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Current Opinion in Environmental Sustainability

Tritrophic defenses as a central pivot of low-emission, pest-suppressive farming systems

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The ongoing COVID-19 pandemic has spotlighted the intricate connections between human and planetary health. Given that pesticide-centered crop protection degrades ecological resilience and (in-)directly harms human health, the adoption of ecologically sound, biodiversity-driven alternatives is imperative. In this Synthesis paper, we illuminate how ecological forces can be manipulated to bolster 'tritrophic defenses' against crop pests, pathogens, and weeds. Three distinct, yet mutually compatible approaches (habitat-mediated, breeding-dependent, and epigenetic tactics) can be deployed at different organizational levels, that is, from an individual seed to entire farming landscapes. Biodiversity can be harnessed for crop protection through ecological infrastructures, diversification tactics, and reconstituted soil health. Crop diversification is ideally guided by interorganismal interplay and plant–soil feedbacks, entailing resistant cultivars, rotation schemes, or multicrop arrangements. Rewarding opportunities also exist to prime plants for enhanced immunity or indirect defenses. As tritrophic defenses spawn multiple societal cobenefits, they could become core features of healthy, climate-resilient, and low-carbon food systems.

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Current Opinion in Environmental Sustainability 2022, **58**:101208

This review comes from a themed issue on **Emerging pests and pathogens**

Edited by **Peter Søgaard Jørgensen**

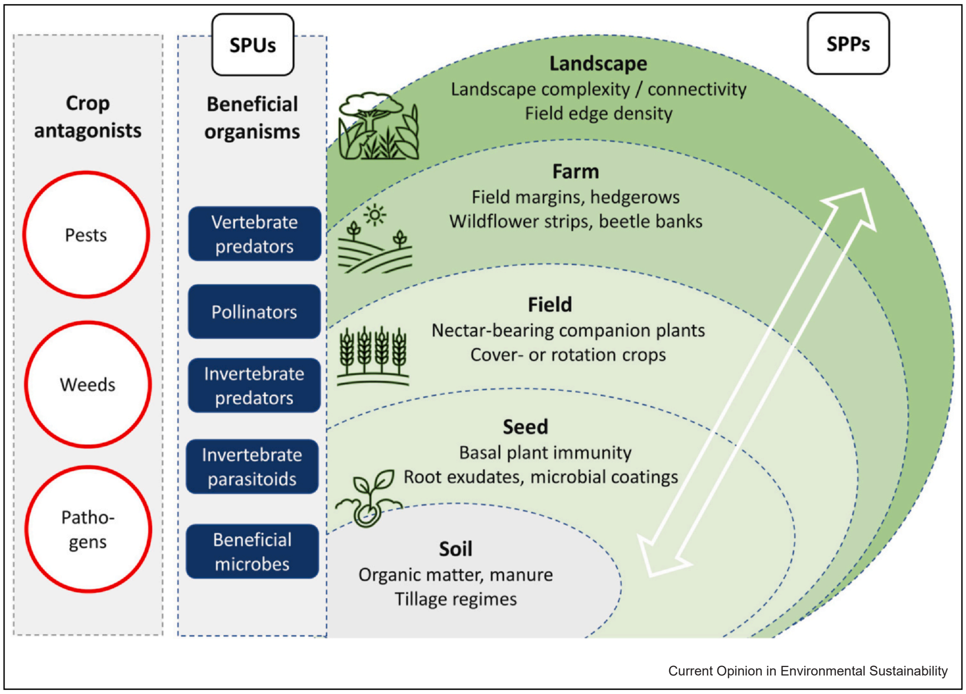
For complete overview of the section, please refer to the article collection, "Re-assessing the challenges of emerging pests and pathogens for sustainable development post-COVID"

https://doi.org/10.1016/j.cosust.2022.101208

Introduction

Since its earliest origins, farming has transformed innocuous herbivores, herbaceous plants, and commensals into debilitating pests, weeds, and pathogens [1]. Domestication and selective breeding have progressively narrowed crops' genetic base [2] and thus directly or indirectly lowered the defenses against various crop antagonists. Over the past century, breeding — often performed under a large pesticide umbrella — has attained noteworthy yield gains but also functionally disarmed plants and exacerbated input dependencies [3,4]. Furthermore, by relying upon genetically uniform, interconnected monocultures and chemical entrants, industrial agriculture has created favorable conditions for recurring pest outbreaks [5•,6]. A steady loss of ecological resilience in these farming systems increases their vulnerability to exotic species' establishment and raises the specter of 'invasional meltdown', that is, population-level feedbacks that continually deepen impacts and facilitate further invasions. These phenomena display

Figure 1



Schematic representation of how tritrophic defenses are influenced by patterns and processes at multiple organizational levels. A nonexhaustive listing is provided of SPPs (and the associated service-providing units (SPUs)) that make full use of ecological regulatory forces. Yet, in order to be effective, all measures need to be accompanied by a progressive pesticide phasedown and balanced fertilization. A simplified listing is given of crop antagonists and beneficial organisms, recognizing that individual species or guilds often act in more than one trophic level. Pests comprise herbivorous arthropods and vertebrates, while pathogens cover fungi, viruses, bacteria, nematodes, and protozoa.

remarkably strong parallels to the increased likelihood of zoonotic disease emergence such as SARS-CoV-2 following a decline in ecosystem integrity and environmental health [7•]. Hence, to safeguard human and natural capital, deliberate efforts are needed to protect biodiversity, bolster ecological regulation, and transition away from pesticide-intensive agri-food production.

As an alternative production paradigm, ecological intensification (EI) harnesses ecosystem services (ESs) to generate copious amounts of nutrient-dense farm produce in an environmentally sound and profitable fashion [8]. Meanwhile, EI helps to sustain yields under variable climatic conditions and over time. The above can also be achieved through sustainable intensification if its goals are properly calibrated [9]. EI thus contrasts with (most) current farming models, which are neither sustainable nor ecologically underpinned [9], and greatly relies on agroecology or conservation agriculture. Under EI schemes, one makes use of regulating forces (e.g. predation, resource availability, and competition) and employs systems approaches to tweak the delicate interplay among three trophic levels, that is, plants, herbivores, and natural enemies. By thus adjusting these forces along the food chain, one can bolster plant defenses and manage crop antagonists (i.e. pests, diseases, and weeds) preventatively. As such, the concept of 'tritrophic defense' [10] helps to marshal breeding, biodiversity conservation, soil science, microbiology, ecology, and crop-protection professionals in a joint quest for more sustainable farming solutions. It transcends disciplinary boundaries, facilitates holistic approaches, and musters collaborative action. In this Synthesis paper, we illustrate how these tritrophic defenses can be fortified at different organizational levels, that is, landscape, farm, field, and the individual seed or plant (Figure 1). At each level, we sketch the current state-of-the-art and (briefly) enumerate prospects for follow-up research or implementation.

Underlying concepts and principles

Across ecosystems, herbivores are regulated by bottom-up and top-down forces. In the former, primary producers (i.e. plants, algae, and many bacteria) mediate herbivore performance. The strength of these bottom-up forces is mediated by varietal resistance, fertilization, organic matter addition, or companion plants [11]. Meanwhile, top-down forces are provided by heterotrophic consumers. Communities of biological control agents (BCAs) that reside within individual fields, farms, or agro-landscapes hereby consistently lower pest numbers and protect crops from herbivore damage [12].

Table 1

Invertebrates as key intermediaries between tritrophic defenses and other regulating ESs in multicrop systems. As an illustrative example, a nonexhaustive listing is provided of how invertebrates respond to various attributes of a legume intercrop, thereby acting as SPUs for a broader range of ESs. For example, in cereal systems, a chickpea intercrop not only fixes atmospheric nitrogen, but also harbors aphid species that act as (alternative) host or prey items for omnivorous BCAs, for example, invertebrate predators such as ladybeetles or big-eyed bugs.

Attribute of legume intercrop	SPU	ESs					
		Climate mitigation	Pollination	Erosion control	Tritrophic defense	Water quality	Soil health and fertility
Nitrogen-fixing nodules	Symbiotic bacteria	+	+		+	+	++
Leaf pubescence	Predatory mites				+		
Repellent/attractant plant volatiles	Invertebrate predators and parasitoids				++		
Floral/EFN	Ants	+	+	+	++	+	++
	Spiders		+		++		+
	Nectar yeasts		+		+		
	Hoverflies		++		++		
	Managed/wild bees		++		+		
Alternative prey or hosts	Invertebrate predators and parasitoids				++		+

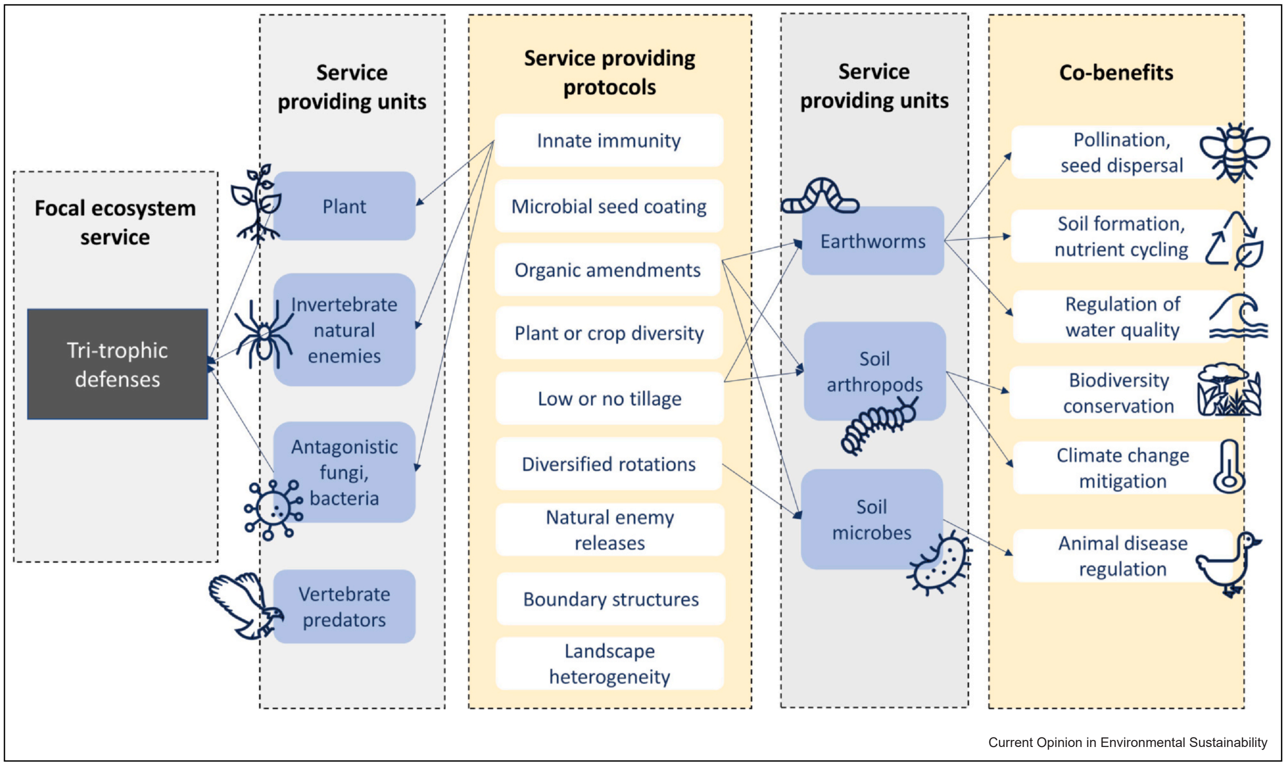
BCAs comprise a highly diverse set of organisms, including arthropod predators and parasitoids, microbial agents, and vertebrates such as insectivorous birds, amphibians, or bats ([13,14•]; Table 1). Their long-term impact on pest densities supersedes that of insecticides [15], while the latter undermine biodiversity-mediated processes [12]. Though the deployment of exotic BCAs is to be guided by scientific selection criteria and comprehensive benefit–risk analyses, the on-farm usage of endemic biota carries little or no risks. However, natural forces (e.g. weather and UV radiation) affect BCA effectiveness and unanticipated feedbacks can never be entirely averted. Multiple BCAs also contribute to (crop and noncrop) pollination or nutrient cycling, while common pollinators (e.g. domesticated and wild bees) act as vehicles for beneficial microorganisms. Similarly, many carabid beetles and ants not only consume pests but also engage in weed-seed granivory — often securing 80–90% seed removal. Through a suite of so-called service-providing protocols (SPPs) ([16••]; Figures 1 and 2), functional biodiversity — including BCAs, alternative hosts, or floral resources — can be put into practice to deliver natural pest, weed, and disease control. SPPs are hereby formulated based upon traits related to environmental filters (i.e. in-field management intensity and landscape simplification), trophic interactions, and the envisioned pest-control services. Bottom-up and top-down forces clearly do not act in isolation; SPPs such as plant diversification or manure application synchronously reinforce both [17]. Yet, as SPPs occasionally fail to translate into desirable yield outcomes (i.e. because of the complexities and uncertainties inherent to any natural system), the underlying science needs to be continually sharpened.

When manipulating this ecological interplay in order to bolster tritrophic defenses, SPPs can be laid out along three dimensions: time, space, and genes [18••]. Management schemes and diversification tactics can thus be chosen based upon a set of experimental decision criteria and theoretical constructs. Arthropod or microbial food webs provide a powerful lens to investigate the resulting outcomes, for example, in terms of pathogen suppression in soils or pest prevention in dynamic agro-landscapes [19–21•]. Meanwhile, decision-support tools have been developed to retain weeds with certain traits that facilitate ES delivery and minimize competition with the focal crop [22]. Along these lines, the Stress Gradient Hypothesis (SGH) provides a suitable analytical framework to deliver testable hypotheses with regard to ecological facilitation under variable (a-)biotic stress ([23••]; Figure 3). As such, the SGH can guide the design of climate-resilient, pest-suppressive systems founded upon (plant–plant, plant–microbe, and/or plant–BCA) ecological interactions. By influencing the magnitude of SGH response to biotic and abiotic stressors, SPPs such as microbial seed coatings or the integration of legumes into crop-rotation sequences may enhance tritrophic defenses [24,25••] but also raise the focal crop's ability to cope with depleted soils, heat waves, or recurrent droughts.

Landscape

At the highest level, the composition of agricultural landscapes affects crop antagonists and BCAs in an inconsistent manner [26]; landscape-level influences are modulated by farm-level management and organismal traits. Nevertheless, landscape heterogeneity and the relative cover of (semi-)natural habitats dictate yield

Figure 2



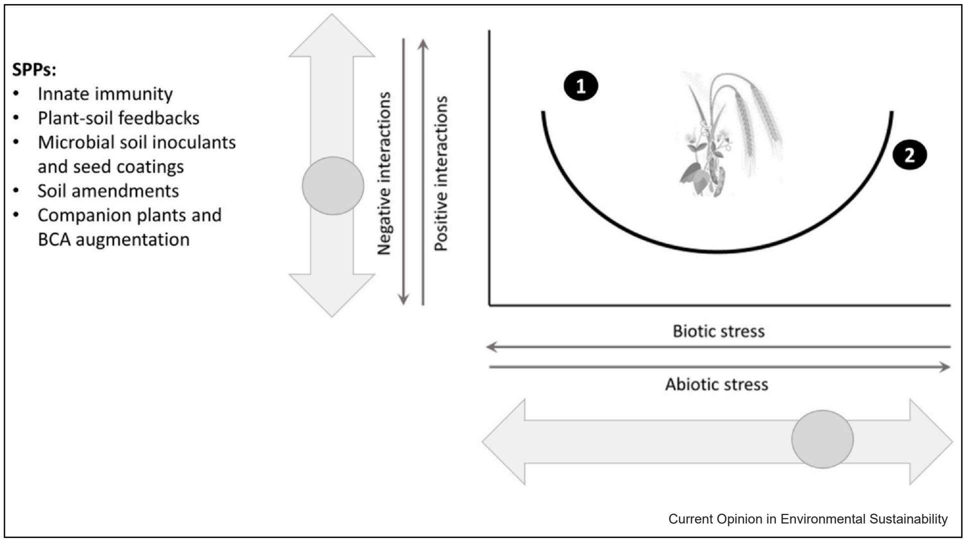
Pathways through which ecological processes can be modulated to synchronously fortify tritrophic defenses and generate a suite of societal cobenefits. As per [16••], multiple SPPs can be used to harness biodiversity for sustainable pest or disease management [20•,31]. Under each SPP, one or more ES providers harbor SPUs such as antagonistic fungi or parasitic wasps. As such, a grass barrier strip directly provides SPUs (e.g. predatory beetles that provide trophic regulation of pests), but also acts on its own as an SPU to improve erosion control. Similarly, a legume-cover crop can bolster insect-mediated defenses, fix atmospheric nitrogen, enhance water infiltration, and suppress weeds. For a subset of pathways, linkages are shown between an initial SPP, its SPUs, and the resulting focal ES. Thus, judiciously defined SPPs can deliver services far beyond tritrophic defense (and pest or disease prevention).

resilience, that is, stability of crop yield under environmental perturbation [27], which is partially ensured through climate-adapted BCAs that colonize fields from noncrop habitats [28•]. Conversely, landscape simplification brings about a net loss of predatory or parasitoid BCAs and weakens tritrophic defenses [12]. The same holds for crop pathosystems: agriculture-dominated settings lower pathogen spillover from wild hosts, but concurrently aid its proliferation and crop host adaptation [6]. These dynamics have implications for field-level management: in heterogeneous landscapes, plant-mediated disease control is optimized and resistance durability is extended [29], while insecticidal (*Bt*) crop clones retain their effectiveness against polyphagous pests even when only established in a fraction of fields [30]. In addition to conserving natural habitats in landscape mosaics, the above biodiversity benefits can be gained through smaller fields, diversified crops, and high field-edge density [31]. Last, though diverse landscape mosaics uphold natural pest control, tritrophic defenses can also be fortified by landscape-independent measures such as periodic releases of sterile insects or BCAs [32,33].

From farm to field

Given BCAs' vulnerability to disturbance (e.g. pesticide sprays, weed removal, and tillage), field- and farm-level action is crucial to mitigate or counteract these processes [34•]. At this level, SPPs such as field margins and hedgerows are particularly effective — providing shelter for BCAs in ephemeral agro-ecosystems and intensely managed landscapes [31]. Hedgerows further contain high levels of functional biodiversity and vital foraging resources (i.e. prey, nectar, and pollen) for BCAs such as spiders or hoverflies. Yet, while our understanding of hedgerows' contribution to natural pest control in temperate settings has advanced considerably, much remains to be learned about their importance in the tropics [35]. Similarly, wildflower strips or grass barriers (regularly termed 'beetle banks') can provide food and shelter to resident BCAs within a standing crop, with the former enhancing pest control by 16% across systems [36]. More

Figure 3



Current Opinion in Environmental Sustainability

Raising the odds for climate resilience and pest suppression in multicrop systems. As per [23••], the SGH serves as an appropriate analytical framework to interpret how (seed, field, farm, and landscape-scale) interventions can alleviate (biotic and abiotic) stressors and modulate the resulting plant-level responses. The odds of facilitation (i.e. positive plant-level interactions) can be raised by improving plants' ability to cope with biotic stress through different SPPs, that is, sowing of tolerant seeds, suitable companion plants, microbial seed coatings, or soil amendments (1), or by lowering plants' vulnerability to abiotic stress through companion plants that raise water holding capacity or improve soil aeration (2). Along these stress gradients, BCAs contribute to pest suppression, receive plant-based food rewards, and are variably guided by DAMPs or repellents. The above SPPs can be deployed along three dimensions, that is, time, space, and genes [18••]. Both empirical and observational assays can account for these stress gradients and diversification dimensions.

so, by integrating them into Bt crops, these ecological infrastructures can also avert resistance development and constrain pollen-mediated gene-flow [37].

Carbohydrates are a coveted commodity within many crops such as cereal grains. While honeydew (i.e. homopterans' sugar-rich excretion product) is arguably the dominant sugar source in many agro-ecosystems [38•], companion plants also provide floral and extrafloral nectar (EFN) for a broad suite of BCAs. EFNs are wielded by plants to reward BCAs for their pest-control services and thus shape the resistance phenotype of individual plants [3], though widespread among the angiosperms, EFNs are especially common in legumes. By thus integrating legumes as strip-, cover-, or rotation crops, tritrophic defenses can be bolstered ([11,34•; Table 1). In addition to securing biological pest control and nitrogen fixation, mixing legumes with crucifers suppresses soil pathogens [39]. Legumes however are not the only plants that provide benefits when incorporated in crop-diversification schemes. In fact, across crops, geographies, and farming contexts, more diverse crops consistently yield higher overall biodiversity and pest control [17,40–•], while an enhanced crop cover boosts yields and soil functioning [41]. Planting trees in arable cropping systems augments BCA density and reduces pest pressure by 25%, though its impact is modulated by management schemes [42]. Much is also to be gained by enhancing interspecific diversity: varietal mixtures regularly bolster pathogen resistance, yield, and yield stability [43]. A classic field study shows how fungicidal sprays prove unnecessary when disease-susceptible rice varieties are grown in mixtures.

Soils constitute the foundation of agri-food production systems, harbor approximately 25% of the world's biodiversity, and offer an important climate-change mitigation pathway. Yet, their contribution to crop protection is routinely overlooked. Science has only started to unravel how soil biota mediate biochemical, physical, or ecological facets of tritrophic defense [11,20,44•,45]. Soil-dwelling invertebrates, plants, and microorganisms however are crucial actors as they link above- or belowground realms, couple energy channels, and connect functional domains, for example, rhizo- and endosphere. Different SPPs can modulate the ecological forces that govern pathogen establishment, crops' resistance phenotype, or even weed-seed decay [46]. Soil-dwelling communities can be steered through microbial inoculants, organic amendments, or plants themselves [44•]. Plants' intimate two-way interaction with soil microbiota is captured within the 'plant–soil feedback' concept (i.e. a process through which plants alter soil properties and thus mediate seedling performance), which constitutes the basis of crop rotation or multicropping. Many of these processes are vulnerable to external disturbance: tillage-intensive systems experience higher herbivore numbers and lowered BCA diversity [47], while pesticide-coated seeds harm beneficial organisms such as earthworms and mycorrhizal fungi [20•,48]. On the other hand, SPPs such as the addition of organic matter and animal manure (when correctly applied) promote plant vigor, raise crop immunity, and strengthen top-down control by supporting resident BCA communities. While organic amendments and mulches have been well-researched, much remains to be learned about the impacts and mechanisms of conservation tillage and cover crops [49]. Across farm and field scales, the added cobenefits of many of the above SPPs and ecological infrastructures (Figure 2) routinely propel their diffusion [34•].

Individual seeds or plants

At the lowest level, plant seeds (or plants) are a key pillar of sustainable pest or disease management. A plant itself (or the plant–microbe holobiome) harbors both constitutive and inducible defenses against a broad suite of crop antagonists. These defenses are moldable and plastic, adapted to specific biophysical conditions, and attuned to the prevailing antagonists [50]. However, for many crops, domestication has directly selected against physical or chemical plant defenses, diluted their titers (e.g. by selecting for larger organs or under yield x defense trade-offs), or lowered their inducibility [1]. Plants' defense traits are often misinterpreted, with seed companies even deliberately breeding for nectarless varieties [51] and thus removing a critical energy source for foraging BCAs. To mitigate this, rewilding constitutes a lucrative new paradigm for plant breeding and entails the reintroduction of natural resistance (e.g. trichomes or nectaries) from a crop's wild relatives [3]. As such, one can diversify breeders' targets without compromising superior yield or abiotic stress tolerance. Classical breeding, marker-assisted selection, and genetic engineering all offer suitable avenues to acquire resistance or tolerance to high-profile antagonists. While the latter approach has attained successes with Bt insecticidal crops or virus-resistant papaya clones [30], transgenics are not a silver bullet, resistance development remains an issue, and societal acceptance is not guaranteed.

In addition, inducible defenses can be customized to aid BCA foraging and host location (e.g. through localized emission of volatile attractants) or to increase BCA fitness (e.g. through heightened nectar secretion) [3]. Considering how damage-associated molecular patterns (DAMPs, triggered through herbivore attack) mediate the plant immune response [25••], marker-assisted breeding can be advanced by pinpointing the relevant signaling systems and metabolic pathways. Defenses can equally be switched on or 'primed' through exogenous sprays of elicitors or by DAMP-releasing microbes, for example, in the rhizosphere [52]. A plant's priming status can further be inherited to its offspring over multiple generations. Another notable advantage of such defense priming is its applicability across farmer-preferred and locally adapted cultivars.

Engineering plants' microbial partners and the plant x microbe interplay carries a lot of promise, and molecular genetics serves as an invaluable compass in such endeavors. Plant roots and the rhizosphere are sites of complex interactions for which the (organismal) actors and chemical signals — even for the world's main food crops — are shrouded in mystery [20•]. Though some microbiota have been inserted into plant tissues, success rates remain low due to a deficient understanding of colonization mechanisms [60]. Nevertheless, coating seeds with plant-beneficial microbes — without necessarily pursuing endophytic establishment — can concurrently boost plant fitness, provide biologically derived nitrogen, and infer broad tolerance to (a-)biotic stressors, including weeds [53]. Brazilian research has elegantly shown how cereal seeds coated with the microsclerotia of *Metarhizium* spp. fungi can simultaneously favor biological control, promote plant growth, and lower pesticide use [54]. As such, manipulating plants' microbial companions can alleviate input dependencies, achieve ecologically sound crop protection, and reduce the carbon footprint of global agriculture [55].

Concluding remarks

The SARS-CoV-2 pandemic has spotlighted the causal linkages between unsustainable land use, biodiversity loss, and animal–human disease spillover. Pesticide-intensive crop protection contributes to these dynamics by weakening ESs, upsetting ecological equilibria, and lowering the immune response of disease-reservoir hosts. Yet, there are myriad other avenues to meet food-security needs without jeopardizing human or environmental health. In this Synthesis paper, we have spotlighted practicable solutions to avert pest-induced losses and resolve the social–environmental externalities of present-day crop protection. The 'tritrophic defense' concept helps to identify ways to mobilize biodiversity for crop protection across disciplinary boundaries, organizational levels, and spatiotemporal scales. Tritrophic defenses can be provided by multiple (plant, animal, and microbial) actors and science is steadily uncovering the processes that act as (fast, slow, large, and small) revolving cogs in its intricate clockwork. Service-providing protocols (as tailored to seeds, farmland soils, standing crops, or landscapes) are continually being designed, trialed, and refined. In some of the world's main cropping systems, best-bet solutions simply wait to be bundled and taken to scale. In principle, a reconstituted agro-ecological balance can generate win–win outcomes for farmers, the economy, and overall societal well-being [32,40•56••], although this could be thwarted through climate-induced regime shifts, species extinction, or food-web collapse [57]. Though this paper centers on its ecological aspects, the social dimensions of sustainable pest management cannot be overlooked [16••]. Many of the solutions are knowledge-intensive and require technical support, economic incentives that align benefits and costs, risk-mitigation schemes (e.g. insurance), and insights into stakeholder behavior. Farms are routinely operated as individual entities and it will require effort to attain critical mass at relevant spatial scales. This however can be supported through targeted investment, as in the new US Department of Agriculture Food System Transformation framework. Also, in degraded (agro-)ecosystems, longer time horizons may be needed for tritrophic defenses to build up to desirable levels and this may stifle adoption rates [58]. Adaptive management and concerted action at all levels of influence are thus crucial to tap the potential of tritrophic defenses. In order to generate impact at scale, disciplinary silos need to be opened up and connected to one another, reductionist visions abandoned, and systems' thinking embraced [59]. By harnessing the full power of biodiversity, low-carbon, climate-resilient, and health-giving farming systems can become a reality.

Author contributions

Kris Wyckhuys: Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Wei Zhang:** Conceptualization, Writing – original draft. **Elisabeth Simelton:** Visualization, Writing – review & editing. **Yelitza Colmenarez:** Writing – review & editing. **Bjorn Sander:** Writing – review & editing. **Yanhui Lu:** Writing – review & editing.

Declaration of Competing Interest

KAGW is the Chief Executive officer of Chrysalis Consulting, an enterprise that promotes nature-based solutions to crop protection.

Acknowledgements

This paper is dedicated to the living memory of Stephen D. Wratten, a tireless advocate of conservation biological control and biodiversity-friendly forms of pest management. The development of this work was enabled through funding from the CGIAR Research Program on Water, Land and Ecosystems (CRP-WLE). We wish to acknowledge the One-CGIAR Initiative "Mitigate+: research for low-emission food systems" for supporting the time and contribution of Wei Zhang.

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Review paper that elegantly describes how biodiversity–ecosystem function effects, and specifically plant–plant mutualisms, can be exploited to advance sustainable agriculture. The authors underline how a mechanistic understanding of (field- or farm-level) ecological interactions can inform breeding efforts and guide future diversification strategies.

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