Habitat Management to Suppress Pest Populations: Progress and Prospects

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Abstract

Habitat management involving manipulation of farmland vegetation can exert direct suppressive effects on pests and promote natural enemies. Advances in theory and practical techniques have allowed habitat management to become an important subdiscipline of pest management. Improved understanding of biodiversity-ecosystem function relationships means that researchers now have a firmer theoretical foundation on which to design habitat management strategies for pest suppression in agricultural systems, including landscape-scale effects. Supporting natural enemies with shelter, nectar, alternative prey/hosts, and pollen (SNAP) has emerged as a major research topic and applied tactic with field tests and adoption often preceded by rigorous laboratory experimentation. As a result, the promise of habitat management is increasingly being realized in the form of practical worldwide implementation. Uptake is facilitated by farmer participation in research and is made more likely by the simultaneous delivery of ecosystem services other than pest suppression.

INTRODUCTION

Since the publication of "Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture" in 2000 (64), the field has expanded dramatically. Reflections of this include the fact that the article has been cited more than 1,000 times, and web searches reveal a high level of research activity and on-farm implementation. A great deal has changed in the 17 years since that review was written including the publication of several excellent reviews of related fields (18, 106, 146). None of these, however, directly covers the field of habitat management for pest population suppression. Accordingly, this new review aims to synthesize the literature with an emphasis on articles that have appeared since 2000 to provide an appraisal of progress and prospects. We expand on our earlier review (64) to include the effects on pests that operate independently of natural enemy activity, thereby providing a more complete synthesis of the ways in which habitat management may be used for pest suppression.

Habitat management: an intervention in an agroecosystem's vegetation with the intended consequence of suppressing pest densities

Push-pull: combined use of a plant to repel pests with a second plant to attract, and possibly trap, pests

Bottom-up effects (resource concentration effects): the action of vegetation (first trophic level) on herbivore pests (second trophic level)

Top-down effects (enemies hypothesis): the action of natural enemies (third trophic level) on herbivore pests (second trophic level)

Conservation biological control: making better use of existing agents via habitat management and the reduction of mortality from pesticides

TERMINOLOGY AND OVERVIEW OF THE DISCIPLINE

Habitat management, sometimes referred to as habitat manipulation, aims to suppress pest densities, often by enhancing the impact of the natural enemy community, though altering vegetation patterns can also act directly on herbivores. Indeed, of the eight hypotheses explaining the effects of vegetation diversity on pests summarized by Poveda et al. (90), seven act independently of natural enemies. Essentially, these direct mechanisms involve disrupting herbivore capacity to locate a suitable host plant by using visual or chemical stimuli (101) that may act by repelling pests from a crop (128), trapping herbivores on a plant other than the crop (46), blocking movement of herbivores with tall vegetation (83), or altering the volatile profile of crop plants (27). Reflecting this diversity of mechanisms, a wide range of strategies for vegetation diversification both within and adjacent to crops has been experimentally explored. Some strategies involve the incorporation of secondary and tertiary crop species (i.e., intercropping), whereas others employ noncrop plants selected for particular functions (e.g., to provide nectar for natural enemy nutrition). Some systems seek to exploit multiple mechanisms, most notably push-pull strategies that use one plant species within a crop to repel pests and another plant species adjacent to the crop to attract pests (18). In a particularly successful form of push-pull, the plant that repels pests also attracts natural enemies (60, 61). Work this century has greatly expanded our understanding of the importance of larger-scale effects extending to landscapes and regions (55, 81, 120). Accordingly, the level of research activity in this area requires a new review to consider progress and prospects (126).

Ecologists view the direct and natural enemy–mediated effects of vegetation on pests in terms of bottom-up or top-down trophic effects, respectively (**Figure 1**). Bottom-up effects refer to the action on herbivore pests (second trophic level) of vegetation (first trophic level). Root (101) referred to this effect as the resource concentration hypothesis. In contrast, top-down effects refer to the action of natural enemies (third trophic level) on herbivores. In this effect, also known as the enemies hypothesis (101), habitat management provides plants that support predators and parasitoids with foods such as nectar and pollen, or it provides additional prey or host species. Alternatively, abiotic conditions may be altered to favor natural enemies; for example, habitats can be manipulated to provide a moderated microclimate that enhances natural enemy survival during overwintering (64).

Reflecting these top-down mechanisms, habitat management is an important component of conservation biological control (**Figure 1**). The second major component of conservation biological control—independent of habitat management—is to reduce the mortality from pesticide use of biological control agents (37), an important issue given their estimated use of 3.5 billion kg per annum (93). This can be accomplished by adopting integrated pest management (93) or

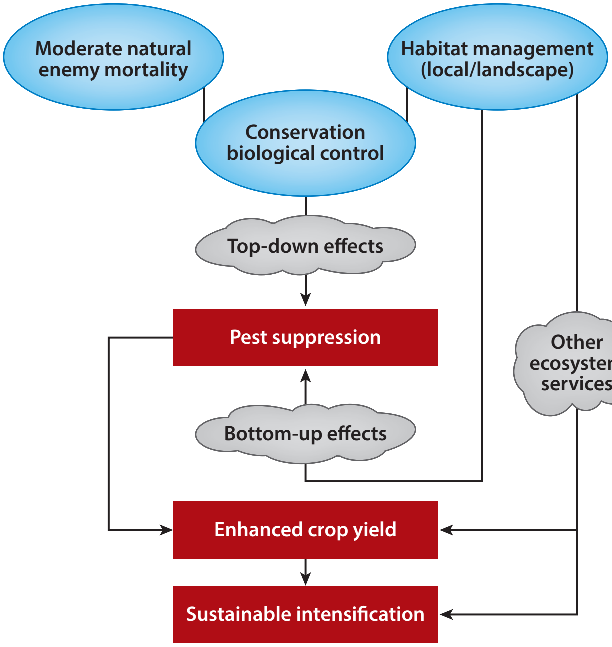

Figure 1

Diagram of habitat management and related research fields (*ovals*), mechanistic effects (*clouds*), and potential outcomes (*boxes*).

switching from broad-spectrum insecticides to insect growth regulators, for example (39). Importantly, habitat management often impacts more than just pest management, with effects on, for example, pollinators, detritivores, and weeds. As explored below, the associated ecosystem services (or sometimes disservices) can lead to broader effects on agricultural systems, including contributing to sustainable intensification.

Ecosystem services: benefits delivered to humanity by biodiversity and its processes

Sustainable intensification: intensification of agricultural production that emphasizes a lessening of effects on the environment

Ecological engineering: a refinement of habitat management whereby the intervention is explicitly supported by evidence to maximize impact

ECOLOGICAL THEORY

Ecological theory is increasingly useful in informing habitat management approaches (40). Advances in the fundamental understanding of biodiversity-ecosystem function relationships (43) mean that researchers now have a firmer theoretical foundation on which to design strategies for enhancing pest mortality in agroecosystems. Similarly, advancing knowledge of the role of landscape structure on natural enemy communities and their impacts on prey populations is increasingly forming the basis for more predictive habitat management at appropriate scales (126). Finally, an explosion of literature on the chemically mediated exchange of information among plants, herbivores, and natural enemies is also beginning to inform habitat management practices (117). Reflecting these effects, some authors (e.g., 149) have recently referred to habitat management as ecological engineering. (See the sidebar titled Selecting Optimal Habitat Management Approaches.)

Biodiversity and Ecosystem Function

Ecologists have been intensely interested in the relationship between biodiversity and ecosystem function (69, 111). Altieri (2) was among the first to outline the role of biodiversity in the function

SELECTING OPTIMAL HABITAT MANAGEMENT APPROACHES

When floral resources are used to enhance biological control, the choice of plant species is often based on laboratory or field studies in which candidate plants are ranked for their effects on parasitoid or predator. However, which aspects of natural enemy biology contribute most to pest population reduction are often unclear. Modeling can help identify these key components, including aggregation, dispersal, search, and reproductive rates. Kean et al. (57) provided a start to this modeling approach, though it remains underused. Empirical ranking of flowering plants is complicated by the fact that cultivars within a species can produce divergent effects on parasitoids (6). Recent work used a combination of laboratory olfactometry with gas chromatography and electroantennography and identified short-chain carboxylic acids as most likely to be responsible for differences among buckwheat cultivars (29). Moving beyond case-by-case empiricism to a more predictive approach may be possible using a trait-based approach (11) to establish guiding principles for which types of vegetation traits and combinations of traits are generally superior for pest suppression.

of pest suppression in agroecosystems. Several decades of subsequent empirical and theoretical studies have refined our understanding. Snyder & Tylianakis (116) reviewed the relationship between biodiversity and biocontrol of pests and showed that pest suppression may increase, decline, or be unchanged by increased natural enemy diversity. Enhanced pest suppression can occur as a result of facilitation or complementarity between natural enemies (70). Alternatively, increased predator diversity can decrease pest suppression via intraguild predation (28). The evenness of predator communities, i.e., the relative abundance of different species, is also important, with more even communities exerting increased pest suppression (19).

Recent studies suggest that the relationship between biodiversity and ecosystem function can change over time. Schmitz & Barton (108) developed a theoretical framework for predicting how habitat management outcomes may shift with climate change. Increasing biodiversity amplifies ecosystem function in plant communities, but it does so more incrementally in mature versus immature communities (98). Thus, as a community matures, greater complementarity can occur. If similar processes occur in insect communities, habitat management practices in perennial crops or those using perennial plants to provide resources will need to be studied over long terms (5–10 years) to accurately assess the shifting interactions of habitat structure and community composition on the function of pest suppression. This is reflected in recent British work in which field margins were diversified with various plants including perennial species (95). Crop yields in diversified fields increased compared with control fields to an extent that tended to be greater in each of the successive 5 years after the experimental interventions.

Complementarity: situation in which enemies attack pests in different ways, times, and/or places, such that overall control is increased

Facilitation: process whereby the action of one natural enemy increases the success of another

Landscape Structure and Biological Control

Ecological theory has also informed the role of landscape structure in supporting biodiversity and pest suppression in agricultural landscapes (125, 126). Specifically, understanding factors that control the exchange of species between habitats is critical for prediction of effective conservation biological control (106, 124). According to one prediction, local habitat management (e.g., creation of diverse floral resource habitats) will increase within-habitat species richness (α-diversity) and contribute to overall species diversity at the landscape level (γ-diversity). However, such practices are likely to be relatively ineffective in landscapes where simplification of the vegetation has left few areas of source habitat and in very complex landscapes where the added diversity is trivial compared with what was already present (125).

Several recent tests have provided support of this "intermediate landscape complexity" hypothesis (55, 131). Theory also suggests that distinctness among communities (β-diversity) should be particularly important in supporting the function of pest suppression and its resistance to disturbance (124). A recent analysis of plant biodiversity-ecosystem function studies showed that the number of ecological functions in modeled landscapes increased with both α- and γ-diversity, whereas β-diversity was related to increasing functionality only in landscapes lacking high overall diversity (82). Agricultural landscapes often lack high γ-diversity. Thus, in addition to pest suppression, the use of habitat management to increase β-diversity will likely be important to maintain or enhance multiple functions (e.g., pollination, decomposition, and crop productivity). This approach could include adding perennial plant strips into largely annual crop landscapes, whereas annual plants may best enhance resources in perennial crops (e.g., orchards).

Attract and reward: combined use of semiochemicals to attract natural enemies and nectar plants to enhance their residency

Several recent meta-analyses have examined the role of landscape structure on natural enemies and on pest suppression and support an emerging consensus. Increasing landscape complexity, typically via inclusion of noncrop habitat, almost always increases natural enemy abundance and diversity (9). Although pest diversity also frequently increases, pest abundance typically declines or remains unchanged. The ecosystem functions of predation and parasitism typically increase, whereas pest population growth rates typically decline (13, 102, 112, 133). More recent work has shown that the extent of disturbance in an agricultural landscape can also have a strong effect (54). Finally, although this finding is based on far fewer studies, plant damage by herbivores typically declines or remains unchanged (13). This collection of empirical studies suggests the potential for generalization, but whether this knowledge can further improve the predictability of habitat management approaches remains undetermined. Such efforts may be supported by modeling, which offers scope to minimize the logistical complexities of research at the landscape scale and which should consider temporal as well as spatial effects (106).

Chemical Ecology and Nonconsumptive Effects

A new frontier in habitat management is the potential to manipulate the exchange of information between organisms in the agricultural landscape to better enhance pest suppression. The field of chemical ecology has yielded tremendous insights into the myriad of ways that organisms communicate (97), and this information is being used to inform habitat management. When attacked by herbivores (or when oviposited upon), plants frequently produce chemical distress signals termed herbivore-induced plant volatiles (HIPVs) that can directly deter pest attack, inform other plants of impeding damage, and attract natural enemies to help defend the plant. Synthetic HIPVs have been used to increase natural enemy abundance and reduce pest damage, and they can also work with floral resource patches to attract and reward natural enemies (114). Australian work in a range of systems (vineyard, broccoli, and sweet corn) showed that significant levels of natural enemy attraction occurred for up to six days after plants were sprayed with synthetic HIPVs, suggesting that treated plants may have been induced to produce endogenous volatiles that attracted insects over this extended period (115). HIPVs are also used in push-pull strategies to repel herbivores from crop plants while simultaneously attracting them to nearby trap plants (58). *Melinis minutiflora*, for example, is widely grown within maize fields in sub–Saharan Africa, where it constitutively emits volatiles such as (*E*)-ocimene, (*E*)-4,8-dimethyl-1,3,7-nonatriene, β-caryophyllene, humulene, and α-terpinolene. These have the dual effect of repelling adult female stem borer moths while attracting adult female parasitoids of the stem borers (59). In the same system, Napier grass (*Pennisetum purpureum*) is established as strips beside maize fields, where it releases volatiles, especially hexanal, (*E*)-2-hexenal, (*Z*)-3-hexen-1-ol, and (*Z*)-3-hexen-1-yl acetate that are attractive to moth pests. Crucially, Napier grass produces more of these volatiles than do maize plants and production peaks in the early evening at the same time moths are seeking host plants. Finally, the larvae of stem borer pests cannot develop on Napier grass, making it highly effective as a trap crop (59).

SNAP (shelter, nectar, alternative prey/hosts, and pollen): the major resources provided by plants to natural enemies

Herbivorous insects can monitor their environment to detect information about the occurrence of natural enemies and alter their behavior to avoid danger. For example, they can detect visual (52) and chemical (44, 79) cues identifying the actual or potential presence of predators. They adjust their behavior in response to these cues, altering their patterns of reproduction, movement (66), and feeding (99). As the push-pull and attract and reward systems demonstrate, a knowledge of chemical ecology can be exploited in habitat management. More widely, in the presence of predators, herbivores frequently drop from plants (78), consume less or lower-quality food (109), and have elevated stress responses (51) that combine to limit reproduction (74, 103). These fear-based effects can reduce herbivore population growth to an equal or greater extent than direct predation (92), thereby representing an exciting future opportunity for exploitation.

MECHANISMS FOR NATURAL ENEMY ENHANCEMENT

Notwithstanding the potential of vegetation attributes to act directly on pest populations by the mechanisms outlined above, an especially active area of habitat management this century has been the study of natural enemy–mediated effects. Ecological resources most often provided in habitat manipulation research and practice are readily captured in the SNAP mnemonic: shelter, nectar, alternative prey/hosts, and pollen.

Shelter

Most crop habitats, especially annual crops, are not favorable for natural enemies because they are instable and have low heterogeneity with frequent disturbance (121). Noncrop habitats, such as flowering strips, banker plants, and hedgerows, can provide shelter and serve as source habitat for natural enemies, thus maintaining their persistence in agroecosystems (58). With the increasing levels of agricultural intensification and simplification that may occur as a result of the need to increase global crop production, forms of habitat management that can be readily accommodated in conventional crop systems will be evermore important. Local-scale management will also need to be complemented by a greater understanding of the contribution—and scope for manipulation—of the wider landscape because doing so is critical for ensuring the availability of source habitat (62, 76).

In temperate annual systems, many species of natural enemies inhabit noncrop habitats such as field boundaries and perennial grasslands during winter because crop fields are fallow or have only young crop plants and much bare ground with few prey (86). Overwintering habitats such as beetle banks can be artificially created to favor beneficial arthropods in farmlands (17). Hedgerows provide overwintering microsites that are suitable for spiders and beetles, with significantly greater richness and abundance than in field margins and bare ground (96). Hedgerow networks can also act as protection against prevailing wind (100) and extreme temperatures in summer or winter (96, 104), and they provide the additional benefits of higher soil water content and organic carbon level (104). Field margins, whether a hedge, shelterbelt of trees, wall, or water course, may also offer refuge from pesticide spray events and other potential mortality factors such as tillage (72). These features are also sources and dispersal corridors for natural enemies, especially at the start of a cropping phase or after a disturbance event (72, 107), and so play important roles in increasing the diversity of predators (12) such as beetles and spiders (107) and in reducing mortality of natural enemies during migration from or into fields (72, 107).

Nectar

Floral and extrafloral nectars are important food sources that can increase longevity (31, 77), fecundity (3, 94), searching and realized parasitism (22, 73), and predation (149) as well as the female ratio (8) of natural enemies. Nectars are also linked to the developmental and predatory performance of their offspring (3, 148). Because their main component is sugars—glucose, fructose, and sucrose—nectars are important primarily as an energy source (123, 135). Nectars can also contain various amino acids that support insect growth and development (71, 84).

Not all flowering plants, however, are equally suitable for providing nectar to natural enemies (87, 140). Their attractiveness and the accessibility of their nectar vary considerably, such that some flowers fail to attract or reward parasitoids and may even repel them (136). Accordingly, the mere presence of flowering plants is no guarantee of benefit to biological control (an assumption of early habitat management efforts). Rather, the choice of plant species is now widely viewed as a critical consideration. Many factors influence flower species suitability: morphology of parasitoids (132), floral architecture (26, 132, 136), flower color (6), floral area (26), flowering time (45), and nectar chemistry and availability (136). Indeed, some nectars can be toxic (1). Furthermore, floral area (7, 10, 26), spatial availability (113), and competition with other species (11, 45) may limit the value of floral resources to natural enemies (35, 45, 105) in the field. The capacity of predators and parasitoids to move between floral resources and the focal crop is particularly important for optimal design of vegetation in habitat management (65, 105, 127). Extrafloral nectar, which is often found on vegetative plant parts, also extends availability compared with floral nectar, which is available only during blooming (32). It can act as an important food source (31, 50) and an indirect defense allowing plants to recruit predators and parasitoids (32).

Alternative Hosts and Prey

Banker plant systems are the most widely exploited method of providing alternative prey. It was first used in the 1970s (118) and has been adopted in Europe, Japan, the United States, and Canada (48, 88, 129). In this approach, some plants preinfested with an herbivore and its natural enemies are added to a crop. For example, *Carica papaya* is used as a banker plant for the parasitoid *Encarsia sophia* against *Bemisia tabaci* in greenhouse tomato production (144), and *Zea mays* was evaluated to support the predatory midge *Feltiella acarisuga* against *Tetranychus urticae* in greenhouse vegetable production (145). As these examples illustrate, banker plants have been used chiefly in greenhouse systems, but some studies have explored their potential for field use (48, 91). A constraint on the wider use of this method is the lack of consensus on optimal systems even for the most frequently targeted pests. Thus, a research priority is to generate an empirical and theoretical body of understanding of how banker plants, crop species, and alternative hosts interact to affect natural enemy preference, dispersal, and abundance (30).

Pollen

Pollen is mainly a source of proteins and amino acids and can supplement available prey to increase the longevity, fecundity, and impact of predators (21, 85, 130). There is little evidence that parasitoid wasps actively feed on pollen (33), though it may be consumed incidentally in nectar. Compared with a prey-only diet, *Capsicum annuum* pollen can reduce developmental time and increase the longevity, survival, and adult size of *Orius insidiosus* (142). As for nectar, however, care is required in species selection because pollen from some plants is toxic to natural enemies. *Lilium martagon* and *Hippeastrum* sp., for example, cause 100% preimaginal mortality of the predatory mite *Amblyseius swirskii* (36).

Honeydew

Agrienvironmental program (scheme): policy initiative in which payments to farmers aim to promote environmental outcomes such as biodiversity conservation

Aside from the SNAP resources covered above, honeydew can be a major alternative nonprey food source for parasitoids and predators, particularly when nectar is not readily available (24, 137). Generally, however, honeydew is a less suitable food source. Compared with other sugar sources, honeydew has lower nutritional value and can be toxic in some cases (67, 134, 137). Importantly, selection pressure on honeydew producers such as aphids favors traits that minimize any advantage to their natural enemies. Accordingly, honeydew tends to have low detectability (119), high viscosity (24), and compounds that limit its nutritional value to species that may attack the honeydew producer (67). Extrafloral nectar yields the opposite scenario: Here, the producer of the resource is advantaged by attracting and providing nutrition to predators and parasitoids. Reflecting this, although female wasps tend to have greater longevity and fecundity when feeding on honeydew compared with control females provided with water only (24, 143), performance is still greater when they feed on other sugar sources.

MULTIPLE ECOSYSTEM SERVICES AND AGRIENVIRONMENTAL PROGRAMS

A common feature of habitat management strategies that have been well adopted is that they each deliver a range of ecosystem services in addition to pest suppression. The most successful is the push-pull system mentioned above that has been adopted by more than 45,000 farmers in East Africa (60). Driving this remarkably high level of adoption has been the fact that a basket of ecosystem services that are strongly valued by end users has been developed and adapted—via farmer-participatory trials—for use in different crops and geographical parts of Africa.

Recent work in Britain provides a clear example of the potential for habitat management strategies to promote beneficial insects by agrienvironmental programs and to deliver wider benefits including, ultimately, yield enhancement (95). Treatments involved converting either 3% or 8% of a field area from low-yielding crop edges to growing vegetation that supports wildlife. Yields in the interiors of these fields were increased in proportion to the increase of yields over the entire field as a result of enhancing pollinators and natural enemies.

However, the willingness of farmers to participate in landscape-scale programs is questionable, despite potential benefits to both ecosystem services and biodiversity (75). Payments may be important in decisions to participate (23), so examples such as those provided by Pywell et al. (95) are important in illustrating that benefits extend more widely than environmental outcomes—the core business of yield can also be enhanced.

Examples from other continents also illustrate the fact that habitat management can deliver multiple ecosystem services other than pest suppression. In the United States, the use of conservation tillage together with cover crops in the cotton-growing state of Georgia is encouraged by complementing pest control with nitrogen fixation, improved soil structure, water infiltration, and reduced erosion (122). Another multifunction habitat management strategy used native ground-cover plants in New Zealand, where biodiversity enhancement and suppression of lepidopteran pests were complemented with erosion management, filtration of winery effluent, and vineyards actively marketing the aesthetic appeal of ground covers for ecotourism (63). Ground covers may also improve fungus disease control by speeding the decomposition of infected prunings (49) and may enhance an endemic species of butterfly (34). The importance of considering multiple ecosystem services was also stressed in recent work on rice-production landscapes (139).

CONSTRAINTS AND OPPORTUNITIES

A recent review considered how the advent of molecular methods such as DNA barcoding-based gut content analysis and the very recent development of CRISPR/Cas9-based gene editing are addressing constraints on conservation biological control (41). Accordingly, this section explores other agronomic, ecosystem, and practical constraints to identify key opportunities for future progress.

Ecosystem disservices (EDS): the negative effects on humanity from biodiversity and its processes

Ecosystem service provider: an organism, interaction network, or habitat that provides ecosystem services (e.g., a hedgerow or woodland)

Service-providing unit: the individuals of one species responsible for providing an ecosystem service to a required level

Agronomic Constraints

Implementing habitat management can require investment in labor, fuel, capital depreciation, and seed. It may also present agronomic challenges such as whether an introduced plant is tall enough to cause impeded airflow, which can lead to frost and disease damage to vines (80). Some practices such as the creation of beetle banks require taking part of the cropping area out of production, which lowers yield (17). Other agronomic problems may arise if growers do not follow recommended habitat management protocols. For example, if added flowers are drilled at an unsuitable time, then species such as buckwheat (*Fagopyrum esculentum*) may be killed by frosts (56) or they may bloom too late to benefit the targeted natural enemy (16). Similarly, the location of flowering strips should be based on knowledge of the dispersal ability of the targeted natural enemy, which can be obtained in studies labeling the plant's nectar with markers such as rubidium chloride (65, 89).

Ecosystem Disservices

Habitat manipulation can have specific unintended negative impacts that promote ecosystem disservices (EDS). For example, the added vegetation may compete with the crop for water, minerals, and light or be allelopathic to the crop (147). Further, some plants used in habitat management may compete with crops for pollinators (47). Perhaps the most important disservice associated with added floral resources is that pests may also feed on them. Begum et al. (5) demonstrated that the fecundity of the moth pest *Epiphyas postvittana* was significantly enhanced by the availability of some nectar plants and stressed the need to identify selective species that allowed feeding only by parasitoids.

The complexities of the wider food web also need to be considered. For example, mealybugs on vines are tended by ants that harvest the mealybug honeydew and prey on many of its natural enemies, including parasitoids, which might otherwise reduce pest numbers (20). Mealybugs also feed on some noncrop plants (42), making the choice of habitat management strategy significant because the naive addition of flowering plants to this food web could exacerbate pest problems (141). To reduce these potential EDS, habitat manipulation modeling can be implemented to enhance pest control by natural enemies (57). More recently, modeling has been used to predict land-use impact on biological control effectiveness and crop damage by pests (53). Similar sophisticated modeling could be used to design robust conservation biological control programs that avoid EDS. However, during the research phase, the extent to which habitat management reduces pest damage as well as a full knowledge of potential EDS need to be established before protocols are deployed. To facilitate this, an ecosystem service provider (such as a strip of flowers of a given species) that supports a service-providing unit (such as parasitoid of a particular type) needs to be clearly identified. To effect grower adoption, however, the further step of developing a service-providing protocol is necessary. This protocol should include all the appropriate and necessary agronomic, floral, and seasonal characteristics so it can be readily implemented by growers.

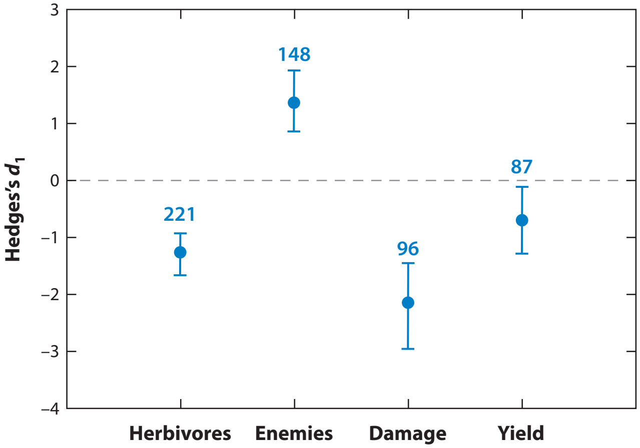

Figure 2

Results of a meta-analysis (68) showing the effects of diverse cropping strategies compared with less diverse systems. Points indicate mean effect size, bars reflect bootstrap confidence intervals, and values are the number of experiments for each parameter. Herbivores decreased significantly, whereas natural enemies were significantly more abundant. Though crop damage was significantly reduced, yields also declined significantly (but see text). Reproduced with permission from Letourneau et al. (68).

Quantitative Analyses of Success and Failure

The now-substantial body of literature on habitat management allows for powerful analyses in which the outcomes of multiple studies are quantitatively assessed. Letourneau et al. (68) considered 552 experiments from 45 articles published between 1998 and 2008, concluding that diversified crops had more natural enemies, fewer pests, and less crop damage than did comparable crops with no or fewer associated plant species (**Figure 2**). An important cautionary finding indicated that a small but significant overall decrease in crop yield can occur in some cases; however, experimental designs in which plants were included in a crop system in an additive (58), rather than substitutive (110), manner exhibited yield increases. Letourneau et al. (68) suggested that future efforts will need to focus on plant species that can be added to a crop with minimal disruptive effect on crop growth while maximizing the extent of benefit from natural enemy enhancement and pest suppression.

The field of intercropping, which is most often pursued explicitly for greater productivity (e.g., 4), potentially offers much to habitat management in terms of useful strategies to maximize the positive outcomes of crop interactions. One general limitation of the meta-analysis of Letourneau et al. (68) was that it considered only the yield of the focal crop and not the yield of the additional plant species, even when the latter was a value crop. Thus, habitat management strategies may be advantageous even when the focal crop produces a lower yield, provided that the secondary crop produces a valuable commodity or other ecosystem services or that it is the target of conservation efforts (25) so it could potentially attract payments to the farmer from an agrienvironmental program (138). A more specific limitation was that, among the studies available for inclusion, crop damage was measured only in annual crops in tropical systems. Thus, there is a clear need for future studies to include yield assessment, particularly for perennial tropical crops and all crop systems in temperate systems.

Recent farmer-participatory work in Asian rice has been unusually comprehensive in evaluating the effects of strips of flowering crops such as sesame and sunflower grown on otherwise unused ridges around rice crops to provide nectar to natural enemies (**Figure 1**). These crops increased

Figure 3

Nectar plant borders added to rice fields promote biological pest control, leading to a trophic cascade that increases grain yields and provides economic advantage (38). Photo credit: H.V. Chien.

rice pest parasitism, leading to reduced planthopper densities to the extent that farmers applied 70% fewer sprays and increased rice yields by 5%. The costs of establishing and harvesting produce from the bordering crops were more than offset by the value of the increased rice yield and savings from fewer sprays, leading to an overall 7.5% economic advantage (38) (**Figure 3**). Detritivore densities also were increased under the regime of reduced insecticide use.

FUTURE PRIORITIES AND PROSPECTS

Aside from an increasingly rigorous foundation of theoretical and empirical work, coupled with farmer participation to develop locally appropriate forms of implementation and effective dissemination, the level of uptake of a habitat management strategy is largely driven by the extent to which a range of ecosystem services is provided. Researchers need to be reminded that farmers manage complex agricultural business systems and are not focused on pests in isolation. Biodiversity can be enhanced in farming systems without a yield penalty (15), and appropriate management of vegetation can promote human well-being as well as ecosystem services and crop yield (14). In the Future Issues section (below), we draw attention to the lines of research we consider most important as habitat management for pest population suppression is embraced by a new generation of scientists.

SUMMARY POINTS

1. Since habitat management for pest suppression first began in the 1970s, ecologists have sought to explain and test aspects of ecological theory, particularly the relative importance of bottom-up and top-down effects on pest populations. This continues with increasing attention on theories related to biodiversity and ecosystem function as well as hypotheses of the effects of landscape on local habitat manipulation.
2. Though many studies demonstrate that natural enemy enhancement by habitat management can lead to pest suppression, syntheses of the available evidence suggest that bottom-up effects that operate independently of predators and parasitoids may be at least as powerful in terms of pest suppression.

3. Farmer participation in habitat management, particularly in the development of locally appropriate strategies (that are based on broad principles derived from more formal research), is likely to be increasingly important for developing locally appropriate habitat management strategies that deliver a basket of ecosystem services as well as encourage wider uptake.
4. The distillation of theoretical and empirical knowledge into service-providing protocols that constitute clear guidelines for growers will be important in promoting uptake.
5. The pattern of land use in the landscape as far as several kilometers from a focal field can markedly influence pest and natural enemy numbers and moderate the impact of local habitat management efforts. However, much remains to be learned about the interplay across spatial scales and the underlying ecological mechanisms.
6. Habitat management for pest suppression is being used in several continents, and adoption appears strongest when a basket of ecosystem services is delivered.
7. Habitat management can strongly promote ecosystem services. Thus, it offers much to the grand challenge of sustainable intensification to meet the escalating needs of humanity while minimizing adverse impacts on the biodiversity on which we ultimately depend.

FUTURE ISSUES

1. Future workers need to assess the effects on crop productivity to remedy the relative paucity of data on crop yield in habitat manipulation studies. This is particularly necessary for perennial tropical crops and all crop systems in temperate systems.
2. Though mechanisms to promote natural enemy function are commonly explored, more work on the bottom-up effects of vegetation on pests is needed to understand their relative importance and scope for exploitation.
3. The field of habitat management for pest population suppression is now well established and increasingly multidisciplinary. Further progress requires closer cooperation among practitioners as diverse as agronomists, landscape geographers, molecular biologists, chemical ecologists, and ecological economists.
4. Future habitat management efforts need to better address real-world complexities including the spatial and temporal effects in agricultural landscapes as well as a wider range of natural enemies (such as nematodes and microbes). They also need to consider below- and aboveground interactions as well as the nonconsumptive effects of natural enemies.
5. Longer-term studies of habitat management are needed because most studies have been short in duration and thus unable to reveal the effects of maturing vegetation and changes in the environment. For example, still unclear are the impacts of pesticide and genetically modified crop use, shifts in land use in the surrounding landscape, and global warming.
6. The extent to which habitat management strategies can deliver a basket of ecosystem services appears to be a key driver for adoption. However, experimental studies of the trade-offs and additive or synergistic interactions among multiple ecosystem services are urgently needed.

7. Agrienvironmental programs in which farmers are paid for stewardship activities offer opportunities for promoting habitat manipulation in which vegetation of conservation value are used to promote pest suppression. Yet, more research is required on the effects differing plant taxa that native to various regions have on pests and natural enemies.

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RELATED RESOURCES

Greening Waipara, Bioprotection Research Center (**http://bioprotection.org.nz/research/programme/greening-waipara**): regional-scale research program promoting the delivery of ecosystem services including pest suppression

Vinh Long Television (Công nghệ sinh thái) (**https://ricehoppers.net/tag/tv-vinh-long-series-on-ecological-engineering/**): mass media programming used to promote habitat management; one episode ran on national television in Vietnam and was awarded the Gold Medal in Science Education at the 32nd National Television Festival December 19–22, 2012, held in Vinh City, Nghe An, Vietnam (see Heong K, Escalada M, Chien H, Cuong L. 2014. Restoration of rice landscape biodiversity by farmers in Vietnam through education and motivation using media. *S.A.P.I.EN.S* 7:7.2)