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REVIEW ARTICLE

Ecological redesign of crop ecosystems for reliable crop protection. A review

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Abstract

To attain food security, we must minimize crop losses caused by weed growth, animal herbivores, and pathogens (or "pests"). Today, crop production depends heavily on the use of chemical pesticides (or "pesticides") to protect the crops. However, pesticides are phased out as they lose efficiency due to pest resistance, and few new pesticides are appearing on the market. In addition, policies and national action programs are implemented with the aim of reducing pesticide risks. We must redesign our cropping systems to successfully protect our crops against pests using fewer or no pesticides. In this review, I focus on the principles for redesigning the crop ecosystem. Ecological redesign aims to enhance ecological functions in order to regulate pest populations and diminish crop losses. Exploring ecology and ecosystems plays an important role in this transition. Guiding principles for redesigning the cropping system can be drawn from understanding its ecology. Ecosystem and community ecologists have identified four principal ecological characteristics that enhance the biotic regulation of ecological processes across ecosystems: (i) advanced ecosystem succession through introducing and conserving perennial crops and landscape habitats; (ii) reduced disturbance frequency and intensity; (iii) an increase in both managed and wild functional biological diversity, above and below ground; and (iv) matched spatial extent of land use (e.g., crop field size) with that of ecological processes (e.g., dispersal capacity of predators). I review the practices that link these ecosystem characteristics to crop protection in grain commodity cropping in both the crop field and the agricultural landscape. The review brings forth how basic understandings drawn from ecosystem and community ecology can guide agricultural research in the redesign of cropping systems, ensuring that technologies, breeding, innovation, and policy are adapted to and support the reshaped crop ecosystem.

Keywords Chemical pesticides · Weeds · Pathogens · Insect pests · Cropping system

Contents

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1 Introduction

To avoid yield loss, we must ensure robust and efficient crop protection. Despite ongoing crop protection efforts, one-third of the global crop yield is estimated to be lost to weeds, animal herbivores, and pathogens (Oerke 2006; Savary 2019). Crop protection promotes and maintains plant health and yields. Crop protection is likely to gain greater worldwide importance as pest outbreaks and abiotic plant stresses increase due to climate change, biodiversity decline, and ecosystem degradation (IPBES 2019; IPCC 2022).

Pesticides are currently a key tool used in protecting our dominant staple crops (Popp et al. 2013). The widespread introduction of pesticides in the mid-twentieth century enabled the growth of a few commodity crops in specialized large-scale cropping systems (Matson et al. 1997; Crossley et al. 2021; Schaak et al. 2023). However, soon after this introduction, serious trade-offs became apparent. Insecticides hit non-target predatory arthropods, which weakened the natural regulation of herbivore populations and caused outbreaks of primary and secondary insect pests, i.e., surges of previously harmless herbivores (Settle et al. 1996; Dutcher 2007). Pesticides have well-documented negative impacts on water quality (e.g., Mahai et al. 2021; Tröger et al. 2021; Stehle & Schulz 2015) and on human health (Kim et al. 2017). They alter abundances of non-target species and hence community composition (Rundlöf et al. 2015; Sanchez-Bayo & Wijkhuis; 2019; Ruuskanen et al. 2023), in turn impeding ecosystem processes such as crop pollination and nutrient cycling (e.g., Stanley et al. 2015; Edlinger et al. 2022; Ruuskanen et al. 2022).

Efforts have been made to mitigate these impacts through the stricter regulation of pesticide use, the withdrawal of registrations deemed too risky, and the implementation of national and transnational risk-reduction programs and policies (Barzmand & Dachbrodt-Saaydeh 2011; Wu et al 2018; Möhring et al. 2020). However, investments in crop protection research and innovation, as well as the implementation of supporting politics, policies, and market initiatives, have not kept pace with the decreased availability of pesticides and pressure to reduce pesticide use. This is evident in the continued use of several retracted pesticides facilitated by temporary emergency authorization within the European Union (EFSA 2022; PAN 2023). The need to find alternatives for crop protection is further underscored by the fact that older pesticides are losing efficacy and are being phased out, while fewer or no alternatives are meanwhile reaching the market (IRAC 2022; Riggi et al. 2016; Owen 2016; Duke 2012; Duke & Dayan 2018).

The challenges for crop protection have not gone unnoticed within the scientific literature. Pesticides are a cornerstone in commodity crop production. Therefore, growing our food with fewer, or no, pesticides calls for transformative change, combining new technologies and breeding (Tataridas et al. 2022; Burgues et al. 2020) with agronomic practices (e.g., Riemens et al. 2022; Maclaren et al. 2020), novel research and innovation approaches (Jacquet et al. 2022), education (Wyckhuys et al. 2019), supporting policies (Mack et al. 2023; Finger & Möhring 2024), and careful landscape management (Deguine et al. 2023).

Literature on the subject often emphasizes the need to develop substitutions for pesticides, such as biopesticides, crop breeding, and mechanical weeding. Yet it also acknowledges that these substitutes are insufficient to ensure reliable crop protection. A redesign of cropping systems is thus called for (Tittonell et al. 2014; van Bers et al. 2019). Pesticides were once essential for the introduction of specialized crop production. Globally, they have, most importantly, facilitated a radical redesign of crop ecosystems across agricultural landscapes. Lower, or no, dependence on pesticides will thus likewise require a redesign or "strong" ecological modernization of crop ecosystems to provide adequate crop protection using fewer pesticides (Jacquet et al. 2022), releasing us from our clear dependence on them (Conti et al. 2021; Clapp 2021).

In order to create conditions under which ecological functions, such as predation, can regulate pest populations at low abundances, we must redesign existing crop ecosystems (Bommarco et al. 2013). Ecology is a central basic science intrinsic to this effort (Deguine et al. 2023). Population, community, and landscape ecological knowledge are engaged and developed and combined with agronomic practices that are often applied to specific taxa separately (van Bruggen et al. 2016; Maclaren et al. 2020; Lundin et al. 2021; Riemens et al. 2022). There is scope to gain further ecological understanding at the ecosystem level to direct which kind of practices to implement, while also understanding their potential impacts on the crop ecosystem as a whole. Such ecological redesign principles could guide policy, research, and transformation pathways strategically.

Each crop ecosystem has characteristic ecological conditions. The biotic and abiotic factors that determine stocks and flows of energy and elements are subject to the exact same biophysical constraints and physical laws of any other ecosystem. Hence, ecosystem and community ecology principles can be employed and further developed to guide crop ecosystem redesign (Smith 2015).

In particular, ecosystem and community ecologists have identified four ecological characteristics that distinctly affect the biotic regulation of ecological processes across ecosystems. They offer guidance for ecosystem redesign that ensures preventative and resilient crop protection:

i. Advance succession by introducing and conserving perennial crops and landscape habitats
ii. Reduce the frequency and intensity of ecosystem disturbance
iii. Increase both managed and wild functional biological diversity above and below ground

Fig. 1 Illustrations of land management for sustainable crop protection: in the landscape (upper left) and in the crop field by managing plant diversity (upper right) and disturbance (lower left) (photos: Ola Lundin), in order to promote biological regulation of pests (lower right) (photo: Sandra Lindström).

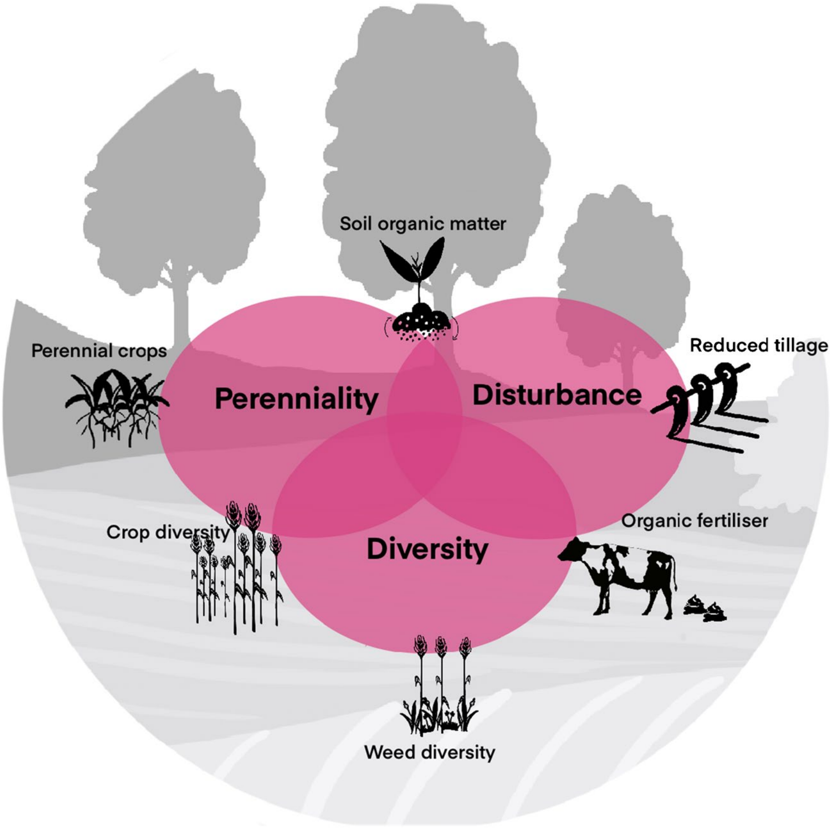

Fig. 2 Ecosystem characteristics to guide crop ecosystem redesign for sustainable crop protection. Crop ecosystem characteristics are identified to guide crop ecosystem redesign toward growing our food with less or no pesticides: perenniality, disturbance, and diversity in the crop fields situated in a landscape with annual and perennial habitat configuration and composition that spatially matches the requirements of beneficial organisms and ecosystem services. Farming practice types are exemplified as having a particular effect on certain ecosystem characteristics: perennial crops, crop and weed diversity, organic fertilizer, and reduced tillage. (Figure created by Janina Heinen).

iv. Match spatial scales of land use and ecological processes

These characteristics affect two main factors governing pest management: the regulation and suppression of pests and the enhancement of plant health, i.e., the plant's capacity to grow and withstand abiotic and biotic stresses, herbivory, and competition. Here, I focus on the former, noting that many of the actions taken to build preventative crop protection are likely to enhance also plant resilience.

In this review, crop ecosystem characteristics and key ecological processes are described in relation to current understandings of ecosystem and community ecology, drawing most of its examples from grain cropping. An overview is then provided of practices within the crop field and landscape that affect the four ecosystem characteristics (Fig. 1 and 2). Finally, it iterates the necessity to consider farm economics, develop technologies, and redefine breeding targets that are adapted to the reshaped crop ecosystem.

2 Characteristics of crop ecosystems

2.1 Succession and disturbance

In ecological terms, industrial commodity grain ecosystems are nutrient-rich ecosystems that are kept in an early successional stage through repeated disturbance and annual cropping. They have a low diversity of crops and associated organisms across large spatial extents.

Growing annual crops that experience a high level of disturbance across large swaths of land (Gaba et al. 2014) keeps the ecosystem in perpetual early secondary succession (Radosevich et al. 2007). Secondary succession describes the evolution of a community of organisms over time after a major disturbance, such as a flood, fire, landslide, or the plowing of an arable field. It drastically affects an area but does not render it entirely lifeless. This distinguishes secondary from primary succession communities, which develop from a lifeless area.

Repeatedly disturbing and resetting agricultural ecosystem succession limits biodiversity build-up, which would usually regulate pests. It instead promotes disturbance-tolerant invasive plants (Buhler 1995; Smith 2015; Maclaren et al. 2020), plant pathogens (McDonald & Linde 2002), and insect herbivores (Wissinger 1997). Maintaining ecosystems at an early stage of succession reduces the biological regulation of resource acquisition and retention (Odum 1969; Gorham 1979). Communities are structured less by biotic processes such as competition and consumption and more by stochastic processes, which require human intervention and resource inputs to pre-empt or subdue outbreaks in order to stabilize primary production (Wissinger 1997; Rist et al. 2014; Smith and Mortensen 2017). In contrast, establishing perennial growth forms improves resource acquisition and retention efficiencies, which are typical characteristics of mid-successional ecosystems (Crews 2018). Introducing perennial crops enhances pools of soil organic matter, enriches organismal communities, and stabilizes ecosystem functions, including those related to crop protection (Duchene et al. 2019; Martin et al. 2020; Heinen et al. 2023).

2.2 Biodiversity

Commodity grain cropping is usually characterized by a low diversity of crops and their associated organisms. The crop is a founding organism of the agricultural ecosystem, similar to how trees are the pillar of the forested ecosystem (Ellison et al. 2005). Despite low crop diversity, the crop is always accompanied by a wealth of organisms above and below ground, many of which participate in and drive functions linked to the primary production of the crop. This diverse community of organisms includes additional primary producers beyond the crop plant, such as weeds and non-crop plants; thousands of consumer species of herbivores, predators, decomposers, and pollinators (Tsiafouli et al. 2015; Dainese et al. 2019); and an immense and multifunctional microbiome (Bender et al. 2016; Trivedi et al. 2020, Banerjee and van der Heijden 2023). The community of organisms assembled in a crop field is drawn from a regional species pool and shaped by a hierarchical set of environmental, landscape, crop management, and biotic filters (Smith & Mortensen 2017).

Together, the organisms drive resource stocks and flows of energy, carbon, nutrients, and water through resource channels that exist both above and below ground (Wardle et al. 2004; Wolkovich et al. 2014). The organisms and processes are affected by the materials and species we put into and remove from the ecosystem (Riggi & Bommarco 2019; Zelnik et al. 2022). They are affected by when and how we till, sow, fertilize, protect, and harvest the crop. Farming operations can build or disrupt already formed macro- and micro-assemblages of organisms. Furthermore, how they are managed affects how the primary production of the crop and its associated ecosystem processes respond to variations in climatic conditions (e.g., Bowles et al. 2020; Costa et al. 2024). Ecosystem functions that are particularly relevant for crop protection outcomes include herbivory, predation, disease, antagonism, and competition, which all affect the primary production we seek to harvest.

Fig. 3 Managing spatial extent (e.g., crop field size) and crop or habitat diversity to match resource requirements of beneficial organisms that contribute to crop protection (e.g., predators to herbivorous pests). Mobile service-providing organisms, such as predatory arthropods, need continuous access to resources and habitats within their movement range for their survival and reproduction. This is in many landscapes decided by us humans, who crop and manage farmland. Purple indicates the probability of survival and reproduction for a predator in two differently cropped landscapes. Colored fields in the landscape indicate different management practices in the crop fields such as crop species, tillage, and fertilization. (Figure created by Janina Heinen).

2.2.1 Relationships between biodiversity and ecosystem functioning

There has been much research into how ecosystem functions are affected by the richness and composition of organismal communities. Ecological understanding of the links between biodiversity and ecosystem functioning holds the potential to inform the redesign of crop ecosystems (Cardinale et al. 2012; Isbell et al. 2017). This research clearly demonstrates that diversity among terrestrial spatially mixed plant communities enhances the regulation of arthropod herbivory (Barnes et al. 2020; Wan et al. 2020) and biomass production (Tilman et al. 2006; Cardinale et al. 2012; Reich et al. 2012). This is due to the effects of species selection and niche complementarity. This relationship is thought to also apply to agricultural ecosystems (Isbell et al. 2017).

Recent research partly confirms this hypothesis. Based on data amassed from multiple agricultural long-term trials, we find that gradually increasing especially crop functional diversity increases cereal yield benefits. This is achieved by rotating crops within a field over time (Smith et al. 2023). There is evidence that increasing weed diversity, e.g., through diverse cropping (Hofmeijer et al. 2021), reduces yield losses (Adeux et al. 2019; Liebman et al. 2021), enhances fungal diversity (Triolet et al. 2022), and potentially enhances weed seed predation by insects.

Species-rich arthropod predator communities with evenly distributed abundances among species are often found to be more efficient in suppressing insect crop herbivores (Crowder et al. 2010; Dainese et al. 2019). However, the strength of this relationship depends on the species and the crop involved, and on which aspect of diversity is measured. Diversity, in terms of species richness, is often a poorer predictor of predation compared with the diversity and distribution of functional groups of predators (Gagic et al. 2015; Feit et al. 2019). Although increasing arthropod predator species or functional diversity more often suppresses crop herbivores, there can be weak or negative effects on predation, resulting from increased intraguild predation and interference among predators as species are added to the community (Letourneau et al. 2009; Jonsson et al. 2018).

Recent research also shows that soil microbial community composition can significantly impact plant health, allowing the prospect of managing or engineering disease-suppressive soils (Mendes et al. 2011; Schlatter et al. 2017; Trivedi et al. 2017). The relationship between microbial diversity and the ability to suppress plant pathogens is not yet fully researched (but see Van Elsas et al. 2012). Researchers are currently identifying the key taxa and genes responsible for disease suppression (Expósito et al. 2018; Mendes et al. 2011; Trivedi et al. 2017). However, increasing a soil's organic matter can enhance its general suppressiveness (Expósito et al. 2017).

Enhancing biodiversity can significantly strengthen crop protection. However, the question of which aspect of diversity to promote, e.g., species or functional diversity, and whether to promote specific organisms are matters that need to be assessed for specific functions, agronomic, and environmental contexts.

2.3 Matching spatial scales of land use with ecological processes

In nature, ecological and physical processes occur over specific spatial scales. Sustained crop production, relying on the biotic pest regulation provided by biodiversity, needs crops and other habitats to be situated within the landscape near the vital resources required for a large number of service-providing organisms. Mobile predatory arthropods exemplify and justify the importance of such spatial and temporal matching (Jonsson et al. 2014). Many predator species depend on continuous access in their life cycle to spatially separated resources and habitats for their survival and reproduction (Rand et al. 2006; Schellhorn et al. 2015). Importantly, all these necessary resources must be within a reachable distance given each species' mobility (Schellhorn et al 2014) (Fig. 3).

In disturbed landscapes with few annual crop species grown in large fields with little or no remnant perennial habitats, e.g., grasslands, hedges, and wood lots, mobile service-providing organisms have difficulty surviving as resources are too far out of reach (Tscharntke et al. 2007).

Arthropod pests, in contrast, often thrive due to their greater dispersal capacity and shorter generation time compared with their predators. This makes them better suited to exploit the rich crop resources and escape predation in the disturbed early succession ecosystems that we have created (Settle et al. 1996; Wissinger et al. 1997). Redesigned landscapes need to satisfy the demands for multiple beneficial organisms and supply adequate resources for a large number of species, all with diverse resource requirements and dispersal capacities (Vasseur et al. 2013).

3 Land-use practices for ecological redesign

Practices and key experiences for ecological redesign and modernized crop protection and production can be drawn from farming practices that employ restricted or actively minimized pesticide use, such as organic and agroecological farming (Mäder et al. 2002; Wezel et al. 2014; van Bruggen et al. 2016). These practices are increasingly evidenced and implemented widely enough to inspire innovation and create a testing ground for adoption. However, more research and more strategically informed investments in innovation are needed so that this can be more widely implemented within mainstream, non-certified farming (in which certain inputs are allowed).

A common denominator among these practices is the improved use and strength of natural processes in the ecosystem in order to reduce dependency on external resource inputs with upheld crop productivity. The aim is to achieve autonomy in production based on efficient and circular resource use via geographic integration of multiple forms of production. A pervading component is adopting practices that enhance biodiversity to strengthen ecosystem functions such as biotic pest regulation and nutrient cycling (Bommarco et al. 2013).

The following section presents practices and research findings that exemplify how the crop ecosystem characteristics of diversification, perenniality, reduced disturbance, and spatial matching can be managed within the crop field and the cropped landscape.

3.1 Redesigning the crop field

The crop field can be redesigned in terms of which crops, cultivars, and support plantings are grown in it. Crop species and cultivars can be grown together within a field in a specified season through inter-, strip-, or patch-cropping. We can plant crops that are either annual or perennial. We decide the duration of the season during which the soil is covered with a crop and the number and sequence of crops that are rotated or relay cropped over time. In addition, the ecology of the field is greatly influenced by how and when we sow, as well as when we till, fertilize, and harvest and what we do with the crop residues. This management regime affects the diversity, disturbance, and successional stage in the crop field, holding great implications for crop protection. The amount of literature on the subject is copious and growing. I will now introduce the main sets of practices, pointing the reader to literature on the subject that they may delve further into.

3.1.1 Crop diversity

As mentioned, the crop is a foundational organism for the cropping ecosystem. A straightforward way to increase biodiversity in the ecosystem is simply to grow more crop species or functionally different crops, such as grasses, forbs, broadleaf, and nitrogen-fixing crops. They can be combined in many ways either sequentially over time, e.g., in a rotation, or in the same field and season associating them in different spatial configurations, such as inter-, relay-, strip-, or patch-cropping. This can have substantial consequences for crop protection.

Diverse crop rotations often prevent pest population build-up by breaking the pest life cycle. This is due to resource competition and interference and the fact that the pests' resources are removed over time (Malezieux et al. 2009; Bennett et al. 2012). The exact mechanisms for observed yield gains in diverse rotation are poorly known, but the creation of disease-suppressive soils could be an important contributing factor (Santhanam et al. 2015; Peralta et al. 2018). By using diverse rotations, attacks by pests that are difficult or impossible to manage curatively can be avoided. These pests are numerous and include several weeds (Liebman & Dyck 1993), such as black grass in winter wheat (Moss 2017), pathogens such as club root disease in oilseed rape (Derbyshire & Denton-Giles 2016), and root rot in peas (Kälin et al. 2022). They also include animals such as cysts and root-knot nematodes in potatoes (Jones et al. 2013).

Long-term agricultural plot experiments have shown that rotations with functionally different crops benefit yields, which, for some crops, increase continually over time (Smith et al. 2023). The gains occur due to a combination of enhanced soil fertility, nutrients, and water use efficiency (MacLaren et al. 2022), resistance to adverse climatic conditions (Bowles et al. 2020; Marini et al. 2020; Costa et al. 2024), and improved pest regulation (Bennett et al. 2012). The latter is, however, likely to be underestimated in agricultural long-term trials as pesticides in many of these experiments are applied equally across treatments. However, trials in which herbicide applications have been optimized in each rotational treatment demonstrate a reduced need for chemical weed control in diverse rotations (Davis et al. 2012; Weisberger et al. 2019). More long-term experiments with a setup such as these, in which crop protection measures are optimized and recorded treatment-by-treatment, would be needed to accurately evaluate the contributions to pest regulation from crop diversification and other farming practices.

We can reduce pest incidence and yield losses to weeds (Petit et al. 2018; Vrignon-Brenas et al. 2018; Gu et al. 2021) and disease (Stomph et al. 2020) by growing mixtures of crop species in intercrops or with service crops in the form of cover crops, green manure, and relay crops. There are concerns that service crops could encourage soil-borne pathogens, but there is as yet little evidence that this would be the case despite widespread implementation in some regions (Šišić et al. 2018). Combinations of intercropped species are also effective for insect control (Hooks & Fereres 2006; Letourneau et al. 2011; Iverson et al. 2014), e.g., as part of "push-pull" pest control techniques (Cook et al. 2007). Varietal mixtures reduce losses to mainly aerial pathogens in cereals and rice (Borg et al. 2018; Reiss and Drinkwater 2018; Hariri et al. 2001; Kristoffersen et al. 2020; Zhu 2000) and can affect insect pests (Tooker and Frank 2012). They do, however, have limited effects on weed control (Lazzaro et al. 2018).

3.1.2 Perennial crops

Perennial cropping, such as with perennial legume-grass mixes for feed and pasture (ley), moves the ecosystem into a later stage of succession. It reduces soil erosion and has well-documented positive effects on soil structure and fertility, nutrient cycling, soil water retention, and also pest regulation (Lemaire et al. 2015; Martin et al. 2020). Perennial crops can outcompete weeds that thrive in annual crops (Meiss et al. 2010a; Schuster et al. 2020). Interestingly, weeds that are found alongside perennial crops (and that are not problematic in annual crops) contribute to a species-rich weed community that is less competitive with the crop (Meiss et al. 2010b).

Perennial crops have a great capacity to increase soil organic matter (Scotti et al. 2015; Thorup-Kristensen et al. 2020; Tang et al. 2024), which increases predator communities that prey on crop herbivores (Tsiafouli et al. 2015; Garratt et al. 2018; Heinen et al. 2024) and increases the soil's disease-suppressive capacity (cf. Expósito et al. 2017). Introducing perenniality and increasing the soil's organic matter are promising options for strengthened ecological functionality, including pest regulation both above and below ground.

3.1.3 Tillage and fertilization

Cropping will inevitably disturb the ecosystem through sowing, managing pests, and harvesting the crop (Gaba et al. 2014; Tooker et al. 2020). Tilling to control weeds and prepare the seed bed significantly disturbs the ecosystem (Lal et al. 2007). Reduced tillage or direct sowing diminishes mechanical disturbance, increases organic matter near the soil surface, and mitigates soil erosion (Stinner & House 1990). Predatory arthropods and insect pest suppression can benefit from conservation tillage (Tamburini et al. 2016). However, some problematic weeds, especially those with a competitive life history strategy (sensu Grime 1977), are less well regulated than with conversion tillage (Gaba et al. 2017; Wittwer & van der Heijden 2020). Volunteer crops (Cordeau 2022) and slugs (Douglas & Tooker 2012) can cause problems and increase dependence on pesticides. A recent global meta-analysis, however, showed no difference in pest incidence between deep conversion and conservation tillage, and foliar pests were somewhat less prevalent in the latter (Rowen et al. 2020). To fully reap the benefits of reduced tillage, more non-chemical options to suppress weeds, such as with mechanical means, would need to be developed (e.g., Bergkvist et al. 2017; Grosse et al. 2021).

Organic fertilizers increase the soil diversity of several taxa by providing resources to the soil micro- and macrobiota (Hines et al. 2006; Birkhofer et al. 2008; Viketoft et al. 2021) and provide food resources to support populations of generalist natural enemies and seed predators above ground (Birkhofer et al. 2008; Riggi and Bommarco 2019). In comparison, inorganic mineral fertilizers feed nutrients more directly to the plant, increasing the plant's nitrogen content and the food quality for the herbivores enhancing their growth and reproduction (Herencia et al. 2007). Organic fertilization, especially with manure, can also boost top-down predator suppression of insect pests (Birkhofer et al. 2008; Riggi and Bommarco 2019; Aguilera et al. 2021; Heinen et al. 2024). Increasing soil's carbon content is beneficial for nutrient cycling and use efficiency and is also a key practice for enhancing crop protection. Combining such management with microbiome inoculation and engineering to build specific and general disease-suppressive soils is a promising development for crop protection (Schlatter et al. 2017; Hartman et al. 2018; Banerjee et al. 2019; Trivedi et al. 2022).

Diversifying farming practices builds associated biodiversity, strengthening multiple ecological functions in the cropping ecosystem, including pest regulation (Tamburini et al. 2020a, b; Dainese et al. 2019). The win-win outcomes from diversification between crop yield and other ecosystem processes that support primary production will become apparent (Tamburini et al. 2020a, b). The concept of "biodiversity farming" can be used to maintain yields under suppressed resource inputs and is aligned with the key aims for future agriculture, such as climate-neutral "carbon farming" and securing food availability (Lehner & Rosenberg 2021).

3.2 Redesigning the cropped landscape

Organisms move, and materials are exchanged among habitats in the landscape (Gounand et al. 2018). Pests disperse widely, and ecological functions that support crop production, such as pest regulation and pollination, are provided by mobile organisms whose occurrence and population sizes are commonly regulated at spatial scales well beyond that of the crop field (Kremen et al. 2007; Moslonka-Lefebvre et al. 2011; Jonsson et al. 2014; Bourgeois et al. 2020). The processes and outcomes we observe in a crop field are thus a combined result of the ecological conditions within that field and of the composition and configuration of the surrounding landscape (Fahrig 2011). Successful pest management requires a landscape perspective and coordinated land use that reaches beyond the individual farm (Kremen and Merenlender 2018).

3.2.1 Landscape composition

A landscape perspective related to pest management can be used for arthropods in conservation biological control, i.e., encouraging naturally resident predators and parasitoids that prey on or parasitize herbivorous arthropods (Tscharntke et al. 2007; Rusch et al. 2017; Landis 2017), pathogen epidemiology (Plantegenest et al. 2007; Meentemeyer et al. 2012), and weed dispersal (Bourgeois et al. 2020).

Perenniality within the landscape plays a key role. If the landscape is covered with stable and diverse perennial crops (e.g., ley) and non-crop habitats, there is more likely to be an abundance and diversity of predators and parasitoids to insect pests (Cronin and Reeve 2005; Chaplin-Kramer et al. 2011; but see Karp et al. 2018) as well as pest regulation (Rusch et al. 2013; 2016; Veres et al. 2013). Grasslands, forests, hedgerows, field margins, road verges, and perennial crops provide continuous access to alternative food and refuge for predators and parasitoids in cropped landscapes dominated by intensively and frequently disturbed crop fields (Vasseur et al. 2013; Schellhorn et al. 2015). In contrast, specialized pests prefer large-scale and continuous growth of their host crop, although they might be temporarily diluted (Delaune et al. 2021). Pests often have higher dispersal and growth capacity and are adapted to exploit ephemeral nutrient-rich plant resources in early succession ecosystems. Their predators are instead more sensitive to disturbance, have lower growth rates and longer generation times, and therefore need local and continuously available resources (Schellhorn et al. 2015; Tooker et al. 2020).

Creation of pest-suppressive landscapes is based on the establishment (Landis et al. 2000; Jonsson et al. 2015; Gurr et al. 2017; Albrecht et al. 2020), preservation, and restoration (Chaplin-Kramer et al. 2011; Gardiner et al. 2018) of perennial (preferably native) (Parry et al. 2015) vegetation within dispersal range to the crop for predators and parasitoids (Rand et al. 2006). However, perennial habitats can also harbor alternative hosts for pathogens, insect herbivores, and other pests. Exotic pests have been known to favor perennial non-crop habitats, probably due to access to added resources (beyond the crop) and the lack of natural enemies adapted to prey on them (Tamburini et al. 2020a, b). The devastating spotted wing drosophila, *Drosophila suzukii* Matsumura, is such an example in Europe.

Future research must seek to understand how perennial habitat quality affects pest, predator, and herbivore communities. This has only recently been gleaned from comparisons between forms of perennial habitat established with the intent to support biodiversity and the functioning of the ecosystem (Woodcock et al. 2008; Boetzl et al. 2019; 2020). Population ecological research is needed on the resource type and continuity needed for arthropods to complete their life cycle and the mortality factors that drive their population dynamics (Schellhorn et al. 2015). This information can also guide the implementation of plantings and off-settings, such as flower strips and hedge rows, targeted to provide vital resources to various organisms (Jonsson et al. 2010; Tschumi et al. 2015).

3.2.2 Landscape configuration

Not only the proportion but also the size, shape, and spatial arrangement, or configuration, of land use types can affect pest regulation (Fahrig 2011; Sirami et al. 2019). We can measure the configuration of agricultural landscapes in several ways, depending on the habitat's size distribution (or grain size), shape complexity, and connectivity. The crop field's size and the amount of perennial edge habitat are two commonly used metrics for agricultural landscapes (Martin et al. 2019; Estrada-Carmona et al 2022). Different taxa respond differently to landscape configuration. For predatory arthropods, carabids, spiders, and coccinellids appear to be less sensitive, while parasitoids, syrphid flies, nabids, chrysomelids, and predatory wasps benefit from fine-grained landscapes. This could be due to their generally poorer dispersal capacity (reviewed in Haan et al. 2020). Configuration was less consequential for the predator community compared with the proportion of perennial habitat in South Korean agricultural landscapes (Martin et al. 2016). Some predators were affected by the landscape configuration, depending on the amount of non-crop perennial habitat and predator traits such as dispersal mode, overwintering, and food requirements (Martin et al. 2019). When devising pest-suppressive landscapes, we would need to consider both landscape composition and configuration (Haan et al. 2020).

The regional pool of species available is affected by regional land use, where a diversity of land uses in the greater landscape supports a richer regional species pool by providing habitat and resources for more species to flourish

(Gering et al. 2003; Tscharntke et al. 2007; Clough et al. 2007). Theory hypothesizes that resilient, stable baseline pest regulation is obtained through a diversity of crops and non-crop habitats spread out through the landscape, which provide contrasting resources asynchronously over time and support a diverse pool of species (Peterson et al. 1998; Tscharnkte et al. 2007).

3.2.3 Landscape effects of farming practices

The crop field is a key habitat for a wealth of organisms, and as we have seen, field management greatly shapes the local community. However, we know less about how farming practices affect associated biodiversity and pest regulation when implemented across large geographic areas. Organic farming, crop diversity, the proportion of perennial ley, and their subsequent effects on the landscape have been examined. Weeds, predatory and herbivorous arthropods, and weed seed and prey predation rates have all been explored.

Employing organic farming in the landscape increases weed diversity and can positively affect predatory insects and predation rates (Inclán et al. 2015; Muneret et al. 2018). However, the effects are poorly documented, and there are also studies that show only marginal effects (Petit et al. 2020). Increased crop diversity within the landscape can affect resource availability and continuity for mobile organisms such as predatory arthropods (Vasseur et al. 2013; Schellhorn et al. 2015). It can also directly enhance predatory ground beetle diversity (Fahrig 2015; Palmu et al. 2014; Carbonne et al. 2022) or when combined with non-crop pastures and forests (Aguilera et al. 2020). The abundance of certain predator species can increase with crop diversity (Bertrand et al. 2016) or in the presence of specific crops within the landscape (Marrec et al. 2017). Others have found no such effects on predatory arthropods (Bosem Baillod et al. 2017). The results are difficult to compare, as analytical approaches and measures to describe the predator and crop communities vary widely. Overall, the taxa of predatory arthropods examined so far seem not to respond strongly to crop diversity within the landscape. However, the biological control of aphids has been noted to increase with landscape crop diversity (Redlich et al. 2018; Scheiner and Martin 2020). Given the strong effects of local field management on biodiversity, it is plausible that more effects on the landscape will become evident if diverse, perennial, and less disturbed cropping is implemented over large areas. This is even more likely if combined with high-quality, non-crop perennial habitat in the landscape.

A key action that has been taken to reduce pesticide use has been to increase the efficiency of crop protection measures in farming. In some places, better-targeted and less toxic chemical pesticides are applied at lower doses and with improved machinery and precision. Treatment decisions based on pest monitoring, forecasting, and economic thresholds are promoted (e.g., Damos 2015). Added to this is the training and licensing of operators, labeling, and pesticide resistance management. Chemical pesticides have, to some extent, been substituted with biological control agents and mechanical weeding. Pesticide use, however, remains high and is even increasing in some regions within the EU (Lapierre et al. 2019; Hossard et al. 2017; European Environmental Agency 2023), and the US (Douglas and Tooker 2015; Douglas et al. 2020), with uncertain risk implications (European Court of Auditors 2020).

Pesticide use efficiency gains and substitutions may have dampened an otherwise even greater increase in pesticide use, but these incremental and substitutive actions have not released us from the apparently locked-in dependence on pesticides for food production (Vanloqueren & Baret 2009; Conti et al. 2021; Clapp 2021). Substitutions for pesticides, e.g., with mechanical means, biological control agents, breeding, and precision farming, will be key for a successful transition toward pesticide-free agriculture. To release us from the pesticide lock-in, future crop protection must be based on preventative rather than curative measures. This requires a shift from incremental changes of existing cropping formats to completely redesigning the cropping ecosystem, underpinned by new and adapted trajectories of innovation (Tittonell 2014; van Bers et al. 2019). The ecology of the cropping system needs to be redesigned.

4 Technologies, breeding, economics, and innovation

Adapted technologies and breeding will be crucial for developing and implementing ecologically redesigned cropping. Farmers will need access to suitable technologies, inputs, and genetic material to sustain and raise yields. For this, crop plants must be bred for the new ecological condition. This will involve using modern tools but setting new breeding targets for an ecologically redesigned crop plant (Rubiales 2023). Furthermore, ecologically redesigned crop production will still require curative actions and management interventions against pests. Promising curative tools to sustain yields include a combination of technologies that substitute chemical pesticides, such as biological control agents, mechanical techniques, and the precise and directed use of available chemical pesticides, inducing minimal exposure and risk.

Productivity and farm economics must be sustained in redesigned crop ecosystems. This is especially important during the transition. There are promising indications that, for instance, crop diversification builds productivity over time (Smith et al. 2023). The final potential benefits are, as yet, unknown and appear promising. However, it is clear that building the biotic regulation of yield-supporting processes takes time.risk.

In any case, it has to be conceded that without pesticides, some crops will likely suffer significant yield reductions in certain regions due to chronic or recurring pest infestations, at least when transitioning away from pesticide dependency (INRA 2010). For instance, it is currently not viable to grow spring oilseed rape without insecticides in south-central Sweden due to recurring insect herbivory both at emergence and the flowering stage (Lundin et al. 2020). It remains to be understood if this is caused by the weak natural regulation of the pest and whether yields would return to economically viable levels with ecologically redesigned cropping. However, it is encouraging that we, already under currently implemented policies and market rules (which continue to promote specialization and enlargement and in turn increased dependence on pesticides), find that adopting agroecological farming practices such as crop diversification can strengthen farm economic performance (van der Ploeg et al. 2019; Nilsson et al. 2022; Sánchez et al. 2022).

The ecological redesign is knowledge-intensive. It requires long-term research commitments and open sharing of co-developed knowledge by practitioners and scientists (Duru et al. 2015). Researchers can take risks to undertake challenges, such as cropping with less or no chemical pesticides (e.g., Ditzler et al. 2021; Cordeau 2022; ZALF 2023). This kind of visionary system-oriented research and demonstration is needed to catalyze the shift needed for the radical innovation of mainstream agriculture (Jacquet et al. 2022). This is particularly warranted for large-scale staple cropping systems (Mortensen and Smith 2020). Basic science plays an important role in this effort. Agricultural sciences draw from all fields of basic science. Among them, ecology is emerging as particularly relevant for the modernization of cropping. An improved understanding of ecological principles and the biophysical processes involved in agricultural ecosystems and integrating this knowledge into agronomy science would strengthen the theoretical and strategic basis for crop ecosystem redesign.

5 Conclusions

The ecological redesign of crop ecosystems aims to reduce pesticide reliance by strengthening the overall biotic regulation of crop pests and, in turn, preventing pest outbreaks. This overview shows that there is further scope to engage knowledge stemming from ecosystem and community ecology, to devise guiding principles for redesign at the ecosystem level. A release from lock-in and a transition of agriculture to low, or no, dependence on pesticides builds on the adoption of a diverse set of locally adapted practices that enhance local biodiversity. This does not ignore the fact that general guiding principles exist, which predictably define ecological processes across ecosystems. In this review, four such principles are suggested based on our understanding of ecosystems and community ecology in relation to perenniality, disturbance, biodiversity, and spatially matched land use. Principal ecosystem characteristics are identified that confer autonomy in production, reduce reliance on costly external inputs, and strategically inform and guide policies related to agriculture, biodiversity, and research.

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