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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 sub-discipline 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 and 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 implementation globally. 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 (65), the field has expanded dramatically. Reflections of this include the fact that this article has been cited over 1,000 times and web searches reveal a high level of research activity and on-farm implementation. A great deal has changed in the seventeen years since that review was written including the publication of several excellent reviews of related fields (18; 107; 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 (65) 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.

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 (91), seven act independently of natural enemies. Essentially these direct mechanisms involve disrupting herbivore capacity to locate a suitable host plant by: visual or chemical stimuli (102) that may act by repelling pests from the crop (128), trapping herbivores on a plant other than the crop (47), blocking movement of herbivores with tall vegetation (84), 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 of these strategies involve the incorporation of secondary and tertiary crop species (i.e. intercropping), whilst others employ non-crop 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 the crop to repel pests a second 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 (61; 62). Work this century has greatly expanded our understanding of the importance of larger scale effects extending to the landscape and region (57; 82; 120) with the level of research activity in this area requiring a recent review to consider evidence for multiple hypotheses (126).

The direct and natural enemy-mediated effects of vegetation on pests are viewed by ecologists 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). This effect was referred to as the resource concentration hypothesis by Root (102). In contrast, top-down effects refer to the action of natural enemies (third trophic level) on herbivores and is known also as the enemies hypothesis (102). This operates by habitat management providing plants that support predators and parasitoids with foods such as nectar and pollen, alternative prey or host species, or by abiotic mechanisms such as providing a moderated microclimate, or serving as source habitat from which crops are colonized (65). 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 reducing mortality of biological control agents from pesticide use (37), an important issue given the estimated use of 3.5 billion kilograms per annum (94). This can be accomplished by the adoption of integrated pest management (94) or switching from broad spectrum insecticides to others such as insect growth regulators (39). Importantly, habitat management often has effects other than on pest management; on pollinators, detritivores and weeds for example. As explored below, the associated ecosystem services (or sometimes dis-services) can lead to broader effects on agricultural systems including contributing to sustainable intensification.

<Fig 1 here>

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 between plants, herbivores, and natural enemies is also beginning to inform habitat management practices (117). Reflecting these effects, habitat management has been referred to as ‘ecological engineering’ by some recent authors, e.g. (149).

Biodiversity and Ecosystem Function

Ecologists have been intensely interested in the relationship between biodiversity and ecosystem function (70; 112). Altieri (2) was among the first to outline the role of biodiversity in the function of pest suppression in agroecosystems. Several decades of subsequent empirical and theoretical studies have refined our understanding. Snyder and Tylianakis (116) reviewed the relationship between biodiversity and biocontrol of pests and showed that pest suppression may either increase, decline, or be unchanged by increased natural enemy diversity. Enhanced pest suppression can occur as a result of complementarity between natural enemies or by facilitation (71). 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, has also been shown to be 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 and Barton (109) developed a theoretical framework for predicting how habitat management outcomes may shift with climate change. Increasing biodiversity increases ecosystem function in plant communities, but does so more incrementally in mature versus immature ones (99). This suggests that as the 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, 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

(96). Crop yields in the diversified fields increased compared with control fields to an extent that tended to be greater in each of the successive five years after the experimental interventions.

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 to predictions of effective conservation biological control (107; 124). A specific predication is that local habitat management (e.g. creation of diverse floral resource habitats) will increase the 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 to that already present (125). Several recent tests have provided support of this "intermediate landscape complexity" hypothesis (57; 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, while β-diversity was related to increasing functionality only in landscapes lacking high overall diversity (83). Because agricultural landscapes often lack high γ-diversity, the use of habitat management to increase β-diversity will likely be important to maintain or enhance multiple functions in addition to pest suppression (e.g. pollination, decomposition, and crop productivity).

This could include adding perennial plant strips into largely annual crop landscapes while resources in perennial crops (e.g. orchards) may be best enhanced by annual plants.

Several recent meta-analyses have examined the role of landscape structure on natural enemies and pest suppression and support an emerging consensus. Increasing landscape complexity, typically via inclusion of non-crop habitat, almost always increases natural enemy abundance and diversity (9). While pest diversity also frequently increases, pest abundance typically declines or remains unchanged. The ecosystem functions of predation and parasitism typically increase, while pest population growth rates typically decline (13; 103; 113; 133). More recent work has shown that the extent of disturbance in an agricultural landscape can also have a strong effect (55). Finally, while based on far fewer studies, herbivory and plant damage typically declines or remains unchanged (13). While this collection of empirical studies suggests the potential for generalization, it remains to be seen if this knowledge can further improve the predictability of habitat management approaches. Such efforts may be supported by modelling, which offers scope to minimize the logistical complexities of research at the landscape scale which should consider temporal as well as spatial effects (107).

Chemical Ecology and Non-consumptive 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 (98), and this information is being used to inform habitat management. When attacked by herbivores (or even 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 can also work with floral resource patches to “attract and reward” natural enemies (115). HIPV’s have also been used in “push-pull” strategies to repel herbivores from crop plants while simultaneously attracting them to nearby trap plants (60).

Herbivorous insects can monitor their environment to detect information on the occurrence of natural enemies and alter their behavior to avoid danger. For example, they can detect visual (53) and chemical (45; 80) cues identifying the actual or potential presence of predators. They adjust their behavior in response to these cues, altering patterns of reproduction, movement (67) and feeding (100). In the presence of predators, herbivores frequently drop from plants (79), consume less or lower quality food (110), and have elevated stress responses (52) that combine to limit reproduction (75; 104). Moreover, these fear-based effects can reduce herbivore population growth to an equal or greater extent than direct predation (93) so represent 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 on natural enemy-mediated effects. The ecological resources most often provided in habitat manipulation research and practice are readily captured in the SNAP mnemonic: shelter, nectar, alternative prey and hosts, and pollen.

Shelter (S)

Most crop habitats, especially annual crops, are not favorable for natural enemies because of their instability and low heterogeneity with frequent disturbance (121). Non-crop 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 (60). 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 ever more 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 since this is critical for ensuring availability of source habitat (63; 77).

In temperate annual systems, many species of natural enemies inhabit non-crop habitats such as field boundaries and perennial grasslands during the winter because the crop fields are fallow or have only young crop plants and much bare ground with few prey (87). Overwintering habitats such as beetle banks can be artificially created to favour beneficial arthropods in farmlands (17). Hedgerows provide overwintering micro-sites which are suitable for spiders and beetles, with significantly higher richness and abundance than in field margins and bare ground (97). Hedgerow networks can also act as a protection against prevailing wind (101) and extreme temperatures in summer or winter (97; 105), and provide the additional benefits of higher soil water content and organic carbon level (105). Field margins, whether a hedge, shelterbelt of trees, wall, or water course potentially also offer refuge from pesticide spray events and other potential mortality factors such as tillage (73). These features are also sources and dispersal corridors for natural enemies, especially at the start of a cropping phase or after a disturbance event (73; 108) and so play important roles in increasing the diversity of predators (12) such as beetles and spiders (108), and reducing mortality of the natural enemies during migration from or into the fields (73; 108).

Nectar (N)

Floral and extrafloral nectars are important food sources that can increase longevity (32; 78), fecundity (3; 95), searching and realised parasitism (22; 74), predation (149) as well as female ratio (8) of natural enemies, and are even linked to the developmental and predatory performance of their offspring (3; 148). The main component of nectars is sugars - glucose, fructose and sucrose - so nectar is important primarily as an energy source (123; 135). Nectars can also contain various amino acids that support the growth and development of insects (72; 85).

Not all flowering plants, however, are equally suitable for providing nectar to natural enemies (88; 140), varying considerably in their attractiveness and the accessibility of nectar 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, plant species choice 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 (46), and nectar chemistry and availability (136). Indeed, some nectars can be toxic (1). Further, floral area (7; 10; 26), spatial availability (114), and competition with other other species (11; 46) may limit the value of floral resources to natural enemies (34; 46; 106) 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 managenent (66; 106; 127).

Extrafloral nectar which is often found on vegetative plant parts extends availability compared to floral nectar, which is available only during blooming (31). It can act as an important food source (32; 51) and an indirect defense allowing the plants to recruit predators and parasitoids (31).

Alternative hosts and prey (A)

The most widely exploited way to provide alternative prey is banker plant systems which involve adding to a crop some plants pre-infested with a herbivore together with its natural enemies (30; 49). This approach began in the 1970s (118), and has been adopted in Europe, Japan, USA and Canada (49; 89; 129). 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 as for supporting 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 potential for field use (49; 92). A constraint on the wider use of this form of habitat management is that there is little consensus on optimal systems even for the most frequently targeted pests so 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 (P)

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; 86; 130). There is little evidence that parasitoid wasps actively feed on pollen (33), though it may be consumed incidentally in nectar. Compared to a prey-only diet, *Capsicum annuum* pollen can reduce the 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

Aside from the "SNAP" resources covered above, honeydew can be a major alternative non-prey food source for parasitoids and predators, particularly when nectar is not readily available (24; 137). Generally, however, honeydew is a less suitable food source, with lower nutrional value compared with other sugar sources and can be toxic in some cases (68; 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 (68). This is the opposite scenario to extrafloral nectar where 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 to the control females provided with water only (24; 143), performance is still greater when fed other sugar sources (24; 143).

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 case is the "push-pull" system referred to above that has been adopted by more than 45,000 farmers in East Africa (61). 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 deliver wider benefits including, ultimately, yield enhancement (96). Treatments involved the conversion of either 3 or 8% of the field area from low-yielding crop edges to grow vegetation to support wildlife. Yields in the interiors of these fields were increased to the extent that yields over the scale of whole fields were enhanced as a result of the enhancement of pollinators and natural enemies.

It has been noted that the willingness of farmers to participate in landscape-scale programs, is questionable despite scope for benefits to both ecosystem services and biodiversity (76). Payments may be important in decisions to participate (23) so examples like those provided by Pywell et al (96) 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 USA, the use of conservation tillage together with cover crops in the important cotton growing state of Georgia, is encouraged by pest control being complemented by nitrogen fixation, improved soil structure, water infiltration and reduced erosion (122). Another multi-function habitat management strategy used native ground cover plants in New Zealand where biodiversity enhancement and suppression of lepidopteran pests were complemented by erosion management, filtration of winery effluent and vineyards actively marketing the aesthetic appeal of groundcovers for ecotourism (64). Groundcovers can also potentially improve fungus disease control by speeding the decomposition of infected prunings (50) and enhance an endemic species of butterfly (35). The importance of considering multiple ecosystem services was also stressed in recent work on rice production landscapes (139).

CONSTRAINTS AND OPPOURTUNITIES

A recent review has 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, is addressing constraints on conservation biological control (41). Accordingly, this section explores other constraints of an agronomic, ecosystem and practical nature in order to identify key opportunities for future progress.

Agronomic Constraints

Implementing habitat management can require investment in the form of labor, fuel, capital depreciation and seed and may present agronomic challenges such as an introduced plant being tall enough to impede air flow which can lead to frost damage to vines (81). Some practices, such as the creation of beetle banks, require part of the cropping area to be taken out of production so lowering yield (17). Other agronomic problems may arise if growers do not follow recommended habitat management protocols. For example, the added flowers may be drilled at an unsuitable time leading to species such as buckwheat (*Fagopyrum esculentum*) being killed by frosts (58) or to 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 labelling the plant's nectar with markers such as rubidium chloride (66; 90).

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 (48). Perhaps the most important disservice associated with added floral resources is that pests may potentially also feed on them. Begum et al (5), demonstrated 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 otherwise have the potential to reduce pest numbers (20). Mealybugs themselves also feed on some non-crop plants (42), making the choice of habitat management strategy significant because the naïve addition of flowering plants to this food web could exacerbate pest problems (141). To reduce these potential EDS, habitat manipulation modelling can be implemented to enhance pest control by natural enemies (59). More recently modelling has been used to predict land use impact on biological control effectiveness and crop damage by pests (54). Similar sophisticated modelling could potentially be used to design robust conservation biological control programs that avoid EDS. However, it is important that 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 deployment of the protocols. To facilitate this, a clear 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 identified. To effect grower adoption, however, the further step of developing a Service Providing Protocol (SPP) is necessary. This should include all the appropriate and necessary agronomic, floral, and seasonal characteristics so that such a 'recipe' can be readily implemented by growers.

Quantitative Analyses of Success and Failure

The now substantial body of literature on habitat management allows powerful analyses in which the outcomes of multiple studies are quantitatively assessed. Letourneau, et al. (69) considered 552 experiments from 45 articles published between 1998 and 2008. The same data were included in an earlier review (91) in which a 'vote counting' approach was used in which the outcomes of statistical tests are simply tallied showed that vegetation diversification reduced densities of herbivores in around half of cases. However, a meta-analysis approach in which effect sizes are used is superior to vote counting because the latter is overly conservative and does not consider the relative size of effects (69). The main conclusion from that meta-analysis was 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**). Whilst this finding lends strong support to the habitat management approach, an important cautionary finding was that there was a small but significant overall decrease in crop yield evident in papers in which yield had been assessed. The analysis did, however, point to how yield might be increased in vegetation diversification because experimental designs in which plants were included in a crop system in an additive (60), rather than substitutive (111), manner exhibited yield increases. That is, strategies such as reducing the area of land over which a crop is grown in order to accommodate a second plant species can lead to a reduction in yield of the focal crop. Letourneau et al (69) suggest that future efforts need to focus on plant species that can be added to a crop with minimal disruptive effect on crop growth whilst maximizing the extent of benefit from natural enemy enhancement and pest suppression.

<Fig 2 here>

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 Letourneau's meta-analysis (69) 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 itself a crop of value. Thus habitat management strategies may be advantageous even when the focal crop does produce a lower yield provided that the secondary crop produces a valuable commodity or other ecosystem services, or is the target of conservation efforts (25) so potentially attracting payments to the farmer from an agrienvironmental program (138). A more specific limitation of that meta-analysis was that, amongst 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 and particularly so for perennial tropical crops and crop systems of all types in temperate systems. In an analysis in which all effects (pests, natural enemies, crop damage and yield) were pooled (69), the strongest benefits resulted from the use of “push-pull” or trap plants within the field.

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

<Fig 3 here>

FUTURE PRIORITIES & 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 rather than being 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 wellbeing as well as ecosystem services and crop yield (14). In the Future Issues box 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. From the beginning of habitat management for pest suppression 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 and this continues with increasing attention on theories related to biodiversity and ecosystem function as well as hypotheses for 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 the development of locally-appropriate strategies (that are based on broad principles derived from more formal research) are likely to be increasingly important for developing locally-appropriate habitat management strategies that deliver a basket of ecosystem services, as well as in encourage wider uptake.
4. The distillation of theoretical and empirical knowledge into Service Providing Protocols (SPPs) 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 but 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 so offers much to the grand challenge of sustainable intensification to meet the escalating needs of humanity whilst minimizing adverse impacts on biodiversity upon which we ultimately depend.

FUTURE ISSUES

1. The relative paucity of crop yield data in habitat manipulation studies needs to be remedied by future workers assessing effects on crop productivity; particularly so for perennial tropical crops and crop systems of all types in temperate systems.
2. Though mechanisms to promote natural enemy function are commonly explored there is a need for more work on bottom-up effects of vegetation on pests so that the relative importance and scope for exploitation are better understood.
3. The field of habitat management for pest population suppression is now well established and increasingly multidisciplinary. Further progress requires closer cooperation between fields such as diverse as agronomists, landscape geographers, molecular biologists, chemical ecologists and ecological economists.
4. Future habitat management efforts need to better address real world complexity including spatial and temporal effects in agricultural landscapes as well as a wider range of natural enemies (including nematodes and microbes), and consider below- as well as above-ground interactions, and non-consumptive effects of natural enemies.
5. There is a need for longer-term studies of habitat management because most studies have been short in duration so unable to reveal the effects of maturing vegetation and changes in the environment such as to pesticide and genetically modified crop use patterns, 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 but an urgent research need is for experimental studies of the trade-offs and additive or even synergistic interactions among multiple ecosystem services.
7. Agrienvironmental programs in which farmers are paid for stewardship activities offer opportunities for promoting habitat manipulation in which vegetation types of conservation value are used to promote pest suppression. But more research is a required on the effects of differing plant taxa, native to various regions, on pests and natural enemies.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding or financial holdings that might be perceived as affecting the objectivity of this review.

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LITERATURE CITED

1. Adler LS. 2000. The ecological significance of toxic nectar. *Oikos* 91:409-20
2. Altieri MA. 1994. *Biodiversity and pest management in agroecosystems*. New York: The Haworth Press. 185 pp.
3. Amoros-Jimenez R, Pineda A, Fereres A, Marcos-Garcia MA. 2014. Feeding preferences of the aphidophagous hoverfly *Sphaerophoria rueppellii* affect the performance of its offspring. *BioControl* 59:427-35
4. Bedoussac L, Journet E-P, Hauggaard-Nielsen H, Naudin C, Corre-Hellou G, et al. 2015. Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. *Agron. Sustain. Dev.* 35:911-35
5. Begum M, Gurr GM, Wratten SD, Hedberg PR, Nicol HI. 2006. Using selective food plants to maximize biological control of vineyard pests. *J. Appl. Ecol.* 43:547-54
6. Begum M, Gurr GM, Wratten SD, Nicol HI. 2004. Flower color affects tri-trophic-level biocontrol interactions. *Biol. Control* 30:584-90
7. Bennett AB, Gratton C. 2012. Measuring natural pest suppression at different spatial scales affects the importance of local variables. *Environ. Entomol.* 41:1077-85

8. Berndt LA, Wratten SD. 2005. Effects of alyssum flowers on the longevity, fecundity, and sex ratio of the leafroller parasitoid *Dolichogenidea tasmanica*. *Biol. Control* 32:65-9
9. Bianchi F, Booij CJH, Tscharntke T. 2006. Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 273:1715-27
10. Blaauw BR, Isaacs R. 2012. Larger wildflower plantings increase natural enemy density, diversity, and biological control of sentinel prey, without increasing herbivore density. *Ecol. Entomol.* 37:386-94
11. Campbell AJ, Biesmeijer JC, Varma V, Wackers FL. 2012. Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity. *Basic Appl. Ecol.* 13:363-70
12. Cardarelli E, Bogliani G. 2014. Effects of grass management intensity on ground beetle assemblages in rice field banks. *Agriculture, Ecosystems & Environment* 195:120-6
13. Chaplin-Kramer R, O'Rourke ME, Blitzer EJ, Kremen C. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14:922-32
14. Classen A, Peters MK, Ferger SW, Helbig-Bonitz M, Schmack JM, et al. 2014. Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 281:20133148
15. Clough Y, Barkmann J, Juhrbandt J, Kessler M, Wanger TC, et al. 2011. Combining high biodiversity with high yields in tropical agroforests. *Proc. Natl. Acad. Sci. USA* 108:8311-6
16. Colley MR, Luna JM. 2000. Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). *Environ. Entomol.* 29:1054-9
17. Collins KL, Boatman ND, Wilcox A, Holland JM. 2003. Effects of different grass treatments used to create overwintering habitat for predatory arthropods on arable farmland. *Agric., Ecosyst. Environ.* 96:59-67
18. Cook SM, Khan ZR, Pickett JA. 2007. The use of push-pull strategies in integrated pest management. *Annu. Rev. Entomol.* 52:375-400
19. Crowder DW, Northfield TD, Strand MR, Snyder WE. 2010. Organic agriculture promotes evenness and natural pest control. *Nature* 466:109-12
20. Daane KM, Sime KR, Fallon J, Cooper ML. 2007. Impacts of Argentine ants on mealybugs and their natural enemies in California's coastal vineyards. *Ecol. Entomol.* 32:583-96
21. De Clercq P, Bonte M, Van Speybroeck K, Bolckmans K, Deforce K. 2005. Development and reproduction of *Adalia bipunctata* (Coleoptera: Coccinellidae) on eggs of *Ephestia kuehniella* (Lepidoptera: Phycitidae) and pollen. *Pest Manage. Sci.* 61:1129-32
22. Diaz MF, Ramirez A, Poveda K. 2012. Efficiency of different egg parasitoids and increased floral diversity for the biological control of noctuid pests. *Biol. Control* 60:182-91
23. Engel S, Pagiola S, Wunder S. 2008. Designing payments for environmental services in theory and practice: An overview of the issues. *Ecol. Econ.* 65:663-74
24. Faria CA, Wäckers FL, Turlings TCJ. 2008. The nutritional value of aphid honeydew for non-aphid parasitoids. *Basic Appl. Ecol.* 9:286-97
25. Fiedler AK, Landis DA. 2007. Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. *Environ. Entomol.* 36:751-65

26. Fiedler AK, Landis DA. 2007. Plant characteristics associated with natural enemy abundance at Michigan native plants. *Environ. Entomol.* 36:878-86

27. Finch S, Collier RH. 2000. Host-plant selection by insects – a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. *Entomol. Exp. Appl.* 96:91-102

28. Finke DL, Denno RF. 2004. Predator diversity dampens trophic cascades. *Nature* 429:407-10

29. Foti MC, Rostas M, Peri E, Park KC, Slimani T, et al. in press. Chemical ecology meets conservation biological control: Identifying plant volatiles as predictors of floral resource suitability for an egg parasitoid of stink bugs. *J Pest Sci*

30. Frank SD. 2010. Biological control of arthropod pests using banker plant systems: Past progress and future directions. *Biol. Control* 52:8-16

31. Géneau C, Wackers FL, Luka H, Daniel C, Balmer O. 2012. Selective flowers to enhance biological control of cabbage pests by parasitoids. *Basic Appl. Ecol.* 13:85-93

32. Géneau CE, Wäckers FL, Luka H, Balmer O. 2013. Effects of extrafloral and floral nectar of *Centaurea cyanus* on the parasitoid wasp *Microplitis mediator*: Olfactory attractiveness and parasitization rates. *Biol. Control* 66:16-20

33. Gillespie M, Gurr GM, Wratten SD. 2016. Beyond nectar provision: The other resource requirements of parasitoid biological control agents. *Entomologia Experimentalis et Applicata In press*

34. Gillespie M, Wratten S, Sedcole R, Colfer R. 2011. Manipulating floral resources dispersion for hoverflies (Diptera: Syrphidae) in a California lettuce agro-ecosystem. *Biol. Control* 59:215-20

35. Gillespie M, Wratten SD. 2013. Enhancing nectar provision in vineyard habitats for the endemic New Zealand butterfly, *Lycaena salustius*. *N. Z. J. Ecol.* 37:67-74

36. Goleva I, Zebitz CP. 2013. Suitability of different pollen as alternative food for the predatory mite *Amblyseius swirskii* (Acari, Phytoseiidae). *Exp. Appl. Acarol.* 61:259-83

37. Guedes RNC, Smagghe G, Stark JD, Desneux N. 2016. Pesticidal stresses in arthropod pests for optimized integrated pest management programs. *Annu. Rev. Entomol.* 61

38. Gurr GM, Lu Z, Zheng X, Xu H, Zhu P, et al. 2016. Multi-country evidence that crop diversification promotes ecological intensification of agriculture. *Nature Plants*:16014

39. Gurr GM, Thwaite WG, Nicol HI. 1999. Field evaluation of the effects of the insect growth regulator tebufenozide on entomophagous arthropods and pests of apples. *Aust. J. Entomol.* 38:135-40

40. Gurr GM, Wratten SD, Snyder WE, eds. 2012. *Biodiversity and Insect Pests: Key Issues for Sustainable Management*. UK: John Wiley & Sons. 347 pp.

41. Gurr GM, You M. 2016. Conservation biological control of pests in the molecular era: New opportunities to address old constraints. *Frontiers in plant science* 6:1255

42. Gutierrez AP, Daane KM, Ponti L, Walton VM, Ellis CK. 2008. Prospective evaluation of the biological control of vine mealybug: refuge effects and climate. *J. Appl. Ecol.* 45:524-36

43. Haddad NM, Crutsinger GM, Gross K, Haarstad J, Tilman D. 2011. Plant diversity and the stability of foodwebs. *Ecol. Lett.* 14:42-6

44. 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

45. Hermann SL, Thaler JS. 2014. Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. *Oecologia* 176:669-76
46. Hogg BN, Bugg RL, Daane KM. 2011. Attractiveness of common insectary and harvestable floral resources to beneficial insects. *Biol. Control* 56:76-84
47. Hokkanen HMT. 1991. Trap cropping in pest management. *Annu. Rev. Entomol.* 36:119-38
48. Holzschuh A, Dudenhöffer J-H, Tscharntke T. 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biol. Conserv.* 153:101-7
49. Huang NX, Enkegaard A, Osborne LS, Ramakers PMJ, Messelink GJ, et al. 2011. The banker plant method in biological control. *Crit. Rev. Plant Sci.* 30:259-78
50. Jacometti MA, Wratten SD, Walter M. 2007. Understorey management increases grape quality, yield and resistance to *Botrytis cinerea*. *Agriculture, Ecosystems & Environment* 122:349-56
51. Jamont M, Crepelliere S, Jaloux B. 2013. Effect of extrafloral nectar provisioning on the performance of the adult parasitoid *Diaeretiella rapae*. *Biol. Control* 65:271-7
52. Janssens L, Stoks R. 2013. Predation risk causes oxidative damage in prey. *Biol. Lett.* 9:20130350
53. Jones E, Dornhaus A. 2011. Predation risk makes bees reject rewarding flowers and reduce foraging activity. *Behav Ecol Sociobiol* 65:1505-11
54. Jonsson M, Bommarco R, Ekbom B, Smith HG, Bengtsson J, et al. 2014. Ecological production functions for biological control services in agricultural landscapes. *Methods Ecol. Evol.* 5:243-52
55. Jonsson M, Buckley HL, Case BS, Wratten SD, Hale RJ, Didham RK. 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. *Journal of Applied Ecology* 49:706-14
56. Jonsson M, Straub CS, Didham RK, Buckley HL, Case BS, et al. 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *Journal of Applied Ecology* 52:1274-82
57. Jonsson M, Straub CS, Didham RK, Buckley HL, Case BS, et al. 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *J. Appl. Ecol.*:doi: 10.1111/365-2664.12489
58. Kalinova J, Moudry J. 2003. Evaluation of frost resistance in varieties of common buckwheat (*Fagopyrum esculentum* Moench.). *Plant Soil and Environment* 49:410-3
59. Kean J, Wratten S, Tylianakis J, Barlow N. 2003. The population consequences of natural enemy enhancement, and implications for conservation biological control. *Ecol. Lett.* 6:604-12
60. Khan ZR, James DG, Midega CAO, Pickett JA. 2008. Chemical ecology and conservation biological control. *Biol. Control* 45:210-24
61. Khan ZR, Midega CAO, Pittchar J, Bruce TJA, Pickett JA. 2012. 'Push–Pull' Revisited: The Process of Successful Deployment of a Chemical Ecology Based Pest Management Tool. In *Biodiversity and Insect Pests: Key Issues for Sustainable Management*, ed. G Gurr, S Wratten, WE Snyder, DMY Read:259-75. UK: John Wiley & Sons, Ltd. Number of 259-75 pp.
62. Khan ZR, Pickett JA, van den Berg J, Wadhams LJ, Woodcock CM. 2000. Exploiting chemical ecology and species diversity: stem borer and striga control for maize and sorghum in Africa. *Pest Manage. Sci.* 56:957-62
63. Kleijn D, Rundlöf M, Scheper J, Smith HG, Tscharntke T. 2011. Does conservation on farmland contribute to halting the biodiversity decline? *Trends Ecol. Evol.* 26:474-81

64. Landis DA, Gardiner MM, Tompkins J. 2012. Using native plant species to diversify agriculture. In *Biodiversity and insect pests: key issues for sustainable management*, ed. GM Gurr, SD Wratten, WE Snyder:276-92. UK: John Wiley & Sons. Number of 276-92 pp.
65. Landis DA, Wratten SD, Gurr GM. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45:175-201
66. Lavandero B, Wratten S, Shishehbor P, Worner S. 2005. Enhancing the effectiveness of the parasitoid *Diadegma semiclausum* (Helen): Movement after use of nectar in the field. *Biol. Control* 34:152-8
67. Lee D-H, Nyrop JP, Sanderson JP. 2011. Avoidance of natural enemies by adult whiteflies, *Bemisia argentifolii*, and effects on host plant choice. *Biol. Control* 58:302-9
68. Lee JC, Heimpel GE, Leibee GL. 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomol. Exp. Appl.* 111:189-99
69. Letourneau DK, Armbrecht I, Rivera BS, Lerma JM, Carmona EJ, et al. 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* 21:9-21
70. Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, et al. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294:804-8
71. Losey JE, Denno RF. 1999. Factors facilitating synergistic predation: The central role of synchrony. *Ecol. Appl.* 9:378-86
72. Lu ZX, Zhu PY, Gurr GM, Zheng XS, Read DMY, et al. 2014. Mechanisms for flowering plants to benefit arthropod natural enemies of insect pests: Prospects for enhanced use in agriculture. *Insect Science* 21:1-12
73. Marshall EJP. 2002. Introducing field margin ecology in Europe. *Agric., Ecosyst. Environ.* 89:1-4
74. Mathews CR, Brown MW, Bottrell DG. 2007. Leaf extrafloral nectaries enhance biological control of a key economic pest, *Grapholita molesta* (Lepidoptera : Tortricidae), in peach (Rosales : Rosaceae). *Environ. Entomol.* 36:383-9
75. McCauley SJ, Rowe L, Fortin M-J. 2011. The deadly effects of "nonlethal" predators. *Ecology* 92:2043-8
76. McKenzie AJ, Emery SB, Franks JR, Whittingham MJ. 2013. FORUM: Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? *J. Appl. Ecol.* 50:1274-80
77. Merckx T, Feber RE, Dulieu RL, Townsend MC, Parsons MS, et al. 2009. Effect of field margins on moths depends on species mobility: Field-based evidence for landscape-scale conservation. *Agric., Ecosyst. Environ.* 129:302-9
78. Nafziger TD, Fadamiro HY. 2011. Suitability of some farmscaping plants as nectar sources for the parasitoid wasp, *Microplitis croceipes* (Hymenoptera: Braconidae): Effects on longevity and body nutrients. *Biol. Control* 56:225-9
79. Nelson EH, Rosenheim JA. 2006. Encounters between aphids and their predators: the relative frequencies of disturbance and consumption. *Entomol. Exp. Appl.* 118:211-9
80. Ninkovic V, Feng YR, Olsson U, Pettersson J. 2013. Ladybird footprints induce aphid avoidance behavior. *Biol. Control* 65:63-71
81. Orre-Gordon GUS, Jacometti MA, Tompkins JML, Wratten SD. 2013. Viticulture can be modified to provide multiple ecosystem services. In *Ecosystem Services in Agricultural and Urban Landscapes*, ed. SD Wratten, HS Sandhu, R Cullen, R Costanza:43-57. UK: Wiley-Blackwell. Number of 43-57 pp.

82. Paredes D, Cayuela L, Gurr GM, Campos M. 2015. Is ground cover vegetation an effective biological control enhancement strategy against olive pests? *PLoS One* 10:13
83. Pasari JR, Levi T, Zavaleta ES, Tilman D. 2013. Several scales of biodiversity affect ecosystem multifunctionality. *Proc. Natl. Acad. Sci. USA* 110:10219-22
84. Perrin RM, Phillips ML. 1978. Some effects of mixed cropping on the population dynamics of insect pests. *Entomol. Exp. Appl.* 24:585-93
85. Petanidou T, Van Laere A, N. Ellis W, Smets E. 2006. What shapes amino acid and sugar composition in Mediterranean floral nectars? *Oikos* 115:155-69
86. Pfannenstiel RS. 2012. Direct consumption of cotton pollen improves survival and development of *Cheiracanthium inclusum* (Araneae: Miturgidae) spiderlings. *Ann. Entomol. Soc. Am.* 105:275-9
87. Pfiffner L, Luka H. 2000. Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agric., Ecosyst. Environ.* 78:215-22
88. Pfiffner L, Luka H, Schlatter C, Juen A, Traugott M. 2009. Impact of wildflower strips on biological control of cabbage lepidopterans. *Agriculture, Ecosystems & Environment* 129:310-4
89. Pickett C, Simmons G, Lozano E, Goolsby J. 2004. Augmentative biological control of whiteflies using transplants. *BioControl* 49:665-88
90. Pickett CH, Roltsch W, Corbett A. 2004. The role of a rubidium marked natural enemy refuge in the establishment and movement of Bemisia parasitoids. *Int. J. Pest Manage.* 50:183-91
91. Poveda K, Gomez MI, Martinez E. 2008. Diversification practices: their effect on pest regulation and production. *Rev. Col. Entomol.* 34:131-44
92. Pratt PD, Croft BA. 2000. Banker plants: evaluation of release strategies for predatory mites. *J. Environ. Hort.* 18:211-7
93. Preisser EL, Bolnick DI, Benard MF. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501-9
94. Pretty J, Bharucha ZP. 2015. Integrated pest management for sustainable intensification of agriculture in Asia and Africa. *Insects* 6:152-82
95. Pumarino L, Alomar O, Lundgren JG. 2012. Effects of floral and extrafloral resource diversity on the fitness of an omnivorous bug, *Orius insidiosus*. *Entomol. Exp. Appl.* 145:181-90
96. Pywell RF, Heard MS, Woodcock BA, Hinsley S, Ridding L, et al. 2015. Wildlife-friendly farming increases crop yield: evidence for ecological intensification. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 282:20151740
97. Pywell RF, James KL, Herbert I, Meek WR, Carvell C, et al. 2005. Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biol. Conserv.* 123:79-90
98. Raguso RA, Agrawal AA, Douglas AE, Jander G, Kessler A, et al. 2015. The raison d'être of chemical ecology. *Ecology* 96:617-30
99. Reich PB, Tilman D, Isbell F, Mueller K, Hobbie SE, et al. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* 336:589-92
100. Reigada C, Godoy WAC. 2012. Direct and indirect top-down effects of previous contact with an enemy on the feeding behavior of blowfly larvae. *Entomol. Exp. Appl.* 142:71-7
101. Ricci B, Franck P, Toubon JF, Bouvier JC, Sauphanor B, Lavigne C. 2009. The influence of landscape on insect pest dynamics: a case study in southeastern France. *Landscape Ecol.* 24:337-49

102. Root RB. 1973. Organization of a plant-arthropod association in simple and diverse habitats - fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43:95-120
103. Rusch RC-K, R.; Gardiner, M. M.; Hawro, V.; Holland, J.; Landis, D.; Thies, C.; Tscharntke, T.; Weisser, W. W.; Winqvist, C.; Woltz,M.; Bommarco, R. 2016. gricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystems & Environment* 221:198-204
104. Rypstra AL, Schmidt JM, Reif BD, DeVito J, Persons MH. 2007. Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. *Oikos* 116:853-63
105. Sánchez IA, Lassaletta L, McCollin D, Bunce RGH. 2009. The effect of hedgerow loss on microclimate in the Mediterranean region: an investigation in Central Spain. *Agrofor. Syst.* 78:13-25
106. Scarratt SL, Wratten SD, Shishehbor P. 2008. Measuring parasitoid movement from floral resources in a vineyard. *Biol. Control* 46:107-13
107. Schellhorn NA, Bianchi FJJA, Hsu CL. 2014. Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. *Annual Review of Entomology* 59:559-81
108. Schmidt MH, Roschewitz I, Thies C, Tscharntke T. 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *J. Appl. Ecol.* 42:281-7
109. Schmitz OJ, Barton BT. 2014. Climate change effects on behavioral and physiological ecology of predator–prey interactions: implications for conservation biological control. *Biol. Control* 75:87-96
110. Schmitz OJ, Beckerman AP, O'Brien KM. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* 78:1388-99
111. Schulthess F, Chabi-Olaye A, Gounou S. 2007. Multi-trophic level interactions in a cassava–maize mixed cropping system in the humid tropics of West Africa. *Bull. Entomol. Res.* 94:261-72
112. Schulze E-D, Mooney HA. 2012. *Biodiversity and ecosystem function*. Springer Science & Business Media. 525 pp.
113. Shackelford G, Steward PR, Benton TG, Kunin WE, Potts SG, et al. 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biol. Rev.* 88:1002-21
114. Silveira LCP, Berti E, Pierre LSR, Peres FSC, Louzada JNC. 2009. Marigold (*Tagetes erecta* L.) as an attractive crop to natural enemies in onion fields. *Sci. Agric.* 66:780-7
115. Simpson M, Gurr GM, Simmons AT, Wratten SD, James DG, et al. 2011. Attract and reward: Combining chemical ecology and habitat manipulation to enhance biological control in field crops. *J. Appl. Ecol.* 48:580-90
116. Snyder WE, Tylianakis JM. 2012. The ecology of biodiversity-biocontrol relationships. In *Biodiversity and Insect Pests: Key Issues for Sustainable Management*, ed. G Gurr, SD Wratten, WE Snyder, DMY Read:23-40. UK: John Wiley & Sons, Ltd. Number of 23-40 pp.
117. Sobhy IS, Erb M, Lou Y, Turlings TC. 2014. The prospect of applying chemical elicitors and plant strengtheners to enhance the biological control of crop pests. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 369:20120283
118. Stacey DL. 1977. 'Banker' plant production of *Encarsia formosa* Gahan and its use in the control of glasshouse whitefly on tomatoes. *Plant Pathol.* 26:63-6
119. Stapel JO, Cortesero AM, De Moraes CM, Tumlinson JH, Joe Lewis W. 1997. Extrafloral nectar, honeydew, and sucrose effects on searching behavior and

efficiency of *Microplitis croceipes* (Hymenoptera: Braconidae) in cotton. *Environ. Entomol.* 26:617-23

120. Thies C, Steffan-Dewenter I, Tscharntke T. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101:18-25
121. Thorbek P, Bilde T. 2004. Reduced numbers of generalist arthropod predators after crop management. *J. Appl. Ecol.* 41:526-38
122. Tillman PG, Smith HA, Holland JM. 2012. Cover crops and related methods for enhancing agricultural biodiversity and conservation biocontrol: successful case studies. In *Biodiversity and insect pests: key issues for sustainable management*, ed. GM Gurr, SD Wratten, WE Snyder, DMY Read:309-27. UK: John Wiley & Sons. Number of 309-27 pp.
123. Tompkins JML, Wratten SD, Wackers FL. 2010. Nectar to improve parasitoid fitness in biological control: Does the sucrose:hexose ratio matter? *Basic Appl. Ecol.* 11:264-71
124. Tscharntke T, Bommarco R, Clough Y, Crist TO, Kleijn D, et al. 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43:294-309
125. Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecol. Lett.* 8:857-74
126. Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, et al. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* 87:661-85
127. Tylianakis JM, Didham RK, Wratten SD. 2004. Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* 85:658-66
128. Uvah III, Coaker TH. 1984. Effect of mixed cropping on some insect pests of carrots and onions. *Entomol. Exp. Appl.* 36:159-67
129. van Lenteren JC. 2000. A greenhouse without pesticides: fact or fantasy? *Crop Protect.* 19:375-84
130. Vandekerkhove B, De Clercq P. 2010. Pollen as an alternative or supplementary food for the mirid predator *Macrolophus pygmaeus*. *Biol. Control* 53:238-42
131. Vasseur C, Joannon A, Aviron S, Burel F, Meynard JM, Baudry J. 2013. The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agriculture, Ecosystems & Environment* 166:3-14
132. Vattala HD, Wratten SD, Phillips CB, Wackers FL. 2006. The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. *Biol. Control* 39:179-85
133. Veres A, Petit S, Conord C, Lavigne C. 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agriculture, Ecosystems & Environment* 166:110-7
134. Vollhardt IMG, Bianchi FJJA, Wäckers FL, Thies C, Tscharntke T. 2010. Nectar vs. honeydew feeding by aphid parasitoids: does it pay to have a discriminating palate? *Entomol. Exp. Appl.* 137:1-10
135. Wäckers FL. 2001. A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *J. Insect Physiol.* 47:1077-84
136. Wäckers FL. 2004. Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. *Biol. Control* 29:307-14
137. Wäckers FL, van Rijn PCJ, Heimpel GE. 2008. Honeydew as a food source for natural enemies: Making the best of a bad meal? *Biol. Control* 45:176-84

138. Wade MR, Gurr GM, Wratten SD. 2008. Ecological restoration of farmland: progress and prospects. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 363:831-47
139. Westphal C, Vidal S, Horgan FG, Gurr GM, Escalada M, et al. 2015. Promoting multiple ecosystem services with flower strips and participatory approaches in rice production landscapes. *Basic Appl. Ecol.* 16:681-9
140. Winkler K, Wackers F, Pinto DM. 2009. Nectar-providing plants enhance the energetic state of herbivores as well as their parasitoids under field conditions. *Ecol. Entomol.* 34:221-7
141. Winkler K, Wäckers F, Termorshuizen A, van Lenteren J. 2010. Assessing risks and benefits of floral supplements in conservation biological control. *BioControl* 55:719-27
142. Wong SK, Frank SD. 2013. Pollen increases fitness and abundance of *Orius insidiosus* Say (Heteroptera: Anthocoridae) on banker plants. *Biol. Control* 64:45-50
143. Wyckhuys KAG, Strange-George JE, Kulhanek CA, Wäckers FL, Heimpel GE. 2008. Sugar feeding by the aphid parasitoid *Binodoxys communis*: How does honeydew compare with other sugar sources? *J. Insect Physiol.* 54:481-91
144. Xiao Y, Chen J, Cantliffe D, McKenzie C, Houben K, Osborne LS. 2011. Establishment of papaya banker plant system for parasitoid, *Encarsia sophia* (Hymenoptera: Aphilidae) against *Bemisia tabaci* (Hemiptera: Aleyrodidae) in greenhouse tomato production. *Biol. Control* 58:239-47
145. Xiao Y, Osborne LS, Chen J, McKenzie C, Houben K, Irizarry F. 2011. Evaluation of corn plant as potential banker plant for supporting predatory gall midge, *Feltiella acarisuga* (Diptera: Cecidomyiidae) against *Tetranychus urticae* (Acari: Tetranychidae) in greenhouse vegetable production. *Crop Protect.* 30:1635-42
146. Zehnder G, Gurr GM, Kuhne S, Wade MR, Wratten SD, Wyss E. 2007. Arthropod pest management in organic crops. *Annu. Rev. Entomol.* 52:57-80
147. Zhang W, Ricketts TH, Kremen C, Carney K, Swinton SM. 2007. Ecosystem services and dis-services to agriculture. *Ecol. Econ.* 64:253-60
148. Zhu P, Gurr GM, Lu Z-X, Heong K, Chen G, et al. 2013. Laboratory screening supports the selection of sesame (*Sesamum indicum*) to enhance *Anagrus* spp. parasitoids (Hymenoptera: Mymaridae) of rice planthoppers. *Biol. Control* 64:83-9
149. Zhu P, Lu Z, Heong K, Chen G, Zheng X, et al. 2014. Selection of nectar plants for use in ecological engineering to promote biological control of rice pests by the predatory bug, *Cyrtorhinus lividipennis*, (Heteroptera: Miridae). *PLoS ONE* 9:e108669

ANNOTATED REFERENCES

1. Crowder et al (19): Evidence that ecosystem function in agriculture requires restoration of species evenness, not just richness.

2. Finke and Denno (28): Evidence that additional consumer species can disrupt predation of herbivores.

3. Gurr et al (38): Evidence that crop yield and farm profits can be boosted by crop-border flower strips.

4. Gurr and You (41): Analysis of how molecular approaches can support habitat management.

5. Jonsson et al (56): Experimental test of the intermediate landscape complexity hypothesis.

6. Kean et al (59): Pioneering attempt to apply population modelling to inform habitat manipulation.

7. Khan et al (62): Key paper on ‘push-pull’ the world’s most successful habitat management strategy.

8. Letourneau et al (69): Important meta-analysis of the success of habitat management approaches.

9. Simpson et al (115): Pioneering work on combining two formerly separate natural enemy enhancement methods.

10. Tscharntke et al (126): Comprehensive analysis of evidence for mechanisms the suppress pests at the landscape scale.

SIDEBAR <to be typeset near the 'Nectar' section of the article>

SELECTING OPTIMAL HABITAT MANAGEMENT APPROACHES

When floral resources are used to enhance biological control, the choice of plant species is often based on laboratory work 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. Modelling can help identify these key components, such as aggregation, dispersal, search and reproductive rates. A start to this modelling approach was made by Kean et al (59) but this approach is still underused. Empirical ranking of flowering plants is complicated by the fact that cultivars within a species can give divergent effects on parasitoids (6). Recent work used a combination of laboratory olfactometry with gas chromatography–electroantennography and identified short-chain carboxylic acids as most likely to be responsible for differences between 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 trait and combinations of traits are generally superior for pest suppression.

RELATED RESOURCES

Bioprotection Research Centre (no date) Greening Waipara (http://bioprotection.org.nz/research/programme/greening-waipara).

<An example of a regional-scale research program promoting the delivery of ecosystem services including pest suppression.>

Vinh Long Television (2012) Công nghệ sinh thái (http://thvl.vn/?p=289142)

<An example of mass media used to promote habitat management: one episode from a series run on national TV in Vietnam and that was awarded the Gold medal in Science Education in the 32nd National Television Festival 19-22 December 2012 held in Vinh City, Nghe An, Vietnam. See Heong et al (44).

Acronyms and Definitions

1. **Sustainable intensification** – intensification of agricultural production that emphasizes a lessening of effects on the environment.
2. **SNAP** – Mnemonic for shelter, nectar, alternative prey/hosts and pollen; the major resources provided by plants to natural enemies.
3. **Ecosystem services (ES) –** the benefits delivered to humanity by the condition and processes of biodiversity.
4. **Ecosystem disservice (EDS)** – the negative effects on humanity from the condition and processes of biodiversity.
5. **Ecosystem service provider (ESP)** – the organisms, interaction networks and habitats that provide ecosystems services (e.g. a hedgerow or woodland)
6. **Service-providing unit (SPU)** – the individuals of one species responsible for providing an ecosystem service to a required level.
7. **Habitat management -** an intervention in an agroecosystem with the intended consequence of suppressing pest densities.
8. **Ecological engineering** - a refinement of habitat management whereby the intervention is explicitly supported by evidence to maximize impact.
9. **Classical biological control** – inoculative release of self-dispersing and self-sustaining agents in a new location.
10. **Inundative biological control** – mass release of reared agents into a system to provide (usually) short-term control.
11. **Conservation biological control** - making better use of existing agents by habitat management and reducing mortality from pesticides.

12. **Integrated biological control** - use of habitat management techniques to increase the efficacy of classical or inundative biological control.
13. **Top-down effects** (enemies hypothesis) - the action of natural enemies (third trophic level) on herbivore pests (second trophic level).
14. **Bottom-up** effects (resource concertation effects) - the action on herbivore pests (second trophic level) of vegetation (first trophic level).
15. **Attract and Reward** – combined use of semiochemicals to attract natural enemies and nectar plants to enhance their residency.
16. **Push-pull** – combined use of a plant to repel pests with a second plant to attract, and possibly trap, pests.
17. **Complementarity -** enemies that attack pests in different ways, times, and/or places, such that overall control is increased.
18. **Facilitation -** where the action of one natural enemy increases the success of another.
19. **Agrienvironmental program (scheme) –** policy initiative in which payments to farmers aim to promote environmental outcomes such as biodiversity conservation.

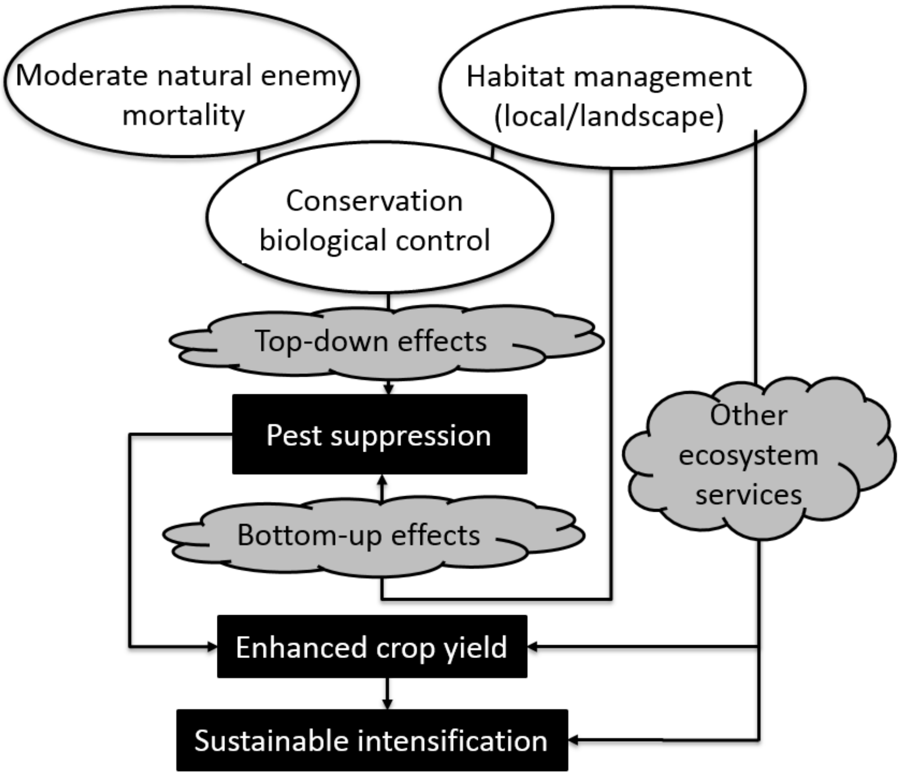

Figure 1

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

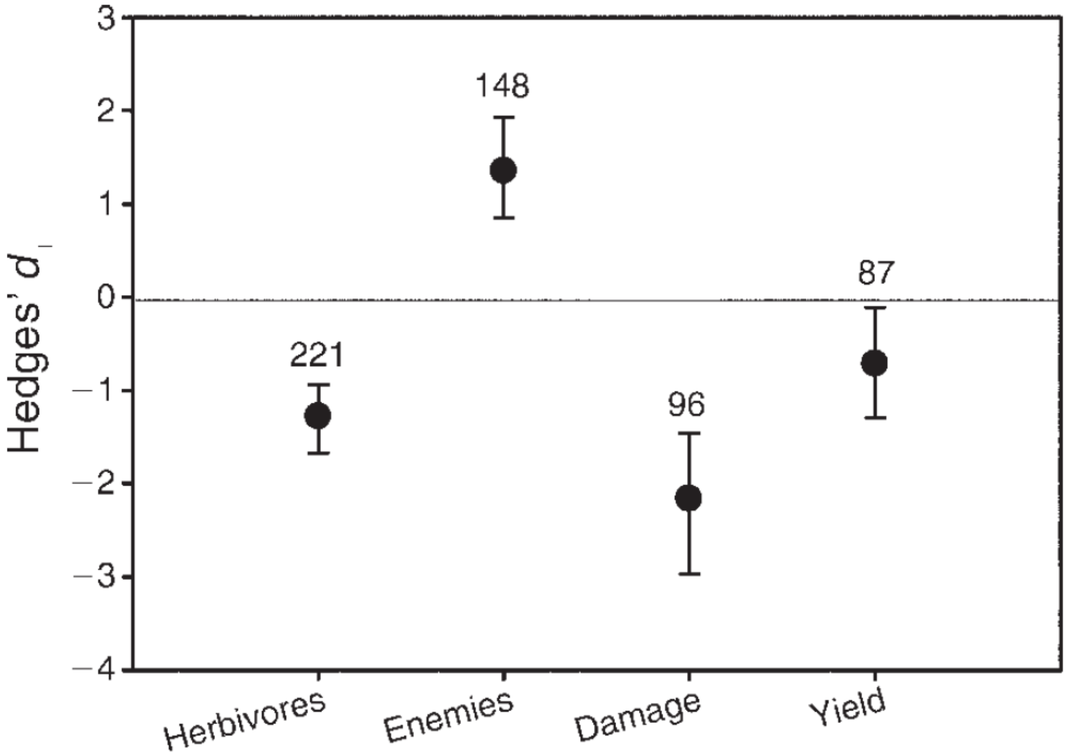

Figure 2

Results of a meta-analysis showing the effects of diverse cropping strategies compared with less diverse systems. Points are mean effect size, bars show bootstrap confidence intervals and values are the number of experiments for each parameter. Herbivores decreased significantly whilst natural enemies were significantly more abundant. Though crop damage was significantly reduced, yields too declined significantly (but see text). From Letourneau, et al. (69), with permission.

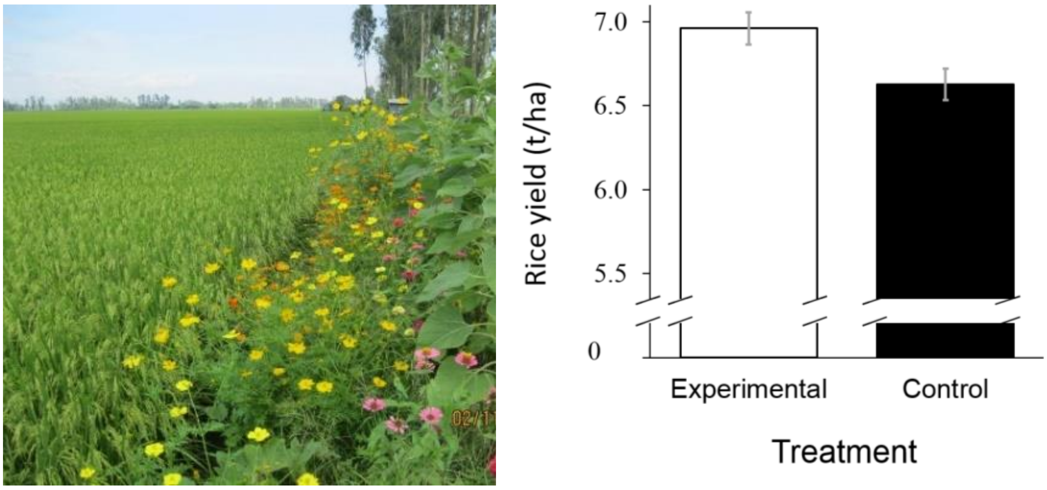

Figure 3

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