Trends in Plant Science

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Opinion

Restoring functional farmland biodiversity for biological pest control

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Roughly 40% of global agri-food production is lost to pests during an era when productivity gains are essential to humanity. Restoring farmland biodiversity for conservation biological control offers potential to secure win-win outcomes for yield and the environment. However, achieving this is hindered by gaps in our understanding of agrobiodiversity, including a lack of data on the occurrence, identity, and interactions of farm-dwelling (plant, animal, microbial) biota. Limited interdisciplinary collaboration and weak policy frameworks exacerbate these issues. Comprehensive data capture using standardized metrics, universal protocols, farmer–scientist cooperation, and next-generation tools could consolidate the evidence base on which to reform farming practice. This will involve ecologists stepping outside their comfort zones to promote behavioral change and make ecological intensification a reality.

Highlights

High-intensity farm management routinely overrides the landscape-level spillover of beneficial biota from natural habitats.

Farm-dwelling invertebrates and microbiota contribute substantially to pest control, but their biodiversity, interactions, and functional roles are poorly characterized.

Farmland biomonitoring through hands-on sampling, (farmer) citizen science, autonomous sensors, and natural language processing should constitute an integral part of global biodiversity research.

Emerging biodiversity, trait, and interaction databases need to be properly curated, upgraded, and tapped to generate actionable information.

Closer engagement with the social sciences allows pathways for behavioral change to occur.

Modern intensive farming systems compromise ecosystem integrity and biodiversity

Modern intensified farming systems are designed in ways that debilitate their functional integrity [1]: in other words, the extent to which ecosystems sustain the provision of ecosystem service 'bundles' mirrors their capacity to adapt, recover, and transform following disturbance. Since the 1940s, agricultural systems have become increasingly species-poor and genetically uniform, devoid of natural habitat, and exposed to recurrent anthropogenic disruption [2]. Industrialized forms of agriculture favor crop-feeding pests, weeds, and diseases (collectively 'pests'), and thereby not only jeopardize food production but also impact on biodiversity conservation and human well-being [3]. Pests destroy up to 40% of crops, representing billions of US dollars in productivity and trade losses annually [4]. This, in turn, has led to unrelenting growth in pesticide usage intensity which magnifies biodiversity loss and disrupts trophic networks [5,6]. The exact reasons for inadequate pest suppression are complex, multifaceted, and mediated by landscape-level phenomena. Most fundamentally, two-thirds of present-day farmland lack the critical amounts (i.e., 20%) of (semi-)natural habitat that can serve as donor habitats for consumer organisms (i.e., natural enemies of pests) [7]. Further, off-farm habitats inconsistently benefit biological control because their effects are context- or taxon-specific, mediated by field and landscape features [8,9], and are usually overridden by intensive field-level management including the use of environmentally disruptive pesticides [10].

If pesticide-related disturbances at the field level can be defused, ecological intensification could be put more effectively into practice to resolve crop yield-gaps sustainably [9,11,12]. Indeed, well-calibrated farm management and integrative 'systems' approaches can take fuller advantage of landscape-level spillover of beneficial organisms into crop fields [13], reconstitute internal

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feedbacks, and deliver win-wins for biodiversity and yield [12,14]. An effective harnessing of on-farm biodiversity for pest control (i.e., conservation biological control) is thus crucial to remediate pesticidal pollution, and therefore constitutes a crucial first step towards achieving ecological intensification [11] (Figure 1). Specifically, habitat management interventions such as early-season plant cover, flower strips, and green manuring can suppress pests in an economically sound manner without a need to resort to synthetic pesticides [15–17]. Conservation biological control can thereby restore key ecological functions, provide complementary benefits, and increase profit [18], although its scaling potential is constrained by context-dependencies that are poorly accounted for under existing decision frameworks.

To advance the effective implementation of conservation biological control, several research gaps need to be filled. We consider four challenges that need to be met. (i) Ecologists need better, internationally coordinated efforts to discover, describe, and study relevant farm biota in temperate and tropical settings. (ii) There are knowledge shortfalls regarding the ecological interactions that drive biological control and (iii) the relative strengths of such interactions in particular systems. (iv) Modern plant breeding must be enriched by incorporating the plant traits that influence natural enemy effectiveness.

The above (field-centric) points infer a need to account for relevant soil- and landscape-level dimensions (a topic which is not treated in this article). To tackle these challenges, next-generation monitoring technologies and farmer–scientist knowledge coproduction models should be embraced. Extending from this [19], localized studies need better integration into multi- and transdisciplinary studies such that agronomic and socioeconomic levers or outcomes are duly considered. In addition, ecologists need to develop stronger theoretical and practical connections between the science of conservation biological control and its on-farm uptake and diffusion. This is a diffuse domain where both political will and enabling policies are imperative to ensure an effective scaling of ecological intensification.

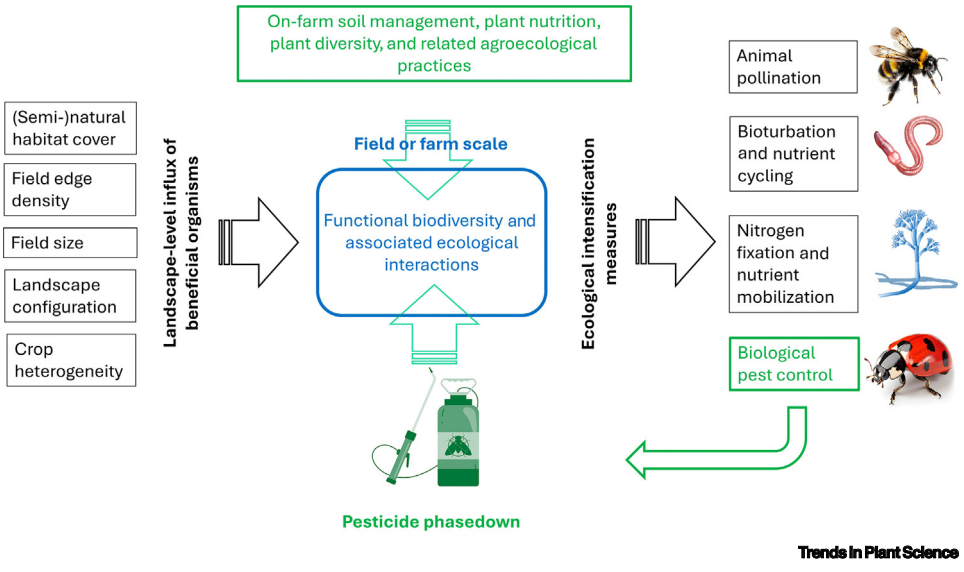

Figure 1. Biological pest control as a crucial lever to attain ecological intensification of agriculture. The implementation of conservation biological control is pivotal to phasing down the usage of synthetic pesticides; this allows farmers and land managers to take advantage of landscape-level spillover of ecosystem providers, restore farmland functional biodiversity, and reconstitute the internal feedbacks of agro-ecosystems – thereby unlocking the potential of ecological intensification.

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Laying the groundwork for agroecosystem recovery

First and foremost, integrative 'systems' approaches are essential to understand and reconstitute the functional integrity of the world's farmlands [9,12], and will ultimately yield ecosystems that are amenable to natural enemy action. However, even interventions that more narrowly seek to promote conservation biological control – arguably a first, resolute step towards ecological intensification – require an in-depth understanding of the underlying role of biodiversity, inter-species interactions, and the ensuing ecological processes [20] (Figure 2). In this regard, mechanistic frameworks that link ecosystem service providers (ESPs), their functional contributions, and community structure [21] carry considerable value – they pinpoint crucial steps towards service delivery, gauge its robustness, and help to translate science into real-world outcomes [22].

These frameworks are distinctively suitable for services in which the contributions of individual species can be easily determined (i.e., biological control) [21], and their effective implementation carries important socioenvironmental dividends. Central to sustainable food production and (agro-)ecosystem functioning, biological control is valued at US$ 95.5–196 billion per annum across biomes [23], adjusted for inflation. In comparative assessments, its monetary value surpasses that of pollination by threefold across biomes and by 50% in cropland. A meta-analysis has indicated that its impact on agricultural productivity is immense: across crop–pest systems, naturally occurring predators alone reduce pest numbers by 73% and increase yield by 25% [24]. As such, biological control features prominently in efforts to redesign agroecosystems [25]. In addition to this 'redesign' approach, 'input substitution' methods such as the on-farm use of factory-grown microbial or arthropod biological control agents (a practice currently adopted by nearly two-thirds of Brazilian growers [26]) can reduce dependence on pesticides, lessen their ill effects on the environment, and rebuild core functionalities. This in turn will unlock further opportunities for system redesign.

Successes in conservation biological control, although these are often localized in nature and have modest outcomes in terms of sustained changes in farmer practice, derive from an effective implementation of these frameworks. Viewing biological control through a network perspective [27], we provide examples of how an in-depth understanding of interspecies interactions and functionalities is key to devising self-sustaining farmland communities in which pests are managed preventatively.

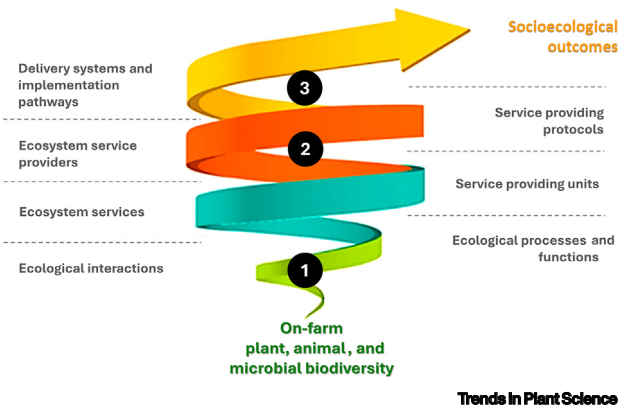

Figure 2. Multistep pathway to effectively harness on-farm biodiversity for biological pest control (adapted, with permission, from Gonzalez-Chang *et al.* [103]). The conceptual figure enumerates eight sequential steps, departing from the foundational principle of biodiversity, through which scientists must proceed to attain concrete socioenvironmental outcomes such as enhanced yield or profit, pesticide phasedown, and reconstituted biodiversity. The last step ideally covers enabling policies and regulations, proper incentives, awareness-raising, and more subtle ways to bring about behavioral change, namely so-called 'nudging' [98]. Skipping one or more steps inevitably reduces the odds of success. Three key leverage points are indicated to advance conservation biological control: ① remediating the taxonomic neglect through next-generation biomonitoring and functional inventories, ② science-based redesign of farming systems, and ③ social innovations to attain behavioral change at scale.

The following sections explain how specific biodiversity shortfalls preclude reliable characterization of core functionalities, interaction networks, and resilience metrics in agricultural settings, thereby slowing or even obstructing the realization of ecological intensification.

(i) Understanding functionally relevant species and guilds

Any effort to restore ecosystem service delivery should be anchored in a profound understanding of agro-biodiversity [25] (Figure 2). Comprehensive inventories of farm biota are the point of departure for further agroecological study. This especially applies to invertebrates and microbiota – key ESPs that maintain diverse communities in agricultural settings but that have been negatively impacted by intensification practices. For example, whereas Arkansas cotton and Florida soybean fields harbored >600–1000 arthropod predator species in the mid-1900s [28], the diversity of on-farm fauna has impoverished greatly in many production systems [29]. In addition, plant-associated entomopathogenic fungi are increasingly impacted by global warming [30].

Invertebrates and microbiota serve pivotal roles in pest regulation. Ants, for instance, are the most abundant predatory invertebrates in the tropics, and their influence on pest regulation extends beyond insect pests because many species, such as *Solenopsis geminata,* consume the seeds of weeds or shape overall community structure [31]. Tactics for manipulating ecosystem services provided by ants include not only mixed cropping and understorey management but also sugar sprays and artificial nectaries. However, the biodiversity of ants and insects overall remains inadequately described [32]. Knowledge is sparse, fragmented, and emphasizes non-crop habitats. Specifically, only 3.4% of ant specimens in the open-access Antweb database, or a respective 0.3% and 4.4% of the world's leaf litter and pitfall trap samples, have been collected from farm settings [33] (Figure S1 in the supplemental information online). Similarly, other ground-dwelling taxa which act as vital prey items for generalist natural enemies such as Acari mites, Collembola springtails, and Isoptera termites have been sampled from cropland in a mere 5.3%, 3.4% and 8.3%, respectively, of cases [34]. There is a similar paucity of knowledge for other functional guilds that are important in pest suppression: DNA barcodes are available for <5% of parasitoids and even the world's most comprehensive collection of entomopathogenic fungal cultures [35] only comprises five or fewer microbial associates for approximately half of the world's top 25 insecticide-resistant pests.

Widely distributed taxa and habitat or dietary generalists are comparatively well covered in inventories, although not necessarily in trophic relationships. However, uncommon natural enemies such as specialist parasitoids and winter-active predators [36], as well as detritivores and non-pest herbivores that can be key to biological control success as alternative prey [37], are overlooked in biodiversity censuses despite their importance. Further, because many farm-dwelling biota are poorly studied or even undescribed, we cannot expect farmers to value and conserve them [38]. By bringing functionally important taxa into the realm of biodiversity assessments and treating on-farm bio-inventories as an integral component of global biodiversity research, this can partially be resolved. For instance, concrete data on the identity, abundance, and population-level impacts of winter-active predators or entomopathogenic fungi at hibernation sites help to reduce early-season pest outbreaks in Spanish clementine orchards and Mexican sorghum fields [36,39]. In light of this, one needs to bear in mind that, aside from performing biodiversity censuses and drawing up simple species lists *per se*, it is crucial to pinpoint the taxa that are functionally relevant and the 'ecological architecture' that upholds such key functionalities. This involves logging inconspicuous, secondary 'support' plant or animal species that occur in both on- and off-farm settings [37,40]. As such, functional approaches are pivotal in deciphering the overwhelming amount of taxonomic data and in judging the relative roles of the innumerable

plants, animals, and microbiota that inhabit the world's farmland. This includes synthesizing and interpreting the wealth of published research findings on predator–prey or host–parasitoid relationships *in silico*, *in vitro*, or *in ecolo* using Big Data analytics or artificial intelligence (AI) [41], among others.

(ii) Characterizing ecological interactions in farm settings

Biodiversity captures the constituent parts of an ecosystem, but ecological interactions constitute the backbone of its structure, stability, and functioning [42]. Besides the ecosystem service of biological control which is central to this article, additional interspecific interactions of importance involve supporting or antagonist species that provide the robustness of food webs and service delivery. By tracing interaction linkages, one can relate the structural and ecological aspects of food webs [43], gain a mechanistic understanding of ecosystems, and steer ecological research. Although anticipating biological control outcomes based upon well-delineated multilayered food webs is not straightforward, species interactions provide a valuable compass in efforts to conserve or restore farm-level functionalities [20,27]. This principle can guide the selection of crop and non-crop plants to optimally leverage the action of resident natural enemies [44] or inform conservation action, for example by clarifying the association of the insect-killing fungus *Metharizium anisopliae* with above- or belowground biota and on- or off-farm habitats. A portrayal of species interactions can guide conservation biological control research and practice [45], especially where assemblages of natural enemies and their associated hosts or host plants [37] rather than individual taxa define the biological control outcomes. For example, the 'push-pull' approach depends upon a combination of companion plants that simultaneously repel crop pests and attract (or reward) their parasitoid antagonists [46]. Similarly, weed biological control relies upon linking the foraging and feeding behavior of granivorous carabids to vegetation structure [47], whereas fungal epizootics in pest populations can be favored by identifying reservoir hosts or plants [48]. Despite the general importance of ecological interactions, and examples of specific value in some agroecosystems, we currently have patchy knowledge of them [49]. Even for biota that trigger unsustainable farming practices, such as pesticide-resistant pests, interaction knowledge is fragmentary (Figures 3 and S2). This state of knowledge of ecological interactions can be assessed by querying data repositories such as GloBI, mangal.io, Web of Life, and the Interaction web database [43], in which the former two are the most comprehensive for predator–prey and host–parasitoid interactions. Specifically, for the world's top-25 insecticide-resistant pests, the numbers of trophic linkages with invertebrate or vertebrate predators logged in the GloBI data repository [50] are startlingly low: 3 ± 7 and 4 ± 6, respectively. For the latter, nearly two-thirds of the respective binary interactions have not received scientific scrutiny. Similarly, for the 25 top herbicide-resistant weeds, merely 27 ± 28 and 7 ± 7 binary interactions with herbivorous invertebrates or vertebrates have been logged (Figure 3).

Accordingly, although searchable repositories represent an important advance, the patchiness of the data available to them is a major constraint [43]. Parasitoid–host interactions are well represented compared to predation linkages because definitive interaction data can be easily obtained via culturing from field-collected pests (although expertise in taxonomy and the presence of hyper-parasitoids are issues). Predation linkages are sparser and can be erroneously assumed from co-occurrence [51] or direct observation, in which the latter are inordinately shaped by organismal body size, identity, feeding, or activity patterns. The growing availability of molecular approaches to infer predation is, however, likely to help to enhance the volume and reliability of records [52]. Nevertheless, given the occurrence of secondary predation, scavenging, and body size or activity-dependent DNA denaturing times, molecular data need to be carefully interpreted and validated by *in situ* observational or manipulative studies. Competition, another

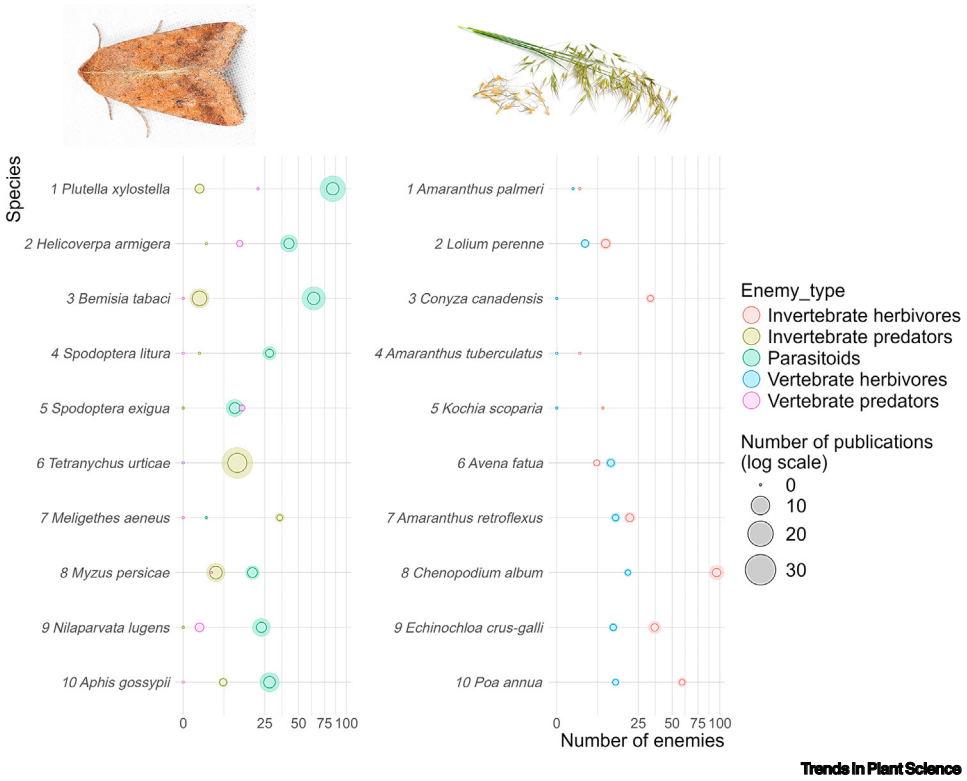

Figure 3. Known and investigated consumer organisms associated with the world's top-10 pesticide-resistant crop pests or weeds. The *x* axis depicts the number of consumer species that are trophically associated with a focal pest or weed (i.e., natural enemies), as determined by querying GloBI [47] using 'host of', 'eaten by', and 'preyed upon by' as search terms. The circle size is proportional to the maximum number of all-time scientific publications that concurrently feature the binomial scientific names of the focal pest and each of its trophic associates, as determined by querying the Web of Science. Plots are drawn for different consumer guilds, and (invertebrate) herbivores include not only folivores, granivores, and root feeders but also nectar-consumers. Dark circles within the transparent circles are the means of the log of the number of publications. The numbers of resistance cases for each pest or weed species are given in Table S1.

key determinant of ecological regulation, as well as volatile-mediated repellency and attraction of pests and natural enemies [46], do not feature in topological metrics and the logging of omnivore interactions is profoundly incomplete (Box 1). Lastly, taxon coverage is possibly shaped by dietary breadth, dispersal capacity, and disturbance proneness [53], and less-mobile specialist feeders are probably under-represented in databases that cover ephemeral agroecosystems. Because network effects and multitrophic interactions often receive lesser amounts of attention under current autecological assessments [19,27], and open-access repositories face important data shortfalls and deficiencies, scientists are unable to effectively harness them for biological control purposes. Addressing these shortfalls is imperative.

(iii) Empirically assessing the strength of ecological interactions

The patchiness of data on the nature and numbers of ecological interactions, dealt with in the preceding text, is compounded by a similar paucity in our knowledge about the strength of interactions. This is a major shortcoming because of the obvious link to species- or population-level dynamics [54] and ultimately to pest impact. Interaction strength cannot reliably be assumed from co-occurrence, range overlap or interspecific encounter rates [51], but ideally is empirically

Box 1. Tracing omnivore linkages

In ephemeral farming systems, generalist ecosystem service providers (ESPs) sustain their populations on a portfolio of resources and play prominent roles in ecological regulation. In addition to attacking crop-feeding herbivores, they feed upon non-pest biota, often in distinct habitats or ecological realms, for example in detrital channels or below the soil surface. Most engage in facultative or obligate omnivory and consume foods across the trophic spectrum, and their feeding habits are often tied to particular life-history stages [104]. Whereas parasitoid immatures develop within animal hosts, the reproductive performance of adults is largely defined by the available carbohydrate food resources. When host and food resources co-occur within the dispersal radius of a species, life-history omnivory may benefit ecological regulation by decoupling predator–prey dynamics [105] but it can also add vulnerability to spatiotemporal mismatches in resource availability. To anticipate the strength and stability of biological control, stage-specific dietary needs must be clarified and trophic interactions traced to animal, fungal, and plant-based dietary resources. Doing so can enable targeted interventions to secure biological control outcomes.

In reality, the detection of omnivorous feeding interactions appears to be skewed towards a single type of resources. Indeed, simple queries on GloBI reveal how (species-level) links to animal hosts are routinely logged for parasitic wasps, but interactions with plants are rarely recorded. This does not mirror reality: most parasitoids are generalized nectar foragers [106] and multiple species visit the inflorescences of individual plants. However, floral or extra-floral nectar does not necessarily present the optimum adult food: aphelinid parasitoids consume homopteran honeydew, and many synovigenic wasps engage in host feeding such as the consumption of host hemolymph. Regardless of these drawbacks, we argue that the life-history omnivory of parasitoids is not comprehensively captured in data repositories.

Data gaps could be ascribed to either unequal detection probabilities or the absence of plant visitation. For instance, linyphiid spiders gain nutritional benefits from pollen consumption that improve their role as predators, but intercept pollen grains in ground-based webs (instead of visiting the plants directly). Because small-bodied, infrequent flower visitors such as parasitoids are often absent in flower-visitor surveys [106], their association with non-pest hosts or extra-floral nectaries may go unrecorded. In addition to parasitoids and spiders, taxa such as carabid beetles and ants extensively switch between predation, nectar, and honeydew feeding, and mycophagy and granivory, based upon environmental context and trophic niche occupancy. Because these parameters shape herbivore–ESP dynamics and define biological control outcomes, omnivore interactions should be traced properly.

measured by recording the 'success' of encounters such as predator-inflicted mortality, parasitism rate, or sentinel prey removal [55]. These data can then be extrapolated by matching the traits of the interacting species, such as weed seed size with mandible width, or flower corolla aperture with parasitoid head size, and linking these with census data [56].

Demographic analysis through ecological life-table studies, preferably enriched with AI-based tools, are crucial in assessing the extent to which ecosystem service providers contribute to population regulation [57]. Elegant work, performed for the major pest *Bemisia tabaci* [58], allowed its main mortality sources, drivers of area-wide population growth, and biological control prospects to be defined. However, among the world's agri-food crops, life-table studies remain scarce. As an illustration, for 13 cereal grain crops, only 2 ± 3 of an average of 14 708 all-time publications report life-table analyses (Figure 4). Adding to scant interaction data (Figure 3), this virtual absence of empirically derived functional data deepens the knowledge deficit for biological control scientists. For instance, life-table analyses for cosmopolitan pests such as *B. tabaci* and the fall armyworm (*Spodoptera frugiperda*) identify invertebrate predation as the main mortality factor [58], but no more than a single predator associate is logged in GloBI for these pests. Because hundreds of natural enemies have been discovered and studied for each of the aforementioned pests, this represents a notable weakness in database integration. More comprehensive data repositories could generate important forward momentum for the science of conservation biological control.

For parasitoid– or pathogen–host systems, assessing interaction strength may appear to be straightforward but common metrics (e.g., point recordings of parasitism rate) vary with sampling methods and poorly reflect population impact. Directly logged predator–prey interactions underrate their population-level impacts because of avoidance behavior, risk cues, or induced plant defenses [59,60]. Tephritid fruit flies, for instance, are affected more by the volatiles of the weaver ant

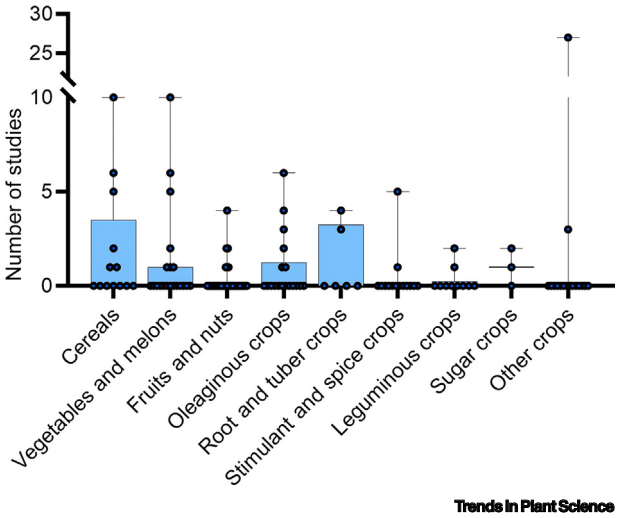

Figure 4. Suboptimal usage of ecological life-table analysis to assess the relative functionality of biological control agents for nine global crop categories. Box and jitter plots show the absolute number of pest-related studies that cover in-field life-table analysis for the individual crops within each crop category. Boxes enclose the 1st to 3rd quartiles, whereas whiskers represent the maximum values. The uncertainties that result from this infrequent use of life-table analysis impede biological control research and practice. From left to right, crop categories comprise 13, 20, 35, 18, 6, 14, 10, 3, and 16 constituent crops. Crop categories were defined based upon the United Nations Food and Agriculture Organization (FAO) Indicative Crop Classification. The underlying search strings are defined in Table S2.

Oecophylla longinoda than by actual ant predation. Exclusive reliance on parasitism or predation rates can thus greatly underestimate interaction strength. For omnivores, interaction strength needs to be gauged accurately (Box 1). For instance, in parasitoid–flower interactions, one cannot simply conflate abundance and activity patterns, and patch time allocation needs to be properly assessed at relevant spatiotemporal scales. For microbial ESPs, combined screening of genetic diversity and pathogenicity can help to pinpoint functional traits [61]. Despite the foregoing challenges, the strength of the key functional interactions needs to be broadly defined, convincingly shown, and empirically assessed given its pivotal role in biological control research [21,45].

(iv) Intertwining breeding science with agroecological research

Plant breeding has been a defining force in shaping both Green and post-Green Revolution agriculture, but has been largely performed under a pesticide umbrella [62], often with a near-exclusive focus on yield gain. In recent years, however, the incorporation of indirect, natural enemy-mediated defenses into breeding science is increasingly pursued [63], especially because their inclusion can sustain yields at reduced (pesticide) expenditure and under unpredictable biotic stress. Traits such as extrafloral nectar secretion, leaf pubescence, shelter structures or 'domatia', and the (induced) emission of volatile attractants can enhance the stability and resilience of pest-regulation networks [64].

Crop wild relatives, the ancestors of modern-day crop cultivars, may be a prime source of such indirect defense traits [65]. The wild relative of tobacco, *Nicotiana benthamiana,* for instance, exhibits high attractiveness and near-100% lethality towards *B. tabaci* [66]. In Mesoamerica, wild relatives of maize host a diverse suite of invertebrate and microbial biological control agents [67,68] while harboring a repertoire of volatile attractants [69]. Online databases for globally important food crops such as maize, rice, *Phaseolus* sp. bean, and potato report 5, 15, 5, and 36 wild relatives, respectively, that harbor one or more traits for (direct) biotic resistance (Figure 5). On the other hand, associations with invertebrate or microbial ESPs have been reported in the global literature for 10, 5, 1, and 3 of the respective wild relatives, although these have received scant scientific attention. Considering that these crops are collectively grown on >400 million hectares, the meager

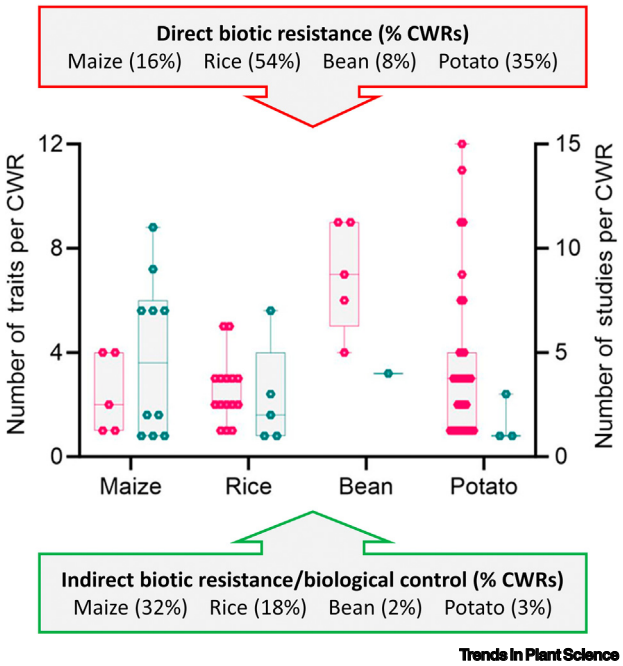

Figure 5. Breeding pipelines of global food crops are skewed towards direct (vs indirect) biotic resistance. Box and jitter plots depict the number of biotic resistance traits of potential breeding interest (red; primary *y* axis) and the number of indexed studies describing associated invertebrate biological control agents (green; secondary *y* axis) for each crop wild relative (CWR) of a given crop. Respective values are obtained by querying the Crop Wild Relatives Project (https://www.cwrdiversity.org/) or GloBI [50] and by performing subsequent literature searches. In call-out boxes, we specify the share of CWRs for which resistance traits or biological control agents are reported. Patterns are shown for maize (n = 31 CWRs), rice (n = 28), *Phaseolus* bean (n = 60), and potato (n = 103). Boxes enclose the 1st to 3rd quartiles, whereas whiskers represent minimum and maximum values. The underlying search strings are defined in Table S2.

scientific attention to indirect defenses does not do justice to the immense potential of ecological regulation, including conservation biological control, in those systems.

To feed this potentially 'game-changing' knowledge forward into breeding pipelines, systematic analyses of genebank collections supported by automation approaches are needed [65], the value of pest tolerance or partial resistance needs to be fully explored [70], and the pace of scientific research on ecologically based defenses needs urgent quickening.

Concluding remarks and future perspectives

Drawing together various strands of evidence, we demonstrate how the service of biological control features dimly in functional ecology or restoration science [14,71], and the crop breeding and agro-ecology domains are crucially disjointed. To restore and make smart use of the natural functionalities of farmland, this knowledge deficit needs to be resolved and pathways should be traced towards behavioral change by various stakeholders (Figures 1 and 6). Although unlocking the potential of biological control can generate vital momentum for ecological intensification, the task at hand is immense because most of the world's cropland is subject to unrelenting simplification and chemical intensification. Key elements of this mission are unglamorous and laborious but necessary. Digital technologies and AI, Big Data analytics, next-generation tools, and closer farmer–scientist interplay (see Outstanding questions) could enable a step-change in the science and practice of biological control. Future research needs to be geared towards three domains.

First, the taxonomic neglect and interaction data gaps can be resolved through bold new biomonitoring programs [72], scalable techniques such as reverse workflows for taxonomic identification [32], and by archiving available records in developed and Global North nations [42]. A quantitative estimation of the relative contributions of biological control agents to ecosystem functioning, resilience, and stability is crucial [20], especially because coarse-grained metrics such as ESP richness (alone) carry limited predictive power [73,74]. Clarifying the role of keystone ESPs

Outstanding questions

Can additional research attention to demographic analyses and life-table studies of pests provide added focus and crucial guidance for conservation biological control?

How can participatory approaches and closer farmer–scientist crosstalk in biological control programs allow the optimization of socioecological trade-offs?

How can advanced pest and natural enemy monitoring be used to promote more sustainable forms of pest management centered on biological control?

What is the relative importance of in-field versus landscape-level interventions for pests of varying mobility, habitat affinity, or host breadth, and how can interventions at different spatiotemporal scales be effectively wedded?

How can emerging digital, AI-powered, or DNA-based technologies allow inclusive, standardized, high-resolution, and globe-encompassing monitoring of farmland biota?

How can data-driven approaches such as automated damage detection, autonomous sensor units, and early-warning systems guide field-, farm-, and landscape-level action and create forward momentum for conservation biological control across varying (agro-ecological, socioeconomic) farming contexts?

Can pests, weeds, and diseases be managed preventatively by integrating conservation biological control with microbial seed coatings and natural enemy releases, soil-targeted interventions, robotic weeders, behavior-modifying infochemicals, defense priming, crop varietal resistance or tolerance, and a further wide array of agroecology tactics?

How can basic ecological knowledge on trophic systems at local and landscape scales be developed into location-specific DSSs for planning and management of agroecosystems?

What are the ways in which partnerships between researchers, practitioners, and policymakers can

such as *S. geminata* in Neotropical maize systems [75] through network approaches will be central in such an undertaking. Further, because interaction data within repositories are noisy and incomplete [43], they should be curated and upgraded with hands-on field sampling, passive crowdsourcing, text mining and natural language processing [76,77], or emerging high-throughput technologies [78]. Crowdsourcing approaches can help to mitigate geographical data biases [79]: farmers can be engaged in biodiversity data collection through low-cost approaches such as deep-learning-based computer vision or soundscape analysis, duly integrated into multi-sensor monitoring platforms [78]. Environmental DNA, meta-barcoding, and microbiome screening can clarify pest–ESP and ESP–plant interactions [80] and identify candidate taxa for biological control [81]. Improvements are required, however, for molecular approaches. Although these have tangible potential to reveal and even quantify community diversity and dynamics or habitat associations [52,82], their usefulness in clarifying the strength of individual bitrophic interactions is restricted due to issues that are difficult (although not impossible) to resolve methodologically. Further, given the impracticality to detect every single interaction on Earth, predictive efforts are crucial and can draw upon co-occurrence patterns or matching traits such as seed size and granivore mandible width [22,56]. In such endeavors, comprehensive, high-quality trait datasets [70,83] and standardized data collection and compilation protocols [84] are essential. In this regard, valuable lessons can be drawn from coordinated, multi-site programs such as the International Long-Term Ecological Research Network (ILTER; https://lternet.edu/international/), the fledgling Long-Term Agroecosystem Research (LTAR; https://ltar.ars.usda.gov/) and the 1000 Farms Initiative run by the grass-roots Ecdysis Foundation (https://www.ecdysis.bio/). Taxon-specific endeavors such as the formal monitoring of tropical forest insects and citizen-science initiatives such as eBird (https://ebird.org/home) and iNaturalist

be enhanced to enable the use of conservation biological control in agricultural systems?

How can inter- and transdisciplinary studies optimally be incorporated into research and implementation pathways?

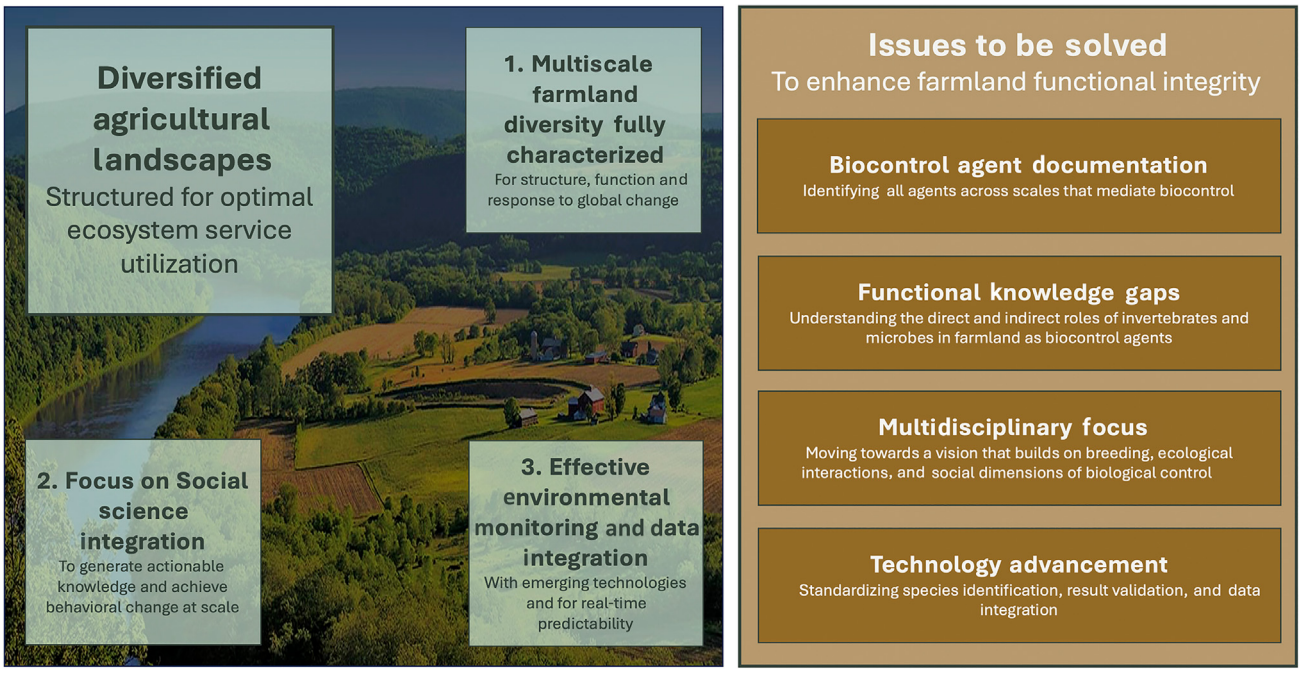

Figure 6. Selected barriers for an effective restoration of functional agro-biodiversity and the main leverage points to advance conservation biological control in global farmland. The background picture was produced by N. Tonelli under CC BY-SA. The entire figure with all its content is licensed under CC BY-SA.

(https://www.inaturalist.org/) provide pointers for bold agrobiodiversity monitoring programs [72,85,86]. Lastly, revitalizing and repurposing historical long-term agricultural monitoring schemes (e.g., [87]) and calibrating those with modern means of data collection could yield comparable population-level data with ease.

Although we argue that the research agenda that emerges from the unresolved issues (see Outstanding questions) will be important for advancing a more robust pest management system, there is an equally important gap that also needs to be addressed. A conservation-focused biological control system needs to guide the design, implementation, and management of a cropping system that enhances on- and off-farm outcomes. At the farm level, a diversity of agronomic measures such as manuring, crop diversification, and conservation tillage have been shown to generate positive effects on services such as soil conservation and nitrogen fixation [9]. However, their outcomes for conservation biological control are variable and context-specific. This creates a practical implementation challenge for biological control because of both its inherent variability in outcomes and the lack of a specific 'recipe' [88] that can be applied to a particular place. Future work can be geared towards characterizing how management that is intended to improve ESP conservation plays out in specific agroecological contexts [89]. This could be achieved by coupling high-resolution monitoring of key ESP groups with predictive models and has the potential to inform ESP-centered management, for example by delineating safe operational spaces [90] and proposing tailored 'redesign' solutions. This eventually can enable the development of decision support systems (DSSs) that can guide diversification tactics and detritus subsidies [25,91], anticipate impacts of soil legacies [92], or inform the addition (or retention) of functional groups with suitable traits. They can inform corrective action to conserve core ecological processes, for example by defusing the drawbacks of ant-based biological control through sugar-feeders [93]. As such, DSSs can provide practical recommendations for precision agriculture with robotic weeders, digitized farms, and patch-wise (biopesticide) spraying. In the end, these tools can generate traction for ecologically centered pest control provided that contextualities are properly accounted for, suitable corrective measures are put forward, management objectives are clearly defined, and the impacts envisaged are made apparent [11,22].

Third, the link between ecological knowledge and the socioecological outcomes that derive from biodiversity (Figures 1 and 2) raises the consideration of how behavioral change occurs in agriculture. Social factors (if not 'people') need to feature in technological trajectories [94] because agrobiodiversity alone does not determine sustainability outcomes [95]. Farmer decisions are also influenced by the social and biophysical context in which their agricultural system resides. The visions and goals of (farmer) end-users and decision-makers determine what changes are practical and desirable [11], and this course of change is modulated by regulatory or policy frameworks [96], proper enforcement, and ultimately by the political will to act on sustainable agriculture. Farm- or landscape-level trade-offs may transpire following the implementation of biological control, for example by decreasing land under cultivation [97]. In addition, biological control interventions often generate important synergies and sustain diverse ecosystem service 'bundles' [9,14]. For instance, fungicide phasedown can enable microbial weed control, benefit plant nutrition, or slow the emergence of antimicrobial resistance, but these win-wins regularly remain unquantified. Equally, the extent to which agronomic interventions such as legume integration or no-till shape pest-control outcomes tends to be occluded. How such contrasting values and priorities are discussed, managed, and negotiated will decide whether or not a given *status quo* is maintained. Further, the actual measurement of spillover benefits can pave the way for market-based instruments or incentive schemes [98], for example through biodiversity credit markets. Social innovations can also enable ecological innovations [99]: these include farmer field schools that rely on peer-to-peer models, innovation brokers, farmer-to-farmer educational videos, and intermediaries

or information and communication technologies (ICTs) that weave innovation systems together [100]. The involvement of farmers in crowdsourcing may also have an educational effect and improve their 'ecological literacy' [38]. In addition, DSSs that visualize how altered management practices result in socioenvironmental outcomes [101] can be used in scenario-based discussions. The incorporation of decision-relevant metrics (e.g., enhanced profit or pesticide phasedown potential) is crucial for DSS appeal and uptake, but such variables are often assessed from narrow, unidimensional perspectives, if at all [11]. Participatory research poses another avenue to hone the scientific underpinnings of biological control and enable transformative change at scale [102]. In short, amending the techno-scientific knowledge gaps of biological control should go hand-in-hand with social innovations and a 'can-do' attitude among decision makers to accelerate its 'real world' implementation.

By thus unveiling the revolving cogs in the socioecological clockwork of biological control, we not only raise the odds of rebuilding the ecological capacities of farming systems to limit pest losses but also lift agroecology science above its current incidental, case-by-case empiricism (see Outstanding questions).

Author contributions

K.A.G.W. led idea generation, writing, analytics, and editing. G.P. contributed to data visualization. All authors actively contributed to writing and editing.

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Declaration of interests

K.A.G.W. is the chief executive officer of Chrysalis Consulting, a firm which provides tailored support to nature-friendly farming and biological control.

Supplemental information

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