Conservation Biological Control of Insect Pests in Two Horticultural Crops

A study of the cabbage root fly *Delia radicum* and the lily leaf beetle *Lilioceris lilii*

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Abstract

Modern farming practices create inhospitable environments for natural enemies reducing their capacity to control pest insects. Conservation biological control (CBC) is a practice that aims to provide natural enemies with the resources they lack. This thesis investigated the potential of CBC for two important horticultural pests, the cabbage root fly *Delia radicum* and the lily leaf beetle *Lilioceris lilii*.

The natural enemy complex of *L. lilii* larvae in Sweden is unknown, so a survey was conducted to collect information on the types of natural enemies present and the levels of parasitism. Four larval parasitoids of *L. lilii* were found, in varying relative abundance depending on the regions surveyed. Parasitism ranged between 21 and 57% depending on year and region.

A three-year field experiment in the south-east of Sweden investigated CBC-based pest management for *D. radicum* that relied on within-field habitat manipulation practices. Nectar resources for the parasitoid *Trybliographa rapae* and perennial grass as overwintering habitat for epigeal predators were combined in conservation strips (CS). It was found that providing vegetative resources within the crop potentially improved the conditions for natural enemies of *D. radicum*. Activity density of the predator and pupal parasitoid *Aleochara bipustulata* was higher in plots with CS, at the time of *D. radicum* egg-laying, in two out of three years. In 2009 this was associated with a significant reduction in the number of infested cabbage plants. Other natural enemies, such as Cynipoidae wasps, were also more abundant in plots with CS. A parallel semi-field experiment showed that *T. rapae* could parasitise significantly more *D. radicum* larvae when given access to flowering buckwheat plants. However, parasitism by *T. rapae* and *A. bipustulata* was not higher in field plots with CS in any study years. On the other hand, egg-laying by *D. radicum* was not enhanced despite the provision of food plants which were not solely selective for natural enemies.

Keywords: Aleochara bipustulata, Brassicaceae, Carabidae, epigeal predators, habitat manipulation, nectar, overwintering habitats, parasitoids, Staphylinidae, survey

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Bevarande biologisk bekämpning av två skadegörare på trädgårdsgrödor. En studie av lilla kålflugan *D. radicum* och liljebaggen *Lilioceris lilii*

Svensk sammanfattning

Det moderna odlingslandskapet kan utgöra ogästvänliga miljöer för naturliga fiender. Viktiga resurser saknas ofta, såsom nektarproducerande växter vilka parasitsteklar kan använda som föda samt ostörda övervintringsplatser för rovlevande skalbaggar och spindlar. Genom att förbättra livsbetingelserna för de naturliga fienderna i odlingslandskapet och i våra hemträdgårdar kan problemen med skadeinsekter reduceras. Detta är en viktig strategi inom *bevarande biologisk bekämpning*.

I min avhandling har jag studerat förutsättningarna för att stärka den biologiska bekämpningen av två olika skadeinsekter på trädgårdsväxter, liljebaggen (*Lilioceris lilii*) som angriper liljor och den lilla kålflugan (*Delia radicum*) som är en svår skadegörare på olika kålväxter.

Det första steget för att skapa en bekämpningsstrategi, som bygger på att förbättra förutsättningarna för de naturliga fienderna, är att undersöka vilka naturliga fiendearter som finns och hur frekvent de förekommer. Detta var inte känt innan denna undersökning. En inventering av förekomsten av naturliga fiender till liljebaggen genomfördes i tre olika regioner i Sverige; Skåne, Småland och Öland samt i Stockholm. Fyra arter av parasitsteklar konstaterades; *Tetrastichus setifer, Lemophagus pulcher, Lemophagus errabundus* och *Diaparsis jucunda*. Förekomsten av de olika arterna varierade mellan regionerna. Larvparasitismen varierade mellan 21 till 57% beroende på region och år och är likvärdig med vad som konstaterats i andra delar av Europa. Effekten av parasitsteklarna kan stärkas t.ex. genom att jorden runt liljorna lämnas orörd under hösten så att det övervintrande stadiet av parasitsteklarna inte skadas genom markbearbetning.

Den lilla kålflugans larver kan göra stor skada på de angripna kålplantornas rötter. Tidiga angrepp kan medföra förluster på upp till 90 % av plantorna om inga bekämpningsåtgärder vidtas. I Sverige finns idag få tillåtna kemiska bekämpningsmedel att använda för kontroll av lilla kålflugan. Det finns dock flera naturliga fiender som angriper kålflugans olika utvecklingsstadium. Parasitstekeln *Trybliographa rapae* kan parasitera upp till 70% av lilla kålflugans larver och angriper även andra skadegörare inom släktet *Delia*, såsom lökflugan (*D. antiqua*) och borststjälkflugan (*D. platura*). *Trybliographa rapae* är beroende av tillgång på nektar av hög kvalitet för optimal utveckling och effektiv parasitering. Många marklevande rovskalbaggar är predatorer på kålflugans ägg och larver. Men de missgynnas av att det finns få bra övervintringsplatser inom odlingsfälten. Därmed reduceras deras överlevnad samt tvingar dem att söka sig till fältkanter för övervintring. Detta försenar predatorernas kolonisation av fälten på våren och ger skadeinsekterna ett försprång i sin populationsuppbyggnad.

Mitt mål var att studera en bekämpningsstrategi som baserades på att gynna de befintliga naturliga fienderna till lilla kålflugan genom att tillföra resurser som saknas i

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fält samt kombinera detta med en växtföljd som skapar ett perent system för parasitstekeln *T. rapae.* Genom en växtföljd bestående av kål och lök ges *T. rapae* kontinuerlig tillgång till värddjur inom *Delia* spp.

Även skadeinsekterna kan gynnas av att blommande växter tillförs odlingslandskapet vilket kan betyda att skadeproblemen i grödan ökar istället för att minskas. Det är därför viktigt att studera hur både skadeinsekterna och nyttoinsekterna påverkas av fältmanipulering. Nio olika blommande växter undersöktes med avseende på hur attraktiva dess blomdofter var för den lilla kålflugan och *T. rapae,* om nektarn var tillgänglig samt hur länge de kunde överleva på två av växterna. Vi fann inga blommande växter som bara *T. rapae* utnyttjade men bovete (*Fagopyrum esculentum*) och dill (*Anethum graveolens*), valdes eftersom de var de mest attraktiva växterna för stekeln som även ökade sin livslängd signifikant på dessa växter.

Ett fältförsök genomfördes på Torslunda försöksstation, Öland, under en treårsperiod. Perent gräs som rovlevande skalbaggar kan använda som övervintringsplatser kombinerades med dill och bovete, i så kallade blomster/gräsremsor. Dessa placerades i mitten av försöksrutorna som 2008 och 2010 alla var planterade med vitkål medan hälften av försöksrutorna var planterad med lök och den andra hälften med vitkål 2009. Som kontroll användes kortklippt gräs som plöjdes ner under hösten.

Bevarande biologisk bekämpning visade potential att förbättra förutsättningarna för kålflugans naturliga fiender men resultaten varierade över försöksåren. Lilla kålflugans äggläggning ökade inte inom eller mellan åren. Detta trots att både dill och bovete kunde användas som en födoresurs i laboratorieförsöken. Få hanar av lilla kålflugan fanns inne i fältet vilket indikerar att flugorna istället aggregerat i vegetationen utanför fältet. Vid aggregationsplatserna söker flugorna skydd, parar sig och födosöker. Troligen fanns andra födoresurser i närheten som utnyttjades istället för dill och bovete.

Antalet kålplantor som var infekterade av den lilla kålflugan var lägre i rutor med blomster/gräsremsor för 2009. Under denna period var signifikant fler *A. bipustulata* aktiva i blomster/gräs rutorna. Vi tror därför att *A. bipustulata* är en viktig predator på kålflugans larver. Förmodligen söker de sig till försöksrutorna med blomster/gräsremsor för att det finns mer tillgång på bytesdjur.

Semifältförsöket visade att nektar från bovete är viktigt för *T. rapae.* Tillgång till blommande bovete medför en 60% ökning i parasitering av kålflugans larver i jämförelse med kontrollerna. Däremot ökade inte parasiteringen av larver eller puppor i rutorna med blomster/gräsremsorna för något av åren. Istället fann vi signifikant högre parasitering i kontrollrutorna 2009 av både *T. rapae* och *A. bipustulata*. Detta berodde troligen på högre täthet av värddjur i kontrollerna.

Den totala parasiteringsgraden ökade dock inom fältet, d.v.s. i båda behandlingarna, från det första året till det sista. Antagligen eftersom antalet kålplantor som var infesterade med lilla kålflugan ökade under samma period men kan också berott på att habitatmanipulering stärkt fältpopulation av *T. rapae.*

Även andra naturliga fiender gynnades av blomster/gräsremsorna t.ex. var Cynopidae spp. mer frekvent förekommande i de försöksrutor som samodlats med blomster/gräsremsor.

Det var inte möjligt att utvärdera vikten av att tillföra alternativa värddjur för *T. rapae* eftersom endast väldigt få lökflugor konstaterades i fält 2009. Vi kunde dock konstatera att kålflugan inte påverkades av växtföljden vilket främst beror på dess förmåga att sprida sig över stora områden.

Framtidens växtskyddskontroll av skadeinsekter på trädgårdsväxter kommer att kräva att många olika strategier används parallellt med *bevarande biologisk bekämpning*. En lovande möjlighet är att applicera insektspatogena svampar och nematoder tidigt på säsongen för att reducera den första generationen av lilla kålflugan. Medan blommande växter kan användas för att stärka den biologiska bekämpningen av den andra generations kålflugor. Dock krävs det mer forskning för att undersöka hur de naturliga fienderna i odlingslandskapet påverkas av insektspatogena organismer så att de olika strategierna inte motverkar varandras syften.

Dedication

To Nils with Love

And then it´s magic…
    Anonymous

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Rämert, B., Kenis, M., Kroon, H. & Nilsson, U. (2009). Larval parasitoids of *Lilioceris lilii* (Coleoptera: Chrysomelidae) in Sweden and potential for biological control. *Biocontrol Science and Technology* 19, 335-339.

II Nilsson, U., Rännbäck, L-M., Anderson, P., Eriksson, A. & Rämert, B. (2011). Comparison of nectar use and preference in the parasitoid *Trybliographa rapae* (Hymenoptera: Figitidae) and its host, the cabbage root fly, *Delia radicum* (Diptera: Anthomyiidae). *Biocontrol Science and Technology* 21(09), 1117-1132.

III Nilsson, U., Eriksson, A., Rämert, B. & Anderson, P. Male and female *Trybliographa rapae* (Hymenoptera: Figitidae) behavioral responses to food plant, infested host plant and combined volatiles. (submitted)

IV Nilsson, U., Rännbäck, L-M., Anderson, P. & Rämert, B. Herbivore response to habitat manipulation with floral resources: A study of the cabbage root fly. (accepted for publication in *Journal of Applied Entomology*)

V Nilsson, U., Rännbäck, L-M., Björkman, M., Anderson, P. & Rämert, B. Assessing the effects of combined beetle bank and flower strips on two natural enemy guilds of the cabbage root fly (*Delia radicum*). (manuscript).

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The contribution of Ulf Nilsson to the papers included in this thesis was as follows:

I   Collected, reared and dissected insects in collaboration with co-authors.

II Planned bioassays and performed part of the experiments. Analysed data and wrote the paper together with co-authors.

III Performed part of the bioassays. Analysed data and wrote the paper together with co-authors.

IV Planned and performed field experiments with help from co-authors. Analysed data and wrote the paper together with co-authors.

V   Planned and performed field experiments with help from co-authors Analysed data and wrote the paper together with co-authors.

Abbreviations

CBC	Conservation biological control
CS	Conservation strip
IFOAM	International federation of organic agriculture movements
HIPV	Herbivore induced plant volatile

1 Introduction

For economic reasons, modern annual agroecosystems are simplified ecosystems designed to produce high yields. Crops are grown in large monoculture units that rely on external inputs of agrochemicals such as synthetic pesticides and fertilisers. Taken together these alterations have resulted in increased production but also in a notable decrease in biodiversity (Chamberlain *et al.*, 2000; Benton *et al.*, 2003).

The negative side-effects of synthetic pesticides were recognized at an early stage by scientists, who argued for the integration of biological control and synthetic pesticides to reduce the environmental impact (Stern *et al.*, 1959). The strategy Integrated Pest Management (IPM) was therefore developed for conventional agriculture. The basic component in IPM is understanding the agroecosystem and the potential consequences of farming interventions (van den Bosch & Stern, 1962). The increased awareness of the potential risks of synthetic pesticides among the European public and politicians has led to a statutory requirement for standards for IPM to be implemented in the member states of the European Union by 2014 (Anonymous, 2009). Biological control of plant pests is considered to be one of the corner stones within the IPM concept.

However, natural enemies to pest insects are often less efficient regulators in simplified ecosystems as there are fewer feeding and microhabitats. This is one reason why agroecosystems are vulnerable to pest insect outbreaks (Pimentel, 1961; Kruess & Tscharntke, 1994).

Augmenting biodiversity *per se* in the agricultural landscape will not automatically improve pest regulation and can even increase the problems (Baggen & Gurr, 1998; Landis *et al.*, 2000; Gurr *et al.*, 2003; Araj *et al.*, 2009). It is therefore important to gain a deeper understanding of how addition of vegetative diversity at the farm scale affects both the herbivore and the natural enemies.

1.1 Biological Control

1.1.1 History and definitions

In biological control living organisms are used to control pests (Ehler, 1998; Eilenberg *et al.*, 2001). This is an old farming strategy, for instance, cats have been used by mankind for thousands of years to control rats and mice in agriculture. Biological control with arthropod control organisms was documented as far back as the third century, when Chinese farmers were able to purchase ants at markets and use them to control lepidopteran pests on citrus trees (Caltagirone, 1981; van Lenteren, 2005). One of the first modern scientific approaches, with clear documentation of the release of control agents and evaluation of the effects, was made in the 1880s in California, when the predatory vedalia beetle *Rodolia cardinalis* (Mulsant 1850) (Coleoptera: Coccinellidae) was imported from Australia to control the cottony cushion scale *Icerya purchasi* (Maskell 1878) (Sternorrhyncha: Monophlebidae), which was a devastating pest on citrus trees at the time (Caltagirone, 1989; Bale *et al.*, 2008).

Eilenberg *et al.* (2001) aimed to unify and clarify the terminology used for the four different strategies within biological control; classical biological control, inoculation biological control, inundation biological control and conservation biological control (CBC). In the first three strategies biological control agents are reared and released, whilst in CBC different measures are taken to improve the conditions for natural enemies already existing in the target area in order to make them more efficient as pest regulators (Landis *et al.*, 2000; Eilenberg *et al.*, 2001).

Classic biological control

The intensive global agricultural trade and the introduction of crops into non-native areas in the last two centuries have resulted in unintentional establishment of exotic pest insects. When an arthropod pest is introduced into a new area, it may escape into an enemy-free space without its co-evolved enemies and can then multiply and spread in an uncontrolled manner (Caltagirone 1981; Bale *et al.*, 2008). The intention with classical biological control is to introduce and establish an exotic natural enemy that can control the pest organism for a long period of time (Eilenberg *et al.*, 2001). There are many examples of successful introductions of exotic natural enemies, for example in control of the mealy bug *Antonina graminis* (Maskell 1897) (Hemiptera: Pseudococcidae) in Texas with the parasitoid *Neodusmetia sangwani* (Subba Rao 1957) (Hymenoptera: Chalcidoidea) that was imported from India (Caltagirone, 1981).

Inoculation biological control

In inoculation biological control the artificially reared control organisms are introduced to control a pest for a longer period, although not permanently (Eilenberg *et al.*, 2001). This is practised by greenhouse growers in Europe, who releases parasitoids and predatory mites early in the cropping season to control different pests in vegetables and ornamentals (Eilenberg *et al.*, 2001; Bale *et al.*, 2008).

Inundation biological control

In inundation biological control the biological control agent is used in a fashion similar to synthetic pesticide application and is normally introduced when the pest population has reached the economic threshold for crop damage (Eilenberg *et al.*, 2001). The biological control agent is released in high doses to get a knock-down effect on the target pest insect population (Bale *et al.*, 2008). Inundation biological control is used, for instance, to control lepidoteran pests with entomopathogenic viruses and the bacteria *Bacillus thuringiensis* (Eilenberg *et al.*, 2001; Dixon, 2006; Zehnder *et al.*, 2007).

1.2 Conservation biological control (CBC)

Interest for CBC has increased substantially over the past two decades (Cowgill *et al.*, 1993; White *et al.*, 1995; Baggen & Gurr, 1998; Stephens *et al.*, 1998; Frank & Shrewsbury, 2004; Fiedler *et al.*, 2008; Jonsson *et al.*, 2008; Jonsson *et al.*, 2010). CBC can be performed either by protecting natural enemies from adverse impacts of the agricultural practices, or by enhancing the elements required for their survival and reproduction in and around the production fields. According to Eilenberg *et al.* (2001), farming practices carried out with the intention of protecting or enhancing a specific natural enemy could be counted as CBC practices. Two important protective measures used in agriculture and home gardens, are to alter the use of pesticides and tillage of the soil in order to be more compatible with pest natural enemies. Farmers can diminish the negative side-effects of pesticides on natural enemies for example by choosing selective pesticides that do not reduce natural enemy fitness or by applying pesticides when the pest and natural enemy are temporally or spatially separated (Ruberson *et al.*, 1998).

Mechanical tillage of the soil is important to create an optimal environment for the crop. Through ploughing the top layer of the soil together with any crop debris and weeds is turned under. However, the soil disturbance and the reduction in plant debris may have a negative impact on epigeal predators and parasitoids overwintering in soil (Thorbek & Bilde, 2004). Fields managed

with reduced or minimum ploughing usually exhibit a higher number of epigeal predators compared with conventional ploughed fields (House & Stinner, 1983; Tonhasca, 1993). In CBC, soil cultivation techniques that minimise the negative constraints on natural enemies should be applied.

Crop rotation is a powerful tool to diminish plant diseases and pest insects that do not easily disperse in the landscape (Hummel *et al.*, 2002). By planting non-host plants, the life-cycles of specialist herbivores can be interrupted by reducing their chances of finding a suitable food source (Walters & Eckenrode, 1996). The use of an appropriate crop rotation that provides alternative hosts or prey for polyphagous parasitoids and predators when their main host is absent could improve the conditions for the natural enemies.

1.2.1 Habitat manipulation

Habitat manipulation is a practice within CBC and the objective is to actively improve the habitats for natural enemies by providing them with the resources required for optimal performance in the field e.g. food, alternative prey, physical refugia and connecting corridors (Landis *et al.*, 2000), resources that are often scarce in the modern agroecosystem. These resources can be enhanced with an increase of the vegetational diversity, which thus forms a corner stone of habitat manipulation. This kind of manipulation can be used on different scales, stretching from within-field, within-farm up to landscape level (Gurr *et al.*, 2003). Two commonly studied within-in field practices are to introduce non-crop nectar plants used by natural enemies as an energy-rich food resource (Leius, 1967; Cowgill *et al.*, 1993; Baggen *et al.*, 1999; Tylianakis *et al.*, 2004; Winkler *et al.*, 2006) and to provide shelter habitats that offer natural enemies protection from the disturbance of agricultural practices and better overwintering habitats (Collins *et al.*, 2002; MacLeod *et al.*, 2004).

1.2.2 Additional food resources for natural enemies

Pollen and nectar produced by plants are important food sources for numerous natural enemies (Bakker & Klein, 1992; Wäckers, 2005). Carnivorous beetles and spiders use pollen and nectar when prey is scarce (Taylor & Pfannenstiel, 2009) while other natural enemies, such as, syrphid flies and some parasitoids, need this food source for survival during their adult stage (Cowgill *et al.*, 1993; Jervis *et al.*, 1993; Wäckers, 2005).

Plant-provided food can positively affect different aspects of the biology of hymenopteran parasitoids, such as increased fecundity, longevity, search efficacy, flight ability and offspring sex ratio (Baggen & Gurr, 1998; Berndt & Wratten, 2005; Vattala *et al.*, 2006). This may result in increased abundance of

natural enemies (Masetti *et al.*, 2010) and improved pest regulation (Tylianakis *et al.*, 2004). For instance, Winkler *et al.* (2006) showed a 10-fold increase in parasitism and a 20-fold increase in reproductive lifespan when the lepidopteran parasitoid *Diadegma semiclausum* (Hellén 1949) (Hymenoptera: Ichneumonidae) was provided with flowering nectar plants in a semi-field study. The spatial arrangement of the intercropped flowers in the field can have a great impact on the outcome of the habitat manipulation. In a study of a aphid parasitoid, Tylianakis *et al.* (2004) found a relationship between aphid parasitism and the distance from the planted floral resource with the highest parasitism closest to the flowers. The effect was completely absent 14 m away from the flowers. However, strong evidence of increased yields, due to the practice of habitat manipulation, for farmers is sparse (Jonsson *et al.*, 2008; Sivinski *et al.*, 2011).

Not all flowering plants are suitable as food for parasitoids. First of all, the plant should flower and produce nectar during the period when the parasitoid is active in the field. Moreover, the plant needs to be attractive and detectable for the food foraging insect (Jervis *et al.*, 1993; Wäckers, 2005). Floral attraction is a function of flower size, colour and odour (Kevan & Baker, 1983; Begum *et al.*, 2004; Sivinski *et al.*, 2011). Parasitoids use these olfactory and visual cues as guidance to the flowers in the field and there is clear difference in attraction to flowers as some are more frequently visited than others (Jervis *et al.*, 1993; Bianchi & Wäckers, 2008). For instance, Wäckers (2004) found differences in the floral odour preferences of naive parasitoids stretching from attraction to repellency.

Flower morphology may obstruct nectar-foraging parasitoids. Parasitoids have short mouthparts and can be restricted from feeding on plants with long tubular flowers and plants with hidden nectaries (Jervis *et al.*, 1993; Krenn *et al.*, 2005; Wäckers, 2005) although some exceptions are known (Jervis, 1998). Consequently, plants belonging to the Apiaceae have often proven suitable as parasitoid food due to their easily reached exposed nectaries (Patt *et al.*, 1997; Baggen & Gurr, 1998; Vattala *et al.*, 2006). In addition, the floral nectar should match the nutritional requirements of the parasitoid and not contain toxic secondary metabolites (Kessler & Baldwin, 2007).

Unless care is exercised, food plants introduced to the agroecosystem with the intention of benefitting natural enemies can also be utilized by crop pests, higher order predators and hyperparasitoids, thus interfering with the intentions of biological control (Rosenheim, 1998; Baggen *et al.*, 1999; Lavandero *et al.*, 2006). It is therefore important to be aware of these risks and use 'selective food plants' in order to make the habitat manipulation more successful (Jervis *et al.*, 1993; Patt *et al.*, 1997; Baggen & Gurr, 1998). The process of selecting

suitable nectar plants to be used in habitat manipulation programmes, generally starts with the screening of different plants in a laboratory based on attractiveness and/or on their effect on the natural enemy and/or pest fitness (Wade & Wratten, 2007). Baggen *et al.* (1999) evaluated the suitability of five plants as food for a parasitoid and its host, an economically important lepidopteran potato pest. They found that three out of five plants were used by both insect species whilst two of them were only utilised by the parasitoid and could thus be considered 'selective food plants'. Difference in plant selectivity between insects could be exploited through differences in floral attraction (Wäckers, 2004), nectar accessibility as a function of weight gain (Wäckers, 2004; Winkler *et al.*, 2009b), increased longevity (Baggen & Gurr, 1998; Irvin *et al.*, 2007; Winkler *et al.*, 2009b), feeding responses (Williams III & Roane, 2007), gustatory responses (Beach *et al.*, 2003) and nectar quality (Vattala *et al.*, 2006). Of these, longevity studies are the most commonly practised (Johanowicz & Mitchell, 2000; Wade & Wratten, 2007).

1.2.3 Shelter habitats

The beetle bank is a shelter habitat created to reduce field size, thereby allowing rapid and uniform predator colonisation in early spring in temperate regions and providing predators with suitable overwintering sites within the field (Landis *et al.*, 2000; Griffiths *et al.*, 2008). The beetle bank consists of perennial grass sown on a raised earth bank within the production field. The dense grass strip undergoes less fluctuation in temperature than the production field during early and mid-winter (Thomas *et al.*, 1992a; Thomas *et al.*, 1992b; Lys & Nentwig, 1994). Bossenbroek (1977) found a positive correlation between stable temperature in winter habitats and the number of overwintering beneficial arthropods. Tussock forming grasses such as *Holcus lanatus* (L.) and *Dactylis glomerata* (L.) have a greater structural diversity and a deeper leaf litter compared with matted grasses and are therefore commonly used in beetle banks (Collins *et al.*, 2002; MacLeod *et al.*, 2004). Different grass species are preferred by different arthropod families. Higher densities of carabids have been found in beetle banks composed of *D. glomerata* and the highest density of staphylinids are reported in beetle banks composed of *H. lanatus* (MacLeod *et al.*, 2004). The depth of the sod layer and the presence of suitable prey may be important overwintering factors for the staphylinids and these vary between different grasses (Dennis & Wratten, 1991).

1.3 Future challenges for CBC

A description of future challenges within CBC is provided by Jonsson *et al.* (2008). The next research step required in order to improve CBC practices is to gain a deeper understanding of the mechanism by which pest suppression is achieved in the field and identify processes that are likely to counteract this (Griffiths *et al.*, 2008). This can only be understood by thorough studies of how the behaviour of the natural enemy and the pest insect is affected by CBC practices in the laboratory and, more importantly, in the field. In addition, a single CBC practice aimed to support one specific natural enemy or guild may not be enough to adequately regulate the target pest insect. Instead, we should aim towards the evaluation of multiple CBC practices that at the same temporal and spatial scale can support a broad natural enemy complex consisting of different guilds with feeding niches that complement each other (Frank & Shrewsbury, 2004; Straub *et al.*, 2008). This is likely to strengthen the biological control of agricultural pests.

2 Objectives

The general objective of this thesis was to explore the potential of conservation biological control of two important horticultural pests, the cabbage root fly *Delia radicum* (Linnaeus 1758) (Diptera: Anthomyiidae) and the lily leaf beetle *Lilioceris lilii* (Scopoli 1763) (Coleoptera: Chrysomelidae).

In Sweden the natural enemy complex of *L. lilii* larvae is not known. Therefore the first tasks were to conduct a survey in order to collect information on the type of natural enemies; to determine the level of parasitism; and to propose measures to improve biological control in the future

The natural enemy complex of *D. radicum,* on the other hand, has been thoroughly studied during the last century. In the second part of the thesis we studied a conservation biological control-based pest management system that relies on combined effects of different within-field habitat manipulation practices, such as, shelter habitats, addition of floral resources, as well as pest lifecycle disruption.

The main focus was on *Trybliographa rapae* (Westwood 1835) (Hymenoptera: Figitidae), the most important larval parasitoid of *D. radicum.* The first step was to compare nectar use and preference in *T. rapae* and *D. radicum* to identify and choose selective food plants for *T. rapae* to be used as food resource in the field. This was done in the laboratory by comparing the following factors for both the herbivore and the parasitoid:

- Olfactory attraction to floral odours
- Ability to access nectar from different flowers
- Effect of flowers on longevity

In addition, we also tested *T. rapae* response to host-associated odours.

In the field we evaluated the impact of habitat manipulation on *D. radicum* and its natural enemies by studying the impact of:

- Floral resources on egg-laying by *D. radicum*

- Selective flower strips on larvae parasitism by *T. rapae*
- Perennial grass strips as shelter habitats for epigeal predators, such as, *Aleochara bipustulata* (Linnaeus 1761) (Coleoptera: Staphylinidae)
- Crop rotation on the lifecycles of *D. radicum* and its natural enemies

3 The studied organisms

3.1 Herbivores

3.1.1 The lily leaf beetle – *Lilioceris lilli*

The lily leaf beetle, *Lilioceris lilii* (Scopoli 1763) (Coleoptera: Chrysomelidae), originates from Asia, and Europe and it is a serious pest on ornamental lilies (*Lilium* spp.) and fritillaries (*Fritillaria* spp.) (Liliaceae). Today it is spread throughout Northern Europe, North Africa and North America (Haye & Kenis, 2004). *Lilioceris lilii* is an introduced pest in Sweden as there are no native lilies or fritillaries. Larvae and adult beetles both damage their host plants by feeding (Fox-Wilson, 1942). The larvae are covered by a faecal shield as a defence against predators and as protection from dehydration (Schaffner & Müller, 2001; Ernst, 2005) (Fig. 1).

Figure 1. Adult *L.lilii* (left) and larvae covered with a faecal shield (right). Photo: Linda-Marie Rännbäck (left)

Biology

Lilioceris lilii is univoltine and overwinter as adult in the soil and start to feed on lilies in early spring (Gold *et al.*, 2001). Copulation occurs shortly after emergence and gravid females deposit orange-red eggs in groups of 3-12 eggs in an irregular row along the midrib on the underside of the leaves (Gold *et al.*, 2001; Ernst, 2005). A female lays on average 200-300 eggs during her life-time (Fox-Wilson, 1942). There are four larval instars and if not controlled, they can completely defoliate the attacked host plant (Haye & Kenis, 2004). Pupation takes place inside a cocoon in the soil close to the attacked plant (Ernst, 2005). A new generation of *L. lilii* emerges from the cocoon and feeds on lilies until autumn and hibernation.

3.1.2 The cabbage root fly – *Delia radicum*

The cabbage root fly *Delia radicum* (Linnaeus 1758) belongs to the family of Anthomyiidae. The *Delia* genus consists of 170 species in the palaearctic region. Besides *D. radicum* six of these are considered to be important pests on various crops, for example, the wheat bulb fly, *Delia coarctata* (Fallén 1825) attacks different cereals, while *Delia platura* (Meigen 1826) and *Delia florilega* (Zetterstedt 1845) feed on the cotyledons of different vegetables (Finch, 1989).

Biology

Delia radicum has long been recognised as an important pest in southern Sweden (Lundblad, 1933 and references therein) and it commonly has two generations in Sweden. If the conditions are favourable a third generation may also occur. The fly overwinter in the soil as a pupa, within a puparium, at a maximum depth of 10 cm (Coaker, 1966). Each puparium is normally less than 1 cm long and a few mm wide, with a red-orange colour (Hughes & Salter, 1959). Adult flies start to emerge in May, when the soil temperature is above 16°C, and adults of the second generation emerge approximately seven weeks later (Coaker & Finch, 1971).

The larvae feed primarily on the root and stem of the host plant and a variety of cultivated cruciferous crops are attacked, for example, Brussels sprout, broccoli, cabbage, cauliflower, radish, turnips and rapeseed (Lundblad, 1933; Coaker & Finch, 1971; Zalom & Pickel, 1985; Finch, 1989; Parsons *et al.*, 2007; Hummel *et al.*, 2009; Hambäck *et al.*, 2010; Ahmed *et al.*, 2011). Plants attacked shortly after planting may be killed or severely reduced in growth by the larvae (Fig. 2). Under suitable weather conditions and high soil moisture, plants can compensate for the loss of root biomass by producing secondary roots and so reducing the damage (Coaker & Finch, 1971).

Cruciferous crops for which the belowground plant parts are used for consumption, such as, radish, horse radish and Swedish turnip, tolerate very little larval damage if they are to be marketable (Finch, 1989).

Figure 2. White cabbage plants killed by *D. radicum* larvae shortly after planting (left) and a plant with the fine roots eaten by the larvae (right).

The cabbage root fly is synovigenic and needs to feed on carbohydrates before it can lay its first batch of eggs, while for the second and subsequent batches both carbohydrates and a hydrolysate protein source are required (Finch & Coaker, 1969a). The cabbage root fly feeds on a variety of different food sources for instance honeydew excreted by homopteran insects, decayed plant material, such as, degraded anthers from flowering grasses and rotten fruit, sap from plants and nectar from flowers (Caesar, 1922; Finch & Coaker, 1969b). Cow parsley, *Anthriscus sylvestris* L., is a food plant of major importance for the first generation of flies while nettle, *Urtica dioica* L., and grasses such as cocksfoot, *D. glomerata* are frequently visited by flies from the second generation (Coaker & Finch, 1971). Life-time fecundity in the laboratory, when provided with an optimal diet, is 376 eggs per female (Finch & Coaker, 1969a). However, in the field flies rarely lay more than one batch (40-60 eggs) (Finch & Coaker, 1969b; Finch, 1971).

3.2 Natural enemies

3.2.1 Parasitoids of *Lilioceris lilii*

In central Europe a parasitoid complex of four larval parasitoids are the most important natural enemies of *L. lilii* (Haye & Kenis, 2004). *Tetrastichus setifer* (Thomson 1878) (Hymenoptera: Eulophidae) is a small gregarious, univoltine wasp that develops on average eight larvae per parasitised host larvae (Gold *et al.*, 2001). All four instars of *L. lilii* are accepted by the egg-laying females (Haye and Kenis, 2004). Overwintering takes place as larvae inside the host

Figure 3. Lemophagus pulcher parasitizing a *L. lilii* host larva. Photo: Tim Haye

cocoon (Gold *et al.*, 2001). This species was found to be the dominant larval parasitoid in France, Switzerland (Gold *et al.*, 2001) and Germany (Haye & Kenis, 2004). *Diaparsis jucunda* (Holmgren 1860) (Fig. 3), *Lemophagus pulcher* (Szepligeti 1916) and *Lemophagus errabundus* (Gravenhorst 1829) (Hymenoptera: Ichneumonidae) are all non-gregarious larval parasitoids that overwinter in a cocoon within the host cocoon (Gold *et al.*, 2001). *Diaparsis jucunda* and *L. pulcher* attack all four larval stages of *L. lilii* whilst *L. errabundus* do not parasitise the first instar (Haye & Kenis, 2004). The geographical distribution and occurrence differ between the species e.g. *D. jucunda* dominates in Switzerland and *L. errabundus* in northern Germany, western France, the Netherlands and Belgium (Haye & Kenis, 2004).

3.2.2 Parasitoids of *Delia radicum*

Trybliographa rapae

Trybliographa rapae (Westwood 1835) (Hymenoptera: Figitidae) is koinobiont, 2.5-4.5 mm long, parasitoid of *Delia* spp. larvae and is considered to be the most important larval parasitoid of *D. radicum* in Europe and North America (Fig. 4) (Wishart & Monteith, 1954; Finch & Collier, 1984; Hemachandra *et al.*, 2007). It was first described in Sweden in 1862 (Lundblad, 1933 and references therein) and is bivoltine in northern Europe (Jones, 1986; Block *et al.*, 1987). *Trybliographa rapae* is oligophagous and in addition to *D. radicum* it can also attack other *Delia* species as for example, the turnip root fly, *Delia* floralis Fallen 1824, the onion fly, *D. antiqua* and the bean seed fly, *D. platura*/*D. florilega* (Wishart & Monteith, 1954).

Figure 4. Trybliographa rapae female. Photo: Linda-Marie Rännbäck

Female *T. rapae* first has to locate host-infested Brassicaceae plants and thereafter find the soil-dwelling larvae within the root system of the plant (Jones, 1986). Female parasitoids are attracted to long range volatiles systemically emitted from root infested Brassicaceae plants (Neveu *et al.*, 2002; Pierre *et al.*, 2011). After host plant

location, females use antennal searching and ovipositor probing to locate host larvae within the root tissue and to evaluate the quality of the potential host (Vet & Van Alphen, 1985; Brown & Anderson, 1998). The parasitoid can parasitise all three larval stage of *D. radicum* (Jones, 1986) but the third larval instar is preferred probably due to faster development of the offspring (Neveu *et al.*, 2000). Female *T. rapae* can parasitise larvae situated 4 cm deep in the soil but not larvae at a depth of 6 cm (Hemachandra *et al.*, 2007). Parasitised pupae are often significantly smaller compared to unparasitized pupae and a cluster of small dark dots that is the meconium of the parasitoid larvae can be seen at the end of the puparium (Hughes & Salter, 1959).

Host-feeding is common among parasitoids (Jervis *et al.*, 1996) but has not been reported in *T. rapae* (Jones, 1986). As *T. rapae* is pro-ovigenic, adult feeding is not required for egg maturation (Jervis *et al.*, 1993). Rather than being egg limited pro-ovigenic parasitoid species are limited by the time available to deposit the eggs (Baggen & Gurr, 1998). Means to increase survival, such as, provision of food to adults will thereby have an impact on the life-time reproductive success (Jervis *et al.*, 1993; Heimpel & Rosenheim, 1998).

Access to carbohydrate-rich food has been found to substantially increase the longevity of a laboratory culture of *T. rapae* (Jones, 1986) and flower visiting has been recorded on Apiaceae plants, *Angelica sylvestris* L., *Heracleum sphondylium* L., *Oenanthe crocata* L., and *Pimpinella saxifraga* L. in the field (Jervis *et al.*, 1993).

Aleochara spp.

Aleochara bilineata (Gyllenhal 1810) and *Aleochara bipustulata* (Linnaeus 1761) (Coleoptera: Staphylinidae) are both pupal parasitoids, as larvae, and predators of eggs and larvae of the cabbage root fly as imagos (Read, 1962; Royer & Boivin, 1999). *Aleochara bipustulata* has a wider host range than *A. bilineata* which is specialised in parasitising hosts within *Delia* spp., for example, *D. platura*, *D. antiqua*, *D. florilega* and *D. floralis* (Fuldner, 1960; Ahlström-Olsson, 1994; Fournet *et al.*, 2000 Andreassen *et al.*, 2009). Jonasson (1994) found that *A. bipustulata* develops less successfully on large cabbage root fly puparia compared with small puparia.

Aleochara spp. females are attracted to patches of host-attacked plants where they deposit eggs (Fuldner, 1960). Newly emerged larvae randomly search the soil around the root system for host puparia to parasitize. Once found, the *Aleochara* larvae gnaw a hole in the wall of puparia, enter it, and start to feed on the fly pupae (Jonasson, 1994). *Aleochara bipustulata* overwinters as adults, whilst *A. bilineata* hibernates as first instar larvae within

the host puparium and start to feed on the host fly puparia in early spring. This means that *A. bipustulata* is active in the field and can predate cabbage root fly eggs and larvae of the first generation at a period when *A. bilineata* is still inside the host puparium (Jonasson, 1994).

3.2.3 Epigeal predators

The egg and larval stage of the cabbage root fly are potential food for various epigeal predators (Coaker & Finch, 1971). Predation by carabid (Fig. 5) and staphylinid beetles has been most frequently studied (Wright *et al.*, 1960; Coaker, 1965; Jonasson, 1994; Finch, 1996; Eyre *et al.*, 2009). In laboratory studies, more than 45 ground beetle species, common in the European agricultural landscape, have been shown to be able feed on *Delia* spp. (Finch, 1996), and egg predation rates of up to 90 % have been recorded in the field (Hughes & Mitchell, 1960). However, under more realistic conditions in field studies predation normally averages 30% (Finch, 1989). In particular, *Bembidion* spp., *Harpalus* spp. and *Aleochara* spp. have the capacity to feed on and destroy *Delia* eggs in the field (Coaker & Williams, 1963; Coaker, 1965; Andersen *et al.*, 1983; Finch & Elliott, 1992).

Figure 5. Carabid beetles caught at Torslunda research station, Öland.

4 Field survey of natural enemies of *Lilioceris lilii*

(Paper I)

For the first time, a field survey was conducted to obtain information on natural enemies of the larval stage of *L. lilii* commonly occurring in Sweden and the frequency with which they occur.

4.1 Materials and methods

Sampling was performed in three regions of southern, south-eastern and central Sweden; Skåne, Småland/Öland and Stockholm. A total of 95 sites were visited in 2006 and 61 sites in 2007. No sampling was carried out in central Sweden (Stockholm) in 2007.

Any *L. lilii* larvae found were carefully removed from the leaves, stems and buds of cultivated lilies found in private gardens and parks. The first instar was not collected due to the high rearing mortality and the risk of underestimating parasitism as *L. errabundus* does not parasitise this instar (Haye & Kenis, 2004). The larvae were taken to the laboratory and placed on wet vermiculite in plastic cylinders at room temperature (20-22° C) and regularly fed with fresh lily leaves until they moved down in the vermiculite and formed cocoons. Adult *L. lilii* beetles and non-diapausing parasitoids hatched from the cocoons were collected with an aspirator and stored in 70 % alcohol in glass vials. Four weeks after the last emergence of insects the cocoons were sifted and the remaining un-hatched cocoons were placed out-doors in a humid and ventilated Styrofoam box until mid-September and thereafter taken inside and kept at 2-3° C. In March the cocoons were transferred to a rearing chamber and kept at 26° C, 70-80% relative humidity and 16:8 h light:dark cycle. Hatched parasitoids were collected daily and stored in 70 % alcohol. Four weeks after

the last parasitoid emerged the un-hatched cocoons were dissected. The emerged parasitoids were identified by taxonomists Britt Åhman (Ichneumonidae), Klaus Horstman (Ichneumonidae) and Hannes Bauer (Eulophidae) to species level.

4.2   Results and discussion

Our survey revealed that four larval parasitoids attacks *L. lilii* in Sweden (Table 1) at parasitism levels comparable to those found in other European countries (Paper I). These findings are important as they show that *L. lilii* is regulated by natural enemies although it is not a native pest in Sweden.

Table 1. Percentage parasitism in larvae of Lilioceris lilii in Sweden, 2006 and 2007.

Year	2006			2007	
Regions	South (Skåne)	South-east (Öland/ Småland)	Central (Stockholm)	South (Skåne)	South-east (Öland/ Småland)
No. of successfully reared larvae (no. sites)	1562 (36)	1547 (50)	133 (9)	155 (9)	1592 (52)
Hymenoptera: Ichneumonidae					
Diaparsis jucunda (Holmgren)		< 1			
Lemophagus pulcher (Szepligeti)	< 1	< 1	4		< 1
L. errabundus (Gravenhorst)	10	7	2	<1	12
Mesochorus lilioceriphilus Schwenke	13	7		5	9
Lemophagus spp.[1]	31	30	5	14	23
Hymenoptera: Eulophidae					
Tetrastichus setifer (Thomson)	2	3	25	< 1	3
Total parasitism	57	49	36	21	48

[1]Non-emerged *Lemophagus* cocoons for which we could not determine whether they contained *L. pulcher, L errabundus* or *M. lilioceriphilus* (hyperparasitoid of *Lemophagus* spp.)

The occurrence of the different species varied between the regions studied in the survey, with the gregarious eulophid *T. setifer* being the most abundant

parasitoid in central regions of Sweden and the non-gregarious ichneumonid *L. errabundus* dominating in southern and south-eastern regions. The bivoltine ichneumonid parasitoid *L. pulcher* was rare in the south but more abundant in central Sweden. The relative abundance of *L. lilii* larvae parasitoids in Sweden is similar to the complex found in northern Germany (Haye & Kenis, 2004). Only one *D. jucunda* parasitoid was found in the survey. This species is the most abundant larval parasitoid in central Europe whilst rarely found in northern Germany and the Netherlands (Haye & Kenis, 2004).

There was high parasitism on *Lemophagus* spp. by the hyperparasitoid *Mesochorus lilioceriphilus* (Schwenke 2000) (Hymenoptera: Ichneumonidae) in the southern and south-eastern regions of Sweden for both years studied, in comparison with the level reported in other studied European countries (Haye & Kenis, 2004). A high level of hyperparasitism is argued to negatively affect biological control by primary parasitoids but it may also have a positive effect through stabilisation of the host-parasitoid system (Höller *et al.*, 1993; Rosenheim, 1998). The effect of *M. lilioceriphilus* on the biological control of *L. lilii* thus needs further study.

At present gardeners either collect larvae and beetles by hand or kill them with a non-specific insecticide (Salisbury *et al.*, 2010). It is likely that there are opportunities to enhance the populations of natural enemies in the domestic gardens through relatively simple CBC operations. For example, all of the parasitoid species found in this survey hibernates in the soil. Keeping the soil undisturbed around cultivated lilies in autumn and early spring may therefore increase the number of parasitoids that successfully emerge in late spring. Soil cultivation by digging may for instance bury the cocoons at a depth from which the parasitoids cannot escape. It has also been speculated that mulching may hamper adult parasitoid emergence and should therefore not be practised around lilies (M. Kenis personal observation). Planting lilies together with flowers that provides easily accessible nectar can also increase the fitness of the parasitoids (Jervis *et al.*, 1993). However, it is likely that sugar deprivation among parasitoids is less common in diverse domestic gardens than in homogeneous agroecosystems with few floral resources.

5 Conservation biological control of *Delia radicum*

(Papers II, III, IV & V)

The cruciferous crop system is a much used model system for the study of plant-insect interactions (Finch & Collier, 2000). Knowledge of the biology and behaviour of the associated insects built up during years of intensive studies can assist in interpreting new results. It is thus not surprising that the cruciferous system has also been used to study the effects of habitat manipulation on cruciferous pest insects. The main focus has been on nectar effects on hymenopteran parasitoids attacking lepidopteran pests in cruciferous crops (Wäckers, 2004; Lee & Heimpel, 2005; Winkler *et al.*, 2006; Pfiffner *et al.*, 2009). The effects of habitat manipulation strategies including nectar resources on herbivores from other orders, such as Coleoptera and Diptera, and their natural enemies have not been as intensively studied.

5.1 Materials and methods

Insects

Reared insects were used for behavioural studies in the laboratory and semi-field (Paper II and III). The insect cultures of *D. radicum* and *T. rapae* were renewed yearly with field-collected individuals from Sweden and Denmark.

Plant material

Plants were grown in a greenhouse chamber at 22°C, 16:8 h light:dark cycle except for *F. esculentum* and white cabbage plants used in the semi-field experiment, which were grown under natural light and temperature conditions.

Plant odour attractiveness – Olfactometer study (Papers II & III)

The moving air Y-tube olfactometer is a valuable and straightforward method to explore insect responses to plant odours (Koschier *et al.*, 2000) and has been used for different hymenopteran parasitoids (Steinberg *et al.*, 1992; Wäckers, 2004; Jönsson *et al.*, 2005). In this thesis it was used to investigate the attraction of *T. rapae* and *D. radicum* to nine different flowering plants that provide nectar and to study the attraction of *T. rapae* to host plant volatiles (Papers II & III). The nectar plants used in Paper II have all been evaluated for use as natural enemy food in other habitat manipulation studies (Table 2) (Wyss, 1996; Wäckers, 2004; Fiedler *et al.*, 2008). The same experimental setup was used for both the herbivore *D. radicum* and the parasitoid *T. rapae* and followed the method described by Jönsson *et al.* (2005).

Table 2. Flowering nectar plants used in the olfactometer study

Family	Scientific name	Common name
Apiaceae	*Anethum graveolens* cv. Communis L.	Dill
	Coriandrum sativum L.	Coriander
Asteraceae	*Matricaria recutita* L.	Chamomile
Boraginaceae	*Borago officinalis* L.	Borage
Brassicaceae	*Lobularia maritima* cv. Snow crystal white Desv.	Sweet alyssum
Fabaceae	*Lotus corniculatus* L.	Birds foot trefoil
Lamiaceae	*Origanum vulgare* L.	Oregano
Polygonaceae	*Fagopyrum esculentum* Moench.	Buckwheat
Tropaeolaceae	*Tropaeolum majus* L.	Nasturtium

Nectar accessibility and Insect longevity (Paper II)

Nectar accessibility can be studied by examining the weight increase/decrease after the insect has been exposed to a nectar plant for a specific time period (Wäckers, 2004). Accessibility to the nectar was assumed when the insect gained in weight after three hours of exposure (Paper II). The method is useful for making a fast screening of suitable food plants. It is considered to be a conservative method, as uptake of small amounts of nectar might not be noticed due to weight loss occurring during the exposure time in the cage (Winkler *et al.*, 2009b). However, plant nectar can contain secondary metabolites that are toxic to arthropods (Wäckers, 2005) and the negative effects of these may be missed if this method is relied exclusively on. Thus, we also made a longevity study were *D. radicum* or *T. rapae* females survival on two different flowering plants were monitored on a daily basis until all insects

in the cage had died. The insect were placed in nylon netting cages (47.5 x 47. 5 x 138 cm, Bugdorm) either in a cage with a flowering plant or in a cage with a plant, of similar size, that had the flowers removed and compared pair-wise (Paper II).

Semi-field experiment (Paper II)

Semi-field experiments represent an important link between the controlled laboratory study and the complex reality of the field experiment (Winkler *et al.*, 2006). To assess the importance of flowering buckwheat plants on the parasitism rate of *D. radicum* larvae by *T. rapae,* semi-field experiments were performed (Paper II) (Fig. 6). Cages (1.5 x 1.2 x 1.2 m) were placed outside in an experimental field at Torslunda research station, Öland, in the south-eastern part of Sweden (56º37´N, 16º30´E). The studied insects were thereby exposed to prevailing weather whilst the risk of cross-treatment movement and predation was eliminated. A total of 15 replicate experiments were conducted over three consecutive years with start in 2008.

Figure 6. Cages used in the semi-field study at Torslunda research station.

Field experiment (Papers IV & V)

The field experiment was conducted at Torslunda research station in 2008, 2009 and 2010 and consisted of eight treatment plots (210 m^2) with conservation strips (CS i.e. flower-grass strips) and eight control plots, divided into four randomised blocks. The CS (1.5 x 10 m) consisted of annually sown *F. esculentum* and *A. graveolens,* with perennial grass strips (*D. glomerata*) on each side (Fig. 7). The *D. glomerata* sown in the middle of control plots was cut to 6 cm height during the season and ploughed under in autumn. Plots were treated according to the organic policy of International Federation of Organic Agriculture Movements (IFOAM) without synthetic pesticides and fertilisers.

In 2008 and 2010 all plots were planted with cabbage plants (cv. Castello) while in 2009 half the plots were planted with onions *Allium cepa* cv. Hytech Eco L. and the other plots with cabbage plants. The following parameters were monitored:

- *Delia radicum* egg-laying was sampled weekly by collecting the soil around the cabbage plants and rinsing it to extract the eggs using a method described by Hughes and Salter (1959) (Paper IV).
- *Delia radicum* puparia were collected at the end of each growing season and reared in the laboratory to examine the occurrence of parasitoids and the rate of parasitism (Paper V).
- The sex ratio of adult *D. radicum* flies and the abundance of aerial natural enemies were monitored using yellow pan traps with an inserted plexiglass window in 2008 and 2010 (Papers IV & V).
- Activity densities of epigeal predators were monitored with pitfall traps. Four traps were placed in each plot (4 and 7 m away from the strip) and emptied once every week. Any epigeal predators caught were determined to species level by taxonomists; Britt Åhman (Carabidae) and Stig Lundberg (Staphylinidae) (Paper V).
- Egg predation rates were assessed by placing out 20 reared *D. radicum* eggs in the field for 24 hours. Eggs with bite-marks and those missing were counted as predated (Paper V).

Figure 7. Conservation strip with *F. esculentum*, *A. graveolens* and perennial grass (*D. glomerata*) in the centre of the experimental plot. Photo: Linda-Marie Rännbäck

5.2   Results and discussion

Responses of Trybliographa rapae *to host-associated odours*

Male parasitoids were not attracted to volatiles from plants infested by *D. radicum* larvae while females showed clear attraction (Paper III). This result for females is in line with findings of others (Brown & Anderson, 1999; Jones, 1986; Neveu *et al.*, 2002). Many parasitoids use plant volatiles, emitted as a response to herbivory by the plant, to locate their host (Steinberg *et al.*, 1992; Mattiacci *et al.*, 1994; Gohole *et al.*, 2003). These herbivore-induced volatiles (HIPVs) are often more detectable than cues descending directly from the host organism (Zangerl, 2003). Furthermore, young females were more attracted to combined volatiles of host and food plants than to those from only the host plant, whereas older females showed similar responses to the two odour sources. This indicates that flowers, besides providing food resources, could also be used to attract parasitoids from the immediate surroundings into the field (Bianchi & Wäckers, 2008) and could be important to consider when designing habitat manipulation programmes.

Selection of plants and the impact of nectar

The nectar produced by flowers proved to be of great importance for the fitness of *T. rapae.* Females survived significantly longer when caged with flowering *F. esculentum* and *A. graveolens* plants compared with the control without flowers (Paper II). Furthermore, the semi-field experiment clearly linked accessibility to nectar with an increase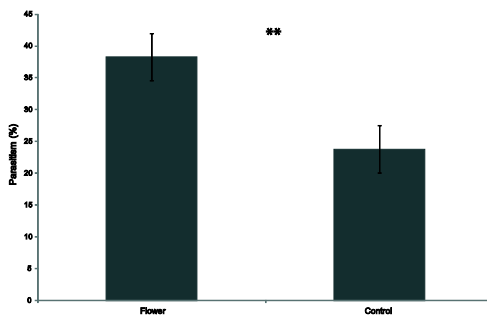 in larval parasitism by *T. rapae,* in a setting similar to field conditions. We investigated the effect of nectar for only three days and still found a 60% increase in parasitism compared with the control with no floral resources (Fig. 8). Increased parasitism rates by parasitoids as a response to habitat manipulation with floral resources have been observed in other herbivore/parasitoid complexes (Leius, 1967; Winkler *et al.*, 2006). In a field study by Berndt *et al.* (2006) parasitism of leafroller larvae, a

Figure 8. Average parasitism rates (±SEM) in host larvae of *D. radicum* parasitised by *T. rapae* in cages with flowering *F. esculentum* plants or *F. esculentum* plants with flowers and buds removed (control). (**P<0.01, n=15).

pest in vineyards, increased by 50% when intercropped with *F. esculentum* at one site but this result was not consistently at the other field site tested.

The screening procedure for nectar plants revealed that *T. rapae* females were selective in their food choice as only *F. esculentum* was found to be attractive whilst two plants were found to be even repellent, *Borago officinalis* and *Coriandrum sativum.* However, this could also indicate that *T. rapae* use both visual and olfactory cues when foraging for food. Indeed, Begum *et al.* (2004) showed the importance of flower colour for a parasitoid which decreased its survival on dyed *L. maritima* plants compared with natural white flowers despite both having similar production of nectar.

The odour from *C. sativum* was repellent for *T. rapae* and the plant was also avoided as a food source despite having exposed nectaries that are accessible to short-tongued parasitoids (Baggen & Gurr, 1998; Fiedler *et al.*, 2008). This finding highlights the importance of studying flower attractiveness and nectar accessibility when choosing flowers to be used in habitat manipulation programmes in the agroecosystem (Bianchi & Wäckers, 2008). A theoretical selection based on flower and parasitoid mouthpart morphology would have led to an erroneous conclusion.

Delia radicum is synovigenic and completely dependent on adult food for oviposition (Finch, 1971). A broad inherent attraction to various flowers would enhance the chances for the flies to successfully find suitable flowers especially as it can have up to three generations in the north of Europe, a period stretching from April until September (Coaker & Finch, 1971). During this time the flora, and the potential nectar plants, changes dramatically. This was confirmed by our finding that *D. radicum* was attracted to the majority of the flowers tested in the olfactometer and could also access nectar from the flowers (Paper II). Moreover, when caged with flowering plants of *F. esculentum* and *A. graveolens,* the life-span of the fly was significantly enhanced compared with the control.

None of the flowering plants tested was solely used by the parasitoid. We found that the *D. radicum* could utilise *F. esculentum* as a food source, but it was less attractive than the other flower species tested. Based on the outcome from the attractiveness, accessibility and longevity tests for *T. rapae*, we chose to include *F. esculentum* and *A. graveolens* as nectar plants in the conservation strips.

Male Trybliographa rapae *responses to food odours*

Male *T. rapae* were not attracted to floral odours from *F. esculentum* at any age tested and this gender disparity is likely to be explained by difference in biology between the sexes (Fig. 9) (Paper III). Females are likely to have a

higher energy demand than males, because they first have to find the patch with the host-attacked plants and thereafter dig down into the soil after the concealed host larvae (James, 1928). Male *T. rapae* are short-lived and mating occurs close to the natal patch (Jones, 1986). Incorporating innate responses to food odours may thus not be as profitable as their energy consumption is lower than that of females. This finding is consistent with other studies where low male parasitoid attraction to food odours also has been reported (Martin *et al.*, 1990; Messing & Jang, 1992).
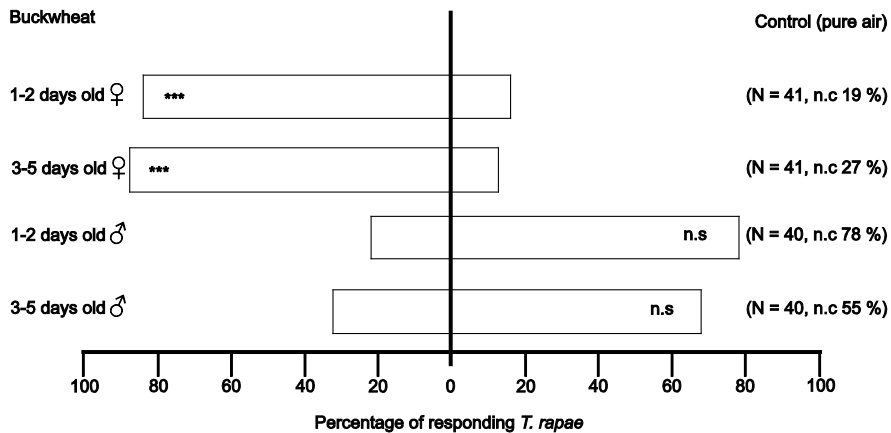
Figure 9. Trybliographa rapae female and male responses in olfactometer experiments to buckwheat flowers and a control (pure air). The responses are presented as percentages. The total number of insects (N) and the percentage not making a choice (n.c) in each experiment are presented on the right. ***P<0.001.

Impact of floral resources on T. rapae *in field*

In the field we found a significant increase in parasitism by *T. rapae* from the first year of study to the last in plots with CS and in the control plots, and this effect was strongest for the CS treatment (Paper V). However, at the same time the number of *D. radicum* infested cabbage plants increased. This may indicate that the field population of *T. rapae* responded positively to habitat manipulation, but could also be a function of an increased host density or a combination of both.

However, no positive effect of CS in terms of increased parasitism was found as compared to the control within years (Fig. 10). Thus either the flowers were not visited by *T. rapae* or they did not provide nectar in the field. It seems unlikely that a long-lived parasitoid such as *T. rapae* would not feed in the field especially since the laboratory and semi-field studies revealed the importance of nectar for *T. rapae* fitness and since flower visiting in the field is

known from earlier studies (Jervis *et al.*, 1993). Moreover, other nectarivores such as bumble bees, bees and hoverflies may have depleted or defended the nectar source from *T. rapae* and thus prevented the latter from utilising it (Winkler *et al.*, 2009a). In line with this, Hogg *et al.* (2011) suggested that selection of food plants should be based on their attractiveness to nectar competitors as well as the herbivore and their biological control agent, as this can have a substantial impact on the outcome of habitat manipulation.

Another possible explanation why nectar provision could not be translated into increased parasitism by *T. rapae* may be found in the experimental setup. The physical limits of the field restricted the distance between experimental plots to 40 m. This distance is likely to have been too short for avoiding cross-treatment movements by the parasitoid, i.e. food foraging parasitoids may have used the flower strips for feeding, whilst egg-laying may have occurred on host larvae found in control plots. Further studies are, however, needed to assess the dispersal capacity of *T. rapae* and to confirm the importance of nectar feeding in the field.
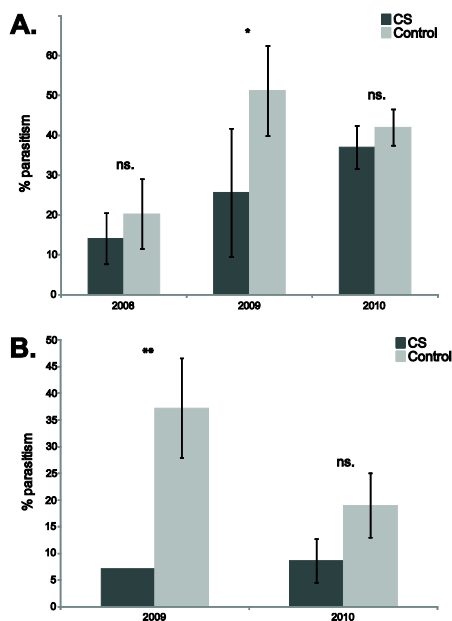

Figure 10. Average parasitism rates in (A) host larvae of *D. radicum* parasitised by *T. rapae* (B) host pupae parasitised by *A. bipustulata* in plots with conservation strips (CS) and without (Control). Based on the proportion of *D. radicum* infested cabbage plants that were parasitised by at least one parasitoid (ns.=not significant, *P<0.05**P<0.01)

Effects of floral resource on Delia radicum

The laboratory result suggested that habitat manipulation in field with floral resources consisting of *F. esculentum* and *A. graveolens* intercropped with white cabbage would elevate the pest density and associated problems.

However, the field habitat manipulation did not increase the overall egg-laying of the second generation *D. radicum* during the three year study and there was no difference in egg numbers between treatments in any of the years (Fig. 11) (Paper IV). Feeding is suggested to take place in the vicinity of fly aggregation sites, where flies also shelter from adverse weather conditions and mate (Hawkes, 1973). Consequently, there was a risk that the flower strips would be used as aggregation sites and thereby increase the pest densities locally in those plots. However, the low occurrence of males in plots with flowers indicates that the males did not use the intercropped flowers as a food resource and that aggregation took place elsewhere (Paper IV). At aggregation sites the sex ratio is likely to be close to 1:1 whilst females are more abundant within the crop than males (Hawkes, 1972; Hawkes, 1973; Nair & McEwen, 1975). It is even possible that the relative abundance of male flies was exaggerated, as Hummel *et al.* (2009) found that yellow bowl traps similar in size and colour to those used in this study caught more *D. radicum* males than females. This was due either to greater activity of males in the field or to a gender difference in attraction to the trap (Broatch *et al.*, 2006; Hummel *et al.*, 2009).

The aggregation outside the planted crop and the distinct feeding and oviposition behaviour of the female flies which involves attraction to host plants first after feeding and mating (Coaker & Finch, 1971), imply that females may be as likely to forage for food outside the crop as within since only one of the resources (food or host plant) is relevant during a specific behavioural period. Moreover, the high mobility of the flies enables food searching over a wide area (Finch & Skinner, 1975). In the vicinity of the experimental fields there was both a deciduous forest and private gardens with a high diversity of potential food sources for the flies that may have been preferred to the flowers in the CS. This is supported by the results from the olfactometer study which found a hierarchy in odour preference, with *L. maritima* being most attractive and *F. esculentum* being less attractive than *A. graveolens* (Paper II)
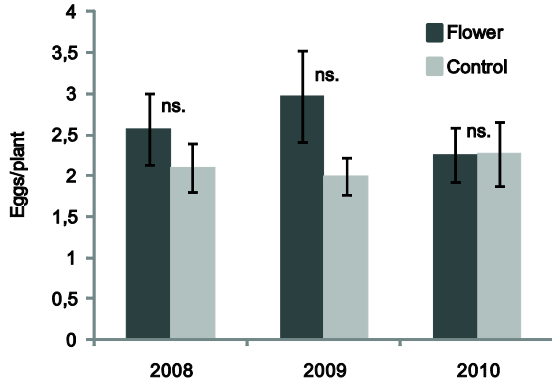
Figure 11. Average number of *D. radicum* eggs per cabbage plant (±SEM) in flower and control treatments between weeks 28-32 in 2008-2010. Egg values are compensated for half the number of planted cabbage plants in 2009. Figure show back transformed values. ns.= no significant treatment difference, *P*>0.05 (PROC MIXED, SAS).

Effects of habitat manipulation on Aleochara bipustulata

Conservation strips had no positive effect on the parasitism of *D. radicum* puparia by *A. bipustulata.* Instead, we found higher parasitism in control plots in 2009, which was probably a density-dependent host response to the significantly higher number of *D. radicum* pupae found in these plots (Fig. 10). *Aleochara bipustulata* and the closely related species *A. bilineata* use info-chemicals, released by cruciferous plants attacked by *D. radicum* larvae, to detect their host (Royer & Boivin, 1999; Neveu *et al.*, 2002; Ferry *et al.*, 2007) and they are known to aggregate in patches with high abundance of hosts and prey (Tomlin *et al.*, 1992). Thus, the significantly higher parasitism of *D. radicum* larvae in cabbage plots without CS in 2009 was most likely an effect of increased patch-finding due to the higher abundance of larvae-infested cabbage plants.

However, the activity density of *A. bipustulata* was significantly higher from the first week of egg-laying by second generation *D. radicum* and in the following three weeks in 2009 and 2010 in plots with CS. In the same time period a significant reduction in the number of *D. radicum* eggs that reached the pupal stage was observed in plots with CS in 2009 and a trend towards a reduction in pupae in 2010. There was no difference in egg predation between the treatments, which suggests that *A. bipustulata* had attacked and fed upon larvae, as proposed in other studies (Fuldner, 1960; Björkman *et al.*, 2010). The higher activity of *A. bipustulata* in plots with CS may have been due to a higher abundance of alternative prey (Kozár *et al.*, 1994). These may in turn have been attracted by the intercropped flowers (Frank & Shrewsbury, 2004).

Effects of habitat manipulation on epigeal predators

During the three years field experiment we caught 10 735 carabids belonging to 55 species and 28 093 staphylinids belonging to 163 species. Among these carabids, three *Bembidion* and two *Harpalus* species were found to be positively correlated to predation of *D. radicum* eggs (Paper V). This is in agreement with other egg predation studies (Mitchell, 1963; Obadofin & Finlayson, 1977; Andersen *et al.*, 1983; Graifus & Warner, 1989). Coaker and Williams (1963) found that five carabid species dominated trap catches and had a high egg predator index including one *Harpalus* and two *Bemibidion*. They are important predators as they are often abundant in the agricultural fields and are of a suitable size to have fly eggs as prey (Finch, 1996).

The activity density of both carabids and staphylinids showed a drastic decrease from the first year to the second, but with a recovery during the third year (Fig.12). This probably explains the increase in *D. radicum* infested cabbage plants in the same period, as the egg-laying of *D. radicum* did not increase during this time span (Papers IV & V).
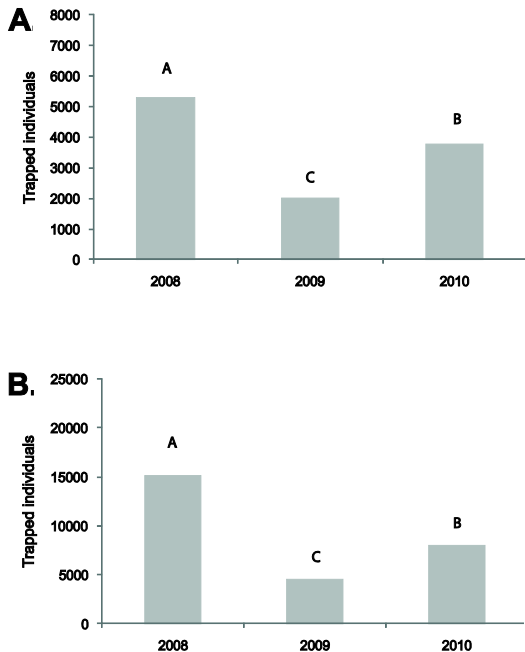

Figure 12. Yearly fluctuations in the activity density of A) Carabidae and B) Staphylinidae in 2008, 2009 and 2010. Figure shows back-transformed values. Different letters indicates significant difference at P<0.05 (PROC GLM, Tukey-test).

The low average number of *D. radicum* eggs found per cabbage plant, 2-3 eggs regardless of treatment and year, indicates that the field herbivore population at the research site was small and stable. A recent field study conducted in Denmark found egg-laying by the second generation of *D.*

radicum to vary between 35 and 185 eggs per plant depending on treatment and sampling year (Meyling *et al.*, 2010). We would have expected a rapid build-up of the *D. radicum* population from the first to the last year, as a host crop was grown at the same location for three consecutive years. It is possible that the ground living predators had a stabilising effect on the population for all three years despite the drastic decrease in activity density in 2009, as proposed earlier by Finch & Collier (1984). For instance, the first generation of *D. radicum* eggs may be more prone to be attacked by polyphagous predators as fewer alternative prey are present in the field at this time of the year. This would suggest that the predators are more efficient as biological control agents of the fly at this period than in July. However, our sampling of egg-laying and abundance of predators started after the egg laying peak of the first generation flies so we cannot compare the effect of predation at the different periods.

We found only minor treatment effects on the activity density of individual carabid and staphylinid species for all three study years, when considering trap catches of each species over the whole sampling season (Paper V). This was also reflected in the lack of difference in the egg predation rate between the treatments. Habitat manipulation with CS is likely to mostly affect the epigeal predators by providing them with suitable overwintering sites within the field and/or by increasing the abundance of prey during the crop season (MacLeod *et al.*, 2004; Griffiths *et al.*, 2008). If the predators used the CS as an overwintering habitat, they are likely to have left them and re-colonized the field in early spring prior to the start of sampling in June (Griffiths *et al.*, 2008). Therefore we cannot show that the CS were used as hibernation sites in the winter 2008/2009 and 2009/2010. However, earlier studies have shown the importance of providing winter habitats within the field for spiders, carabids and staphylinids (Thomas *et al.*, 1992a; Lys & Nentwig, 1994; Pfiffner & Luka, 2000; MacLeod *et al.*, 2004).

Effects of habitat manipulation on aerial natural enemies

Other natural enemies e.g. Cynipoidae wasps responded positively to CS with an increase in abundance whilst two other groupings of parasitoids, Ichneumonoidae and Parasitica spp., were more abundant in one out of two sampling years.

Effects of crop rotation

A sound crop rotation regime is important to avoid a build-up of soil-born plant pathogens and depletion of nutrients, but can also be used as a pest management strategy against insect pests with a limited dispersal capacity (Zehnder *et al.*, 2007). The crop rotation practice in this study was primarily

intended to support *T. rapae* with additional hosts when *D. radicum* was not present thereby creating a more stable perennial system where it did not have to migrate between fields each year to find its host. For instance, the onion fly *D. antiqua*, a severe pest on onions, is reported to be a potential host to *T. rapae* (Wishart & Monteith, 1954). Onion was therefore planted in 2009 to explore whether *T. rapae* is able to shift hosts from *D. radicum* to *D. antiqua*. Unfortunately, it was not possible to evaluate this hypothesis as very few onion flies were found in the field in that season (Paper IV). However, preliminary laboratory experiments with reared *T. rapae* indicate that at least this sub-population could not shift from *D. radicum* to *D. antiqua* (unpublished results). *Delia radicum* was, as expected, not affected by the crop rotation with onions (Paper IV). Egg-laying was similar in plots planted with onion in the previous year and in those planted with cabbage. The high mobility of *D. radicum* and their need to feed for egg-laying forces the flies to relocate in the field every new generation, making isolation with crop rotation impractical (Finch, 1989; Zehnder *et al.*, 2007).

6 Conclusions and future perspectives

Our home garden and park survey of natural enemies to *L. lilii* revealed that four different larval parasitoids exist in Sweden which was not known before. Two of these were more abundant, the eulophid *T. setifer* and the ichneumonid *L. errabundus.* The parasitism rate was similar to that elsewhere in northern Europe. CBC is an important strategy for home gardeners, as few synthetic pesticides are available against insect pests. Possible CBC measures to strengthen the biological control of the *L. lilii* could be to plant flowers with accessible nectar that the parasitoid can feed on close to the lily plants and, even more important, to provide suitable and undisturbed overwintering sites for the parasitoids. For instance, avoiding digging the soil in autumn could reduce the risk of destroying parasitoid cocoons. Another important part of this work is to inform and teach home gardeners how to recognise *L. lilii* and its parasitoids.

Our results showed that CBC within the crop, comprising floral resources and perennial beetle banks has the potential to improve the conditions for natural enemies of *D. radicum* and other pest insects in the Brassicaceae agroecosystem. The activity density of *A. bipustulata* was higher in plots with CS compared with the control at the time of egg-laying by second generation *D. radicum* in two out of three years. In 2009 this was also linked to a significant reduction in the number of infested cabbage plants. Other natural enemies, such as Cynipoidae wasps, were also more abundant in plots with CS, whilst two other groups of parasitoids, Ichneumonoidae spp. and Parasitica spp., were more abundant in one of two study years. Moreover, the main larval parasitoid *T. rapae* increased its capacity to parasitise *D. radicum* larvae by 60% when given access to flowering buckwheat plants in our semi-field study which covered a three-day period.

At the same time, egg-laying by the key pest *D. radicum* was not enhanced in the field even though the food plants provided were not solely suitable for

natural enemies. Other food sources for the fly may have been found closer to the aggregation sites at the field edges.

Parasitism by *T. rapae* and *A. bipustulata* the two dominant parasitoids at our field site, was not higher in plots with CS than in controls for any of the study years. The treatment effect may have been masked having too short a distance between the experimental plots although *T. rapae* is considered to be a weak flyer. Cross-treatment effects may have arisen through parasitoids feeding in one plot and host foraging in another. Our knowledge of how *T. rapae* moves in the field and the distances covered is limited and needs to be further improved since this is an important issue when designing future Brassicaceae crop systems with added food resources.

However, there was an increase in *T. rapae* parasitism from the first year to the last in plots with CS and controls plots. This was most likely a function of the increase in the host population for the same period, but could also have been partly a response by the parasitoid to the CS, especially since the increase was more pronounced in plots with CS.

Future pest management in Brassicaceae crops to control *D. radicum* will require multiple management practices to achieve adequate control without a reliance on synthetic pesticides. For instance CBC to increase natural enemies should be combined with other practices e.g. timing of sowing or planting to avoid the peak egg-laying of the first generation of *D. radicum* or physical barriers to reduce oviposition.

CBC could also be complemented with inoculation or inundation biological control with entomopathogenic fungi and nematodes. However, these multiple management practices need to be thoroughly evaluated before being promoted to farmers. For instance, the knowledge of whether and how entomopathogenic organisms, besides regulating pest insects, can also reduce the fitness of the natural enemies is today rather limited.

To strengthen our findings from the study of *D. radicum* I suggest further evaluation of this practice for a longer period at our experimental field, preferably not less than a seven year crop rotation, as well as at production areas with a less diverse landscape than that found at Öland.

General conclusions from one single short-term field trial should only be done with some caution because the results of CBC are largely determined by the surrounding landscape, the time scale used for studying population effects on natural enemies and the timing of habitat manipulation. Future CBC of horticultural pests will require a deeper understanding of the dynamics of pest insects, natural enemies and higher order predators and how they interact at different scales. Many studies have shown the importance of increasing the vegetative diversity both within the crop field, at farm level and at the

landscape level to improve pest suppression. A more diverse landscape can support a larger pool of natural enemies and these can be recruited and maintained within the field through periods when prey is scarce, by intercropping with flowering plants. Besides enhancing pest control, this can also improve other ecosystem services for example improved pollination of horticultural crops.

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