

Efficacy and economics of shelter habitats for conservation biological control

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Abstract

Provision and manipulation of shelter habitat features within the agroecosystem provide a strategy for enhancing the effectiveness of natural enemies for biological pest control. Evidence from numerous studies indicates that aspects of natural-enemy diversity, abundance and distribution can all be affected by shelter habitats. However, data demonstrating impacts on pest populations and crop yield are few. Accordingly, voluntary adoption of this approach to conservation biocontrol has been limited. We argue that utility of the approach could be enhanced through an improved mechanistic understanding of the relationship between biodiversity of natural enemies and resulting pest control function, including an understanding of the influence of local ecological context and spatial and temporal scale. We also identify the need to consider socio-economic as well as ecological factors to better understand and manage adoption of such conservation biocontrol technologies.

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1. Introduction

Conservation biological control (CBC) represents a sustainable means of enhancing the potential of naturally occurring predators and parasitoids to control crop pests (Eilenberg et al., 2001). Its basic aim is to identify potentially important components of the natural-enemy community, categorize agronomic and ecological constraints that appear to limit effectiveness of these natural enemies and adjust practices and/or modify ecosystem features to ameliorate these constraints. There are a range of approaches to achieve this but in this paper we review examples of habitat manipulations with a particular focus on the use of non-crop vegetation as shelter habitat within arable cropping systems in Europe. This focus partly reflects the

knowledge and experience of the authors, but also that some of the best information and data on the use and effects of shelter habitats for CBC are derived from such systems. Moreover, whilst the voluntary adoption of shelter habitats by farm managers has been limited (an issue we return to later), a range of policy measures in Europe now provide financial incentives to promote their use for organic farming (Haring and Dabbert, 2004) and as a means of integrating sustainable agriculture with biodiversity conservation (Curry, 2002). As the uptake of shelter habitats is becoming increasingly wide spread, it is pertinent to review their value for pest control and examine their future development.

We focus on shelter habitat features that are known to influence the abundance and distribution of natural enemies and exhibit some potential to affect top-down control of herbivore prey (for broader reviews considering field margins, vegetational diversity, intercropping and habitat management readers are referred to, for example, Risch

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et al., 1983; Andow, 1991; Landis et al., 2000, 2005; Marshall and Moonen, 2002; Bianchi et al., 2006). We begin by reviewing characteristics of shelter habitats and their effects on natural-enemy abundance, diversity and distribution, and then examine the mechanisms and extent to which manipulation of shelter habitats delivers improved biological control. We then go on to consider some economic perspectives and issues that relate to adoption of CBC, before concluding with recommendations for further research to maximize the utility of the approach.

2. Shelter habitat features and effects on natural-enemy populations

From a biocontrol perspective, the general function of shelter habitats is to provide beneficial arthropods with semi-permanent habitats offering suitable biotic and abiotic conditions for overwintering, aestivation and reproduction, and a refuge from the perturbations of farming practices (e.g. plowing, spraying, harvesting). In so doing, shelter habitats facilitate reinvasion of areas where population reductions have occurred (Lee et al., 2001; Holland et al., 2000). In addition to targeting specific natural enemies or natural-enemy communities, shelter habitats will also affect the richness and abundance of crop associated biodiversity, although the extent to which this ‘unplanned’ biodiversity is beneficial, varies (Vandermeer and Perfecto, 1995).

Shelter habitats can be either external to (at crop or field edge) or lie within a crop. Linear features such as hedgerows, ditches, fence lines, fencerows, shelter belts and field margins are the most common external habitat features that abut cropped fields, along with woodland and grassland (Haines-Young et al., 2000). These linear features form a composite of habitat characteristics and may include an herbaceous ground flora, a woody or shrubby canopy and/or emergent trees (Forman and Baudry, 1984). The complexity of the habitat structure and the plant species composition will determine the range of niches and hosts available and consequently the diversity and abundance of associated beneficial arthropods (Burel and Baudry, 1995).

Within-crop shelter habitats tend to be herbaceous (perennial or annual) and are designed not to impede farm machinery or practice. Arguably the most iconic within-field shelter habitats in Europe are semi-permanent features known as “beetle banks”, which are composed of an earth bank sown with perennial, tussock-forming grasses located centrally in larger arable fields (Thomas et al., 1991, 1992b). Their function, as elaborated below, is to provide improved overwintering conditions for a range of polyphagous predators and maintain populations within the field to facilitate rapid colonization of the crop when predators leave overwintering sites in the spring.

Within intensively managed cropping systems, polyphagous predators that have overwintered in field boundary habitats are more likely to be present and even dominate the arthropod fauna early in the season (Wissinger, 1997;

Ribera et al., 2001), when predators have greatest potential to control pest population outbreaks (Chambers et al., 1986). In particular, generalist predators within the Coleoptera (Carabidae and Staphylinidae) and Araneae (Lycosidae and Linyphiidae) are numerically dominant in temperate fields and a large proportion overwinter as adults or juveniles in non-crop areas (Sunderland et al., 1987). Many of these species show seasonal migration between crop and shelter habitats at different stages in their life cycle (Coombes and Sotherton, 1986; Duelli et al., 1990). Certain species of polyphagous predators will also use shelter habitats during summer as sites for refuge from unsuitable microclimatic conditions, oviposition and larval development (Wallin and Ekblom, 1988).

Optimal shelter habitat can improve overwintering survival and subsequent fecundity of polyphagous predators by ensuring availability of pre-overwintering food for the build up of fat reserves, and drier microhabitats with stable but relatively low temperatures to limit direct mortality and the depletion of fat reserves (Sotherton, 1985; Van Dijk, 1994; Dennis et al., 1994; Zhou et al., 1995; Petersen et al., 1996; Petersen, 1999). Prey availability in shelter habitats in early spring can also influence post-overwintering mortality, fecundity of surviving individuals and phenology of dispersal into the crop (Thomas et al., 1992a; Bommarco, 1998a; Petersen, 1999). Although generalist predators vary in their degree of polyphagy, several studies have indicated the value of a mixed diet in maximizing growth and survival (Toft, 1995; Jorgensen and Toft, 1997; Toft and Wise, 1999) and enabling polyphagous predator populations to be maintained when the pest is absent or present at low levels (Settle et al., 1996). Plant diversity, density of herbaceous vegetation and leaf litter can all influence the distributions of soil-dwelling species that are prey items for polyphagous predators (Altieri and Letourneau, 1982; Dennis et al., 1994; Hovermeyer, 1999).

In addition to provision of food, certain attributes of shelter habitats have been associated with preferential microclimatic conditions to benefit overwintering arthropods. A raised bank can improve drainage (Sotherton, 1985) and different vegetation types and cover will also affect fluctuations in temperature, with tussocky grasses appearing to provide favorable, stable temperatures for overwintering polyphagous predators (Thomas et al., 1992a; Collins et al., 2003). Grass mixtures also increase the structural diversity of the vegetation and thereby that of the beneficial arthropods (Baines et al., 1998). Web-building spiders have been shown to prefer a closed structure (Robinson, 1981), and litter depth is an important determinant of spider community composition (Bultman and Uetz, 1982). Overall, a positive relationship is considered to exist between plant diversity in uncropped habitats and the diversity and abundance of beneficial arthropods (Dennis and Fry, 1992; Asteraki et al., 1995). However, some relatively simple habitats (e.g. fencelines) can support a high number but low diversity of beneficial arthropods that may contribute to pest control (Griffiths et al., 2007).

Hedgerows may be expected to encourage beneficial arthropods within fields because of their high associated biodiversity (Pollard and Holland, 2006). More floristically diverse hedges support a greater diversity of faunal species (Pollard et al., 1974), although the number of arthropod species associated with individual plant species found within hedges can vary enormously (Kennedy and Southwood, 1984). Predators from five orders (Araneae, Coleoptera, Diptera, Hemiptera and Hymenoptera) were found to be the dominant functional group associated with hedgerows in southern Britain, accounting for 90% of all arthropods captured (Pollard and Holland, 2006).

The presence of a range of shelter habitats and composite features will enhance habitat heterogeneity at the farm and landscape scale, contribute to higher invertebrate diversity and decrease the probability for overall extinction of rare species (Marino and Landis, 1996; Colunga-Garcia et al., 1997; Holland and Fahrig, 2000; Bianchi et al., 2006; Griffiths et al., 2007). Bommarco (1998b) found that fecundity and body size of a carabid generalist predator was positively correlated with the degree of landscape heterogeneity within its range of mobility. By manipulating landscape structure and composition, the condition of polyphagous predatory carabid beetles could be improved, thereby potentially increasing populations of these beneficial insects (Ostman et al., 2001). Additionally, by enhancing habitat heterogeneity, it is more likely that cross-taxon biodiversity (e.g. plants, birds, mammals and other arthropods) can be maintained (Lombard, 1995), together with additional ecosystem services including pollination, nutrient recycling and food chain linkage.

3. Influence of shelter habitats on natural-enemy distribution and dispersal

As indicated, in the spring a proportion of polyphagous predators will disperse into crops from boundary overwintering sites. Such movement between habitats is especially true for Coleoptera, whereas spiders show a greater species differentiation between uncropped and cropped areas, and consequently the presence of boundary habitats will have less impact on abundances within the adjacent crop (Kromp and Steinberger, 1992; McLachlan and Wratten, 2003). However, even for the Coleoptera, not all individuals will disperse from their shelter habitats (Thomas et al., 2001). For those that do, the rate and extent of colonization are determined by the boundary habitat quality, field:boundary ratio, field size and dispersal ability. To achieve an even field coverage before pest populations develop, overwintering arthropods within boundaries must disperse rapidly across fields. This can be more readily achieved by aerial dispersers, such as Linyphiidae and certain Staphylinidae (Hunter et al., 1991), than less mobile species. Most medium-sized Carabidae and Lycosidae, for example, disperse by walking and remain in relatively close proximity (~60 m) to the field boundaries (Coombes and Sotherton, 1986; Holland et al., 2004a). It was to

address this colonization constraint that beetle banks were developed and ultimately recommended for use through the center of fields greater than 16 ha (Thomas et al., 1991). Indeed, a common aim of within-crop habitat manipulations is to minimize dispersal constraints of beneficial arthropods by providing shelter, plant resource subsidies, alternative hosts and prey within and around the crop at a scale relevant to species' mobility.

In contrast to herbaceous shelter habitats, woody features may inhibit movement of arthropods between fields depending on the vegetation structure and species in question, and reduce the possible benefits of shelter habitats (Duelli et al., 1990; Mauremooto et al., 1995; Thomas et al., 2001; Fernández Garcia et al., 2000). Vegetation structure at the ground level has been shown to strongly influence foraging and movement behavior of ground-active predators, with absence of cover, and increased structural complexity of vegetation reducing movement rates (Mauremooto et al., 1995). Large scale mark-release-recapture studies investigating the season-long permeability of hedgerows to predatory carabids have produced contrasting results demonstrating potential for inhibition (Fernández Garcia et al., 2000; Thomas et al., 2001), or facilitation (Holland et al., 2004b) of between-field movement (differences which may be attributable to hedgerow structure (Joyce et al., 1999)). The fractal geometry of the ground surface may be important in increasing the effective distance dispersed by an epigeal arthropod (Wiens et al., 1993; Mauremooto et al., 1995; Thomas et al., 2001). Furthermore, insects can also encounter field boundaries as impediments to flight between fields and this will be influenced by the canopy structure (Wratten et al., 2003).

4. Efficacy of shelter habitats for biological control

From the above it can be seen that shelter habitats have the potential to influence the abundance, diversity and distribution of natural enemies in the agroecosystem but what does this mean for pest control? The answer to this central question appears somewhat equivocal. Whilst ecological theory supports the general basis of CBC, there is very little quantitative evidence to optimize this practice (Gurr et al., 2003). Where evidence exists, it tends to demonstrate potential for impact rather more than confirming actual impact. For example, at the semi-field and field level numerous studies have shown that fungal pathogens, aphid specific predators, parasitoids and polyphagous predators can considerably reduce peak aphid numbers and/or yield loss (Chambers et al., 1986; Ostman et al., 2003; Schmidt et al., 2004; Winder et al., 2001, 2005; Holland et al., 2006). Additional evidence for generalist predators indicates potential to reduce cereal and sugar beet aphid populations in their early colonization phase, mainly by foraging on aphids that have fallen from the vegetation (Kromp, 1999). With regards to the influence of shelter habitats, the creation of field margin refuges around arable

fields has been shown to enhance the within-field activity-density of polyphagous predators, as well as increase the availability of food for predators and their subsequent fecundity (Lys et al., 1994; Dennis et al., 1994). However, the spatial extent of such effects appears limited. Collins et al. (2002) reported a detectable impact of generalist predators originating from a beetle bank up to 58 m into the crop. This agrees with intensive studies on the spatial distribution of boundary overwintering predators showing that the overall numbers of predatory arthropods are highest within 60 m of the boundary (Holland et al., 2004b, 2006). Similarly, a study on the use of unharvested refuge strips in lucerne (*Medicago sativa* L.) suggested that strips should be spaced less than 30 m apart to enable natural enemies to contribute to herbivore suppression over the entire width of the intervening crop (Hossain et al., 2002).

At larger scales, landscape heterogeneity has been shown to contribute to greater invertebrate diversity and to the increased effectiveness of natural enemies (Colunga-Garcia et al., 1997; Bommarco, 1998b; Holland and Fahrig, 2000; Bianchi et al., 2006; Marino et al., 2006). In a recent review, Bianchi et al. (2006) identified that in 74% of studies examined, natural-enemy populations were higher in complex versus simple landscapes. The review further identified that in 80% of the cases, enhanced natural-enemy activity could be associated with herbaceous habitats, such as fallows and field margins. However, data to confirm impacts on actual crop damage or yield were generally wanting. Moreover, the patterns revealed in the literature are complex. In a study examining the effect of agricultural landscape structure on parasitism and parasitoid diversity, Menalled et al. (1999) found that in some sites, complex landscapes comprising cropland intermixed with mid- and late-successional non-crop habitats, had higher rates of parasitism and parasitoid diversity compared with simple (primarily cropland) landscapes. This pattern, however, was not consistent across all sites and so no clear effect of landscape complexity on parasitism could be determined. Similarly, Weibull et al. (2003), reported a general increase in species richness with landscape heterogeneity at the farm scale, but also showed that changes in diversity do not clearly lead to effects on natural pest control. For example, although parasitism was higher in more complex landscapes, so too was aphid colonization, resulting in no net gain in biological control compared with simpler landscapes (Thies et al., 2005). Part of the observed variation may result from threshold effects associated with landscapes of differing complexities. In simple landscapes, increasing non-crop habitat can have an impact on biological control but in structurally diverse landscapes that already have a high proportion of non-crop areas, increasing the proportion of non-crop areas further has little effect (Thies and Tschardtke, 1999).

It appears, therefore, that in many cases the actual benefits of shelter habitats for pest control tend to be implicitly assumed rather than explicitly demonstrated. Indeed, the development of CBC overall has been limited by a lack

of studies examining impact on herbivore populations and cascading effects on crop yield or value (Risch et al., 1983; Bianchi et al., 2006). The lack of data is compounded further by the fact that our understanding of the relationship between biodiversity (as affected by these habitat manipulations) and pest control functioning remains poor, and the mechanisms through which natural enemies interact to determine the extent and stability of pest control, are unclear. For example, in a recent study of the effect of landscape, habitat diversity and management on species diversity in cereal systems, Weibull et al. (2003) revealed that there was no straightforward relationship between species richness of carabids, rove beetles, and spiders, at either the farm level or in individual cereal fields, and biological control. They concluded that species richness in itself is not as important as a high diversity of different guilds of predators, such as ground and foliage predators, spring and summer breeders, day and night active species, for the overall efficiency of biological control. In effect, this argues that the key to successful natural control is in maximizing functional complementarity among the natural enemies of pest species. Unfortunately, our understanding of complementarity and the factors determining the emergent properties of multi-species predator assemblages is limited (Schmidt et al., 2003). While there is evidence that there is significant niche partitioning across microhabitats and functional complementarity among spider species for example (Sunderland, 1999), few other studies have shown significant complementarity among natural enemies (but see Snyder and Wise, 1999; Wilby and Thomas, 2002; Wilby et al., 2005). Similarly, whilst examples of synergistic interactions between predators exist (e.g. foliar predators eliciting dropping responses in aphid prey which increases their vulnerability to ground-foraging predators (Losey and Denno, 1998)), processes such as intraguild predation (Rosenheim et al., 1995; Finke and Denno, 2004) can severely disrupt biological control. A particularly pertinent example in this regard is the recent study of Prasad and Snyder (2006) which revealed that intraguild predation between large and small predatory beetles could negate potential biocontrol benefits of beetle banks in vegetable cropping systems in the US. Additionally, the expression of these different diversity effects will be dependent on ecological context, with factors such as habitat complexity (Finke and Denno, 2006), extent or diversity of prey resource (Wilby et al., 2005) and higher (Sullivan and Völkl, 1999) or lower (Thomas, 1999) trophic level effects strengthening and/or weakening the emergent properties of even the same assemblages of natural enemies (Fridley, 2001).

Alternative hypotheses regarding the role of biodiversity in ecosystem functioning present contrasting implications for the benefits of CBC strategies that affect measures of enemy diversity such as richness and abundance. Within classical biological control programs, for example, although multiple species of natural enemy might be released, in the majority of cases effective control is deliv-

ered by a single species of natural enemy (Denoth et al., 2002). This observation is consistent with the results of a recent meta-analysis of biodiversity–ecosystem function experiments that indicated that the widely reported positive effects of biodiversity were likely generated by the so-called ‘sampling effect’ (Cardinale et al., 2006). This argues that as diversity increases, so does the probability of including a functionally effective species (in our case natural enemy) within the assemblage and it is this species that is responsible for the majority of the function. Prevalence of the sampling effect would imply that habitat manipulations for CBC would be most effective if they targeted the functionally dominant species of natural enemy (or enemies) rather than enemy diversity per se. However, this conclusion is highly crop and scale dependent; scaling up from the field to the farm or landscape level will broaden the range of pest species and ecological scenarios under which a natural enemy has to act. Hence, although just one species of natural enemy might contribute substantially to control of one pest species in one crop at one site, in line with the ‘insurance hypothesis’ (Naeem and Li, 1997; Petchey et al., 1999; Yachi and Loreau, 1999), in order to cope with a full range of pests, crops and environmental conditions in successive years, it is likely that different species of natural enemy will be required to deliver effective control over time and space. Placed in a broader ecological context, while a saturating function may be a common biodiversity–ecosystem function relationship (Schwartz et al., 2000; Hooper et al., 2005; Cardinale et al., 2006), the minimum diversity at which maximal functioning is obtained will be dependent, in part, on the spatial–temporal-process extent of the study (Wilby and Thomas, 2007).

5. Economics of CBC and technology adoption

Clearly, in many production systems, much research remains to be done to quantify the role of shelter habitats in natural pest control and to provide management recommendations on optimal shelter habitat design. As a consequence, voluntary adoption of CBC techniques has been limited and is highly influenced by prevailing policy and commercial contexts that determine the costs–benefits associated with implementation (Falconer and Hodge, 2000; Pietola and Lansink, 2001). These potential economic costs and benefits of CBC can be compartmentalized into those accruing to the grower, and the external costs and benefits accruing to the rest of society. Considered together, these dual components will determine the incentives for adopting technologies such as habitat manipulations.

To further explore the relative costs and benefits accruing to growers and society, we take as our starting point the aim that a CBC measure, such as a beetle bank, will deliver a degree of pest control sufficient to prevent pests exceeding economic thresholds, enabling insecticide inputs to be avoided. In this case, the benefits for the grower derived from protection of the crop are zero since in the absence of CBC this level of pest control would have otherwise been

achieved through use of chemicals. The costs associated with implementing CBC practices relative to the marginal cost of the insecticide application avoided would, at a minimum, include the avoidance of chemical insecticide purchase. However, the farmer might also save the costs associated with application of the product, including energy, machinery depreciation and possibly labor costs, if the product was to be applied singly and not as a tank-mix. Of course, this ignores the possibility that pesticide efficacy might be declining due to development of resistance, that pesticide regulation becomes more stringent over time, and that pesticide taxation has yet to be introduced (Falconer and Hodge, 2000), all of which will make CBC relatively more appealing.

The costs associated with the use of CBC are more difficult to characterize and quantify. The implementation of a CBC strategy largely consists of switching potentially productive land out of crop production and into the production of habitat designed to produce pest control function, together with increased labor inputs in the form of system monitoring and human capital (in the form of one-off information or knowledge acquisition). The grower, therefore, faces a cost equal to the reduction of saleable crop output that could have been produced from the diverted land. However, farmland quality may vary, even over a relatively small scale, and so a field margin habitat could present the farmer with a lower opportunity cost than a within-field habitat feature due to existing edge effects on crop yields and crop quality. This potential for differential opportunity costs could result in economic pressure for the adoption of sub-optimal management prescriptions for CBC (for an example of this pressure see Fraser, 2001). Of course, diverting land from production means the farmer should net from this the costs of inputs (such as seed, fertilizers, other chemical sprays and the marginal operations costs such as energy, machinery depreciation and the value of any labor input) which are avoided due to the diversion of land from crop production. Lastly, the farmer must consider whether the diversion of land for CBC presents any additional negative impact on economic yield through unintended increase of harmful organisms such as weeds, pests or diseases.

Given our starting assumption (i.e. that chemical and biological pest control are equally effective), there will be an economic incentive for a farmer to adopt CBC if the grower costs are lower than those of using chemical insecticide alternatives. If, however, the efficacy of CBC falls short of chemical control then we need to calculate differences in total benefit as well as costs. It is important to note that a comparison of efficacy must consider variation in pest control and not just mean levels. Variation in efficacy and differences in predictability between the alternative strategies can have a discernable impact on the relative risk that farmers face and this must be factored into the cost:benefit calculation. Risk perception can have a strong impact on the willingness of farmers to adopt alternative pest management strategies, and risk-averse growers may

be prepared to accept greater overall costs in exchange for stable outputs (Lu et al., 1999). However, added benefits will be received by those farmers adopting CBC techniques that are eligible for subsidies during transition to organic production, or able to sell their products with certified organic premiums. These benefits provide a strong incentive for organic conversion, with premiums allowing certain organic cropping systems to be more profitable than conventional production, although this raises questions regarding long-term viability (Lohr and Salomonsson, 2000; Smith et al., 2004). Furthermore, our estimates of variability in natural pest control efficacy are likely to be a function of the relative volume of research activity and experience (Cowen and Gunby, 1996), which will likely be unfavorable to the assessment of a new CBC technology compared with an established chemical approach (in simple terms 20–30 years of experience with an incumbent technology count for more than perhaps 3–5 years data on a new one).

To society, the switch from insecticide use to CBC presents an opportunity to benefit from two potential impacts. First, the reduction in chemical use is likely to reduce loadings of toxicants in ground waters, rivers and other water bodies and hence, off-site environmental damage. Reduced application also reduces the incidence of operator ill-health and the probability of encountering residues of insecticides in animal and human foodstuffs. Such reductions can enhance the welfare of society as a whole (Chalak et al., 2006; Foster and Mourato, 2000). Second, the promotion of an increased level of biodiversity in the agricultural landscape can also produce a positive external value when the public attaches importance to such things (Chalak et al., 2006). However, it is somewhat ambiguous whether the public will always value more biodiversity and here the nature of the changes and taxa affected matters (Crane et al., 2006). Moreover, farming practice will be informed in the first instance by whether or not the benefits outweigh the costs for farmers (although some farmers will, of course, place large personal values on the sustainability and environmental neutrality of their farming system which may encourage adoption of CBC even if it presents some loss). If farmers risk a net cost, but the marginal external benefits to wholesale adoption are positive, then implementation of CBC will likely require some form of government intervention. These interventions could include a physical ban of certain insecticides, pesticide taxes or subsidies for CBC to drive up the relative marginal cost of insecticide strategies. In addition, increased public funding of CBC research could redress technology lock-in problems and engage in knowledge exchange and extension activities to improve commercial understanding of CBC and increase farmers' confidence (Cowen and Gunby, 1996; Lohr and Salomonsson, 2000).

Central to quantifying either grower or public benefit is a need to understand how effects of habitat manipulations are influenced by scale. We illustrate this in Fig. 1 with three conceptual models describing different relationships

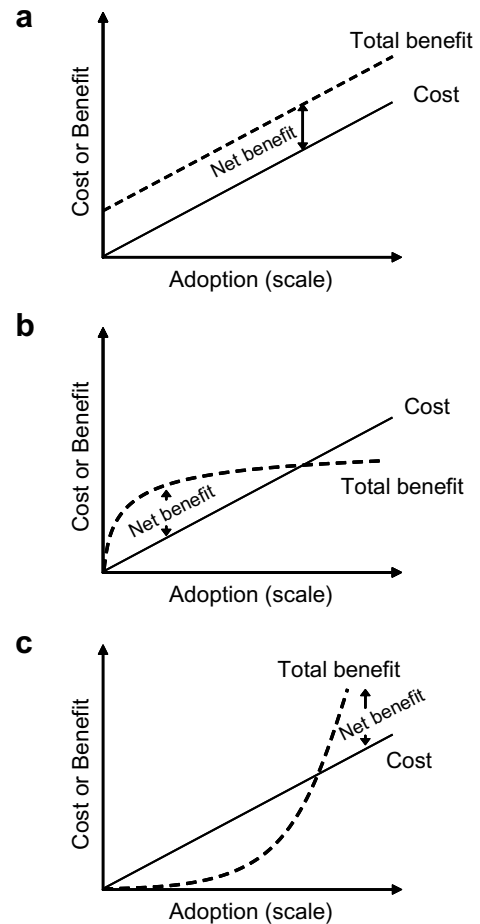


Fig. 1. Illustrative examples of possible relationships between costs and benefits of a conservation biocontrol strategy and the level of adoption of that strategy. (a) A simple linear relationship whereby effect on biocontrol is independent of level of adoption and hence, net benefit remains constant. (b) A non-linear relationship where effectiveness is greatest at small scales such that net benefit decreases as adoption increases. (c) A contrasting non-linear case where impact increases with adoption. Here adoption needs to exceed some threshold level before a net benefit is derived. Implications of these models are discussed in more detail in the main text.

between benefits of a CBC technology, such as manipulation of shelter habitats, and scale of adoption. In the first scenario (Fig. 1a) we assume benefits to be independent of scale. In this instance, increased adoption leads to an increase in total cost and total benefit of the approach, but net benefit remains constant. In Fig. 1b we present an alternative scenario whereby benefit saturates with increasing adoption. This could arise if, for example, the effects of a habitat manipulation derive largely from redistribution of natural enemies; at small scales (e.g. single field level) natural enemies might be drawn from adjacent habitats boosting pest control, but at larger scales (e.g. multiple fields) this effect diminishes as the species pool for redistribution becomes exhausted. The implications here are that a technique might look promising initially and favor early adopters but then fail as it becomes implemented more widely. The contrasting scenario is that benefit of a technology

could be negligible initially but then increase with scale of adoption (Fig. 1c). This could occur if habitat manipulation alters natural-enemy richness and abundance and numbers build up the more habitat there is. In this case, there might be little incentive for adoption by an individual farmer unless the technology is going to be implemented widely. Such an effect is also consistent with negative transition effects that produce short-run declines in yield following the initial shift from chemical to biological control (see Cowen and Gunby 1996). Any negative scale or transition effects will likely hinder adoption whenever farmers trial, or partially adopt, a practice in order to evaluate its performance. Which of these (or other) relationships apply will depend on the specifics of the technology and the local ecological context (cf. Thies et al., 2005) but on the whole, we understand very little about scaling effects.

6. Conclusions and recommendations

The development of biological alternatives to chemical pest control has been an area of intensive research for some decades. However, on a global scale, penetration of biological control technology into agriculture has been minimal—less than 1% of global pest control sales of US\$30 billion involve biological methods. In particular, the negligible uptake of biologically based pest control in annual, arable crop systems is striking. Based on insights derived from the review above we can identify a number of key priorities for future research to address this technology gap. First, whilst there are numerous studies examining and demonstrating effects of different habitat features on various measures of natural-enemy abundance, diversity and distribution, data confirming and quantifying the contribution of these manipulations to reductions in pest populations and cascading effects on crop yield or quality are few. We need more research to quantify impact and how this varies across time and space (since it is not just mean impact that is important but also variation).

Second, in addition to quantifying what impacts certain habitat manipulations have on pest control, we need a better understanding of the mechanisms involved and how practices might be modified to further increase impact. To design optimum (integrated) management prescriptions we need to understand the full complexities of the biodiversity–ecosystem functioning relationship and the ecological circumstances under which interactions (sometimes extending across 3 or 4 trophic levels) reduce or enhance natural-enemy function at the appropriate level of field or farm. At present we are attempting to manipulate natural enemies without a clear understanding of the consequences (which might be negative as well as positive), and without prior knowledge of what components of enemy diversity, abundance and distribution we need to manipulate in order to deliver effective control.

Third, common to both of the above is the need to better understand the role of ecological context and functional spatial scale. This call is not new (e.g. Kremen, 2005; Thies

et al., 2005; Urban, 2005) and the research challenges here are numerous. What we can say, however, is that ‘standard’ research programs that evaluate a technology over may be 1 or 2 fields for 3 years, likely provide a weak foundation for effective translation to farm or landscape levels.

Finally, it is essential to understand the economic costs and benefits accruing to the grower of adopting CBC technology. Evaluating the costs is relatively straightforward but, in line with the fact that few studies have demonstrated actual impact of habitat manipulations on pest densities and crop yields (see above), the benefits remain unquantified in many cases. Potential public benefits also tend to be poorly quantified but these (and the associated policies) may be as, or more important than grower benefits in determining ultimate adoption; factors such as retailer or regulatory constraints on pesticide use and compliance requirements for farm subsidy schemes, strongly determine farmer behavior. These insights identify the need to place CBC research in a more interdisciplinary context and to recognize the importance of socio-economic factors, and not just technological innovation, in changing management practice.

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