

HABITAT MANAGEMENT TO CONSERVE NATURAL ENEMIES OF ARTHROPOD PESTS IN AGRICULTURE

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■ **Abstract** Many agroecosystems are unfavorable environments for natural enemies due to high levels of disturbance. Habitat management, a form of conservation biological control, is an ecologically based approach aimed at favoring natural enemies and enhancing biological control in agricultural systems. The goal of habitat management is to create a suitable ecological infrastructure within the agricultural landscape to provide resources such as food for adult natural enemies, alternative prey or hosts, and shelter from adverse conditions. These resources must be integrated into the landscape in a way that is spatially and temporally favorable to natural enemies and practical for producers to implement. The rapidly expanding literature on habitat management is reviewed with attention to practices for favoring predators and parasitoids, implementation of habitat management, and the contributions of modeling and ecological theory to this developing area of conservation biological control. The potential to integrate the goals of habitat management for natural enemies and nature conservation is discussed.

INTRODUCTION

Conservation biological control involves manipulation of the environment to enhance the survival, fecundity, longevity, and behavior of natural enemies to increase their effectiveness. Such conservation efforts may be directed at mitigating harmful conditions or enhancing favorable ones. Conservation practices can be further categorized as those that focus on reducing mortality, providing supplementary resources, controlling secondary enemies, or manipulating host

plant attributes to the benefit of natural enemies (129, 160). Because of its importance in enhancing natural enemy performance, conservation biological control should be a keystone of all biological control efforts (61). Of the major forms of biological control, conservation biological control has received the least amount of attention (53). However, this trend has begun to reverse (12, 125).

Habitat Management and Conservation Biological Control

Habitat management can be considered a subset of conservation biological control methods that alters habitats to improve availability of the resources required by natural enemies for optimal performance. Habitat management may occur at the within-crop, within-farm, or landscape levels. Underlying these practices is the understanding that agricultural landscapes often do not provide resources for natural enemies at the optimal time or place. The need for habitat management is directly linked to the biology of specific pests and natural enemies, and the qualities of the environment in which they occur. As a result of frequent and intense disturbance regimes, many agricultural systems are recognized as particularly difficult environments for natural enemies (91, 96, 127, 156). This is especially true for annual monocultural cropping systems where the rates of establishment of imported natural enemies and their success in controlling the target pest are lower than in more stable cropping systems (14, 63, 64, 147). Many of the proximate factors identified as limiting the effectiveness of natural enemies in agricultural systems (pesticides, lack of adult food, lack of alternative hosts) (48, 127, 129) can be viewed as direct results of the disturbance regimes imposed on these systems (93). In particular, the ubiquity of pesticide use in crop production systems has posed a limitation to the successful implementation of biological control. A focus of many past conservation efforts has been to seek more selective pesticides, or to time the use of pesticides to minimize their negative impacts on natural enemies (135). Recently, increasing attention has been paid to conservation practices that seek to alter the quality of the natural enemies' habitat (93a).

Provision of Resources: Short Versus Long Term

Conservation efforts can take various routes to mitigate undesirable conditions. For example, well-timed food sprays have been used to supplement in agricultural systems lacking pollen and nectar resources (62, 113). Alternatively, the establishment of perennial flowering plant habitats may provide similar resources in a more stable fashion over the entire season and for years to come (98). While food sprays address the immediate symptom (i.e. lack of food resources), they fail to address the ultimate problem (i.e. herbicide and land use intensity that reduces the diversity and spatial availability of flowering plants). Similarly, removal of broad-spectrum pesticides from crops may be of limited benefit if habitats supporting populations of natural enemies are not spatially and temporally available in the landscape.

Scope of this Review

Interest in the role of habitat alteration on pests and natural enemies can be traced to observations of insect outbreaks in relation to increasing crop monoculture (3), early empirical work (162) and the subsequent study of the role of plant diversity on insect stability in agricultural ecosystems (126, 165).

The role of non-crop plants on beneficial insects was first summarized by van Emden (163) and later reviewed by Altieri & Whitcomb (4) and Altieri & Letourneau (3). Subsequent studies focused on examining the role of uncultivated corridors (83) or adjacent habitats on influencing the natural enemy communities of fields (13, 31, 44, 47, 80, 86, 168, 169). In this contribution, we will focus on the practice of habitat management to enhance the impact of arthropod predators and parasites of arthropod pests, with an emphasis on the recent literature. For information on enhancement of pathogens, nematode natural enemies of arthropods, conservation of natural enemies of plant pathogens, and weeds, see Barbosa (12).

Just as habitat management can reduce pest attack by top-down effects operating via an enhancement of the third trophic level (natural enemies), pests may also be suppressed by bottom-up effects operating via the first trophic level (flora) of diverse habitats. These resource concentration effects (134), though an important complementary area, are beyond the scope of this review. The relative contribution of top-down and bottom-up effects and the interactions between the resource concentration hypothesis effects and natural enemy-mediated pest regulation have been explored recently (59, 177).

MECHANISMS FOR HABITAT MANAGEMENT OF ARTHROPOD PREDATORS AND PARASITOIDS

Providing the “Right” Diversity

Diversity in agroecosystems may favor reduced pest pressure and enhanced activity of natural enemies (2, 5, 136, 144). However, several authors have noted that to selectively enhance natural enemies, the important elements of diversity should be identified and provided rather than encouraging diversity per se (59, 143, 164, 165, 170). Indeed, it has been shown that simply increasing diversity can exacerbate certain pest problems (7, 10, 29, 59). Identifying the key elements of diversity may be a difficult process, but the process can be guided by an understanding of the resources needed by natural enemies (177, 178). Potential mechanisms include improving the availability of alternative foods such as nectar, pollen, and honeydew; providing shelter or a moderated microclimate in which natural enemies may overwinter or seek refuge from factors such as environmental extremes or pesticides; and providing habitat in which alternative hosts or prey are present. In addition, the temporal availability of such resources may be manip-

ulated to encourage early season activity of natural enemies. Finally, the spatial arrangement of such resources to enhance natural enemy activity within the crop must be considered.

Alternative Food Sources

While some parasitoids are able to obtain needed resources from hosts (76), others require access to non-host foods. Floral nectar is taken by many species (78), and can result in increased rates of parasitism (127). Extrafloral nectar is produced by various plants such as faba bean (*Vicia faba* L.) and cotton (*Gossypium hirsutum* L.), and is an important food source for adult parasitoids (21, 157). Pollen may also be consumed directly (68, 75) or as a contaminant within nectar. The presence of honeydew-producing insects has been suggested as desirable for some parasitoids (54). While most habitat management attempts with alternative food sources have involved hymenopteran parasitoids, Diptera may benefit as well (155).

Quantifying the impact of different nectar sources on parasitoid survival and fecundity has yielded important information on which plant species to retain or introduce into an agroecosystem. Studies have examined a range of wildflowers as nectar sources (74) and identified significant differences in the accessibility of nectaries as a result of floral architecture (119). Work with *Pimpla turionellae* L. showed that rapid weight loss occurred for insects caged on flowers with inaccessible nectaries, illustrating an important advantage of nectar over pollen in providing water as well as nutrition (167). Laboratory experimentation has been used to identify which plants to use in the field. Patt et al (120) screened a range of flowers to determine which were most favorable to *Edovum puttleri* Grissell and *Pediobius foveolatus* Crawford, parasitoids of the Colorado potato beetle (*Leptinotarsa decemlineata* Say). They found that floral architecture influenced the selection of nectar plants, with *E. puttleri* feeding effectively only upon flowers with exposed nectaries, while *P. foveolatus* could also utilize flowers with partially concealed nectaries. Provision of nectar resources may provide increased benefits to herbivores as well as parasitoids (183), but careful selection of plants can reduce this possibility (11, 11a).

Substantial work has been conducted on the enhancement of aphidophagous syrphids by provision of flowering plants. Several of these studies (69, 70, 71, 100) have used the North American annual plant *Phacelia tanacetifolia* Benth, since it produces large quantities of pollen and nectar, though some work has examined other food plants (39, 104). Borders of *P. tanacetifolia* have also been explored in cabbage, *Brassica oleracea* L. (172), where syrphid numbers increased, and aphid populations declined. Patt et al (121) screened a range of flowers to determine which were suitable for Colorado potato beetle (*Leptinotarsa decemlineata* Say) predators. They found that that dill (*Anethum graveolens* L.) and coriander (*Coriandrum sativum* L.) had flowers compatible with the head morphology of *Coleomegilla maculata* (Degeer) and *Chrysoperla carnea* Ste-

phens. Field observations of foraging behavior supported the utility of these plants and their subsequent use in eggplant (*Solanum melongena* L.) led to enhanced predator numbers, increased consumption rates of *L. decemlineata* egg masses and decreased larval survivorship.

Other studies have focused on the management of existing plants rather than the use of artificially introduced plants. Smith & Papacek (139) showed that the mite *Amblyseius victoriensis* (Womersley), a predator of the phytophagous eriophyid *Tegolophus australis* Keifer, was favored where growers of orange *Citrus aurantium* L. retained and allowed flowering of the widely established ground cover plant, Rhodes grass (*Chloris gayana* Kunth). The wind-blown pollen of the Rhodes grass provided a supplementary food source, and growers are now advised to maximize the benefit by mowing alternate grass strips between tree rows. Crop plants can also be important in providing pollen and nectar resources. Bowie et al (16) studied the effect of a crop of flowering canola (*Brassica napus* L.) on arthropod distribution in an adjacent crop of wheat (*Triticum aestivum* L.). Dissection of adult syrphids from within the canola and at varying distances into the wheat showed that these natural enemies made extensive use of canola pollen, resulting in lower densities of the aphid, *Rhopalosiphum padi* (L.) from sample positions close to the crop interface.

Food sprays can also benefit natural enemies, but this approach may be economically viable only in relatively high-value crops. In cotton, field testing of the product "Envirofeast" showed treated areas to be attractive to various natural enemies including Coccinellidae and Melyridae (Coleoptera); Lygaeidae and Nabidae (Hemiptera); and Chrysopidae (Neuroptera) (113). Though no effects of these predators on prey were reported, separate mesh-house and field testing indicated that treated plants were relatively unattractive to ovipositing *Helicoverpa* spp. (112).

Shelter and Microclimate

Perennial crop systems are potentially more amenable to conservation biological control than are ephemeral annual systems because they are subject to lower levels of disturbance. Thus, resident populations of natural enemies may persist from year to year in perennial crops. However, in some perennial crops such as alfalfa (*Medicago sativa* L.), the normal practice of harvesting entire fields causes disruption to the resident arthropod fauna (159). Among the earliest examples of habitat management were attempts to provide a refuge for natural enemies of alfalfa pests displaced by cutting (148, 158). This practice has also been explored in more recent work where strip harvesting was associated with lower pest densities and lower aphid-to-predator ratios, except in spring (24). Altered harvesting patterns also offer refuge to the brown lacewing *Micromus tasmaniae* (Walker) (95) and a range of coccinellid and hemipteran predators (72a). In these approaches, the provision of a moderated microclimate of uncut alfalfa is likely to be important (158). Overwintering of natural enemies has also been investi-

gated in a number of temperate perennial systems. Shelter has been provided by augmenting leaf debris on the orchard floor with peppermint (*Mentha x piperita* L.) (115), wrapping the bases of apple (*Malus domestica* Borth.) trees in vegetable debris held in place with plastic, placing similar debris around the base of smaller trees (43), or providing on-tree refugia of burlap and aluminum in peach, *Punus persica* (L.) Batsch (149).

Perennial crop systems may be disrupted by unavoidable pesticide applications, so refugia outside the treated area can be critical. The predatory mite *A. victoriensis* was able to re-colonize citrus orchards more readily after pesticide-induced disruption where the nearby windbreaks were of *Eucalyptus torelliana* F. Muell. (140). This tree species has also been tested in citrus-growing areas of South Africa, where high populations of the predatory mite *Amblyseius tutsi* Pritchard & Baker occurred on trees nine months after release of mites at the density of one per leaf. Use of this tree is believed to aid in the management of phytophagous mites and thrips (58). An equivalent refuge within tea (*Thea sinensis* L.) production systems exists because the tea bush is stratified into the plucking surface and the interior of the perennial bush. The latter constitutes a refuge for natural enemies that are able to contribute to pest suppression even where pesticides are used (81).

In annual crop systems, maximizing the overwinter survival of natural enemies may be critical in ensuring adequate biological control in the following growing season. This consideration has led to efforts to identify optimal overwintering habitat for arthropod predators of British cereal fields. Overwinter survival of these natural enemies is low because field interiors contain very little vegetation. For this reason, the vast majority of predators overwinter in the field margins and disperse into the crop in the spring (152, 154). However, such colonization of the crop is too slow for optimal pest regulation. Attempts were made to provide suitable overwintering habitat within fields by creating a raised earth bank, termed beetle banks, sown with perennial grasses (174). Comparisons of several grass species led to a recommendation to use cocksfoot (*Dactylis glomerata* L.) and Yorkshire fog (*Holcus lanatus* L.), perennials that have a dense tussock-forming growth habit and harbor the greatest numbers of predators (153, 154).

During the growing season, high temperature and low humidity may constrain natural enemy populations or the activity of individuals. Orr et al interplanted ryegrass (*Lolium multiflorum* Lambert) in seed maize (*Zea mays* L.) fields to reduce the temperature of the soil surface, increasing survival of augmentatively released *Trichogramma brassicae* Bezdenko (118). Alderweireldt reported dramatic increases in spider densities after holes 10 to 12 cm deep were made in the soil surface (1). The microclimate within such depressions is certain to be different from that of untreated soil and is likely to be part of the explanation for the observed effect. However, the observation that web-building spiders (Linyphiidae) were favored more than non-web-building species, combined with the fact that holes with diameters of 5 or 9.5 cm were preferred over smaller holes, sug-

gests that the structural heterogeneity of the manipulated environment influenced web construction.

Non-crop vegetation may be favored by natural enemies as oviposition sites. It has been observed that *Coleomegilla maculata* (Coleoptera: Coccinellidae) lays more eggs on a native weed, *Acalypha ostryaefolia* Ridell than the sweet corn (*Zea mays* L.) crop, even though the plant supported few prey. Larvae then disperse from the weed and climb maize plants. Maize plots bordered by *A. ostryaefolia* contained significantly more *C. maculata* than did plots without a border (38).

Other examples of ground covers or intercrops influencing natural enemy density, activity or impact include carabids in maize (18), parasitoids in cabbage (*Brassica oleracea capitata* L.) (151), mite predators in citrus (97), and various natural enemies in pecan (*Carya illinoensis* Koch) (123) and cotton (180). Although microclimate factors are likely to be involved, in at least some cases the availability of alternative foods in the form of floral resources and/or prey or hosts in the non-crop vegetation may have contributed to the observed effects (142). It is important to note that other studies indicate inconsistent or limited benefits of ground covers or intercrops on natural enemies (22, 28, 37, 40, 72, 139) or even negative effects (35, 36).

Alternative Prey or Hosts

Given sufficient alternative prey, populations of generalist predators may establish within a crop before the arrival and seasonal increase of pests (164). Kozar et al showed that for homopteran pests of apple the distribution of predators was determined by the presence of alternative prey on weeds or in surrounding vegetation (85). Management of crop residues or organic matter may also be effective in enhancing natural enemy populations. A classic demonstration in rice, *Oryza sativa* L., involved increasing the amount of organic matter in test plots leading to increases in detritivores, plankton-feeders, and generalist predators (138). Further, early-season insecticide applications that killed predators led to pest resurgence later in the season. Thus ensuring that natural enemies are protected from the adverse effects of pesticides is a prerequisite for successful habitat management.

Organic matter can also be beneficial when applied to the soil surface of field crops. Manure and straw increased numbers of the carabid *Bembidion lampros* (Herbst), an egg predator of the cabbage root fly *Delia radicum* (L.), and increased total carabid populations in cabbage. This increase was apparent even into the year following the last application and was attributed to increased reproduction by the predators, which in turn may have been the result of the observed increase in alternative prey availability (73). No-tillage production systems that leave crop residue on the soil surface increased the populations and impacts of predatory carabids (18, 26, 27).

Providing alternate hosts may be more difficult for parasitoids, which are often host- or habitat-specific (127). The best known example is of *Anagrus* (Hymenoptera: Mymaridae) parasitoids of the grape leafhopper (*Erythroneura elegantula* Osborne) (46). These egg parasitoids must overwinter on alternative hosts outside the grape (*Vitis vinifera* L.) vineyard because the grape leafhopper does not overwinter in the egg stage. Wild plants in the genus *Rubus* support overwintering eggs of alternative leafhopper hosts, as do cultivated French prune (*Prunus domestica* L.) trees. Prune refuges adjacent to vineyards as well as nearby riparian areas containing *Rubus* spp. increase *Anagrus* parasitism and contribute to control of grape leafhopper (34). As observed by van Emden (164), there may be many unknown examples of parasitoids with requirements for alternate hosts. This lack of alternative hosts may be a contributing factor in the observation that, although many biological control introductions result in establishment, most are unsuccessful in reducing pest densities (61).

Using the ability of some parasitoids to parasitize more than one host species has been explored by Stary (145) in glasshouse crop production. Beans were selected as a model crop and *Myzus persicae* (Sulzer) as the target pest. In this approach, the aphid parasitoids, *Aphidius colemani* Vierck and *Lysiphlebus testaceipes* Cresson were introduced into a pest-free greenhouse along with wheat plants infested with *Schizaphis graminum* (Rond.) as the alternative host. Any subsequent infestation of *M. persicae* within the glasshouse could result in parasitoids moving from the alternative host reservoirs to the target pest population.

Timing the dispersal of natural enemies by manipulating alternative prey has also been explored. The fact that faba beans are commonly infested with aphids was used as a rationale for their selection as a groundcover in hops (*Humulus lupulus* L.) to encourage natural enemies of the hop aphid, *Phorodon humuli* Schrank (57). In this habitat management approach, cutting the bean plants when aphid infestation was detected within the hops was planned as a means of encouraging dispersal of natural enemies to the crop. Though no hop-aphid infestation was observed in this study, dispersal of natural enemies was elicited by cutting the ground cover plants. Cutting is also likely to be important in other cases. Bugg et al showed that the weed *Polygonum aviculare* L. provided both floral resources and alternative prey and was attractive to many natural enemies, especially *Geocoris* spp. (Hemiptera) (20). The authors suggested the plant should be tolerated at field edges as a breeding site for natural enemies, and they speculated that timely removal of the weeds would be useful in encouraging natural enemy dispersal.

Multiple Mechanisms

Habitat management may benefit natural enemies by the simultaneous operation of more than one mechanism. Work with *Eriborus terebrans* (Gravenhorst), the primary parasitoid of *Ostrinia nubilalis* (Hübner) in maize in Michigan showed that females were most frequently captured in maize fields close to wooded field

edges and that parasitism of *O. nubilalis* was higher in these areas (90). Laboratory, greenhouse, and field cage studies showed that adults lived longer when provided with sugar and that longevity increased at 25°C versus 35°C (49). The wasps were also shown to be more active on hotter days, which could result in their leaving crop habitats to find shelter in adjacent wooded areas (50). It was suggested that wooded edges benefited *E. terebrans* by providing both a source of adult food (nectar and honeydew) and access to a moderated microclimate (51). Intentionally established “insectary hedgerows” containing a diversity of shrubs and herbaceous plants to provide continuous sources of pollen, nectar, and shelter have been studied (98). Marking studies showed that natural enemies utilize these habitats and disperse into adjacent crops. Up to 47% of the marked *Hyposoter* wasps and 23% of lady beetles were found up to 75 m into the crop.

Because of the potential for natural enemies to be simultaneously favored by more than one mechanism, the small number of studies that have explicitly sought to elucidate which mechanism is most important are noteworthy. Irvin et al used ground covers of either buckwheat (*Fagopyrum esculentum* Moench) or faba bean to increase the impact of natural enemies of leafrollers (Tortricidae) in apple orchards (75). Sticky trap catches of the leafroller parasite *Dolichogenidea tasmanica* Cameron were significantly greater in plots of flowering buckwheat than in plots of buckwheat where flower buds were removed. This showed that floral rewards, rather than either availability of shelter or presence of alternative hosts on the buckwheat foliage was responsible for enhancement of parasitoid activity (60).

In a second study, buckwheat had the greatest effect on *Anacharis* sp., a parasitoid of the brown lacewing (*Micromus tasmaniae* Walker), itself an important natural enemy (146). In these trials, sticky traps in the buckwheat plots caught more parasitoids than those in the control except in the period prior to buckwheat flowering. This indicated that feeding upon flowers, rather than the presence of aphids on the buckwheat upon which host lacewings were feeding, influenced parasitoid catches. Vacuum sampling the buckwheat confirmed the very low densities of lacewings and *Anacharis* suggesting they were not using plants for shelter.

IMPLEMENTING HABITAT MANAGEMENT

Here we address five key issues in the implementation of habitat management: (a) the selection of the most appropriate plant species; (b) the predator/parasitoid behavioral mechanisms which are influenced by the manipulation; (c) the spatial scale over which the habitat enhancement operates, with implications for the area, shape and spacing of resources and refugia for predators and parasitoids; (d) the negative aspects associated with adding new plants to an agroecosystem, such as the use of the plant resources by the pest being targeted; (e) the degree of uptake by the agricultural/horticultural community of the proposed habitat changes.

Plant Species Selection

Several publications have attempted to rank candidate plants based on their use by the targeted natural enemy (25, 100, 103). These rankings are often carried out on replicated blocks of candidate plants and the only criterion used for the ranking is the number of predators found on, or in traps near, the candidate plants (25). Annual flowers may require repeated planting or cutting of the plants to promote regrowth of flower buds (75). These practices can be labor intensive and may interfere with growers' practices. The advantage of annuals, however, is that there is no persistence of the vegetation into the next growing season, although they may contribute to the seed bank. For perennial crops, the ideal plant may be a species that spreads within or between years and is a good competitor with weeds. One such candidate is *Lobularia maritima* (L.) Desv. (alyssum) (Brassicaceae) (25). Though initially slow-growing and susceptible to weed competition, it persists through most "Mediterranean" climates, behaves as a perennial, and spreads well (75). While an excellent source of pollen and nectar, it, like most other potential companion plants, may also be used by certain pests (25).

Phacelia tanacetifolia has been used extensively in Europe and Australia (10, 11, 69, 172). The annual nature of *P. tanacetifolia* however, may be a disadvantage, as discussed, and possibly more importantly, its deep corolla makes the nectar unavailable to short-tongued insects such as hover flies (69). Despite these limitations, significant reductions in aphid populations were achieved by the use of *P. tanacetifolia* around cereal fields in the United Kingdom (69), and around cabbages in New Zealand (172).

Selection of plants for habitat management should consider their suitability in the agricultural or horticultural regime in which they will be placed. On beetle banks, two tussock-forming grasses, *D. glomerata* and *H. lanatus* (174), offered the best overwinter habitat for aphid predators (152, 153, 154, 178). These European species were formerly important components of many pasture seed mixes. They are not particularly invasive, and to date, have not become problems in adjacent fields. However, where arable systems include livestock in the rotation, the palatability of such refuge grasses and other plants should be considered. Evidence from New Zealand and elsewhere indicates that, although livestock such as sheep may graze these grasses, they are not preferred over more common pasture grasses such as *Lolium* spp. (52). However, if grazed the grasses usually recover from their tussock base. In non-European countries, resistance to using these grasses on such banks because of a desire to use a native species is an important consideration (82). Because of the multitude of factors which may influence the choice of plant species for habitat management, the use of a semi-quantitative decision-making tool, the graded weighted checklist, (122), has been suggested (59).

Behavioral Mechanisms

Understanding the behaviors of natural enemies that may be altered by habitat management is a key to success. For example, parasitoids also make extensive use of semiochemicals in host location, some of which emanate from plants (41).

Recently it has been observed that use of semiochemicals may hold potential to manipulate an agroecosystem in a “push-pull” or stimuldeterrent diversionary strategy. Kahn et al studied lepidopteran stem borers and the parasitoid *Cotesia sesamiae* (Cameron) in Africa (84). In this study, the grass *Melinis minutiflora* Beauv. produced volatiles that repel female stem borers and attract the foraging female parasitoids. Intercropping maize with this grass led to reduced infestation by the stem borer and increased rates of parasitism compared with a maize monoculture.

Various techniques may be used to investigate how habitat management alters natural enemy behavior (77). Rubidium has been employed as a marker with notable success. Rubidium levels in plants can be artificially enhanced and this can result in marking of the host and subsequent transfer to natural enemies (34). Alternatively, marking of plant nectar has been used to trace movement of natural enemies as they disperse from refuge habitats (98). Pollen can also be a useful marker, particularly if the plant is not native to the area (e.g. *Phacelia* in Europe) or otherwise easy to identify (68, 75). For *Phacelia*, saffranin staining of predator or parasitoid gut contents can be used to answer questions about the proportion of individuals containing pollen over time or in relation to the distance from the pollen source (178a). This information can help in decision making regarding the size, shape and location of pollen sources. Once the value of a habitat has been established, a crucial but very difficult question to answer is the extent of pest suppression resulting from the emigration of the predators and parasitoids into the adjacent crop. Given the sporadic spatial and temporal distribution of many pests, and the experimental difficulties of evaluating predation and parasitism rates in field populations (77, 175), some sort of experimental crop or refuge manipulation may be needed to evaluate predation rates associated with the refuge (110).

Scale and Spatial Arrangement

Habitat structure may influence arthropod natural enemies over a variety of spatial scales (19, 88, 92, 93, 94, 133, 176) and impact the structure of natural enemy communities (93, 106). Increasing habitat fragmentation at a local scale can result in the loss of parasitoid species and the release of herbivores from parasitism (87). Corbett & Rosenheim showed that arrival of *Anagrus* parasitoids into a vineyard was affected by both the presence of adjacent prune refuges (via a wind-break effect) as well as the distance from presumed overwintering sites in riparian areas (34). The importance of landscape heterogeneity was also shown for predatory coccinellids that were favored by the presence of uncultivated habitats in the landscape (30, 104). A similar association was evident for hymenopteran parasitoids of *Pseudaletia unipuncta* Haworth, where increased parasitism was associated with complex landscapes characterized by smaller field sizes and higher proportions of edges with woodland or wide hedgerow (105). A similar result was shown for oilseed rape (canola) in Germany (151a). Subsequent work has shown this association to be related to the specific landscape composition

rather than landscape complexity per se. (111). Structural diversity in the landscape may sometimes impede natural enemy movement between fields as in the case of certain Carabidae (55, 107), although, for others, it may also facilitate natural enemy movement (23).

The question of the optimal shape and distribution of habitats to enhance natural enemies is not well understood. In the spring carabid beetles emigrate from beetle banks to a distance of at least 60 m on either side (152, 153, 154). This finding led to a recommendation in the United Kingdom that these banks should be spaced at least 100 m apart (174). In that work there was a 5 to 10 m gap between the end of the bank and the existing field margin to allow for farm machinery to pass without crossing the bank. Concepts of landscape connectivity (55) indicate that connecting such refugia with existing boundaries may facilitate their initial colonization and interchange within the field margin predatory community. Given that field margins can also act as impediments to predators, connecting such refugia to existing boundaries is even more important to maximize colonization from the boundary to the refuge (175) and to facilitate movement along such features.

Negative Aspects of Added Habitat Diversity

Probably the most obvious potential disadvantage of increasing habitat diversity is that some land may be taken out of production. This potential disadvantage may be a major consideration for high-value crops and, for example, mitigate against the use of alfalfa strips within cotton as proposed by Mensah & Khan (114). In the case of beetle banks in wheat (*Triticum aestivum* L.) fields, such losses have been shown to be more than offset by savings from reduced need for pesticides to control aphids (141). Where within-crop botanical diversification is used, an additional concern is that any advantage from increased natural enemy activity and pest suppression may be more than offset by a reduction in yield resulting from competition (42).

Once a habitat is established, little can be done to control the community of organisms by which it is colonized. Ideally, basic experimental work should quantify these effects (175), but surprises may still occur (25, 146). An example of such a surprise is the use of pollen and nectar sources to enhance parasitism of the potato tuber moth *Phthorimaea operculella* (Zell.) by *Copidosoma koehleri*. In this work the first sources of pollen and nectar selected, although enhancing parasitism rates, were also exploited extensively by tuber moth adults. Subsequent laboratory work exposed moths and parasitoids to a range of candidate pollen and nectar sources, which led to the decision to use borage (*Borago officinalis* L.) in subsequent fieldwork. Borage enhanced parasitism of the moth but was not used by the pest itself, providing a rare example of the careful selection of a “selective food plant” as a pollen and nectar source, taking into account pest and parasitoid use (10, 11).

Another hurdle is grower reluctance to establish plants that could become invasive in the future. Selected plants should have minimal weed status, and/or knowledge should be gained concerning herbicides that control them. Sometimes selective herbicides that do not affect the companion plant will also be necessary, especially during the establishment phase. Selective herbicides have been used effectively to manage the dicotyledenous weed species in crop edges (146). Agonomic factors such as plant phenology, flowering periods, and performance in different seasons of the year, assume increasing importance as the research approaches the technology-transfer stage. Simple repeat-planting experiments can be carried out to measure agronomic characteristics independent of the insects involved (17).

Producer Acceptance

Relatively few cases of widespread grower adoption of habitat management to enhance natural enemies have occurred. These include beetle banks (153), weed strip-management in agriculture (116, 117), cotton-wheat intercropping systems in China, and use of pollen-producing ground covers in citrus orchards in China (97) and Australia (140).

Adoption of beetle banks is widespread in Europe with hundreds occurring in Britain, the Netherlands, Scandinavia, and elsewhere (N.W. Sotherton, personal communication). The term "beetle bank" is about to be included in the Oxford English Dictionary (D Pudley, personal communication). Recommendations on how to manage these habitats continue to evolve and include periodic mowing every few years (8). Such banks are also being turned into a multiple function habitat manipulation sites as the needs of other predators and parasitoids are incorporated. For example, Boatman (15) has added the concept of "conservation headlands" (146) to the banks as well as drilling winter brassicas alongside the headland. The strip of winter brassicas provides a refuge and some food for gray partridge (*Perdix perdix* L.) in winter. Current work in New Zealand is evaluating alyssum for beneficial insects (25), as well as adapting beetle banks for southern hemisphere conditions. One strong option for the future will be some form of beetle bank with alyssum in strips alongside it.

"Weed strip management" has been researched in Europe for several years (117). The practice involves establishing diverse mixtures of native flowering plants in strips in and around fields. These strips have achieved a degree of acceptance in Swiss agriculture where they contribute to increased activity density of Carabidae (Coleoptera) (101, 102), spiders (Araneida), Nabidae (Hemiptera), Dolichopodidae (Diptera) and Syrphidae (Diptera) (67). The results for spiders have indicated only a minor benefit (79). Weed strip management appears to increase the availability of food for carabids and result in enhanced reproduction (181, 182).

Cotton-wheat relay intercropping is practiced on 2.3 million hectares in northern China (179). The primary benefits are reduced damage by cotton aphid, *Aphis*

gossypii Glover on seedling cotton and increased productivity. Natural enemies are maintained in the field because they feed on prey in wheat and then easily disperse to emerging cotton seedlings where they can prevent population increase by *A. gossypii*. In the absence of wheat, predators arrive in cotton too late for effective control (180).

Citrus growers in China are reported to have planted or conserved “weeds,” principally *Ageratum conyzoides* L., on 135,000 ha of orchards. These plants are beneficial to natural enemies of the citrus red mite, *Panonychus citri* (Mc. G.), primarily *Amblyseius* spp., through the provision of alternative food in the form of pollen (97). A similar case is evident for citrus growers in Queensland, Australia where *A. victoriensis* is important in the management of eriophyid mites (140). Of growers in the major districts of Central Burnett, Bundaberg, and Emerald, occupying some 3,000 ha, it is estimated that between 80% and 95% actively encourage the flowering of Rhodes grass during the fruit-growing season to provide pollen as an alternative food for the predatory mite. Doing so typically involves mowing alternate inter-rows every three weeks, allowing time for the grass to produce pollen while maintaining a neat orchard. Further, between 30% and 50% of growers used *Eucalyptus torelliana* (F.v. Muell) trees in windbreaks, making use of its hairy leaves to intercept grass pollen and provide an alternative refuge for the predator (D Papacek, personal communication).

CONTRIBUTIONS OF THEORY AND MODELING TO HABITAT MANAGEMENT

While individual researchers have been guided by theoretical considerations, habitat management as a whole has proceeded largely on an empirical basis (6). Increasingly, however, modeling and ecological theory are beginning to inform habitat management decisions.

Modeling

Models can be used to investigate the interaction of refuge habitat arrangement and natural enemy dispersal on colonization of crop habitats (32). Corbett & Plant (33) showed that a simple model could explain a wide variety of observed natural enemy responses to refuge habitats based on the dispersal capability of the enemy, refuge placement, and timing. Others used simple models to investigate critical parameters for biological control of aphids by predators and compared these models to the results of field experiments (161). Under the assumptions that best simulated reality, this model indicated that initial predator density and immigration rate were critical parameters determining if prey suppression would occur. Van der Werf concluded that the landscape features that influenced these rates should be investigated to allow advances in model precision (161). The role of landscape heterogeneity on linyphiid spiders was modeled by Halley et al (65), who found that inclusion of small amounts of grassland in a cereal landscape

greatly increased the population size of spiders in cereal fields, while pesticide use and crop rotation decreased population size, and field size had no effect up to a size of 4 km², revealing the importance of the dispersal capabilities of spiders.

Ecological Theory

Several authors have summarized the contributions of ecological theory to the practice of habitat management. Gurr et al explored the ecological principles guiding habitat management, including diversity and stability arguments, the natural enemies hypothesis, and life history strategies (59). They integrated these principles with practical considerations to suggest crop system effects, habitat management strategies, and spatial factors that should guide habitat management practices. Landis & Menalled reviewed the ecological and entomological literature on the effect of disturbance on landscape structure and its effects on limiting parasitoid communities within agricultural landscapes (93). They suggested that moderating disturbance regimes through habitat management is a key to conserving parasitoids in agricultural landscapes. Letourneau examined the conservation biology, island biogeography, and metapopulation ecology literature for lessons related to conservation of natural enemies (96). She pointed to the need for landscape-level management if conservation biological control is to succeed on a large scale and concluded that policy and economic strategies are at least as important as the ecological strategies if success is to be achieved. Andow examined the use of vegetational diversity to augment natural enemies (6) and Schellhorn et al reviewed the role of cultural practices to enhance natural enemies from an ecological perspective (137). Theoretical and applied considerations of the role of generalist predators in regulating prey populations have been examined (128, 131, 132, 175).

Finally, a novel contribution has been the synthesis by Wissinger, who contrasted the life history traits of many insects that cyclically colonize ephemeral habitats (173). He argued that annual crops are ephemeral, but predictable, habitats. He outlined a series of life history traits for cyclic colonizers that include (a) dispersal from overwintering sites prior to reproduction, followed by (b) reproductive onset and loss of flight ability following migration, (c) one or more generations of highly fecund but sedentary individuals, and finally (d) emigration with delayed reproduction. Wissinger suggested that effective biological control strategies in annual crops must include provision of permanent habitats to act as reservoirs for cyclic colonizing natural enemies.

SYNTHESIS

Implementation

We have reviewed the growing literature on habitat management for natural enemies in agricultural systems. Applying these concepts is a challenge because of

the complexity and frequently case-specific nature of the interactions. Landis & Menalled outlined several principles to guide habitat management for parasitoids (93) that are expanded below to include other natural enemies.

Many of the factors that limit the effectiveness of natural enemies in agricultural systems (pesticides, lack of adult food, lack of alternative hosts) are direct results of the disturbance regimes imposed on these systems. Subsequently, conservation of natural enemies by amelioration of these conditions ultimately must be achieved by managing disturbance, not just the symptoms it produces. Habitat management to reduce disturbance may need to occur at various spatial scales. For example, while eliminating a pesticide treatment within a field may permit the establishment or persistence of a natural enemy population, if viable meta-populations (66) do not exist at the landscape-level to provide immigrants, the within-field effort may be ineffective.

Successful implementation of natural enemy conservation involves assessing levels of disturbance in agricultural systems. Practices such as cover cropping, intercropping and reduced tillage relax the overall disturbance regime, although they may require some new disturbances (i.e. herbicides) in order to manage weeds. Alternatively, some new technologies such as transgenic maize expressing *Bacillus thuringiensis* Berliner toxins may appear to reduce disturbance by eliminating pesticide treatments, but may in fact represent a more pervasive disturbance through the potential for cascading multitrophic level impacts.

Habitat management may not always demand a radical change in farming practices as illustrated by the relative ease with which beetle banks and border plantings can be introduced into annual row crop systems. The success of these tactics within such economically important systems indicates that habitat management can be packaged in an agronomically acceptable form. Moreover, the introduction of perennial vegetation does not always require that land be taken out of productive use. Habitat management may be as simple as taking into consideration adjacent crops when planning rotations. Observations such as those by Bowie et al could lead to very simple recommendations such as “wherever possible plant canola and wheat in neighboring fields” (16). However, improved methods for extending conservation methods to producers are needed (166). Synergistic interactions of habitat management for natural enemies with agroforestry (45, 124), weed management (24a, 104a, 111a), and soil and water conservation (89) may help in this process.

Finally, habitat management will normally be complemented by other methods and should not be promoted as a standalone method. Commonly these will employ biological control agents that have been released in classical or augmentative manners. In such instances habitat management holds considerable potential for enhancing the success rates of classical agents, and to maximize the persistence and impact on pest population of augmentative agents. In the future, these formerly separate branches of biological control will be merged to synergistic effect in “integrated biological control” (sensu 61).

BENEFITS TO NATURE CONSERVATION

Because of the difficulties of nature conservation within reserves alone, it has been argued that the agricultural ecosystems, which occupy large areas of land, are critical in maintaining biodiversity (108). Thus the encouragement of natural enemies by strategic increases in habitat diversity offers potential to align the goals of agriculture with those of nature conservation (56). The benefits arise partly from the lessened need for synthetic pesticides and the attendant direct and indirect off-target impact on organisms such as butterflies (99), birds (130), and small mammals (15a, 150); and partly from the introduction or maintenance of structural heterogeneity, for example, as observed for skylarks *Alauda arvensis* L. (141). Flora, too, may be conserved. One approach is to establish and preserve a matrix of native vegetation in which agriculture is nested. This process would lead to the creation of a “variegated landscape” (109) which, in the case of rangelands of New South Wales, Australia, has been suggested as an approach to conserve native grassland flora. Initiatives such as these may be made more palatable to economic rationalists if the potential value of conserved species is stressed. Such species might include direct biocontrol effect of previously unrecognized predators such as the big brown bat, *Eptesicus fuscus* Palisotde Beauvois, which was shown only recently to feed extensively on pest insects (171).

CONCLUSION

The science of habitat management is still in its infancy. Publications on the topic date from the first half of the century, but close to 80% of the literature reviewed herein was published after 1990. While this is in part attributable to our intention to focus on recent literature, within the current decade a marked trend toward increasing activity is evident. The international community of scientists engaged in this field appear well poised to meet the challenge of making agricultural pest management more effective, and production systems more sustainable, as well as being increasingly compatible with nature conservation.

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