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Balancing Disturbance and Conservation in Agroecosystems to Improve Biological Control

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Abstract

Disturbances associated with agricultural intensification reduce our ability to achieve sustainable crop production. These disturbances stem from crop-management tactics and can leave crop fields more vulnerable to insect outbreaks, in part because natural-enemy communities often tend to be more susceptible to disturbance than herbivorous pests. Recent research has explored practices that conserve natural-enemy communities and reduce pest outbreaks, revealing that different components of agroecosystems can influence natural-enemy populations. In this review, we consider a range of disturbances that influence pest control provided by natural enemies and how conservation practices can mitigate or counteract disturbance. We use four case studies to illustrate how conservation and disturbance mitigation increase the potential for biological control and provide co-benefits for the broader agroecosystem. To facilitate the adoption of conservation practices

that improve top-down control across significant areas of the landscape, these practices will need to provide multifunctional benefits, but should be implemented with natural enemies explicitly in mind.

1. INTRODUCTION

Viewed from an ecological perspective, farming can be seen as a series of disturbances imposed upon early successional systems to produce plant-based commodities. Disturbances are necessary features of agricultural systems, allowing crops to be established, managed, and harvested, but disturbances can cause challenges (56), including limiting the role of beneficial arthropods (152) and facilitating insect pest outbreaks (10, 59). Research, however, is revealing how conservation-based practices can moderate the negative influence of these disturbances so that farms can benefit from ecological interactions, such as predation and parasitism (17, 71, 83, 134).

Crop production practices disturb periods of stability during which crops and associated plant, microbe, and animal communities develop. These communities can benefit or antagonize crop production, with the individual species acting as key participants that influence the productivity of agricultural systems. Similarly, noncrop portions of agroecosystems contribute at various scales to dynamics of plant and animal communities that inhabit arable fields (119). Therefore, it is necessary to consider the entire interconnected system to understand the influence of disturbance on agroecosystems, the potential for conservation practices to decrease the influence of disturbance, and how to maximize benefits of arthropod-mediated ecosystem services.

Our goal is to explore ways to balance disturbance and conservation to improve the biological control of crop pests. To prevent yield loss, agricultural entomologists have often focused narrowly on interactions among plants, insect pests, and their natural enemies, without accounting for the larger system (i.e., the agroecosystem at farm, regional, and/or landscape scales, including noncrop habitats); however, a more realistic understanding of arthropod populations and possible influences and management options emerges when the larger agroecosystem is considered (**Figure 1**). Globally, the amount and form of disturbance associated with agriculture have increased (41), resulting in a decrease in land residing in a natural, noncropped state. Once established as farmland, variation in the inputs used within farms affects the impact that disturbances have on both pest and beneficial insects. We explore these two types of disturbances, focusing first on the influence that the lack of noncrop habitat around a farm has on natural control of pests and then on how on-farm disturbances can further exacerbate this issue. We highlight examples that have addressed aspects of on-farm disturbance for a range of crop types, from annual to perennial, largely in the context of temperate crop production typical in large portions of North America and Europe. We address a range of possible disturbances and strategies that can minimize the negative influence of disturbances. The central theme of disturbance and the influence of vegetational diversity, habitat manipulation, and noncrop plants on biological control has been the basis of previous *Annual Review* articles (2, 71, 95, 118, 145). However, we focus mostly on articles published within the past 15 years and, where possible, meta-analyses, which provide quantitative measurements of the impact that disturbances have on natural enemies, insect pests, and crop yield. We finish by considering recent case studies of conservation projects rooted in pest control or other aspects of farm management (e.g., erosion control) but that carry co-benefits for biological control and beyond. From the perspective of multifunctional agriculture, these case studies represent possibilities for meaningfully improving biological control across substantial crop acreage.

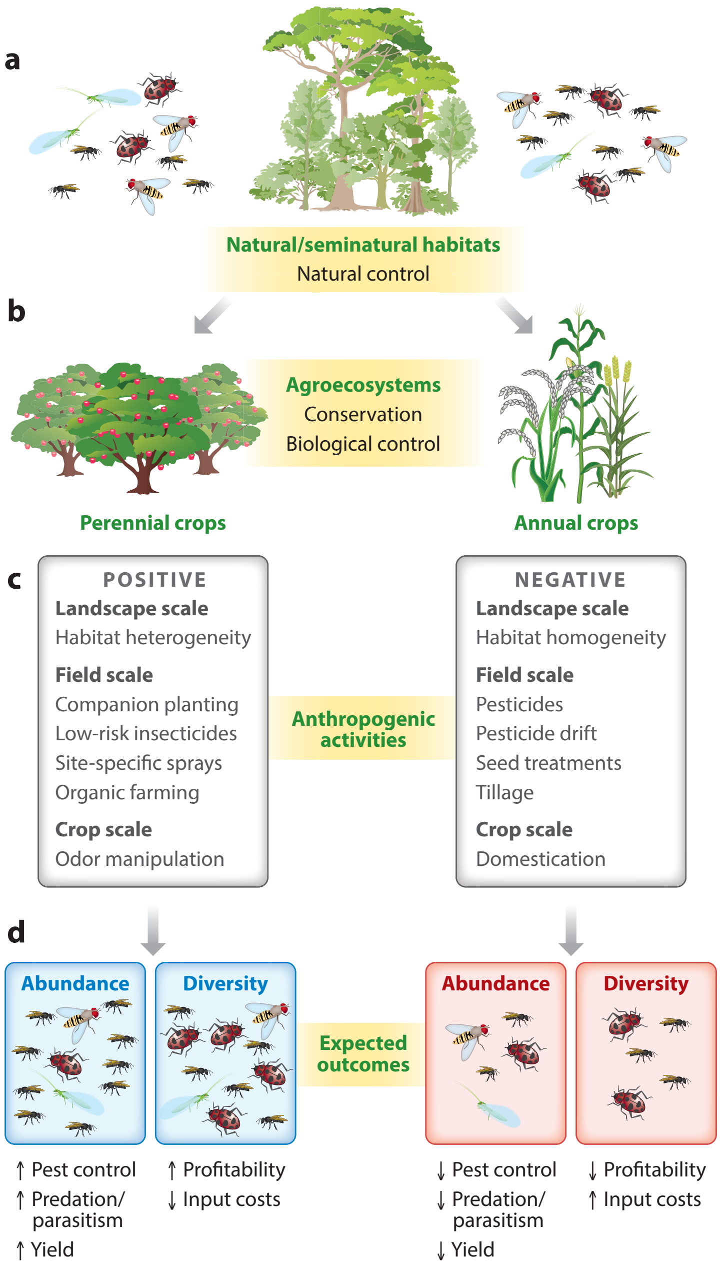

Figure 1

Conceptual framework for the effects of human disturbances on biological control. (*a*) Natural control effectively regulates herbivore populations in natural and seminatural habitats, where abundance and diversity of natural enemies are often high. (*b*) These natural enemies can spill over to agroecosystems; however, human disturbances can dampen natural control. Conservation biological control is then needed to restore these ecosystem services. (*c*) Human disturbances and methods to mitigate them affect natural enemies at various ecosystem scales from large (landscape) to small (crop). (*d*) The balance between negative and positive anthropogenic practices will determine the abundance and diversity of natural enemies in agroecosystems, which can affect levels of pest abundance, yield, and management costs.

1.1. Definition of Biological Control

To pursue our goal, we first need to settle on a definition of biological control (also known as biocontrol) from those provided by several authors (e.g., 29, 39, 52). We prefer "a pest management tactic involving purposeful natural-enemy manipulation to obtain a reduction in a pest's status" (99, p. 311). This definition is effective because it includes the key element of intent—biological control resulting from tactics implemented to improve pest control. Purposeful manipulation differentiates biocontrol from natural control, which is a base level of population control from biotic (or abiotic) sources that occurs without implementing any tactics (**Figure 1**) (99). This distinction is key because manipulations implemented to improve biocontrol ought to significantly increase natural-enemy-mediated mortality above natural control. If they do not, then we can conclude that the biocontrol tactics were unsuccessful. However, when natural control is insufficient for pest management, this is not an example of a failed biocontrol program. Rather, this is a situation where the purposeful selection of a biocontrol tactic (i.e., importation, augmentation, and conservation) may be necessary for successful management. As a final comment on this topic, note that determining whether top-down control is natural or biological (i.e., intentional) is not always simple. In our view, helping natural enemies by avoiding an insecticidal treatment or not removing a hedgerow would qualify as practices that facilitate biological control, but one would have to gauge growers' intent to be certain.

1.2. Disturbances in Agroecosystems and Their Influence on Biocontrol

Where modern, high-input farming is practiced, several common features limit the potential for natural control to prevent pest outbreaks. These features contribute to an intensification syndrome [as defined by Andow & Hidaka (4)] that includes landscapes dominated by large crop fields planted to monocultures of just a few crop species with limited genotypic diversity (85). These crop fields experience limited, if any, crop rotation and are established with effective weed-control tactics in landscapes converted largely to arable fields with little remaining natural or seminatural habitat (85); therefore, overall plant diversity in many agricultural landscapes is low (38). As a result, insect pests are more abundant, and natural enemies are less abundant, in these simplified, limited environments, forcing growers to rely on insecticides (82, 88). Given the importance of plant species and genetic diversity for driving arthropod diversity (24, 124, 137), these simplified agroecosystems tend to have depauperate natural-enemy fauna (82, 85).

In addition to this general intensification syndrome, many crop fields will likely be further disturbed by in-field management practices, such as pesticide use, tillage, fertilizer use, and crop harvest. These activities tend to decrease abundance of natural enemies and the control that they can provide. Insecticide use, of course, can limit natural-enemy populations, often resulting in pest resurgence or outbreaks of secondary pest species that can decrease crop productivity (33, 36). Ideally, farmers would utilize integrated pest management (IPM) to protect natural-enemy populations (addressed in detail below; see 130), but management-intensive systems tend to use insecticides preventatively. Furthermore, other pesticide use (i.e., herbicides and fungicides) can also negatively influence natural-enemy populations. Herbicides limit abundance of noncrop plant species in agroecosystems and can have direct and indirect effects on herbivore and natural-enemy populations within crop fields and on field edges (15, 37, 94, 103). Fungicides can disrupt natural or biological control of some insect and mite pest species, as many are toxic to entomopathogenic fungi (66, 127). Tillage tends to be used as a weed-management tactic and to prepare seed beds (69) but can also have strong influences on soil-dwelling arthropod populations, including natural enemies (131). Tilled fields tend to have fewer predators than no-till fields, whereas herbivorous insects tend to occur equally often in the two types of fields, suggesting that crops in tilled fields may be more vulnerable to pest damage because of an absence of top-down control (14). Fertilizer use (organic or inorganic) can also disrupt natural control by increasing growth rates of pest populations. This effect is often associated with plant nitrogen content, but other nutrients may cause similar effects (6, 86, 114). Crop harvest can also be viewed as a disturbance, mostly from the perspective of natural-enemy populations, the absence of which can allow pest populations to build (10, 128, 152). Altering harvest regimes can help maintain natural-enemy populations (121).

Lastly, low-diversity agriculture systems tend to suffer from invasive species and climate change, which cause additional disturbance. Invasive pest species appear to more easily invade simplified communities of agricultural fields, which are scouted more frequently than natural areas and are typically recovering from a disturbance, offering abundant food to consumers that are adapted to early successional habitats (116). Recent examples in North America include the soybean aphid (*Aphis glycines*), brown marmorated stink bug (*Halyomorpha halys*), and spotted wing drosophila (*Drosophila suzukii*). Their populations have grown explosively, resulting in profound changes in the management of entire systems, in large part because their newly invaded habitats lack the natural control provided in their native range (108, 149, 156). When climate change is layered onto these disturbances, pest populations may become more abundant and diverse in some parts of the temperate world (18).

2. METHODS TO CONSERVE BIOCONTROL AGENTS IN THE FACE OF DISTURBANCE

Decades ago, the "world is green" hypothesis argued that natural enemies are a primary force regulating herbivore populations in natural ecosystems (50). More recently, a meta-analysis revealed that, in general, consumer control (top-down forces) in natural and cultivated environments exerted stronger effects on herbivore fitness than resource forces (bottom-up effects) (147). The ecosystem service provided by natural pest control in agroecosystems has been valued in the United States at $4.5 billion per year (81). As mentioned above, crop-management tactics can disrupt natural control in various ways; the following sections address how conservation can be used to mitigate some of the negative influence of disturbance from management tactics (**Figure 1**).

2.1. Disturbances at the Landscape Level

With global human expansion, agricultural intensification has reduced natural ecosystems to a minority of the world's land cover (41). This widespread disturbance has reduced landscape heterogeneity, resulting in an associated decline in biodiversity (41). Diverse noncrop habitats in agricultural landscapes can harbor natural-enemy populations that provide substantial amounts of pest control in agroecosystems (140, 141); therefore, global declines in biodiversity, which include arthropod predators and parasitoids, are concerning for pest control. Noncrop areas can provide natural enemies with shelter from insecticides, alternative food resources (e.g., nectar or pollen), alternative hosts and prey, and overwintering sites (49, 71). Several meta-analyses have explored land-use complexity and diversity to explain variation in abundance, diversity, and impact of natural enemies on insect herbivores (8, 23, 27, 72, 76, 111, 146). A general trend has emerged from these studies indicating that, as landscape complexity and diversity decrease at several scales (i.e., simplification), natural-enemy abundance and diversity also decrease.

Farms located in landscapes with lower amounts of noncrop habitat are anticipated to experience less natural control because general losses in biodiversity affect trophic cascades (20). Because reductions in abundance and diversity often occur simultaneously within agroecosystems, it can be challenging to identify which differences in natural-enemy communities between simple and complex landscapes contributed to pest suppression. However, improvements in diversity can increase biocontrol of pests in agricultural systems (19). Regardless of which aspect of the community is responsible (greater diversity or abundance), farms located within a landscape with less complexity have fewer and less diverse natural enemies contributing to pest control (49, 80). For example, parasitism of the rape pollen beetle *Meligethes aeneus* in oilseed rape (*Brassica napus*) was lower in simple than in more structurally complex landscapes (135). For soybean fields, decreases in landscape diversity reduced soybean aphid predation (44). Similar relationships have been observed for perennial crops. European vineyards, for example, experienced 46% less pest control in homogeneous landscapes dominated by cultivated land than in more complex landscapes (115). A message emerging from this research is that, in heterogeneous landscapes, efforts should be made to forestall landscape simplification to prevent degradation of potential pest-control services (among other benefits to the broader system), whereas in more homogeneous landscapes, pest control would likely benefit from meaningful increases in abundance and/or quality of noncrop habitats.

The impact of landscape heterogeneity on pest damage has been shown to increase crop yield (48, 79), although this effect has been less studied (23). A review of 72 studies showed that farms embedded in landscapes with a higher proportion of seminatural areas had lower pest abundance or higher pest control (146). In addition to evidence that farms in heterogeneous landscapes experience more natural control, there is evidence that the opposite is also true. Agricultural intensification correlates with higher pest populations and increases in insecticide use (74, 88, 89). For example, in regions where both soybean and maize are produced, increases in maize production decreased landscape diversity, reducing natural control of soybean aphid by 24% at a cost of $58 million per year in reduced soybean yield and increased insecticide use (70). Such data argue for trying to avoid landscape simplification and, if possible, working to diversify simpler landscapes that contribute to conservation of natural enemies in ways that are practical for farmers.

Despite substantial evidence that increasing land-use diversity improves the natural control of pests, inconsistencies in the effects of noncrop habitats on pest control, insecticide use, and yield have been reported (62, 73, 90, 139). The impact of the surrounding landscape on natural control is not always significant and may vary by natural-enemy taxa; the magnitude of the effect can be stronger on measures of diversity than abundance for at least one taxon [spiders (123)]. Furthermore, there may be limitations to meta-analysis when shared parameters (e.g., land use around a targeted field) are estimated without a shared methodology (62). Karp and colleagues (62) pooled data from 359 separate studies but did not observe a consistent effect of noncrop features on natural-enemy abundance and pest activity. Pest control in an equivalent number of cases was either positively or negatively affected by surrounding noncrop habitat. This overall finding contradicts the trend described by multiple meta-analyses (8, 23, 27, 72, 76, 111, 146). This difference likely resulted from the broad analysis by Karp et al. that lumped studies together regardless of important differences (62), suggesting that context-dependent sources of variation can disturb a general relationship between land use, natural-enemy communities, and their impact on pests.

For those interested in drawing inferences from meta-analyses on the value of noncrop habitats (23, 27, 72, 76, 111, 146), especially that of Karp et al. (62), it should be noted that rarely have these quantitative reviews focused on studies that explicitly explored the impact of a conservation program on management of a target pest. Rather, these reviews have drawn from studies that explored land-use diversity as a pre-existing feature contributing to natural control, and not on active efforts to manipulate the environment for natural enemies and, thus, biocontrol. For example, the oft-cited work by Gardiner et al. (44) revealed that land use surrounding soybean fields explained soybean aphid mortality from natural enemies and concluded that landscape diversity enhanced biocontrol of this invasive pest. Given our definition, this study measured natural control, not biological control. Of the three approaches to biological control (importation, augmentation, and conservation), none were implemented in the soybean-aphid system in North America prior to the work of Gardiner et al. (44). A key exotic predator of the soybean aphid was introduced to a different region of the United States prior to the arrival of soybean aphid (67), and parasitoids were not recovered, suggesting that importation biocontrol was not a contributing factor (53). Moreover, few, if any, efforts to actively conserve endemic natural enemies were in place during the time of the study. If anything, as noted earlier, further simplification of the Midwest US landscape was occurring, reducing the impact of natural enemies on soybean aphid (70).

A broader inference is that natural control in this specific system, and many others, could be improved by implementing conservation tactics that increase natural-enemy populations and allow them to persist over time in proximity to crop fields. Exploiting relationships between natural-enemy communities and landscape diversity is challenging because the scale at which landscape can influence pest control is often beyond the control of one farmer (138, 140). The collective action of multiple farmers and landowners, possibly facilitated by local or federal policy, may alter land use and decrease homogenization of landscapes, but specific actions that farmers can take to exploit this relationship tend to be limited to the farm scale. Finally, we note that habitat manipulation may result in ecosystem disservices (49). For example, hyperparasitoids may also respond positively to landscape complexity, which may dampen the mortality that pests suffer from primary parasitoids (106). In the next section, we discuss how disturbances that produce simplified agroecosystems can be moderated or even reversed at the farm level.

2.2. Disturbances at the Farm and Field Levels

We discuss three key limits on diversity in agroecosystems: habitat, insecticide use, and soil management. We focus on methods to reduce their negative effects on natural enemies and top-down control, in part by highlighting studies that tested the combined effects on natural enemies of these three factors at local and landscape scales.

To more effectively manipulate noncrop habitats, we need a better understanding of factors on farms that limit natural enemies. Several studies have recently compared the relative importance of local- versus landscape-scale structure and composition on abundance of natural enemies and the control that they provide (43, 47, 84, 90, 117, 133). Local management can compensate for limitations of simplified landscapes (117, 133). For example, planting flowering strips in winter-wheat fields reduced cereal leaf beetle damage by 61%, irrespective of landscape complexity (142). In addition, aphid predators benefited more from provisioning of floral resources than from overwintering habitats (105), suggesting that conservation measures need to be tailored to specific natural-enemy taxa. In most cases, however, both landscape and local effects are important. For instance, lady-beetle abundance in soybean was higher in buckwheat field margins and in fields with higher amounts of seminatural vegetation in the landscape, but there was no interaction between these two spatial scales (154). Similarly, colonization of tomato crops by mirids increased in landscapes with fallow fields but decreased in landscapes with orchards, possibly due to crop management practices, indicating the importance of sink-source dynamics of the landscape (5, 118). Although both local- and landscape-scale complexity enhanced the control of cabbage aphid in broccoli, landscape simplification influenced the time of natural-enemy arrival (22), again highlighting the importance of the source habitat for successful biocontrol.

Insecticides, of course, can have negative effects on natural enemies residing in crop fields and those that move in from surrounding habitats (112). By providing more abundant and diverse sources of predators and parasitoids, a heterogeneous landscape may compensate for the negative influence of insecticides on natural-enemy communities. Although this hypothesis is appealing, the studies that have addressed this question thus far have generated mixed results (155, 158). For example, in landscapes with increasing annual crop cover, insecticide use was the main driver of decreased parasitism of two crop pests, rather than landscape-level decreases in habitat diversity (60). Similarly, in apple orchards, predation of sentinel codling moth (*Cydia pomonella*) eggs was mostly dependent on local farming practices (insecticide use), rather than landscape factors (91). In contrast, landscape diversity (e.g., fallow fields), rather than insecticide use, was the main driver of spider populations in rice fields (7).

In-field soil management (e.g., tillage) and vegetation cover (e.g., cover crops) can negatively or positively affect natural-enemy populations, particularly soil-dwelling predators, in agroecosystems (98). In fact, practices that minimize negative effects of tillage on the soil environment, such as conservation tillage, can enhance natural-enemy populations and pest control (98, 134), as well as mitigate negative effects of landscape simplification on biocontrol (133).

2.3. Disturbances at the Crop Level

Physical and chemical traits of host plants directly and indirectly influence natural-enemy populations (102, 144), but it is unclear whether landscape factors mediate tritrophic interactions in agroecosystems (42, 125). Plants produce a wide array of secondary metabolites that can reduce performance and preference of herbivores as well as of their natural enemies (64). Similar to applications of insecticides, these plant compounds may reduce natural-enemy populations and the control that they can provide (102). Selection of genotypes resistant to pests may harm natural enemies, but we are unaware of studies that explored the interactive effects of host-plant resistance (HPR) and landscape complexity on biocontrol, although for specific examples, HPR and biocontrol can be compatible (e.g., 87). We predict that biological control would work best in diversified cropping systems within which both resistant and susceptible varieties are utilized because susceptible plants may promote pests and resistant plants decrease the landscape's carrying capacity for natural enemies. Such a combination of cultivars is consistent with resistance management plans that employ a refuge of susceptible varieties.

Humans have domesticated plants for approximately 13,000 years with a focus on higher yield (24, 30). Domestication can alter traits in plants, such as reducing emission of herbivore-induced plant volatiles (HIPVs), which may negatively influence foraging by natural enemies (24, 107, 109). Restoring HIPVs in crops via synthetic lures can mitigate these negative effects (110) and has been tested in combination with companion planting as an attract-and-reward strategy (96, 126). However, more studies are needed to determine if this strategy for enhancing biocontrol is affected by landscape variation. For example, is the impact of synthetic lures limited when they are deployed in crops surrounded by limited noncrop habitat? Moreover, because the effects of HIPVs on natural enemies can be influenced by field size (1, 61), such studies need to be done at a scale relevant to the crop species of interest.

Soil amendments can also mediate indirect interactions between plants and natural enemies. Although fertilizers affect herbivores by altering nutrient availability in plants (2, 129), less is known about their effects on the third trophic level. For example, fertilization increased parasitism of tephritid flies in creeping thistle (148). Similarly, nitrogen fertilization increased aphid populations and the number of hoverfly pupae in wheat fields (21). In contrast, fertilization negatively affected plant-species richness, herbivores, and their natural enemies (54). Besides nutrient availability, fertilizer regime can affect natural enemies directly by changing levels of plant secondary metabolites or altering levels of HIPVs (151), or indirectly by providing increasing populations of alternative prey (114).

3. CASE STUDIES

Below we highlight four farming systems that have included conservation practices and/or addressed aspects of agricultural disturbances. We highlight these particular examples because their conservation efforts were intended, in part, to move natural control to biological control, and as the efforts range from simple to more complex, other agricultural benefits emerge. Going forward, conservation tactics that provide multiple benefits, also called co-benefits, will have the best chance of being adopted for the long-term.

3.1. Reincorporating Native, Perennial Plants Back into Farm Systems

We present three case studies that illustrate conservation tactics implemented in nonorganic agricultural settings to improve natural-enemy populations and the control that they can provide (**Supplemental Figure 1**). In each case, researchers compared a conventional production system to one that they enhanced with perennial conservation plantings, featuring native flowering-plant species selected based in part on their attractiveness to natural enemies. Importantly, each of these improvements provided significant benefits beyond biocontrol; the conservation planting improved other animal populations or even helped improve other features of the agricultural landscape (e.g., limiting sediment and nutrient loss).

Supplemental Material >

3.1.1. Case study 1: the hedgerows of Central California tomato fields. In California, tomato fields adjacent to semimanaged, nonnative weeds had fewer parasitoid wasps, fewer lady beetles and more pests than fields adjacent to hedgerows constructed from at least five native perennial plants in strips of varying size [7 m wide and up to 550 m long (93; see **Supplemental Figure 1**)]. The abundance and diversity of native bees were also greater in hedgerows than in control sites (92), and this difference persisted up to 100 m into adjacent tomato fields (93). Hedgerows also increased bird diversity and abundance (51), with increased community diversity as the perennial plants matured, 10 years post-establishment (101).

3.1.2. Case study 2: prairie borders along blueberry fields. Before European settlers arrived, prairies dominated the landscapes of the Midwestern United States, including the southwestern corner of Michigan. Beyond the grasses, prairie flora included perennial plant species attractive to natural enemies (40) and pollinators (143). When planted together, species selected for this attractiveness (based on abundance and diversity of insect species visiting plant species) can support natural enemies throughout the growing season (46). In Michigan, these mixtures (12–15 species) were planted in patches ranging from 0.06 to 1.0 ha, adjacent to blueberry fields, a crop that suffers injury from multiple insect pests and requires bee pollination (**Supplemental Figure S1**). These mixtures increased natural-enemy abundance (13), pollinator abundance and diversity, and blueberry yield (12). The yield response resulted from improved pollination, but sentinel prey assays suggested that the prairie borders also may have increased pest mortality in adjacent fields (11).

3.1.3. Case study 3: prairie strips within corn and soybean fields. The Science-based Trials of Row-crops Integrated with Prairie Strips (STRIPS) project in Iowa used prairie plant species but embedded them into fields in a corn–soybean rotation. The primary goal of STRIPS was to determine if adding small amounts of reconstructed prairie back into Midwestern watersheds committed to annual crop production delivers multiple ecosystem services [e.g., reduced sediment loss, improved water quality, and pest control (25, 122)]. Researchers added prairie patches to watersheds along field edges and in strips distributed across a field. Replicated

Supplemental Material >

watersheds (0.5 to 3.2 ha) received varying amounts of prairie to achieve three levels of habitat incorporation (0, 10%, or 20% prairie per watershed; see **Supplemental Figure S1**). Once established, these prairies averaged approximately 15 species, accounting for a 380% increase in plant biodiversity compared with the adjacent crop (55). Overall, these prairies significantly increased the diversity of insect species (122), including several predators of the soybean aphid. Prairie strips contained more natural enemies of aphids, especially before the adjacent soybean emerged (25). After emergence, however, the abundance and diversity of natural enemies in the adjacent soybean crop and their influence on artificial infestations of soybean aphids later in the season did not increase (25). To date, the value of prairie strips for conserving natural enemies and improving biocontrol of other insect pests of corn and soybeans has not been explored. However, corn and soybean fields that had prairie strips within or adjacent to them had significantly more insect pollinators, as well as a greater species richness and abundance of native birds (122). Furthermore, 20-fold less sediment was lost from fields with prairie strips, as well as 4.3 times less phosphorus and 3.6 times less nitrogen in groundwater emerging from these fields, suggesting a role for prairie strips in addressing water quality issues exacerbated by crop fertilization (i.e., hypoxic zones).

These three case studies highlight a constant response of beneficial insects to conservation in conventional agroecosystems. Regardless of the cropping system, each effort increased abundance and diversity of natural enemies and pollinators by adding native, perennial, flowering plants. Note that none of the studies avoided pesticide use. Although yield improvement was only observed in one case, none of the studies observed a decrease in yield. Two of the three studies observed improvements to other ecosystem services, including increases in biodiversity of noninsect species. This was most noticeable in the STRIPS project, which also documented increased sediment and soil nutrient retention. These additional co-benefits highlight the potential for conservation biological control programs to be part of a larger effort to improve delivery of ecosystem services.

3.2. Reduced Disturbance via Organic Agriculture

As a fourth example of conservation-based farming that moderates disturbance and facilitates top-down control, we highlight organic agriculture. In general, farming organically facilitates delivery of natural control, in part by fostering diversity that appears to compensate for disturbance caused by farming tactics (e.g., tillage), ultimately maintaining natural-enemy communities. Organic farms tend to have higher crop diversity, which enhances arthropod abundance and richness, including those of predators (78). As a result, organic farms tend to harbor robust natural-enemy communities that significantly contribute to pest control and help produce larger plants (26). The diversity and abundance of natural-enemy communities on organic farms tend to be most influenced by local farming practices (104), but these communities, and the control that they provide, can also be enhanced by higher levels of landscape complexity (31, 57, 97, 150). For example, aphid predation was highest in organic cereal fields in complex landscapes and declined with increasing landscape homogeneity (150). The response of natural enemies to farming practices (local factors) and landscape (regional factors), however, will likely differ according to taxa (32, 150). Mixed results emerged at the landscape level when models were used to predict the response of aphids to parasitoids and increasing amounts of organically managed fields within a farm landscape dominated by conventional agriculture (9). The impact of parasitoids on an aphid species varied as the amount of farms under organic management varied at a landscape level (9). Accounting for multiple sources of pest suppression resulting from organic practices may produce more robust management. For example, organic soils can increase crop resistance against insect pests (100), potentially interacting positively with biocontrol to reduce pest populations even further.

Organic farmers' achievement of this level of natural control may be attributed to an approach to pest management that will sound familiar to the initial description of IPM (130). Arthropod pest management in organic crop production has been broken into four phases, starting with preventative practices and leading to more direct strategies as needed (157). Initial methods focus on cultural practices that limit pest outbreaks by reducing the pests' carrying capacity. The second and third phases are biocontrol tactics (conservation, inundative and inoculative release of biocontrol agents). The fourth phase is the use of organically approved behavioral modifiers and, finally, approved insecticides. The former include repellents and attractants that are often based on semiochemicals, such as sex pheromones. For certification as an organic farm, the latter, of course, cannot be of a synthetic origin. Despite this limitation, organic insecticides are available, including those derived from plants (e.g., Neem extract and pyrethrum), microbes (e.g., *Bacillus thuringiensis* and granulosis viruses), and fungal pathogens. Use of insecticides approved for organic use may result in greater cost than synthetic, broad-spectrum insecticides due in part to differences in toxicity, residual activity, and price (157).

Because insecticide use is possible, this general approach to pest management (i.e., first making use of phases 1–3) aligns remarkably well with the original vision of IPM, which was developed to decrease reliance on insecticides to avoid problems associated with overusing them (130). IPM was originally meant to imply that natural enemies will contribute to pest control, and scouting and applying economic thresholds prior to using insecticides (or other control tactics) will minimize unnecessary disturbance to natural-enemy populations (68, 130). Notably, a complaint of more current implementation of IPM is that it often inverts the four phases of pest control (157), relying first on insecticides, many of which are relatively inexpensive, and only exploring phases 1–3 to develop more ecologically based control options once ecological or environmental problems have emerged from overuse of insecticides (77).

4. CONSTRAINTS TO ADOPTION OF CONSERVATION TACTICS

Humans have disturbed agroecosystems at various scales, from artificially selecting crop species to modifying landscapes. Mitigating the negative effects of these disturbances on natural enemies depends on their life-history traits and the environmental contexts in which they live (79). Because we are unable to change the former, we need to address the latter to make progress on conserving natural enemies in agricultural landscapes and effect biocontrol. Unfortunately, responses of natural enemies to crop disturbances and conservation practices tend to be variable in space and time and can be pest and crop specific. This variability will likely influence adoption of conservation tactics that can promote biocontrol. We separate disturbances in this review into two scales: in the surrounding landscape (Section 2.1) versus within the farm (Sections 2.2 and 2.3). We are left with a question: Which more strongly limits biocontrol—within-farm disturbances or homogenous landscapes surrounding farms? Few attempts have been made within a variable landscape (i.e., simple versus complex landscapes) to measure the impact of organic versus conventional agricultural practices on delivery of insect-derived ecosystem services (but see 57, 150). One study found that, across 153 European farms, farming practices (organic versus conventional) interacted with landscape complexity to influence predation of aphids in cereal fields (150). Such fully crossed experiments would be helpful in prioritizing which features of agroecosystems are most likely to respond to conservation efforts, so that we can enhance natural control and provide greater pest management via biocontrol.

We need to recognize that most of our knowledge on the moderating effects of conservation on predation and parasitism comes from large-acreage annual crops (e.g., corn, soybean). For example, in the meta-analysis discussed above (62), 90% of the data came from annual agricultural systems. Although research on perennial crops has increased in the past decade (13, 58, 132), more research is needed to understand how conservation tactics can benefit from the stability of perennial systems to limit the influence of disturbance and improve top-down control.

5. CONCLUSIONS

Conservation strategies and tactics can mitigate or offset disturbances that lower the capacity of natural enemies to provide top-down suppression. In some agroecosystems, the noncrop habitat that can help maintain natural enemies and the natural control they provide may be insufficient to suppress pest populations below economic injury levels. To justify additional habitat that provides for natural enemies well enough to effect biological control, agricultural systems may need to adopt technology allowing farmers to more precisely estimate yield [for example, for corn and soybean production (see 16)]. By targeting conservation efforts (e.g., prairie STRIPS) to replace persistently low-yielding areas, profit can be maximized in part by the delivery of additional ecosystem services. The more farmers are able to rely on conservation biocontrol, the more it will be able to help move agriculture toward sustainable intensification by employing practices that more intensively use natural capital to reduce negative environmental impacts of farming (45, 136). Natural capital harnessed to better manage agroecosystems will allow natural enemies to impose top-down control (56) and may deliver additional benefits to wildlife of conservation concern (e.g., pollinators, birds), soil health, and water quality.

A key to greater adoption of biocontrol in agricultural landscapes is developing conservation strategies that include practices that provide these multiple benefits to agroecosystems. Bundled with other benefits, strategies and tactics that help move farming from simplified systems that are reliant on insecticide use to more diverse systems that rely on biological control will have a better chance of being adopted if farmers adopt specific conservation efforts that deliver, for instance, soil-quality-improving benefits. A conservation practice that delivers such a range of benefits is cover cropping, which is widely promoted to decrease erosion and improve soil quality, nutrient cycling, and weed control, among other ecosystem services (120). Although these benefits are generally considered to be primary, cover crops can provide a secondary benefit of improving top-down control. Cover crops can provide habitat for predators and help increase their populations early in the growing season, leading to improved pest control (75, 83, 120). Similar to landscape diversity, however, the beneficial impact of cover crops on natural enemies is not guaranteed; the impact can be limited (34), particularly if implemented without IPM (98). Moreover, if not managed well, cover crops can increase the risk of damage from insect pests (35). Similar bundled benefits (e.g., weed control, water quality, and crop productivity) can also be derived from farming strategies like extended crop rotation (28), which influences insect pests by disrupting insect life cycles and fostering populations of predators (153). A more recent development that should help deliver numerous conservation benefits, including biological control, is the rising interest in soil health and its associated practices (e.g., no-till, cover crops), which can improve soil quality and help foster a more complete range of soil biological functions, all of which are attracting widespread interest from farmers (65). Further research should focus on developing other conservation-based approaches to farming and accounting for the multifaceted benefits received by farmers beyond biological control.

In the end, facilitating widespread adoption of biocontrol through conservation may require adopting practices that provide a range of benefits that decrease the footprint of agriculture while contributing to productivity and profitability (63, 115). As noted above, organic farming minimizes local disturbances and benefits from greater control of pests. However, agriculture is not static because new pests often arrive (i.e., invasive species) and require novel management. As researchers develop conservation tactics to improve the resilience of agroecosystems against new threats, the pest management approach used by organic practitioners may provide the best conditions for more multifunctional agriculture to include insect-derived ecosystem services. This is not meant as advocacy for organic agriculture per se, but rather as an approach to pest control that is consistent with how IPM was originally envisioned [i.e., insecticides used as a last resort (130)].

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