



## A functional overview of conservation biological control



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### ABSTRACT

Conservation biological control (CBC) is a sustainable approach to pest management that can contribute to a reduction in pesticide use as part of an Integrated Pest Management (IPM) strategy. CBC is based on the premise that countering habitat loss and environmental disturbance associated with intensive crop production will conserve natural enemies, thus contributing to pest suppression. The abundance and diversity of natural enemies increases in response to a variety of conservation measures, including plant and habitat diversification, a reduction in cropping intensity, and increased landscape complexity. However, the response of natural enemy populations to conservation measures is not consistent; often it fails to translate into pest suppression or improved crop yield, and is seldom utilised in commercial crop production settings. CBC is a complex strategy drawing on a number of ecological and behavioural processes, operating at multiple scales, and mediated by management actions that are, potentially, targeted at a wide range of pest organisms. Given this inherent complexity, it is not surprising that the scientific understanding of CBC is incomplete, or that the design and adoption of reliable CBC prescriptions have proved elusive. To tackle this, we consolidate existing knowledge of CBC using a simple conceptual model that organises the functional elements of CBC into a common, unifying framework. We identify and integrate the key biological processes affecting natural enemies and their biological control function across local and regional scales, and consider the interactions, interdependencies and constraints that determine the outcome of CBC strategies. Conservation measures are often effective in supporting natural enemy populations but their success cannot be guaranteed; the greatest limitation to the development of effective CBC is due to a failure to adequately direct biological control services to achieve suppression of the target pests. By considering the performance of these and other components of CBC within the context of an integrated system, we believe that the limiting factors can be identified, and removed, allowing effective CBC strategies to be implemented.

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### 1. Introduction

Conservation biological control (CBC) seeks to contribute to the management of pests by supporting populations of natural enemies present in the agroecosystem and promoting their effectiveness as

predators, parasitoids or pathogens (Ehler, 1998; Pell et al., 2010; Seastedt, 2014). Natural enemies were fundamental to pest regulation in the holistic crop-production systems that preceded the widespread adoption of synthetic pesticides during the second half of the 20th century. However, agricultural intensification involving greater reliance on pesticides and the accompanying simplification of landscapes, dominated by highly disturbed crop habitats, has threatened natural enemy populations and the stability of crop production by increasing the frequency and severity of pest

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outbreaks. Despite this, natural enemies continue to provide a valuable ecosystem service; estimates rank their contribution to the management of crop pests well ahead of other measures, including pesticides (Pimentel and Burgess, 2014), and place a value on this service of \$4.5 billion annually in the United States alone (Losey and Vaughan, 2008). It is clear, therefore, that the conservation of natural enemies is of fundamental importance to the sustainability of crop production and that encouraging natural pest management through the “Protection and enhancement of important beneficial organisms” is a basic tenet of Integrated Pest Management (e.g. Principle 1 - Annex III of Framework Directive, 2009/128/EC, see Barzman et al., 2015; Lamichhane et al., 2016).

To date, CBC strategies have focused on reversing the negative effects of intensification on natural enemies. These include reducing disturbance associated with the extensive use of pesticides, tillage, and other agronomic interventions, as well as the establishment of beneficial habitats to compensate for the general reduction in quality and diversity of habitats in the agricultural landscape. Sufficient research has now been done to establish that natural enemies respond positively to such conservation strategies; including plant diversification (Letourneau et al., 2011), reduced cropping intensity (Attwood et al., 2008; Garratt et al., 2011; Sunderland and Samu, 2000), and enhanced landscape composition or complexity (Chaplin-Kramer et al., 2011; Veres et al., 2013). However, it is also clear that such strategies do not always benefit natural enemy populations and, more significantly, they often fail to result in effective pest regulation (Chaplin-Kramer et al., 2011; Veres et al., 2013) or improved crop yield or quality (Letourneau et al., 2011). The adoption of CBC-specific strategies by farmers is limited to a few examples (Landis et al., 2000; Tracy, 2014), among them the introduction of perennial beetle banks (Collins et al., 2002; MacLeod et al., 2004) and the sowing of flower-rich margins (Marshall, 2004; Haaland et al., 2011). More extensive initiatives such as the “Greening Waipara” programme (Gillespie and Wratten, 2012) which has coordinated the introduction of native plants to support a range of ecosystem services, including pest suppression, to vineyards in the Waipara Valley, New Zealand, being rare exceptions.

CBC is a complex pest suppression strategy drawing on a number of ecological and behavioural processes. It operates at multiple scales and is mediated by management actions that could be targeted at a wide-range of pest species and their associated natural enemies. Efforts continue to elucidate the workings of CBC but habitat management remains the dominant consideration (Gillespie et al., 2016; Holland et al., 2016; Philips et al., 2014), albeit with an expanded perspective that recognises the multiplicity of resource requirements, scales, ecosystem services, natural enemy and pest species (Gillespie et al., 2016; Philips et al., 2014). Furthermore, consideration has also been given to an increasing number of other issues relevant to CBC including nutritional (Labruyere et al., 2016; Tena et al., 2016) and chemical ecology (Rodriguez-Saona et al., 2012), molecular genetic approaches (Gurr and You, 2016), natural enemy dispersal and habitat connectivity (Schellhorn et al., 2014), trophic interactions (Chailleux et al., 2014), landscape effects (Chaplin-Kramer et al., 2011; Veres et al., 2013), impact assessment (Macfadyen et al., 2015), and societal and economic aspects (Naranjo et al., 2015; Tracy, 2014; Uyttenbroeck et al., 2016). This expansion of CBC research has been accompanied by an increasingly integrative view; for example, considering interactions between scales (Schellhorn et al., 2015b) and between farming systems and landscape structures (Rusch et al., 2010). Given the inherent complexity, it is not surprising that, despite these research efforts, the scientific understanding of CBC is incomplete. Neither is it surprising that the design and adoption of reliable management prescriptions have proved elusive (Jeanneret et al., 2016).

In response to this challenge, we propose that the development of successful CBC strategies will be made easier if a systemic view of CBC is taken. This approach would identify and integrate each of the relevant biological processes affecting natural enemy populations and individuals, be explicit about their interactions, constraints and interdependencies, and provide a framework within which management interventions can be located. To guide this process, we propose a simple conceptual model that organises the functional elements of CBC into a common, unifying framework. The framework is then used to synthesise existing knowledge, providing a comprehensive overview of CBC and a guide for the development of CBC strategies. Our focus is on placing existing knowledge in the context of this systematic framework which we do by reference to existing published studies, supplemented by more detailed examples from our own recent research.

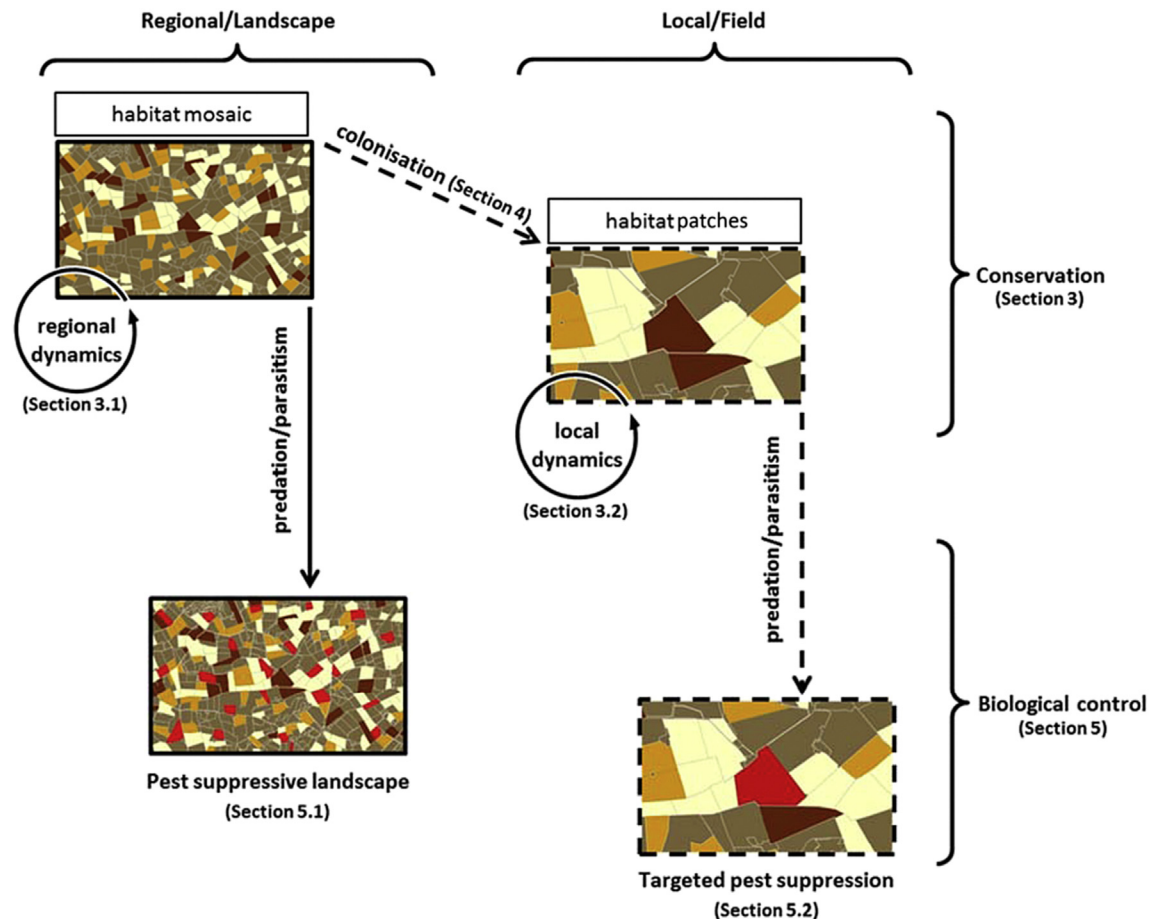
## 2. A conceptual model for CBC

The framework recognises that CBC is inherently multi-scalar and that, although spatio-temporal scale is a continuum perceived differently by each pest and natural enemy species, farming practice produces characteristic structures at, more or less, fixed scales. On this basis, two scales that are relevant to CBC and common to many crop production systems are identified: the local scale, which consists of a cropped field and the surrounding habitats, and the regional or landscape-scale, which comprises multiple fields and areas of non-cropped land and semi-natural habitats (Fig. 1). In addition to scale, the framework decomposes CBC on the basis of the processes that operate, primarily those that contribute to the conservation of natural enemies versus those that subsequently deliver biological control. At the regional scale, spatial population dynamics, influenced by the composition and configuration of habitat types within the landscape, determine the abundance and diversity of species that make up the regional species pool. The local and regional scales are linked by the colonisation of local habitat patches. Regional conditions impose constraints on the local dynamics and hence on population growth and abundance of natural enemies within fields or in surrounding habitats. In principle local population dynamics may be isolated within a field or other habitat patch. However, for many species of natural enemy, populations move between crop and non-crop habitats, driven either by heteroecious life-cycles or within-field disturbance. Together, regional and local population dynamic processes underpin the conservation of natural enemy populations. However, to deliver biological control, i.e. the suppression of pest populations and protection of crop yield and quality, requires the cascade of trophic interactions from natural enemies to crop to proceed unimpeded. Enhancing natural enemy assemblages at the landscape-scale has the potential to increase predation (or parasitism) pressure leading to the general and widespread suppression of prey populations, including crop pests. Additionally, colonisation of habitats at the local scale can concentrate the benefits of landscape-scale natural enemy conservation in the vicinity of target crops from where active or passive dispersal into the cropped areas could result in targeted biological control as a result of increased rates of predation and parasitism.

## 3. Natural enemy conservation

### 3.1. Landscape-scale conservation

It has been proposed that more effective biological control will be achieved in complex landscapes that contain a higher proportion of semi-natural habitat and less intensively-managed farmland than simple landscapes, and consequently support a greater



**Fig. 1.** A conceptual model or framework for conservation biological control (CBC) which decomposes CBC into conservation and biological control elements and identifies two scales at which these processes operate and interact. Two alternative routes to successful pest management are shown. Route 1 (solid arrow) identifies the general suppression of insect herbivores that results from the non-specific conservation of natural enemy populations at the landscape scale, possibly resulting in the suppression of crop pests across the region (indicated in red). Route 2 (dashed arrows) identifies the steps to achieve the targeted suppression of a pest species at the field scale. Natural enemies colonise local habitats from the regional species pool, localising their abundance and enhancing it via local population dynamics in the vicinity of target fields. Subsequent dispersal into the crop results in pest suppression through increased predation and parasitism (indicated in red). The framework is described in more detail in section 2, the text in parentheses identifies those sections of the paper that expand on each component of the framework, and the routes to pest suppression are discussed in section 6. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

abundance and diversity of natural enemies (Landis et al., 2000; Tschamtkke et al., 2007). Recent reviews of the effect of landscapes on the conservation of natural enemies and on biological control provide compelling evidence that natural enemies benefit from increased landscape complexity. Bianchi et al. (2006) found that 74% percent of studies examined reported an increase in natural enemy abundance, a meta-analysis of 46 landscape-scale studies by Chaplin-Kramer et al. (2011) found a consistent positive effect of landscape complexity on natural enemy abundance and diversity, and Veres et al. (2013) found a positive effect on pest control or predation rates in more than three quarters of the studies they considered.

Increasing landscape complexity may promote the abundance of natural enemies across the landscape due to either the cumulative effect of increased fitness across multiple local populations resulting from the introduction of beneficial semi-natural habitats (Landis et al., 2000; Tschamtkke et al., 2008) or due to a reduction in chemical and physical disturbance associated with intensive crop management (Jonsson et al., 2012). However, the ability of natural enemies to disperse between habitat patches means that such effects are likely to be mediated by spatially-explicit processes. It is uncertain how increasing landscape complexity affects the population dynamics of natural enemies on a regional scale as these are

inherently complex and non-linear. Consequently the outcome of introducing fitness increasing measures into the landscape is uncertain. Field trials at this scale are almost inconceivable although modelling studies can provide useful insights (e.g. Bianchi and van der Werf, 2003; Bianchi et al., 2010; Jongejans et al., 2008; Box 2).

In addition to its impact on natural enemy abundance, landscape complexity, or more specifically, habitat heterogeneity, can affect biodiversity via various species-coexistence mechanisms. Increasing the heterogeneity among habitat patches leads to greater beta-diversity as long as species exhibit a degree of habitat specialism, while introduced semi-natural habitats possess greater within-patch vegetation diversity leading to an increase in alpha-diversity across trophic levels (Crist and Veech, 2006; Tschamtkke et al., 2007). Variation in habitat quality is also the basis for mechanisms such as the source-sink effect, which have the potential to promote species coexistence by allowing both competition and predation to be avoided (Kneitel and Chase, 2004).

Changes in landscape configuration may also affect natural enemy populations. The fragmentation of habitats that accompanies land-use intensification can, through patch isolation, lead to local extinction and pressures on regional persistence (Fahrig, 2003; Fraterrigo et al., 2009). In theory, a trade-off between the tendency for the isolation of habitat patches to reduce alpha-diversity

but promote beta-diversity (Tschamntke et al., 2012) may result in scale dependent effects of fragmentation. Modelling studies also suggest that natural enemy populations will be sensitive to habitat fragmentation and connectivity (e.g. Bianchi and van der Werf, 2003; Benjamin et al., 2008; Visser et al., 2009). This has been corroborated by some empirical studies, showing that the spatial configuration of beneficial habitats is more important than its area alone in determining arthropod abundance (e.g. Perović et al., 2010) while others have shown insect diversity can be more sensitive to habitat area than fragmentation (With and Pavuk, 2011).

The effect of landscape on the biodiversity and functioning of agricultural systems has typically been assessed in terms of landscape complexity, defined as the proportion of semi-natural, or conversely, agricultural land present (Chisholm et al., 2014). Recently, an increasing number of studies have attempted to understand the impact of landscape composition by resolving the effect of land-use in more detail. Research carried out as part of the EU FP7 project PURE found that particular habitat types, both crop and semi-natural, and their management contributed to landscape effects on the within-field abundance of predatory and parasitic arthropods (Box 1). These results are part of a growing body of work establishing that habitat specificity, including crop type, and complementarity between habitats, are important landscape-scale determinants of natural enemy abundance and diversity (Chisholm et al., 2014; Diekötter and Crist, 2013; Rusch et al., 2013; Sarthou et al., 2014; Schellhorn et al., 2015a).

### 3.2. Local and within-field scale conservation

A wide range of treatments have been tested at the local and within-field scale as part of attempts to conserve populations of natural enemies. These either involve a change in crop management to reduce non-target effects via some form of de-intensification, such as reduced tillage or pesticide use, or a diversification of habitat by the introduction of additional crop types or non-crop vegetation (Orr and Fox, 2012). Treatments may also be combined within a prescribed management approach as is the case in organic production or agri-environment management schemes.

By drawing on the reviews of Batáry et al. (2011), Bengtsson et al. (2005), Letourneau et al. (2011), and Langellotto and Denno, (2004) and examining the effect sizes representing 82 independent tests we can establish that, overall, conservation strategies have a positive effect on entomophagous arthropod groups (Fig. 2). However, variation in the effectiveness of treatments is substantial and a fifth of the 82 studies reported a decrease in the abundance of natural enemies (Fig. 2).

Habitat manipulation, through the introduction of semi-natural or non-crop vegetation in or around fields, has been the focus of natural enemy conservation strategies (Rusch et al., 2010; Orr and Fox, 2012) and is widely promoted by agri-environment schemes. The majority of trials support the effectiveness of this approach in conserving natural enemies (Andow, 1991; Gurr et al., 2000; Rusch et al., 2010), including floral margins (Haaland et al., 2011; Pfiffner and Wyss, 2004), arable-woodland boundaries (Bennewicz, 2011), riparian margins (Cole et al., 2012), and grass margins (Holland et al., 2012). In these and other cases the introduction of semi-natural habitats benefit natural enemy populations by providing: alternative food supplies; shelter from disturbance and predation; an improved microclimate; or by enhancing over-wintering survival and reproduction, (Landis et al., 2000; Rusch et al., 2010; Orr and Fox, 2012).

Many natural enemies require additional resources to supplement those obtained from pest prey or hosts. Floral resources, particularly nectar and pollen, are important dietary components for various natural enemies (Heimpel and Jervis, 2005; Wäckers

et al., 2008) and by providing these, the fitness of individual insects can be increased through enhanced survival (van Rijn and Wäckers, 2016), longevity (Wäckers, 2001) and fecundity (Tylianakis et al., 2004; Winkler et al., 2006). This provides a plausible mechanism for the conservation benefits that result from adding flowering plants in or around crops (Hickman and Wratten, 1996; Wäckers et al., 2008; White et al., 1995) though the frequent non-linear nature of population dynamics means that such effects may not necessarily lead to increased rates of population growth or density (Andow and Risch, 1985; Poveda et al., 2008). As an alternative mechanism, food sources may attract and retain natural enemies, leading to an aggregation response rather than population growth (Wäckers et al., 2008).

Semi-natural habitats can also provide supplementary resources by supporting populations of alternative prey and host populations. These are a valuable resource for natural enemies, increasing fitness and allowing populations to persist in the absence of pest species and enabling a rapid response to the appearance and increase in pest populations (Landis et al., 2000; Rusch et al., 2010). This mechanism is perhaps of greater importance to generalist predators, even though there are examples of parasitoid populations being maintained on an alternative herbivore host species which was itself maintained by the introduction of its preferred host plants (Bugg et al., 1987).

Beetle-banks (Collins et al., 2003) and hedgerows (Maudsley, 2000) are classic examples of habitat amendment strategies that conserve natural enemies through the provision of shelter. In these cases, the vegetation improves overwintering survival of ground-dwelling arthropods that would otherwise suffer from substantial disturbance in annual arable cropping systems (e.g. Varchola and Dunn, 2001; Pywell et al., 2005; Geiger et al., 2009).

De-intensification strategies may act to conserve natural enemies by mitigating the physical and chemical disturbance associated with intensive crop production. For ground dwelling species such as carabids or species such as some parasitoids whose life cycles include over-wintering in the soil (Nilsson, 2010), reduced tillage reduces mortality directly but may also influence arthropod communities, including natural enemies, through changes in the weed flora of fields (Norris and Kogan, 2000) or increases in ground cover as a result of the retention of stubbles and crop residues (Roger-Estrade et al., 2010). Non-target impacts of pesticides are an enduring environmental concern and are a strong motivation for pesticide reduction strategies (Frampton and Dorne, 2007; Meehan et al., 2011; Simon et al., 2010). Intuitively, any reduction in insecticide use would be predicted to have a positive effect on natural enemy populations (Geiger et al., 2010). However, in an extensive review of the effects of reduced pesticide use on field margins, a common agri-environment scheme prescription, the only consistent response was by herbivores to reduced herbicide application (Frampton and Dorne, 2007). Pesticide treatments also have a huge impact on the availability and stability of food resources in the crop and indirectly affect ecological processes such as field recolonization from their edges (Frampton et al., 2007).

The suppression of pests, weeds, and diseases is a significant driver for the traditional use of diverse cropping systems and its retention or reintroduction into modern practice (Vandermeer, 1989; Newton et al., 2009; Ratnadass et al., 2012; Tooker and Frank, 2012). Of the mechanisms by which diverse cropping can act to suppress pests, the bottom-up disruption of pest life-cycles and behaviour has been a favoured explanation (Bale et al., 2008; Ratnadass et al., 2012). However, several reviews provide convincing evidence that intercropping and other crop diversification schemes benefit natural enemy populations, i.e. the basis for top-down effects (Andow, 1991; Russell, 1989; Letourneau et al., 2011). Why natural enemies benefit in this way is not clear (Bale

**Box 1**

Evidence from PURE of landscape effects across cropping systems.

In the EU FP7 project PURE three contrasting cropping systems were investigated and the response of pest and natural enemy populations to system-specific measures of habitat quality explored across scales from field to landscape.

**East of Scotland arable cropping system (Quesada et al. pers com)**

- Activity abundance of ground beetles, spiders and rove beetles was measured in 40 fields and field margins in 2008 and related to local crop management intensity, field and boundary type, and landscape composition.
- The area of broadleaf woodland, heath, and specific crop types in the landscape were important determinants of predator abundance (Fig B1.1).

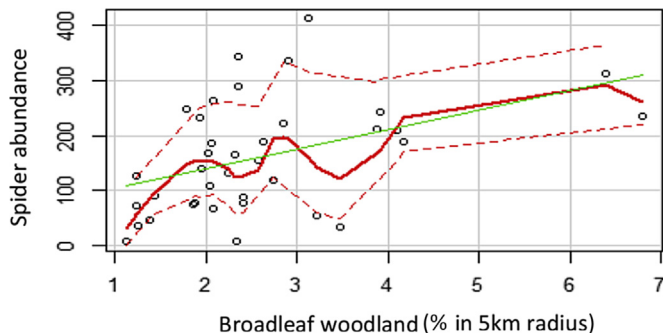


Fig. B1.1 Variation in the within-field activity density of spiders in relation the percentage of broadleaf woodland within the surrounding landscape (5 km radius of the fields).

**South-East France pome-fruit system (Maalouly et al., 2013)**

- Density of codling moth larvae and parasitism rate were measured in 37–49 apple orchards from 2006 to 2010 and related to local crop management intensity, orchard and boundary characteristics, and landscape characteristics, including the extent of semi-natural features such as hedgerows, crop management intensity and composition.
- Organic production was associated with increased parasitism at orchard and landscape scales but codling moth population also increased in organic orchards suggesting the positive contribution to conservation biological control did not compensate for the change in pesticide usage.

**North-Eastern France arable cropping system (Alignier et al., 2013)**

- Presence/absence of 13 common weed species was recorded in 58 fields from 2004 to 2011 and related to crop characteristics and field management, boundary characteristics and the crop type and management of neighbouring fields.
- Weed species occurrence was frequently influenced by the cropping history and management experienced at the field-scale, characteristics of the field boundary also contributed to the occurrence of the majority of species, while the management of surrounding fields also influenced the occurrence of several weed species (Fig. B1.2).

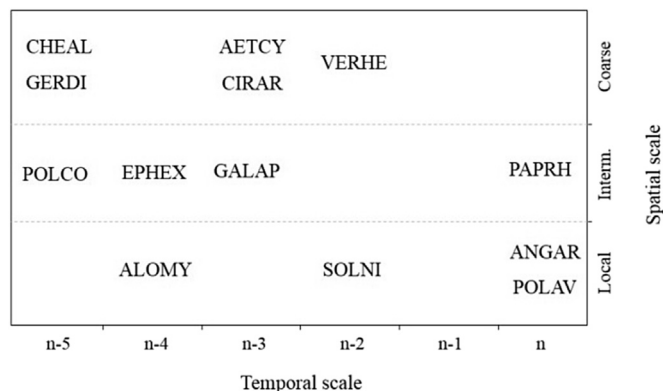
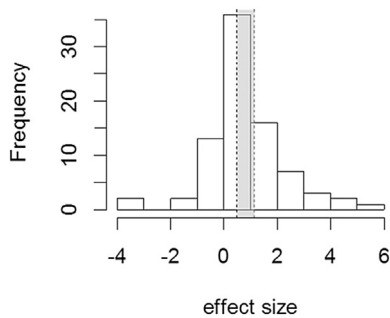


Fig. B1.2. Maximum spatial (local, intermediate, coarse) and temporal (current year = n, preceding year = n-1, etc.) scales included in best fitting statistical models of weed occurrence. The temporal scale corresponds to the shorter scale of significant management variables. AETCY: *A. cynapium*, ALOMY: *A. myosuroides*, ANGAR: *A. arvensis*, CHEAL: *C. album*, CIRAR: *C. arvensis*, EPHEX: *E. exigua*, GALAP: *G. aparine*, GERDI: *G. dissectum*, PAPERH: *P. rhoeas*, POLAV: *P. aviculare*, POLCO: *P. convolvulus*, SOLNI: *S. nigrum*, VERHE: *V. hederifolia*.

Conclusions: Together these studies examined the multi-scalar effects of crop management and land-use on the conservation of natural enemies and the impact on pest populations. Despite the contrasting nature of the systems, the results were consistent in: (1) demonstrating the sensitivity of natural enemy and pest populations to conditions across scales from field to landscape, (2) resolving detailed landscape effects on CBC, including specific crop management or land-use conditions, (3) highlighting the potential to develop multi-scalar crop and land-use management strategies to promote CBC.



**Fig. 2.** The distribution of effect size (ES) from 82 experimental tests of the response in natural enemy abundance to a range of conservation biological control treatments. ES varied from  $-3.64$  to  $26.89$ . The two largest ES reported ( $14.95$  and  $26.89$ ) came from maize intercropping systems in Africa (Midęga et al., 2008; Sekamatte et al., 2003). On the exclusion of these studies the maximum ES reported was  $5.55$  and the overall mean ES was  $0.81$ , significantly greater than zero ( $t$ -test:  $t = 5.108$ ,  $P = 2.12 \times 10^{-6}$ ). An ES of this magnitude is considered large (Cohen, 1988) and is equivalent to an increase in abundance from the 50th percentile (ES = 0, i.e. no effect) to the 80th percentile of the underlying distribution in natural enemy abundance. The shaded interval indicates the 95% confidence interval [0.49, 1.31]. Data taken from Langellotto and Denno (2004), Bengtsson et al. (2005), Batary et al. (2011), and Letourneau et al. (2011).

et al., 2008; Orr and Fox, 2012). Some of the same mechanisms underlying the beneficial effect of semi-natural habitats such as the provision of additional food sources and favourable microclimatic conditions may be involved (Bugg and Waddington, 1994; Landis et al., 2000). However, other mechanisms may also operate that are specific to crop diversification. For example, host selection behaviour of pests is disrupted by mixed cropping; this could also make pests more vulnerable to natural enemies, either due to depleted energy or fitness (and so the ability to defend themselves) or by increasing their apparency to natural enemies (Ratnadass et al., 2012).

#### 4. Spatial processes and scale interactions

Organisms, as individuals or populations, are seldom restricted to a single local habitat and so the effects of local treatments propagate through the landscape and link processes across scales (Tscharrntke et al., 2007). For example, the success of local conservation strategies must depend, at least in part, on interactions with meta-populations or communities that are defined at a larger, regional scale (Tscharrntke and Brandl, 2004). At its simplest, this interaction may take the form of a downscaling, in which conditions within local patches (crop fields or semi-natural habitat) act on those natural enemies that have been filtered or sampled from the surrounding species pool (Fig. 1). The importance of this process to CBC has been noted (e.g. Landis et al., 2000; Sunderland and Samu, 2000; Tscharrntke et al., 2007; Bale et al., 2008) but the effects have not been elaborated fully. However, the interaction between local and regional scales has been considered with respect to the conservation of biodiversity in agricultural systems more generally and in particular to explain the variable performance of local conservation initiatives (Dainese et al., 2015; Kleijn et al., 2011). The emphasis placed on the regional to local colonisation processes in the CBC framework (Fig. 1) is consistent with the ‘intermediate landscape-complexity’ hypothesis (Tscharrntke et al., 2012). The key argument here is that a landscape of intermediate complexity is associated with intermediate diversity; this is greater than in an overly simple landscape (<2% semi-natural habitat) in which the regional species pool is too depauperate for colonisation to take place, but less than a complex landscape, in which the regional species pool is so rich that re-colonisation continues even in the absence of local conservation measures.

Implicit in the introduction of beneficial habitats is the assumption that the natural enemies will not be restricted to these new habitat patches but will disperse or ‘spill over’ into other adjacent or nearby habitats including cropped areas (Woodcock et al., 2016). The positive effect of landscape complexity on within-field diversity of natural enemies supports this assumption (Flohre et al., 2011). However, the extent of such spill-over into cropped areas can be limited (Tscharrntke et al., 2005b; Tylianakis et al., 2004; Wamser et al., 2011). This limitation can be explained by dependence on a number of factors including the degree of habitat specialism exhibited by the species involved; the relative productivity or quality of the respective habitats, the proximity and connectivity between them; and the synchronisation in resource availability (Inclan et al., 2015, 2016; Neuville et al., 2016; Rand et al., 2006; Tscharrntke et al., 2007). Where spill-over does occur, it may be the result of passive diffusion of individuals from areas of high population density (Rand et al., 2006). Alternatively, movement could be driven by the foraging behaviour of individuals between habitat types (Blitzer et al., 2012; Gillespie et al., 2016) seeking complementary resources, either as a consequence of omnivory (Rand et al., 2006) or because of seasonal changes in resource availability, a feature common in arable cropping systems (Gillespie et al., 2016; Tscharrntke et al., 2005b). Where complementary resources are spatially separated, spill-over becomes a necessary mechanism to maintain natural enemy populations (Box 2).

#### 5. Biological control

A degree of optimism about the potential to conserve natural enemy populations is justified and a number of studies have shown positive effects of this in terms of increased predation or parasitism and reduced pest density. For example, Letourneau et al. (2011) concluded that, on average, local scale plant diversification strategies were successful in achieving a reduction in pest abundance. At the landscape scale, beneficial effects on predation and parasitism and subsequent pest suppression have also been reported, for example in the parasitism of pollen beetles in oilseed rape (Thies and Tscharrntke, 1999) and the predation of soybean aphid (Gardiner et al., 2009). Using a vote counting approach, Veres et al. (2013) found a beneficial effect of landscape complexity on biological control, with 18 out of 23 studies showing either reduced pest abundance or increased predation/parasitism in response to an increase in the proportion of semi-natural habitat within a landscape.

However, the presence of natural habitats can fail to enhance biological control (Tscharrntke et al., 2016). For example, the effect sizes reported by Batary et al. (2011), Bengtsson et al. (2005), Letourneau et al. (2011), and Langellotto and Denno (2004) suggest that, on average, the conservation strategies of the type deployed are insufficient to achieve pest suppression even when natural enemy populations have been enhanced; the average effect size of 25 experimental tests of the effect of CBC strategies on pest populations were not significantly different from zero (Fig. 3). This conclusion is consistent with that of other reviews; Bianchi et al. (2006), Chaplin-Kramer et al. (2011) and Veres et al. (2013) found the abundance of pests to be unresponsive to landscape complexity, indicating that positive landscape effects on natural enemies do not automatically translate into enhanced biological control; an echo of previous findings on the performance of habitat manipulation at the local scale (Gurr et al., 2000).

The question posed by these findings is why, given an increase in the abundance and diversity of natural enemies, do conservation strategies often fail to show evidence of pest regulation? To explore this it is necessary to consider how conservation strategies might

**Box 2**

Simulating the effect introducing flower rich habitats aphids and a parasitoid natural enemy.

AgBioscape software developed in the EU FP7 project PURE was used to construct a spatially explicit model of a crop – aphid – parasitic wasp system in order to simulate the effects CBC strategies. It was assumed that crop habitats are characterised by insufficient floral resources to maintain the survival of adult parasitoids leading to low-survival instability of parasitoid populations in crop monocultures (e.g. Fig. B2.1A). Targeting the survival of adult parasitoids through the provision of supplementary floral resources is a recognised strategy for conservation biological control (Bianchi and Wäckers, 2008; Vattala et al., 2006). To simulate this approach to CBC, conservation habitats were characterised by low aphid survival, i.e. lower than that experienced on the crop, but high parasitoid survival, again leading to unstable parasitoid population dynamics of the sort exemplified in Fig B2.1B.

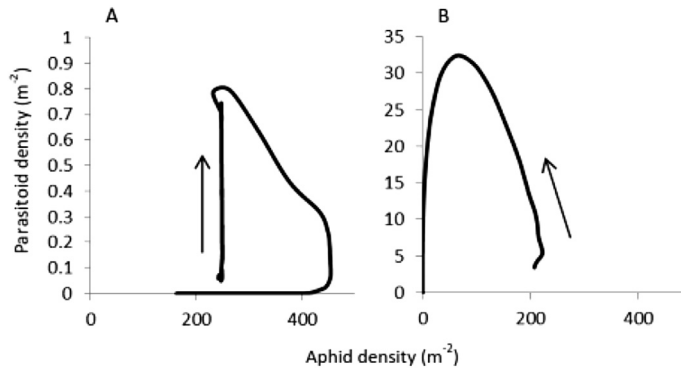


Fig. B2.1 Phase planes showing the seasonal dynamics for example years during which parasitoid extinction occurred. (A) Low parasitoid survival leading to instability and (B) high parasitoid survival leading to instability. Arrows indicate direction of seasonal changes in aphid and parasitoid density from mid-May.

Two patch systems coupled by dispersal, representing a crop with floral margin, became stable for a very wide range of conditions indicating the potential of such systems to promote natural enemy conservation through the provision of complementary resources. The beneficial effect of the floral margin extended into the crop, maintaining parasitoid populations and suppressing aphids populations. The effect diminished with distance from the margin until the parasitoid populations become extinct in those crop patches beyond the zone-of-influence of the floral margin (Fig. B2.2).

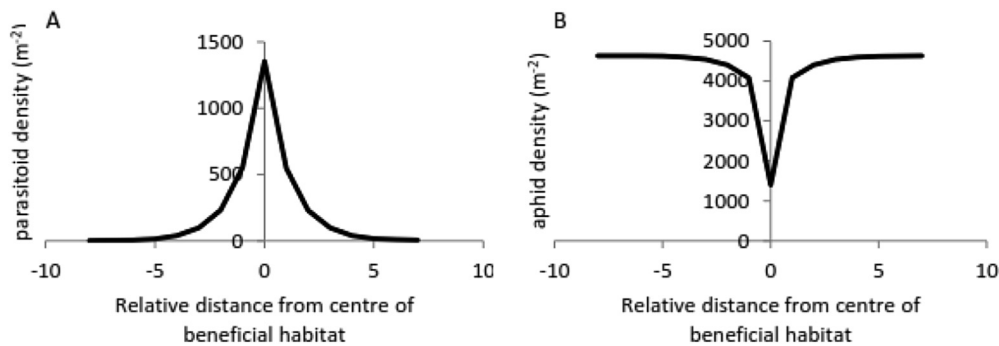


Fig. B2.2 Spill-over of parasitoids from the floral margin located at zero on the x-axis leads to stable but declining parasitoid populations (A) with distance and a diminishing impact on aphid density (B).

At the landscape scale, increasing the area given over to floral margins had positive effects on natural enemy conservation and aphid biocontrol while floral habitat fragmentation caused by small patch size at low habitat density lead to greater rates of parasitoid extinction. The formation of stable spatial patterns in the population densities is a characteristic of these systems leading to areas of unpredictably high or low pest density not correlated with the underlying distribution of floral habitats (Fig. B2.3).

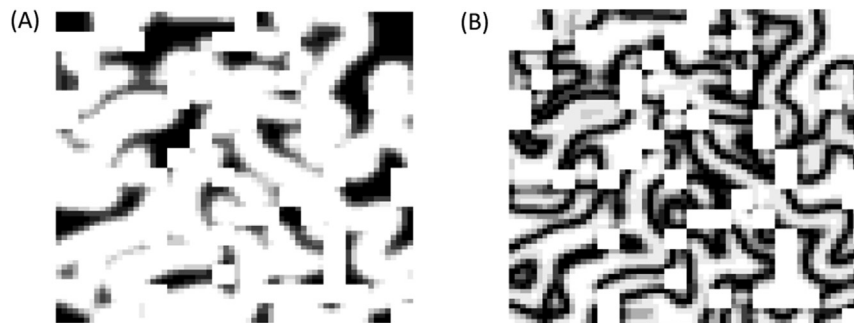
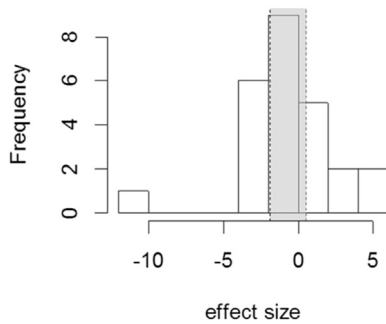


Fig. B2.3 Heat maps showing the distribution of aphids (A) and parasitoids (B) across a 3 x 3 km landscape comprised of 80% crop monoculture and 20% floral habitats (empty squares). The formation of spatial structures in population densities is characteristic of these systems.



**Fig. 3.** Distribution of effect sizes from 25 experimental tests showing range of responses in prey abundance to conservation biological control strategies. The shaded interval indicates the 95% confidence interval [-1.87, 0.55]. Data taken from Langellotto and Denno (2004), Bengtsson et al. (2005), Batáry et al. (2011), and Letourneau et al. (2011).

deliver biological control. Returning to the CBC framework we can identify two routes (Fig. 1).

### 5.1. Biological control at the landscape-scale

The first route relates to landscape-scale modifications that, when effective, promote both the abundance of natural enemies and their diversity at one or more spatial scales. This can lead to the suppression of within-field populations of crop pests (Martin et al., 2013), a result that is consistent with local-scale habitat management strategies being ineffective and perhaps unnecessary when set in complex landscapes (Kleijn et al., 2011; Tscharntke et al., 2012). However, there is no doubt that landscape-scale strategies are very likely to be indiscriminate in their effects and offer little control over when, where or which natural enemies and pest species are affected. This non-specific approach is not without its benefits as an increase in the abundance and diversity of natural enemies across habitats is likely to both increase and stabilise rates of parasitism and predation (Shackelford et al., 2013; Tscharntke et al., 2005a) leading to “preventative pest management” (Tscharntke et al., 2016), an objective that is entirely consistent with the ‘prevention and suppression’ principle of an IPM approach (Barzman et al., 2015). Furthermore, such a non-targeted approach has, by its very nature, the added advantage that it is likely to support farmland biodiversity and valuable ecosystem services more generally (Lescourret et al., 2015; Tscharntke et al., 2005a). However, by understanding the landscape ecology of natural enemies and resolving in detail the interaction between particular species and different habitats, more targeted landscape treatments may be developed (Diekötter and Crist, 2013; Ekroos et al., 2014; Mitchell et al., 2014; Box 1). This may lead to more effective natural enemy conservation but could also avoid unintended and undesirable effects such as conserving pests (Tscharntke et al., 2016). These could include the management of cropping patterns at the landscape-scale or the introduction of particular semi-natural habitats into the agricultural landscape. The former may have the advantage of not taking land out of production, while both could be achieved through policy instruments of the types currently in use, such as the greening measures of the EU Common Agricultural Policy (Regulation (EU) No 1307/2013 (EUR-Lex, 2013)) and the Scottish national policy for woodland expansion (Forestry Commission Scotland, 2009). Despite the potential value of landscape-scale approaches to CBC, it is clear that conserving natural enemies at this scale cannot be universally effective in delivering biological control and it should be accepted that some pest problems will be resistant to this approach (Tscharntke et al., 2016).

### 5.2. Biological control at the local-scale

The second route to CBC focusses on the conservation of natural enemies at the local scale, possibly within the cropped area (field), but more typically by providing beneficial habitats around the cropped area, such as field margins. As discussed in the preceding sections, these strategies are often effective in increasing the abundance and diversity of natural enemies yet have been less effective at delivering biological control. This could arise because, although present in greater numbers, the natural enemies are in the wrong place or present at the wrong time. This approach requires the natural enemies to access the crop from their area of conservation, often a non-crop habitat, and in synchrony with the growing pest populations (Neuville et al., 2016). This often requires natural enemies to be active early in the season before pests reach sufficient densities to cause damage, reduce yield, and outstrip the ability of the natural enemies to suppress their populations (Schellhorn et al., 2014).

Manipulating the foraging behaviour of natural enemies provides a possible route to achieve their appropriate spatio-temporal deployment. Increasing accessibility to the crop by ensuring conservation measures are located in close proximity to the crop will maximise the spill-over of natural enemies (Rand et al., 2006), at least locally. This is an important element of existing CBC strategies but it could be enhanced by the use of habitats as green corridors or stepping stones to facilitate natural enemy movement (Perović et al., 2010). The active manipulation of foraging and host selection behaviour of natural enemies using visual, chemical and physical cues may provide a way to enhance CBC in the future. Synthetic herbivore-induced plant volatiles (HIPVs) can be used to attract natural enemies into the field (Zhou et al., 2016; Kaplan, 2012). This approach has the potential for use in sophisticated forms of behavioural intervention, for example as one half of an ‘attract and reward’ strategy that uses a semio-chemical-based approach to draw natural enemies into a crop combined with nectar producing plants to support them once they are there (Simpson et al., 2011). These strategies can even induce a selective response from components of the natural enemy guild, manipulating trophic interactions in a way that avoids problems associated with the complex food webs described below (Kaplan and Denno, 2007). Though the chemical manipulation of natural enemy behaviour is at the experimental stage, the manipulation of pest foraging behaviour and host selection is a well-developed IPM strategy known as ‘stimulo-deterrent diversion’ or ‘push-pull’ (Cook et al., 2007; Hassanali et al., 2008; Eigenbrode et al., 2016). In this approach pests are deterred from the crop and attracted to another resource. This has the potential to improve the efficacy of CBC if the relocation can direct pest/prey towards the habitat of natural enemy populations and possibly even more effective if combined with the deployment of cues to attract natural enemies into crops (Cook et al., 2007; Khan et al., 2000; Ferry et al., 2009).

It has been argued that a general biodiversity-ecosystem function relationship (Tscharntke et al., 2005a) cannot be relied upon as the basis of an effective CBC strategy and that ‘hit and miss’ approaches should be replaced with targeted diversification schemes that provide the ‘right kind’ of diversity rather than diversity *per se* (Jeanneret et al., 2016; Tschumi et al., 2015). Targeted approaches using the identification and provision of preferred floral food resources has been effective for a range of predatory and parasitic natural enemies (Olson and Wäckers, 2007; Box 3). There may also be negative side-effects of the indiscriminate increase of biodiversity such as the promotion of alternative or additional pest species (Tscharntke et al., 2016) or the disruption and complication of the trophic cascade leading to intraguild predation (e.g. Finke and Denno, 2004; van Veen et al., 2006). The trophic cascade that is



### Box 3

Designing multifunctional margins for biological control in wheat-oilseed rape rotations in Europe.

#### Introduction

Field margins are an important part of European agri-environment schemes. Grass margins can support cereal aphids and their natural enemies but do not support the specialist natural enemies of oilseed rape, the second most important crop in most arable rotations. As part of the EU FP7 project PURE, two complementary experiments were carried out in the UK and Denmark to test the effect of including brassicas in margins on biocontrol in adjacent crops within the wheat-oilseed rape rotation.

#### Experimental approach

Both experiments replicated similar treatments designed to compare the effect of brassica and grass margins over a two-year period. Arthropod communities, pest and natural enemy guilds, were sampled using pit-fall traps and suction sampling, while parasitism and predation rates were estimated by deploying live and artificial sentinel prey (Fig. B3.1).

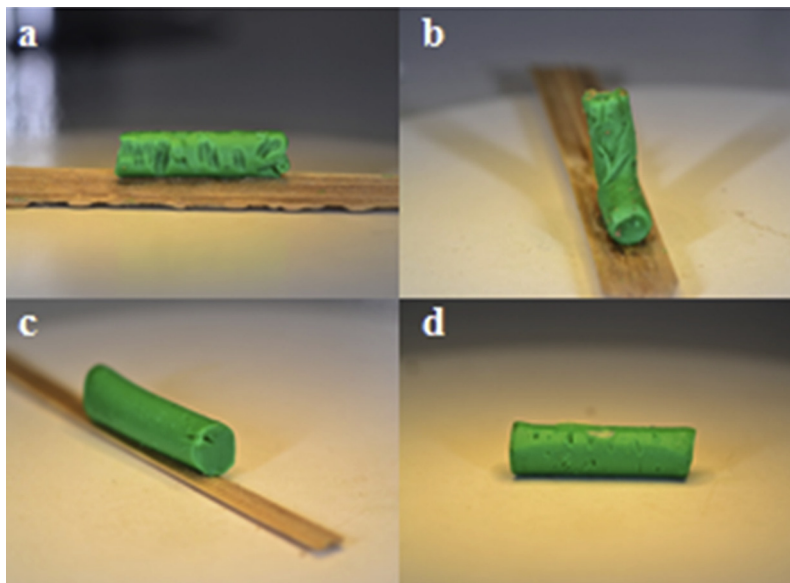


Fig. B3.1 Artificial sentinel prey (caterpillars) showing different predation marks: (a) mammal, (b) bird, (c) and (d) chewing insects.

#### Results

Within-field effects of the margin treatments were elusive but some benefits from the inclusion of brassicas in field margins were observed. Including brassicas in the margin when next to oilseed rape crops increased the abundance of specialist parasitoids of oilseed rape pests within the margin; this was also true for the pests themselves, although within-field pest abundance was unaffected. When next to wheat fields the inclusion of brassicas also appeared to benefit populations of specialist aphid predators, possibly due to the provision of nectar or alternative hosts. Combined with a significant reduction in the lifetime of aphid colonies in flowery margins observed in Denmark, the results suggest that biological control may be increased by the targeted use of brassicas in field margins.

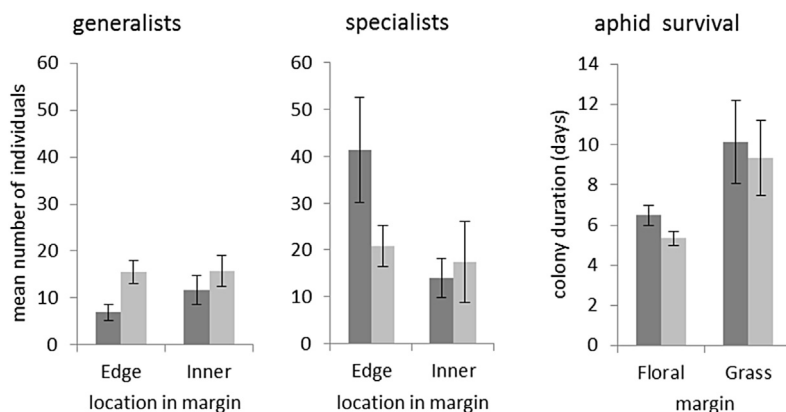


Fig. B3.2 Abundance of generalist and specialist natural enemies (mean  $\pm$  S.E.) caught by vacuum sampling in the edge and inner area of floral (brassica) and grass margins, and the survival of aphid colonies located on crops adjacent to floral or grass margins at Flakkebjerg, Denmark in 2014.

the basis of biological control should be most effective as a short, linear food-chain in which the natural enemy feeds directly on the pest (Maalouly et al., 2013; Montoya et al., 2003). Conservation strategies that increase the abundance of functionally similar species is likely to lead to negative interactions such as competition, predation and hyper-parasitism. The disruptive effect of intraguild competition (Caballero-López et al., 2012) has been observed, while intraguild predation has been documented in many systems (e.g. Rosenheim et al., 1995; Xue et al., 2012; Messelink et al., 2013), and even as a response to increased landscape complexity (Martin et al., 2013) that may disproportionately benefit 4th trophic level generalist predators compared with specialist 3rd trophic level natural enemies (Rand et al., 2012). Therefore, intraguild predation appears to be a significant risk to CBC, although it should be noted that positive intraguild interactions can arise, for example through species complementarity, and that there are theoretical results to suggest that intraguild interactions may not always result in the reduced predation of pests (Janssen et al., 2006). The importance of trophic interactions underlines that apart from tracking changes in the densities and composition of the natural enemy complex, direct measures of the intensity of desired functions (e.g. predation, Howe et al., 2009) should be deployed (Box 3).

The general and non-targeted effects of habitat diversification and reduced intensification may have a greater impact on the abundance of generalist natural enemies than specialists (Chaplin-Kramer et al., 2011), and perhaps on more mobile species (Rand and Tschardtke, 2007). Colonisation of local habitats may be active, stimulated by behavioural cues, or result from passive spill-over. The interventions that rely on passive colonisation should be biased towards mobile generalists who display greater spill-over between habitats (Rand et al., 2006), while attraction may be necessary to stimulate colonisation by specialists in the absence of prey aggregations. The degree of host and prey specialism expressed by the natural enemies may also be influential in the realisation of biological control at the crop scale. For example, the ability of generalist predators to utilise alternative prey enables them to persist in the absence of a pest population and to respond quickly to increasing pest density by changes in their foraging behaviour (Symondson et al., 2002; Tschardtke et al., 2005b). However, the more complex feeding interactions present within a guild of generalist predators, e.g. the presence of alternative prey and negative intraguild interactions, have the potential to weaken the trophic cascade on which successful biological control relies. Which of these competing effects hold sway is not clear, though Symondson et al. (2002), found that in three quarters of the cases reviewed, generalist predators reduced pest numbers significantly, suggesting that the positive effects usually outweigh the negative ones. In contrast, the trade-off is reversed for specialist natural enemies with a delayed numerical response to increasing prey numbers being off-set by a reduced risk that the trophic cascade will be disrupted (Symondson et al., 2002; Tschardtke et al., 2005b).

## 6. A systemic approach to CBC: using a conceptual framework to unify existing knowledge and identify research gaps

The development of the conceptual model, or framework, proposed in this study is based on the principle that a systemic approach is necessary to develop effective CBC strategies. As such, the framework seeks to provide a comprehensive overview of the elements that contribute to the functioning of CBC and their interactions across temporal and spatial scales. The framework is structured around a scale-explicit consideration of the conservation and biological control processes, distinguishing conservation and biological control elements at landscape and local scales.

Natural enemy conservation is viewed as emerging from population and community level processes spanning scales from the local/field scale to the regional/landscape scale. The interaction between scales is important, particularly the colonisation of local habitats with biological control taking place at the local scale, usually on crops but also on non-crop habitats due to the targeting of different life-cycle stages of a pest. However, biological control varies in the extent to which pest populations are targeted in space and time. At the landscape-scale, habitat diversification and management de-intensification (e.g. reduction in pesticide use) might promote generalised biological control, moderating pest suppression at multiple, unspecified sites across a region. Local, field-scale treatments are typically implemented with the intention of achieving targeted biological control of specific pests within a particular locality (field).

As a systematic overview of CBC functioning, the framework described here may also prove useful as a check-list for the development of CBC strategies. The relevant questions include: Does the landscape support a rich natural enemy community of appropriate generalist and specialist species that can respond adaptively to changing pest densities? Given the landscape, is local-scale conservation needed, and if so what form will it take? Can local measures be targeted to support populations of specific natural enemies and can they be directed to suppress key pests before they reach damaging levels on crops? However, before such a check-list could be used in practice, it is necessary to establish the extent to which these questions may be answered. In using the framework to set-out our understanding of CBC, it serves equally to identify where the gaps in CBC knowledge lie.

Evidence shows that neither the conservation of natural enemies nor their success in delivering biological control can be taken for granted. At the landscape scale, attention has focussed on the loss of semi-natural habitats and the resulting reduction in landscape complexity. Schemes to increase landscape complexity are promising options for the conservation of natural enemy assemblages at the regional scale. Without additional intervention, these may enhance the diversity of natural enemy assemblages leading to stable, pre-emptive pest suppression across a range of pest species; they could also accrue additional benefits by conserving functional biodiversity and ecosystem services more generally, although taking land out of crop production may undermine any economic advantage. In addition, the latest research into landscape effects provide a strong indication that more targeted CBC prescriptions might be possible. As we gain greater insight into the habitat requirements of natural enemies, the role of habitat complementarity, and the effect of their configuration in the landscape, it may become possible to devise conservation prescriptions targeted at particular natural enemies, species or functional groups. In addition to the role of landscape complexity, results from the EU PURE project highlight the contribution that landscape-scale cropping patterns and patterns of crop management, particularly pesticide use, can have on natural enemy and pest populations. This offers an alternative approach to promoting CBC and pest suppression across a landscape through geo-spatial or area-wide approaches to crop management at a farm or regional scale (e.g. by crop rotation design; Woltz and Landis, 2014) that also has the advantage of retaining land in production.

Conservation of natural enemies at the landscape scale, although often not an effective biological control strategy in its own right, can provide appropriate conditions for the success of CBC strategies deployed at smaller spatial scales that impact more directly on the crop. For depauperate regions, reinstating a degree of landscape complexity will be necessary to rebuild the natural enemy species pool. This provides the essential ingredient on which local conservation strategies must draw although, according

to the ‘intermediate landscape-complexity’ hypothesis, there may be an optimally complex landscape above which the introduction of a conservation measure at the field-scale is redundant. However, the evidence for this refers largely to non-specific local conservation measures. There is a need to consider whether interventions might be devised that are capable of taking advantage of a diverse species pool in order to maximise and target biological control delivery.

Local conservation measures appear to offer significant opportunities for CBC. The empirical evidence contained in this review suggests that the local implementation of one or a number of conservation strategies to reduce cropping intensity and provide beneficial habitats is likely to be effective as long as consideration is given to the surrounding landscape, and that this might be used as a ‘black-box’ approach without the need to fully understand the mechanisms operating. On the other hand, such an approach is not wholly reliable. Recent research has made progress in unravelling some of the ecological and behavioural detail affecting the outcome of local conservation strategies and we can be confident that further progress will be made; for example, in selecting the correct composition and configuration of habitats needed to provide supplementary resources.

Currently, the greatest limitation to the development of effective CBC lies not in the conservation of natural enemies but in their ability to deliver effective, reliable and robust biological control of pests. These limitations can be offset to an extent by ensuring CBC is used as part of a comprehensive IPM approach (Lamichhane et al., 2016). In this review we identify two factors responsible for the disruption of biological control: the spatio-temporal asynchrony in pest and enemy activity, and the disruption of the trophic cascade by alternate trophic interactions. Several approaches offer potential solutions to these problems including the combination of complementary generalist and specialist natural enemies to provide multiple biological control opportunities, targeting specific components of the food web by deploying appropriate combinations of plant species, and the use of chemical or other cues to modify the behaviour of natural enemies. In addition to these limitations, the effect that deployment of local measures across a landscape may have on their effectiveness is not well understood. We have illustrated here how this could lead to unpredictable patterns in the distribution of natural enemies and their suppressive impact on key pests (Box 2). If such risks are to be avoided, more research is needed to establish the best approaches to area-wide deployment of conservation measures that are effective in delivering biological control at the field-scale and that farmers are willing to invest in via actionable management, as part of a wider IPM strategy for the farm and the region.

In addressing these knowledge gaps, the specifics arising from location, cropping system, and the prevailing pest and natural enemy communities (with differing habitat resource requirements) will always create idiosyncrasies that demand case-by-case consideration. However, much is to be gained by seeking some general rules in this area and we expect that a systemic approach to CBC of the type presented here will provide a useful guide to this process.

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