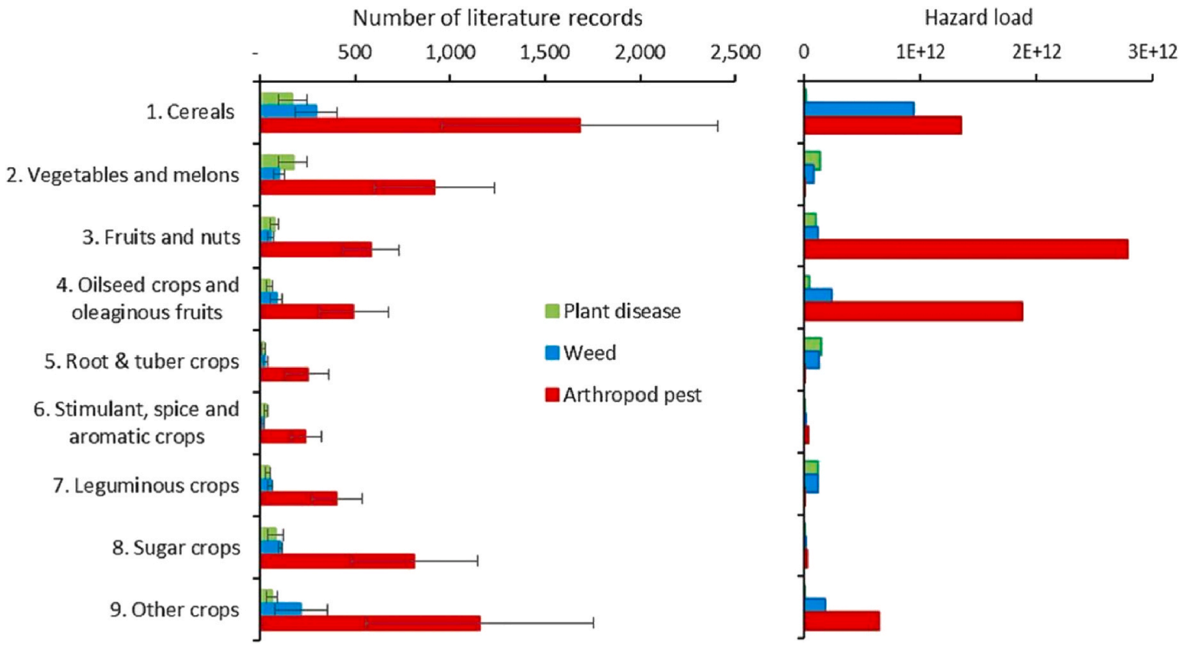

Fig. 2. Scientific underpinnings of biological control in the world's agricultural crops as contrasted with their respective pesticide hazard load. Per crop category, we plot the average (mean ± SE) number of all-time scientific publications on biological weed, disease and arthropod pest control (left panel) and the overall hazard load for fungicides, herbicides and insecticides (right panel) for its constituent crops. Hazard load (kg body weight) was computed based on the total applied toxicity indicator (TAT) concept, indicating the non-target organism (birds and mammals) mass required to absorb the applied pesticides without experiencing adverse effects (Wyckhuys et al., 2023b). Underlying queries were run on Web of Science over 1900–2023, using search strings designed to capture scientific output on biological weed, plant disease and pest control (Supplementary Table 1). Per query and crop, the number of logged literature records serves as an (imperfect) proxy of the respective scientific activity. Crop categories were defined based upon the Indicative Crop Classification by the Food and Agriculture Organization.

grains, vegetables and cash or sugar crops. No less than 8400; 7600; 5900 and 5700 all-time peer-reviewed publications cover arthropod biological control in corn, cotton, tomato or pasture systems, respectively (Suppl. Table 1). In particular, their potential to reduce pesticide-related hazards in fruits and nuts, oilseed crops or cereals is immense. Advances in their use for disease or weed control are more modest, though notable progress is still being made e.g., in cereal grains such as wheat, maize or rice, vegetables and melons and other crops such as cotton or tobacco. Though some forms of biological control are wielded as responsive controls i.e., tailored measures for pesticidal input substitution, they all contribute to preventative management (Fig. 1) and are predominantly safe for applicators, consumers and the environment. Their tactical integration is central to achieving a wholesale redesign of farming systems (Tittonell, 2014). This with regard to ensuring biodiversity gains without yield trade-offs (Gong et al., 2022) while bolstering functional integrity and, eventually, resilience (Rist et al., 2014).

4.1. Augmentation biological control: methadone of IPM

Under augmentation biological control, BCAs are mass-reared and released to provide instantaneous or season-long pest control (van Lenteren, 2012). While BCA releases were traditionally used as responsive controls, their early establishment in production systems at the beginning of the season is increasingly pursued, in particular in glasshouse production and other protected cultivation systems (Pijnakker et al., 2020). In recent years, augmentation biological control has become a full-fledged commercial undertaking with a US$ 3–5 billion market value i.e., 5% of the total crop protection market and with a 15–20% annual growth (Marrone, 2019; Robin and Marchand, 2019). In the European Union, BCAs now comprise 40% of registered crop protection products and most greenhouse vegetable crops are under biological control, e.g. over 50% in Southern Spain and 95% in the Netherlands (van Lenteren et al., 2018; Acebedo et al., 2022). Its progress is largely market-driven and dominated by private sector actors: numerous (small-scale) enterprises and bio-factories backed by governments or farmer cooperatives produce BCAs (Mason, 2021; van Lenteren et al., 2018), and agrochemical corporations prove increasingly supportive of biological control. Even in African countries, augmentation biological control is increasingly adopted by growers in the floriculture sector to manage pests such as red spider mites, thrips and mealybugs (Wainwright and Labuschagne, 2009; Gacheri et al., 2015; Akutse et al., 2020). In India, sugarcane stem borers are frequently managed with biological control (Sithanantham et al., 2013; Srikanth et al., 2016). However, its adoption in other sectors in Africa and Asia is minimal due to lack of availability of cost-effective biological control interventions, but see Zang et al. (2021) for China's notable progress in the use of *Trichogramma* spp. in multiple field crops.

Globally, at least 360 species of arthropods are mass-reared and used for pest control. Further, environmentally-sound pest, weed or disease control is provided by a respective 62, 46, 33 and 3 individual (sub-) species of fungi, bacteria, viruses and yeasts (Fig. 3), discounting the countless microbial strains and isolates that are continually cultured, screened and employed worldwide (Lacey et al., 2015; van Lenteren et al., 2018). For the management of high-profile pests such as true bugs or butterflies and moths, no less than 176 and 71 invertebrate BCAs are commercially available. While a wide spectrum of BCA solutions is available in the greenhouse sector of Europe or North America, ever more agents are becoming available for use in field crops and other continents. Meanwhile, many microbial BCAs are geared towards plant disease control, and Asian countries play an (increasingly) prominent role in their development and upscaling (Jiang and Wang, 2023). In Brazil and China, sophisticated rearing technologies enable the use of *Trichogramma* spp., micro-wasps that parasitize lepidopteran pest eggs, on millions of hectares of corn, rice, soybean and sugarcane fields (Zang et al., 2021; Parra and Coelho, 2022). These technologies have recently also spilled over into Europe's maize crop, as enabled through digital technologies such as automated drone-based delivery systems (Finger,

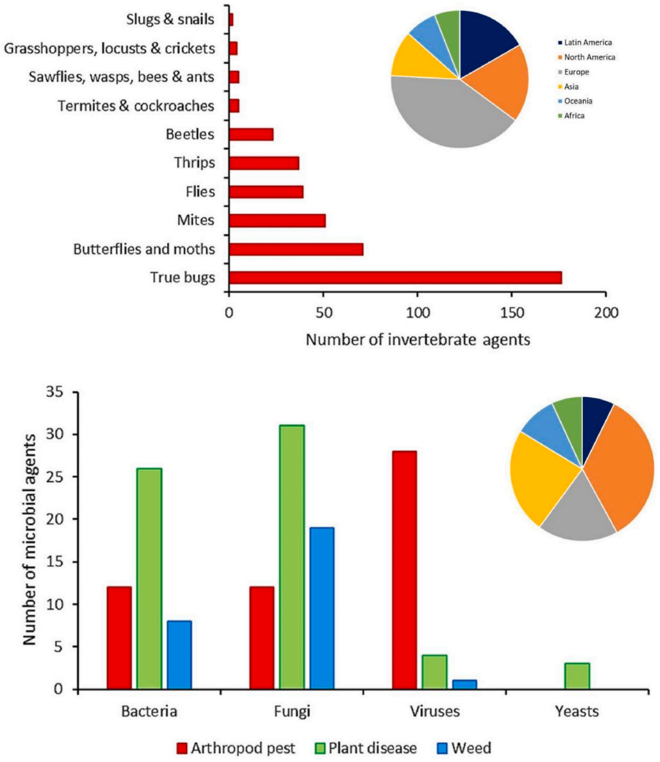

Fig. 3. Number of biological control agents (BCAs) that are globally available or registered for augmentative use. The upper panel depicts the total number of invertebrate BCAs that are commercially available for use against various target pests. Pests are organized by taxonomic order, with the number of BCAs plotted for the ten main targets. The lower panel depicts microbial BCAs (historically) registered for plant disease, weed or arthropod pest control for use across (agro-)ecosystem contexts - not accounting for their actual commercial availability and formulation as mixtures. Microbial BCAs are listed at the species, subspecies, *forma specialis* or variety level. Microbial BCAs only comprise living organisms, excluding essential oils, natural product extracts, microbial metabolites or allelochemical-based products. Separate microbial strains or isolates are not accounted for. Bacteriophages and microsporidia are either listed under viruses or fungi, respectively. Records are drawn from Van Lenteren (2012), Van Lenteren et al. (2018) and Morin (2020), complemented with recent data for India, China, Brazil and African countries (Supplementary Table 2). In either panel, availability or registration status of BCAs is broken down per geography.

2023). Since the 1970s, similar set-ups have been in place for the management of Mexican bean beetle in US soybean crops, for sugarcane borers and spittlebugs in Brazil or for the control of the European corn borer in Europe. Crystal proteins from *Bacillus thuringiensis* (Bt) are used in arthropod pest control in myriad systems, while the fungus *Metarhizium acridum* (Green Muscle™) is mass-produced across Africa and South Asia for use against locust swarms (Lomer et al., 2001; Lacey et al., 2015). In Europe, Canada, and Japan, *Beauveria bassiana* is widely used against whitefly, aphids, and thrips (van Lenteren et al., 2018). Soil microbial inoculants provide satisfactory control of debilitating diseases e.g., wheat take-all or cabbage club-root (Woo et al., 2014; Miljakovic et al., 2020), in tandem with enhancing plant performance, conditioning defenses and raising yields (Nerva et al., 2022). A comparatively small number of (microbial) BCAs have been registered for arable weed control e.g., against common dandelion, but face obstacles during commercialization (Cordeau et al., 2016; Morin et al., 2020; Duke, 2024). These include a relatively narrow action spectrum i.e., often targeting one single weed species, unreliable efficacy under variable environmental conditions, higher costs as compared to synthetic herbicides, technological hurdles related to large-scale BCA production or product formulation, and the general lack of an enabling environment. Some of the biological issues possibly can be circumvented by using killed microbial products such as cell-free filtrates (Duke, 2024) or by paying considerably more research attention to allelochemical compounds (Khamare et al., 2022). Meanwhile, notable obstacles in the upscaling of non-native weed BCAs (see below) include concerns over direct or indirect nontarget effects, evolved host shifts or dispersion into unwanted areas i.e., concerns that are theoretically possible but for which on-the-ground evidence is scant (Walsh et al., 2023).

BCA research pays off: its success rate for new product development (1:10) and development costs (US$ 2.6 million) compare favorably to those of chemical pesticides i.e., 1:160,000 and US$ 286 million (McDougall, 2016; van Lenteren, 2012). Often, the use of BCAs (singly or combined) protects crop yields in an efficacious, profitable manner without a need to resort to chemical inputs e.g., in Spain's sweet pepper crop (Calvo et al., 2012). By thus preserving resident biota, crop-specific BCA packages are instrumental in nurturing systems back to resilience and act as the 'methadone' (withdrawal therapy for chemical addiction) for IPM (Waage, 1994). As science progresses, novel formulations and delivery modes e.g., drone-based applications of predacious mites, fungal seed coatings, small-scale autodissemination, or bee-mediated vectoring, are taking proven technologies to scale (de Lira et al., 2020; Mweke et al., 2023). For other BCAs such as nematodes, phages, and insect- or mycoviruses, *in vitro* production constitutes a game-changer (Oliveira-Hofman et al., 2023). Next-generation bioreactor systems now manufacture insect-killing viruses at a cost of US$ 4.7 per ha - competitive with chemical pesticide pricing (Reid et al., 2023).

However, the semi-contained nature of greenhouse cultivation is often critical to the success of BCA augmentation and can serve to mask potential pitfalls and intrinsic limitations of this approach in open systems (Michaud, 2018). For example, Perez-Alvarez et al. (2019) show that landscape context shapes the effectiveness of augmentative BCA releases by modulating interactions between the introduced predators and the local enemy community. In Brazil where augmentation biological control presents a series of new opportunities to advance more sustainable forms of agriculture, biological control is not always aligned with the aims and philosophy of organic agriculture and agroecology. Indeed, biological control research is oftentimes geared towards the development of therapeutics that are to be used in a prescription-like fashion (Wyckhuys et al., 2023b). For example, fewer than 3% of all-time studies focusing on the management of the fall armyworm *Spodoptera frugiperda* addressed the radical modification of conventional practices that is essential to transform farming systems (Melo et al., 2024). New research thrusts are thus needed to devise strategies that integrate BCA augmentation with measures that conserve resident biota (Togni et al., 2019a) and which pursue a broader transformability of farming systems (Melo et al., 2024). By exploring so-called conservation biological control options (as outlined below) exhaustively before committing investment to augmentation (Michaud, 2018; Togni et al., 2019a), one potentially builds further momentum towards a wholesale 'redesign' of farming systems by skirting the 'input substitution' step. This is essential in efforts that are aimed at achieving deep instead of shallow sustainability (Hill and MacRae, 1996; Tittonell, 2014).

4.2. *Conservation biological control: fortifying Nature's inherent defences*

Conservation biological control (CoBC) entails a deliberate manipulation of the agroecosystem with an aim to enhance the abundance, performance and biological control action of resident BCAs (Landis et al., 2000). CoBC is the oldest form of biological control: as early as 304 AD, date palm and citrus growers in Yemen and (sub-)tropical Asia inoculated their orchards with ant nests and built up their populations using kitchen scraps (Huang and Yang, 1987; Van Mele, 2008). CoBC is central to preventative pest management: naturally occurring (polyphagous or omnivorous) BCAs slow pest build-up and avert population outbreaks (Fig. 1). CoBC is an area of active scientific inquiry - largely propelled by academia and the public sector, often in partnership with farmers - holding significant yet underused potential.

In addition to preventing mortality from chemical or mechanical disturbance, CoBC tactics aim to provide BCAs with suitable microclimates, shelter, complementary foods (e.g., nectar or pollen) and non-pest hosts or prey. In doing so, CoBC measures seek to re-establish functioning agroecosystems in which BCAs maintain viable populations. CoBC tactics can be deployed along space, time and gene (plant diversity) dimensions across the agroecosystem, involving the establishment of floral margins, grass strips or hedgerows, cropland diversification and landscape-level natural and/or semi-natural habitat (Albrecht et al., 2000; Tscharntke et al., 2021). For instance, flower strips or natural habitat patches provide sugar-rich nectar for predators such as syrphid flies or dolichopodids and thereby contribute to pest suppression (Amaral et al., 2013; Medeiros et al., 2018; Harterreiten-Souza et al., 2021). A plethora of CoBC schemes are tailored to specific BCAs e.g., arable weeds can be suppressed by favoring native grasses or "neutral weed communities", while dynamic thresholds or climate-based prediction systems take advantage of virus or fungus epizootics – the latter naturally inflicting almost 100% mortality in aphids (Wagemans et al., 2022; Esposito et al., 2023). For example, by predicting epizootics of the aphid-killing fungus *Neozygites fresenii*, cotton farmers can postpone or avoid pesticide application (Steinkraus, 2007). CoBC constitutes a key lever to redesign farming systems and some of its tactics have been in use for millennia e.g., in maize-bean-squash polycultures or agroforestry systems in the Americas (Morales and Perfecto, 2000; Perfecto and Armbrecht, 2003; Peñalver-Cruz et al., 2019; Venzon et al., 2019), though surprisingly receive scant attention (Wyckhuys et al., 2013). Scientific research however is imperative to further validate or refine these (indigenous) practices and integrate them with novel tools and innovations.

Sugar dispensers or pollen sprays (in-)directly enhance biological control by predacious ants or mites in fruit orchards (Pijnakker et al., 2020; Pérez-Rodríguez et al., 2021), and their deployment can even suppress apple scab disease through the action of ants' antimicrobial secretions (Jensen et al., 2023). Similarly, the application of fish soup recruits natural enemies to maize and enhances biological control in Africa's maize crop (Niassy et al., 2024). By revisiting agronomic practices, crop arrangements and breeding strategies, above- or below-ground plant-BCA synergisms can be better exploited (Pickett et al., 2014; Stenberg et al., 2015; Morin, 2020; Mariotte et al., 2018). Many CoBC measures also offer valuable co-benefits, with crop diversification not only bolstering natural pest suppression but also providing decisive win-win support for multiple ecosystem services including yield (Tamburini et al., 2020). Measures such as annual (or ideally perennial) flower strips consistently reduce pest pressure, though their impacts on pollination and crop yields are more variable (Tschumi et al., 2015; Albrecht et al., 2020; Toukem et al., 2023). Further, legume integration curbs nitrogen fertilizer needs and stabilizes the soil, but also contributes to pollinator conservation and CoBC – though its scientific underpinnings stand inordinately weak (Wyckhuys et al., 2023a). Alternative host plants in or near farm settings maintain biological control over space and time (Kahuthia-Gathu et al., 2008), while agriculturally subsidized BCAs in turn contribute to vegetation conservation and ecosystem restoration at a landscape scale (Wyckhuys et al., 2024).

Oftentimes straightforward CoBC measures can be economically rewarding: avoiding pesticide sprays or establishing nectar-bearing plants to conserve resident BCAs offers returns of $262-2850 per ha above normal farm practice (Naranjo et al., 2015; Gurr et al., 2016). As the backbone of UN-supported IPMFarmer Field Schools (IPM-FFS) during the 1980–90s, CoBC permitted pesticide reductions of up to 80–90% on millions of Asian rice farms and raised profit by 19% (Van den Berg and Jiggins, 2007; Waddington et al., 2014). With the current state of CoBC science, replicating or reviving those achievements is entirely feasible.

4.3. Classical biological control: restoring ecological balance

Classical or Importation biological control (IBC) involves the scientifically-guided introduction of non-native organisms to attain a perpetual, self-sustaining suppression of invasive biota. IBC is founded upon the principle that invasive species' success relates to an absence of effective, coevolved BCAs, and their suppression to a cautious restoration of such ecological balance (Hoddle, 2004). This IBC-induced balance is central to preventative management (Fig. 1). Following the dramatic 1888 suppression of cottony cushion scale insects in California citrus groves by the vedalia ladybird imported from Australia (Caltagirone and Doutt, 1989), over 6000 parasitoids or predators have been introduced against about 600 insect pests (Kenis et al., 2017). IBC campaigns have brought a respective 226 and 57 invasive arthropod pests and weeds under control on 10% of global land surface (Cock et al., 2010, 2015). Microbial BCAs and nematodes have further been deployed against 22 invasive weeds and 85 arthropods (Morin, 2020; Hajek et al., 2021). IBC initiatives are largely led by governmental and non-governmental organizations, with close stakeholder engagement during implementation. Overall, private sector engagement in IBC is largely limited – as IBC tends to provide self-sustaining control and thus limits its business prospects.

IBC is touted for offering permanent, energy-efficient and non-polluting control of high-profile pests (Culliney, 2005), which has reconstituted food and livelihood security in numerous instances over its 100+ year history. One single monophagous species of micro-wasp permanently controlled the invasive cassava mealybug, resolving famine in sub-Saharan Africa (Herren and Neuenschwander, 1991) and slowing commodity-driven deforestation in tropical Asia (Wyckhuys, 2019b). Highly virulent insect- or fungus-killing viruses ensured self-sustaining control of the rhinoceros beetle - a debilitating invasive pest of coconut, the 'tree of life' across the Pacific (Hajek et al., 2021) and restored commercial viability of comestible chestnut production in southern Europe (Nuss, 2005). Introductions of specific rust fungi, folivorous caterpillars or root-feeding beetles cleared millions of hectares of rangeland in the USA, Australia or Chile from invasive weeds, with immense, annually recurring benefits for local livestock operations (Van Driesche et al., 2010). Similarly, introduction of co-evolved natural enemies of invasive pests such as the cassava mealybug, Asian stemborer, diamondback moth and oriental fruit fly have resulted in significant economic and societal impacts in Africa (Zeddies et al., 2001; Soul-kifouly et al., 2016; Mohamed et al., 2022; Agboka et al., 2023). IBC against arthropod pests has long been motivated solely by economic incentives. However, in the last decades, it has been also increasingly developed for the primary purpose of protecting biodiversity and natural ecosystems (Van Driesche et al., 2010), such as the release of a coccinellid predator to control the invasive orthezia scale in St Helena to save an endemic gumwood tree to extinction (Fowler, 2004).

Importing and releasing an exotic BCA into a new region has to be done with utmost caution. In the nearly 150-year history of IBC, a small number of these exotic BCA releases turned bad, affecting native biodiversity through various mechanisms (Howarth, 1991; Suckling and Sforza, 2014; Van Driesche and Hoddle, 2016). However, in the last decades, international guidelines, national regulations and risk assessment procedures have been developed and are being implemented, with emphasis on host specificity assessments to prevent the introduction of generalist natural enemies (Hajek et al., 2016; Hinz et al., 2020). Nowadays, regulators routinely overrate ecological risks of IBC, whereas it is advisable to conduct comprehensive *ex ante* benefit/risk analyses (De Clercq et al., 2011; Heimpel et al., 2024) and to judiciously assess those risks in light of the prevailing mitigation alternatives, typically inaction or pesticidal control (Abram et al., 2024). In nearly 70% of IBC programs, success is linked to the action of one single, highly efficacious BCA (Hawkins et al., 1999), oftentimes a so-called specialist that is evolutionarily adapted to its pest target in their common region of origin and thus interacts with non-target biota to limited or no extent. As a result, weed IBC has an impressive ecological safety record while less than 1% of all-time arthropod pest IBC efforts have proven harmful to native biodiversity (Heimpel and Cock, 2018).

With a (public) benefit:cost ratio that can reach >1000:1 (Cock et al., 2015; Wyckhuys et al., 2020b), IBC can offer a powerful, coevolved solution for the unrelenting establishment of invasive pests (Seebens et al., 2017). Across tropical Africa, IBC consistently provides the quickest, most profitable way to control invaders (Mohamed et al., 2022; Neuenschwander et al., 2023), while in the Asia-Pacific, historic BCA introductions now annually provide on-farm benefits up to US$ 23.1 billion yr^{-1} through yield-loss recovery in critical food, feed and fiber crops (Wyckhuys et al., 2020b). By banking on the decades-long progress in IBC efficacy and safety while consciously accounting for the risk of inaction, this practice can be confidently deployed across the globe (Heimpel and Cock, 2018; Heimpel et al., 2024).

5. Rebooting biological control science

To effectively bolster agroecosystem resilience, one needs to methodically steer its core knowledge domains. Given that biological control faces numerous obstacles that are often located outside its core disciplinary boundaries i.e., social, technical, or institutional aspects (Lacey et al., 2015; van Lenteren et al., 2018; Morin, 2020), it is vital to calibrate its scientific underpinnings. Further, biological control science cannot bud serendipitously but should progressively accrue along a multi-step pathway starting from the foundational principle of biodiversity (González-Chang et al., 2020), with a view towards fortifying resilience-enhancing mechanisms and attaining concrete social-ecological outcomes (Oliver et al., 2015). To achieve this, crop protection is to be systematically treated as an integral part of farm or agro-landscape management and with due consideration of the social or behavioral sciences (Chaplin-Kramer et al., 2019; Deguine et al., 2021; Wyckhuys et al., 2023b). Remediation action on the following fronts can prove rewarding and carries most potential to reconstitute a broad bundle of foundational ecosystem services in global farmland. We argue that this action can be especially rewarding in tropical regions of the Global South, where most of the world's biodiversity is concentrated and where pesticide usage is rising near-exponentially (Shattuck et al., 2023).

1. Fortify ecological underpinnings. To manage pests preventatively, a solid ecological foundation must be built. In addition to advancing BCA discovery and description, gaining biodemographic insights (Bellows Jr et al., 1992) and charting organismal interactions (Yang et al., 2021). Scientific progress can be catalyzed through innovative means of biodiversity monitoring e.g., camera traps, remote sensing or environmental DNA and by mobilizing, archiving and making biodiversity or biostructure data interoperable (Eisenhauer et al., 2019; Segoli et al., 2023).
2. Embrace complexity. Research should involve ecologically-relevant experiments and networked trials, leveraged on existing (on-farm) research networks (Robertson et al., 2008; Lacoste et al., 2022). Doing so can transcend current case-by-case empiricism, account for cross-scale feedbacks, and assess long-term impacts (Gonzalez et al., 2020). Coordinated on-farm trials further help to tweak tractable solutions incrementally or adaptively through learning-by-doing (DeFries and Nagendra, 2017) and permit an integrated *in silico* assessment of management decisions (Bondad et al., 2023).
3. Engage in interdisciplinary collaboration. Biological control scientists need to strive to avoid further disciplinary fragmentation and 'silo' attitudes (Brodeur et al., 2018). Individual BCAs often act synergistically, interact with myriad non-pest organisms in above- or below-ground realms, and contribute to the delivery of multiple services. Hence, collaboration with plant breeding, pollination ecology, chemical ecology, modeling and agronomy domains is crucial to operationalize multi-service, multi-functionality or tri-trophic defense concepts (Stenberg et al., 2015; MacLaren et al., 2020; Schipanski et al., 2014; Couëdel et al., 2019). Equally, biological control science has to intersect with the (political) economy field to understand power imbalances and its implications for pricing and access to information (Möhring et al., 2020) or so-called path dependencies and 'technology lock-in' (Cowan and Gunby, 1996).
4. Integrate application of ecologically sound technologies. As stand-alone technologies seldom achieve their envisioned outcomes (Herrero et al., 2021), biodiversity-based and agroecological solutions need to be tactically integrated even in conventional i.e., non-organic systems (Stenberg, 2017; Finger and Mohring, 2024). This includes pairing microbials and arthropod BCAs under inoculative and/or inundative release modes (Pijnakker et al., 2020; Koller et al., 2023) and combining them with various other measures. These include soil-targeted interventions (Mariotte et al., 2018; Nerva et al., 2022), sensor-equipped robotic weeders, sterile insect technique (Horrocks et al., 2020), behavior-modifying volatiles e.g., synthetic predator cues or (biological) defense priming (Rizvi et al., 2021; Yassin et al., 2021), ant-derived antibiotics (Offenberg et al., 2022), a targeted use of varietal resistance or 'dead-end' trap crops (Lu et al., 2012; Han et al., 2024) and tailored farm-or landscape-level management (Fig. 4). While many interventions are indeed geared towards the field scale and involve above-ground processes (Wyckhuys et al., 2023), only limited research involves below-ground realms and landscape-level dynamics (but see Pineda et al., 2017 or Perez-Alvarez et al., 2019). Also, the vast techno-scientific advances in (arthropod) biological control can now be used as a springboard to tactically link to cultural control or host plant resistance.
5. Meaningfully relate to people. To effectively steer decision making and action by farmer end-users, governments or conservation groups, assessments need to adopt decision-relevant endpoints such as profit, wellbeing, consumer demand, biodiversity x pest control win-wins, energy use or pesticide phasedown potential (Kleijn et al., 2019; Chaplin-Kramer et al., 2019; Wyckhuys et al., 2022). Accounting for the true cost of pesticide-induced externalities (Bourguet and Guillemaud, 2016) permits a just evaluation of BCA benefits. Public health and food safety concerns can also motivate policy changes toward restricting chemical pesticide use and trigger policy overhaul in favor of biological control, as exemplified by recent experiences in China and Switzerland (Finger, 2021; Li et al., 2021).

6. Taking biological control to scale

To support sustainable food production, farmland functional integrity needs to be fortified (Schneider et al., 2023). To achieve such, the reduction of pesticide use risks has become an essential policy goal (Candel et al., 2023). To achieve these objectives and bring these goals to life, policy has to stimulate the development and uptake of alternative, biodiversity-based and agroecological approaches. Irrespective of context dependencies and system-level variabilities (Karp et al., 2019), a sustained on-farm implementation of biological control is likely to achieve short-term (social-ecological) gains and long-term resilience. Hence, its current adoption on 1–10% farmland does not do justice to the promise of biological control.

Though biological control carries substantial promise, its global mainstreaming is obstructed through myriad socio-technical hurdles. Despite a robust scientific foundation and a fortified evidence base, the step towards decisive action appears small (Pongsiri et al., 2019), though the road from science to practice is often long and circuitous. By enhancing the salience, credibility and legitimacy of biological control knowledge (Cash, 2003), (reinvented) institutional settings can steer the course of technological change in the pest management domain (Jefferson et al., 2018; Walker et al., 2023) and, more importantly, tactically integrate pest-centric practices with other regenerative

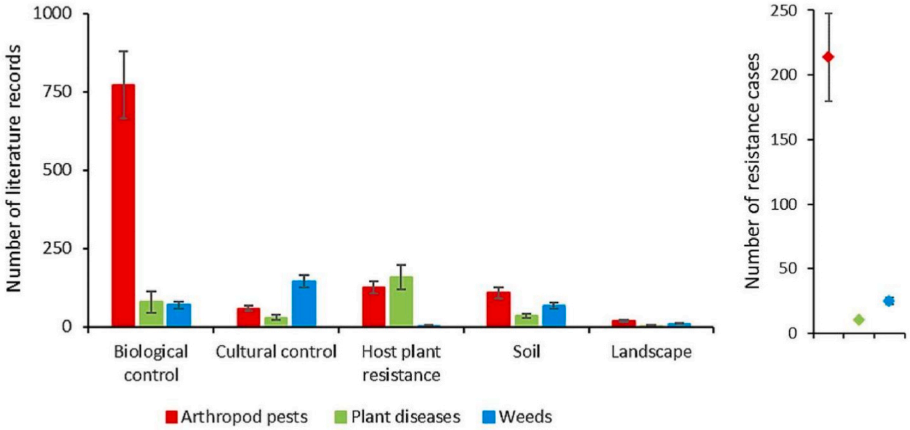

Fig. 4. Scientific underpinnings of the agroecological management ‘solutions space’ for the world’s most prominent biocide-resistant pests. Patterns are plotted for the world’s top 50 pesticide-resistant pests, weeds and plant pathogens. Per pest category, we plot the average (mean ± SE) number of all-time scientific publications addressing five core non-chemical control strategies. Underlying queries were run on Web of Science over 1900–2023, using search strings designed to capture relevant scientific output (Supplementary Table 1). Per query and biotic constraint, the number of logged literature records serves as an (imperfect) proxy of the respective scientific activity. In the right panel, the average number of (species-level) biocide resistance cases is plotted as per global databases i.e., Fisher et al. (2022), Mota-Sanchez and Wise (2023) and Heap (2023).

farming solutions. The necessary steps encompass all actors in the food value chain as well as ambitious policies and tangible policy instruments addressing all these actors (Möhring et al., 2020). To take this practice to scale, action is warranted on the following fronts.

1. Raise awareness. What farmers do not know cannot help them (Bentley, 1989). Given contemporary farmers’ low levels of ecological literacy and undervaluation of biological control - especially when provided by less conspicuous BCAs (Wyckhuys et al., 2019a) - bold awareness-raising efforts are needed. This can entail demonstrating the economic viability of biological control to farmers, decoupling agro-advisories from pesticide sales, bolstering public extension (Wyckhuys et al., 2019;Wuepper et al., 2021) and engaging farmers in citizen-science networks, ideally conducted *in sync* with targeted education of value chain actors including the general public. As an added plus, human appreciation of the value and role of biodiversity motivates ecological stewardship (Turner et al., 2022).
2. Involve farmers. Farmers are resourceful experimenters and tireless innovators (Lacoste et al., 2022). Engaging them through participatory extension efforts e.g., farmer-to-farmer video sharing or (digital) IPM-FFS, nodular on-farm research hubs or ‘living laboratories’ and multi-actor, cross-sectoral innovation niches (Pigford et al., 2018) can benefit the diffusion of biological control. On-farm research allows to perform (networked) experiments with standardized protocols in order to holistically evaluate impacts on crop yield, farm profit, biodiversity, biostructure and broader ecosystem functionalities to thus prove that biological control can be effectively used in real world settings. In such impact or outcome evaluations, the use of multidimensional One Health metrics -co-recorded together with participant farmers-carries notable advantages over the far more restrictive, though predominant cyclopean view on yield. Farmers can also extend the reach of augmentation biological control e.g., through a (properly certified) cottage-style production of beneficial invertebrates, fungi or nematodes with limited or no true market potential (Grimm, 2001; Nzioki et al., 2016; Oliveira-Hofman et al., 2023). A reliable supply of high-quality BCAs is a fundamental prerequisite to a successful use of (augmentation) biological control. Cottage-style BCA production represents the humble origins of the professional biological control industry (van Lenteren et al., 2018). It may also embody its future, as there is ample potential to engage farmers themselves in this production modality. On-farm production remains a largely under-explored approach for bolstering BCA supply in rural areas, but also for enhancing farmers’ familiarity with functional biodiversity, promoting autonomy and diversifying their income sources. This is evident in Brazil, where farmers now routinely mass-produce microbial BCAs on-farm, challenging the traditional role of input suppliers and agrochemical corporations (Goulet, 2023). To move this production modality forward and to avoid reputation loss from unsafe, low-quality or spurious organisms, strict quality control and assurance systems, external certification and a close, two-way interaction with the established biological control industry are imperative (Morales-Ramos et al., 2022).
3. Streamline or harmonize registration and legislation. Complex, lengthy and expensive product registration constitutes the biggest hurdle in the (commercial) diffusion of BCAs (Lacey et al., 2015; van Lenteren et al., 2018; Wagemans et al., 2022). This severely restricts the participation of small and medium-size enterprises in the up-scaling of biological control. Simple registration procedures that are aligned or reciprocated at continental or global scales, with fast-track processes or registration waivers e.g., for endemic biota can provide instant relief. For example, in Brazil, the regulatory environment provides a stimulus for biological control by prioritizing the registration of BCA-based solutions over chemical pesticides (Togni et al., 2019a). Moreover, streamlined, priority registration in Brazil and other South American countries made the entire continent one of the most attractive markets for augmentative biological control in the world (Bullor et al., 2024). On the other hand, with a rather complex, costly and protracted registration process in Europe (Balog et al., 2017; Van Lenteren et al., 2018) - where the registration of BCAs takes 6–10 years as compared to 1–3 years in other parts of the globe, local farmers miss out on solutions that are protective of human and environmental health while biological control becomes a ‘revolution in waiting’ (Helepciuc and Todor, 2022). Similarly, IBC is often hampered by risk-averse attitudes and indecisiveness on behalf of legislators (De Clercq et al., 2011; Barratt et al., 2018; Abram et al., 2024) or the independent implementation of the Nagoya Protocol on Access and Benefit Sharing by each country, which often renders the exchange of natural enemies difficult if not impossible (Mason et al., 2023). These hurdles could be circumvented by explicitly considering the risks and benefits of IBC, including the consequences of inaction or pesticide-centered control (Abram et al., 2024).

4. Incentivize biological control. To overcome the current over-reliance on chemical pesticides, ambitious policies need to be combined to incentivize biological control (Möhring et al., 2020). To avoid that such policies e.g., those that underpinned the European Farm-to-Fork strategy, are inordinately shaped by or fall victim to public pressure (so-called availability cascades; Kuran and Sunstein, 1998), they are to be built upon careful objective analysis in which (scientific) experts serve as a bulwark against cognitive biases, irrational fears and external lobbying.
    i) Command and control/regulation can reduce pesticide use and thereby make alternatives more attractive. This can entail admitting specific low-risk pesticides and regulating their use. This policy type also addresses biological control e.g., making it rapidly available to the market is a key factor.
    ii) Market-based instruments such as taxes on (medium- to high-risk) pesticides to make alternatives more attractive (Nielsen et al., 2023); subsidies to procure BCAs; effective implementation of product standards, certificates and labeling that support price markups for pesticide-free products (Jacquet et al., 2022; Möhring and Finger, 2022; Finger and Mohring, 2024); payments to adopt biological pest control and more sustainable forms of crop protection increase their uptake by farmers.
    iii) Information, education and extension e.g. providing information to farmers is a prerequisite for behavior change. Even the type of extension matters for an effective promotion of non-chemical solutions (Wuepper et al., 2021). In low-income countries, a more extensive use of mass-media campaigns, social media and ICTs is critical to overcome weak and chronically underfunded extension systems (Klerkx, 2021) and thus help to prevent messages to be 'drowned out' by agrochemical marketing campaigns.
    iv) Moreover, nudging may be used to incentivize farmers to use non-chemical alternatives (Balew et al., 2023; Zachmann et al., 2023).
    v) Usually, alternatives to pesticides are (perceived to be) more risky, disincentivizing farmers to adopt them (Möhring and Finger, 2022). Policies to reduce risk exposure and risk perception associated with non-chemical alternatives such as biological control (coupled with transition support) can be efficient.
    vi) Exploiting the power of networks: there are strong peer effects in the uptake of non-chemical alternatives, as farmers learn from each other, share knowledge, experiences, machinery, etc. (Wang et al., 2023). Policies to exploit these network effects and farmer-to-farmer knowledge exchange can be useful complements to other policies.
    vii) Act proactively: When a new (invasive) pest problem arises, biological control is often considered when other methods have shown their limitations (i.e., contrary to core IPM principles). Instead, biological control should be systematically treated as 'first line of defence' and even considered pre-emptively, before a high-profile pest makes it appearance (Hoddle, 2023; Avila et al., 2023).

5 Align funding with desirable tactics. The current lack of public investment in biological control, including in the vital (long-term) research that underpins this practice, reflects the relative influences of different power brokers in policy processes. Biological control receives less than 1% of overall pest management funding (van Lenteren, 2012) and pollution control or even agroecology scarcely figure in development assistance (Fuller et al., 2022). Those budgetary shortfalls are causing an erosion of core academic and scientific capacity (Warner et al., 2011; Brodeur et al., 2018) and slow progress in more sustainable forms of crop protection or production. True cost accounting can reveal the "full" monetary value of biological control either individually or when smartly intertwined with agroecology, and justify such a funding boost. Such stimulus, coupled with a conscious repurposing of public spending and a phase-out of harmful subsidies, carries substantial economic payoff (Gautam et al., 2022). Long overdue, this funding boost and the associated reconstitution of critical techno-scientific capacity may prevent humans from being caught in a decades-long, ever-deepening 'pesticide catastrophe' (Van den Bosch, 1978).

7. Conclusions

The recent state of food systems report established an urgent need to change the way we grow food in order to safeguard foundational ecosystem services (Schneider et al., 2023). Indeed, since the 1940s, input-intensive agriculture has boosted food production, while compromising the natural self-regulation capacity of global agro-ecosystems and undermining their functional integrity. This Perspective provides scientifically-grounded evidence to show that a tactical integration of (on- and off-farm) agroecological and biodiversity-driven solutions can resolve these critical issues. Specifically, biological control offers an environmentally-friendly, economically-viable approach to preventatively manage crop antagonists and thereby fortify the broad functionalities and long-term resilience of agroecosystems. Yet, despite notable scientific progress over the past decade, persistent (socio-technical) barriers obstruct a mainstreaming of biological control. Moving forward, it is crucial to embrace the intricacies of ecological interconnectedness and to tactically integrate biodiversity-based, pest-centric solutions with a wider array of agroecological measures and landscape-level action. To take biological control to scale, we equally urge to increase farmers' awareness and engagement, streamline registration of biological control agents, establish supportive policies that render biological control more economically viable than pesticide-intensive measures, and increase funding. By thus looking beyond the narrow confines of crop protection, critical momentum can be built in regenerating the ecological functionality of farmland ecosystems amidst rapid global change. As such, one could meet future food needs without jeopardizing farmer livelihoods, societal wellbeing or Earth system resilience.

CRediT authorship contribution statement

Kris A.G. Wyckhuys: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Baogen Gu:** Writing – review & editing, Funding acquisition. **Ibtissem Ben Fekih:** Writing – review & editing. **Robert Finger:** Writing – review & editing, Writing – original draft. **Mark Kenis:** Writing – review & editing. **Yanhui Lu:** Writing – review & editing. **Sevgan Subramanian:** Writing – review & editing. **Fiona H.M. Tang:** Writing – review & editing, Data curation. **Donald C. Weber:** Writing – review & editing. **Wei Zhang:** Writing – review & editing. **Buyung A.R. Hadi:** Supervision, Funding acquisition.

Declaration of competing interest

KAGW is the chief executive officer of Chrysalis Consulting – a firm which provides tailored support to nature-friendly farming and biological control.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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