Integrated pest management across spatial scales

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Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2017

Acta Universitatis agriculturae Sueciae
2017:28

Cover: Predators and preys in the landscape
(Picture: Laura Riggi)

ISSN 1652-6880
ISBN (print version) 978-91-576-8829-3
ISBN (electronic version) 978-91-576-8830-9

Print: SLU Service/Repro, Uppsala 2017

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Abstract

Despite spectacular increases in agricultural productivity per unit of land and labour and a continually growing awareness of the importance of sustainable agriculture, modern agriculture faces serious problems at scales ranging from individual fields to regions. Such problems include increased resistance of pests to pesticides, loss of soil fertility, and loss of diversified habitats in the landscape. In my thesis I aim to better understand how field and landscape scale management affects integrated pest management with a particular focus on pest abundance, pest resistance, and biological pest control by naturally occurring enemies.

Using large scale landscape field studies, we investigated the effect of landscape composition on pollen beetle pesticide resistance and abundance, and on abundance of its natural enemies in oilseed rape (Papers I and II). We found that the amount of oilseed rape crop in the landscape increased pest abundance and pesticide resistance in the target pest. Negative effects of landscape intensity were found on specialist but not on generalist natural enemies. This suggests that generalist predator communities are well adapted to crop-dominated landscapes. Therefore, management of natural pest control services by generalist predators in oilseed rape in Sweden should prioritize local scale management practices.

At the local scale, we investigated the impact of four major herbivores on oilseed rape yield. We found that under specific combinations of pests, attacks by several different pests have a positive effect on oilseed rape yield (Paper III). Increasing our knowledge about multiple pest–plant interactions has a potential for directly increasing yield while reducing pesticide input.

Finally, we tested how local scale long-term fertilisation affects soil communities and natural pest control (Papers IV and V). Our results suggest that in intensively managed agricultural systems, biennial organic fertilisation is insufficient to promote diversity within the soil community in the long-term. Generalist predators, however, benefitted from high quality organic fertilisation in the long-term, which in turn exerted top-down control on the aphid pest.

Keywords: Biological control, pesticide resistance, landscape ecology, organic and mineral fertilisation.

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To whom it may concern…

If the observer always affects the observed, changing it from moment to moment, from glance to glance, then the observed also changes the observer.

Donald Worster, Nature's Economy

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 **Riggi LG**, Gagic V, Bommarco R & Ekbom B (2015). Insecticide resistance in pollen beetles over 7 years - a landscape approach. *Pest Management Science* (72), 780–786.

II **Riggi LG**, Gagic V, Rusch A, Malsher G, Ekbom B & Bommarco R. Pollen beetle mortality is increased by ground-dwelling generalist predators and soil clay content, but not landscape complexity (manuscript).

III Gagic V, **Riggi LG**, Ekbom B, Malsher G, Rusch A & Bommarco R (2016). Interactive effects of pests increase seed yield. *Ecology and Evolution* (6), 2149–2157.

IV **Riggi LG**, Taylor A, Viketoft M, Hallin S & Bommarco R. Long-term organic and mineral fertilisation affects soil communities composition and associations (manuscript).

V **Riggi LG** & Bommarco R. Subsidy quality mediates the direction of trophic cascades in an agroecosystem (manuscript).

Papers **I** & **III** are reproduced with the permission of the publishers.

The contribution of Laura Riggi to the papers included in this thesis was as follows:

I Main author. BE designed the experiment and led the collection of the data. LR performed the analysis. All co-authors contributed to interpretation of results and the writing of the manuscript.

II Main author. VG, RB, BE and AR designed the experiment. LR, VG and GM collected the data. LR performed the statistical analysis. All co-authors contributed to interpretation of the results and the writing of the manuscript.

III Second author. VG designed the experiment together with RB, BE and AR. VG, LR, GM collected the data. VG performed the statistical analyses and led the writing with contributions from all the co-authors.

IV Main author. LR and RB designed the experiment. LR and AT collected the data. LR performed the statistical analyses. All co-authors contributed to interpretation of the results and the writing of the manuscript.

V Main author. LR and RB designed the experiment. LR collected the data and performed the statistical analyses. LR and RB interpreted the results and wrote the manuscript.

Abbreviations

Bt	*Bacillus thuringiensis*
DDT	dichloro diphenyl trichloroethane
FAO	Food and Agriculture Organization
IPM	integrated pest management
kdr	knock-down resistance
OSR	oilseed rape
OSR_{t0}	present year OSR
OSR_{t-1}	past year OSR
Pb	pollen beetle
qPCR	quantitative polymerase chain reaction
SN	semi-natural habitat

1 Introduction

Although not always aware of the fact, humanity depends on nature for its survival and welfare. Over millennia, we have shaped our environment in dramatic ways, with agriculture being the most ancient and prevalent example. Agriculture covers more than one third of global land area, making it the principal form of land management worldwide (FAO 2016). In the face of increasing demand for food from a growing human population and an inherently production driven economy, agriculture has been intensified at both local and landscape scales. Agricultural expansion has entailed the extension of homogenous landscapes, preserving few and fragmented semi-natural habitats. As a result, many species have experienced a reduction in habitat diversity and quality (Stoate et al. 2001, Robinson and Sutherland 2002). Meanwhile, local field management intensification, including machine-driven farming with higher inputs of fertilisers and pesticides, alongside lower crop diversity and increased sizes of arable fields, has resulted in the reduction of soil fertility (Stoate et al. 2001, Tscharntke et al. 2005). These issues are not novel. In his book *Nature's Economy* (1994) historian Donald Worster refers to John Steinbeck's *The Grapes of Wrath* (1939) and indicates that the miseries inflicted on the Joad family were a result of changing farming practices on the American prairies in the 1930s, an event known as the Dust Bowl. A human and an environmental disaster, the Dust Bowl was a prolonged series of dust storms brought on by drought, agricultural practices and human ecological ignorance. This event in many ways framed the discipline of agroecology, in which this thesis belongs (Worster 1994).

1.1 Agroecology: historical context and current perspectives

Bensin (1930) coined the term "agroecology" to describe the use of ecological methods on commercial crop plants. However, up until the 1960s, agricultural ecosystems were primarily managed to maximize the provisioning of food, fuel, and fibre with little guidance from the science of ecology. This approach, that viewed the land as a resource provider, led to overexploitation both of the soils and those whose livelihoods depended on them. Some of the most striking examples come from the USA with the Dust Bowl in the 1930s followed by post-WWII technology, such as the deployment of DDT (Carson 1962, Worster 1994). These disasters, along with an increasing awareness of the fragility of nature, paved the way for a more humble approach to the management of agricultural landscapes. Since then there has been a growing appreciation of the importance of applying ecological principles to crop management.

In its several conceptions, agroecology has emerged as a scientific approach used to study, diagnose and propose alternative low-input management of agroecosystems. Severe pest outbreaks in the early 1970s in the USA (e.g. gypsy moth, Douglas fir tussock moth, and southern pine beetle), and the lack of adequate substitutes for DDT, which had been banned since 1957 for use in forest pest control, converged to encourage the development of **integrated pest management** (IPM) (Stern et al 1959, Kogan 1998). IPM sought to radically modify the philosophy of crop protection, de-emphasizing the chemical control aspect in favour of a management approach. This involved a deeper understanding of insect and crop ecology and the deployment of several complementary tactics such as the application of economic thresholds and biological control (Rabb and Guthrie 1970). More recently, the concept of **ecosystem services** coined by Ehrlich and Mooney in 1983, and subsequently defined as "*the functions and products of ecosystems that benefit humans, or yield welfare to society*" (MA 2005) has taken both ecology and policy literature by storm. This concept, originally intended as a metaphor (Norgaard 2010), has now become a major ecological framework aiming to measure, assess, and value aspects of societal dependence on nature. For example, natural pest control services in crops were valued to US$ 417 billion per year worldwide (Costanza et al. 1997, Losey & Vaughan 2006). Other examples of services provided by nature in agroecosystems are pollination, soil biodiversity, and nutrient turnover (Zhang et al. 2007).

Despite spectacular increases in agricultural productivity per unit of land and labour and a continually growing awareness of the importance of sustainable agriculture, current agriculture faces serious problems at scales ranging from individual fields to regions. These include loss of soil fertility, increased resistance of pests to pesticides, and loss of diversified habitats in the landscape. In this context there is a necessity to implement cautious actions that limit agricultural intensification at both field and landscape scale. The challenges facing IPM are to increasingly rely on naturally occurring ecosystem services while maintaining high productivity and keeping pest damage low.

This thesis fits into the growing field of agroecology that aims to better understand how field and landscape scale management impact pest management, with a particular focus on pest damage, pesticide resistance and natural pest control.

1.2 Integrated pest management and scales of management

The need to consider the total ecosystem is the first principle of IPM (Smith 1962). Nevertheless, IPM programs, including some of the most successful, have been implemented with little consideration of ecosystem scale processes (Maredia et al. 2003).

Throughout the 1990s, the focus of pest management was the crop field. The prevailing IPM strategy has been on monitoring programs in which pest thresholds are established, and chemicals (or biologically based products) are used on an as-needed basis (Nicholls and Altieri 2004). However, such treatments are therapeutic and do not aim to control the causes of pest outbreaks or decrease the vulnerability of agroecosystems. This strategy almost inevitably carries the risk of promoting pest resistance. A striking example of pest resurgence is the blue alfalfa aphid (*Acyrthosiphon kondoi* Shinji), which had been successfully managed since 1975 in western USA through host plant resistance, economic thresholds and insecticides. Since 2013, however, it is once again causing severe economic losses, likely due to the development of insecticide resistance and the depletion of its natural enemies (Natwick et al. 2014). Truly satisfactory and sustainable solutions to pest problems require a shift to understanding why is the pest a pest, and should seek to address the underlying processes in ecosystems and/or agronomic practices that have allowed organisms to reach pest status (Lewis et al. 1997). The current objectives of IPM are thus to optimize agroecosystems by maximizing their abilities to regulate natural pest control, by improving their resilience to pest damage and by preventing pesticide pest resistance. An important part of IPM is hence to understand the ecology of naturally occurring enemies of the pest in order to find options to support them. The other tools (e.g. thresholds, chemicals, control agents) remain important, but need to be applied with caution, such that the natural control is not disrupted. To achieve IPM objectives we need to move from a reductionist view of pest management (e.g. applying economic thresholds) to a systemic view of agroecosystems, integrating the crops within an ecosystem perspective (Lewis et al. 1997).

Pest damage, pest resistance, and biological control depend on ecological processes at multiple scales ranging from field to landscape (Bianchi et al. 2006, Tscharntke et al. 2007, Chaplin-Kramer et al. 2011). For example, Zaller et al. (2008a,b) found that the damage caused by stem weevils in oilseed rape was positively correlated with the soil quality of the field and with proportion of wooded areas in the landscape. Furthermore, a recent review suggests that field and landscape management can have an interactive effect on pest abundance and biological control, with local management having a smaller effect in promoting natural enemies in more complex landscapes than in simple, intensified landscapes (Tscharntke et al. 2012). However, the relationships between crop and non-crop habitats are complex and can be antagonistic (e.g. Thies and Tscharntke 1999, Valantin-Morison et al. 2007, Zaller et al. 2008c, Tscharntke et al. 2016). On the other hand, investigations of landscape features promoting the incidence of pest resistance over time are rare and have mostly focused on the effect of refuges on pest resistance to Bt crops (Onstad and Carrière 2014).

This thesis aims to include both landscape and local scale approaches to investigate sustainable pest management, including biological control and pest resistance.

2 Aims and objectives

The overall aim of this thesis is to identify drivers that explain natural pest control and pest resistance, components of IPM, at various spatial scales. More specifically the aim was to investigate how landscape and local management affect biological control (**Paper II** & **V**), insecticide resistance management (**Paper I**), soil community composition (**Paper IV**) and crop yields (**Paper III** & **V**).

The specific objectives are to:

- Examine the effect of landscape composition on the occurrence of pyrethroid pesticide resistance in a major oilseed rape pest, the pollen beetle, across Sweden (**Paper I**).
- Explore the most important local and landscape components of agricultural intensity that affect biological control of the pollen beetle in oilseed rape (**Paper II**).
- Identify the impact of multiple pest species on oilseed rape yield and implications for the application of economic thresholds for single and multiple pests (**Paper III**).
- Explore how long-term mineral and organic fertilisation management affects communities of soil organisms in a conventional cereal agro-ecosystem (**Paper IV**).
- Examine the effects of long-term mineral and organic fertilisation on aphid biological control and cereal yield, using large cage experiments (**Paper V**).

My ambition is that the different aspects of this thesis will contribute to the growing knowledge base on the importance of investigating multiple scales for the management of naturally occurring pest control and resistance.

3 Landscape perspective

3.1 Landscape ecology: Background

Landscape ecology investigates the relationship between spatial organization (composition, connectivity, and configuration of habitat patches) and ecological processes at scales generally larger than the ones typically explored in ecology. The definition of a landscape varies with the question (Turner et al. 2001). In this thesis, landscape is defined as a level of organization greater than, and encompassing, the level of the ecosystem. It is characterized by heterogeneous and dynamic interactions between habitats (Rusch 2010).

One useful approach to quantify the effect of landscape on the population dynamics of a species is to use a functional approach that identifies the habitats in the landscape and the resources utilized by the species throughout its life-cycle (Dunning et al. 1992). A first step in landscape ecology is therefore to examine the size or the proportion of habitats relevant to the biology of the investigated species, at an ecologically relevant scale. In general, larger habitat patches harbour both more species and more individuals of each species (MacArthur and Wilson, 1967; Turner et al. 2001). Loss of favourable habitat in the landscape has been identified as a major driver for decreases in species abundances, while the consequences of habitat configuration (i.e. fragmentation and distance between habitat patches) vary depending on traits of the species in question. Habitat configuration has, for example, been shown to have little effect on species with high dispersal abilities (Wiegand et al. 1999, Fahrig 2003, Haynes et al. 2007, Banks and Gagic 2016). To conclude, the effects of landscape on a given population will primarily depend on the amount of habitats relevant to the investigated process and the ability of the focal species to disperse among habitats (Tischendorf and Fahring 2000, Baguette and Van Dyck 2007).

Another important feature of agricultural landscapes is crop rotation, which leads to inter-annual variation in the distribution of habitats (i.e. focal crops). Inter-annual variation in the amount of crop patches in the landscape was shown to influence pest population dynamics via dilution and concentration processes (see Table 1). These temporal dynamics are particularly relevant when investigating univoltine species (i.e. species with only one generation per year) (Thies et al. 2008). Therefore it is important to integrate a temporal dimension when investigating agricultural landscapes.

In this thesis, I investigated the effect of landscape composition across different years on the abundance of pollen beetles, on the occurrence of pesticide resistance in pollen beetle populations, and on natural pest control.

3.2 Study system: pollen beetle in oilseed rape

Traditionally used to give soils a good break between cereal crops, cultivation of oilseed rape (OSR) (*Brassica napus* L.) has boomed in Sweden in recent years, as demand for its oil has soared (Figure 1). But the bright yellow flowers have also attracted a variety of pests, of which the most significant are the pollen beetles (primarily *Meligethes aeneus* F., Coleoptera, Nitidulidae).

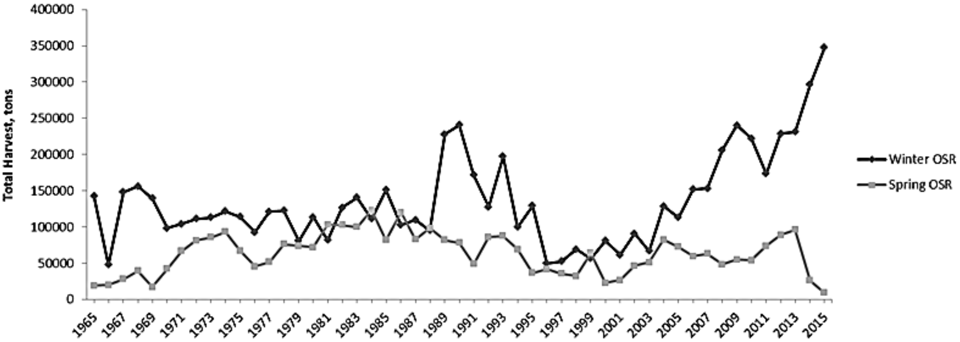

***Figure 1**: Total harvest of oilseed rape crops (tons) in Sweden between 1965 and 2015.*

Pollen beetles produce one generation per year, and adults overwinter outside the field (Rusch et al. 2011). In the spring, the beetles emerge and begin feeding on pollen of various plants. As temperatures rise, the beetles migrate to winter OSR fields where they oviposit in the flower buds. The larvae feed on pollen and when fully grown drop to the soil for pupation. As the winter crop matures, adult beetles move to spring OSR, if available, and continue to feed and reproduce. The next generation of adult beetles emerges in the middle of the summer, and it is these which will overwinter (Figure 2). Pollen beetles can move up to 10 km in 2 days (Tamir et al. 1967), and genetic analysis suggests high rates of gene flow among regional populations across Sweden (Kazachkova et al. 2007).

Feeding by the pollen beetle reduces the number of buds that are able to develop into seed pods. Crops are particularly susceptible at the early green bud to yellow bud stages. Although OSR has high compensatory abilities for damage (Free and Williams 1978, 1979), yield losses of 70–80% have been recorded in untreated OSR (Hansen 2003).

Pesticides have been widely used against pollen beetles and, as a consequence, resistance has been rising across Europe. This has led to the strict implementation of pesticide bans within the European Union (Hillocks 2012) and the necessity of finding alternative methods of control. Due to its complex life cycle - with different stages requiring different habitats - and its high dispersal ability, pollen beetle abundance and resistance management require a multi-scale approach.

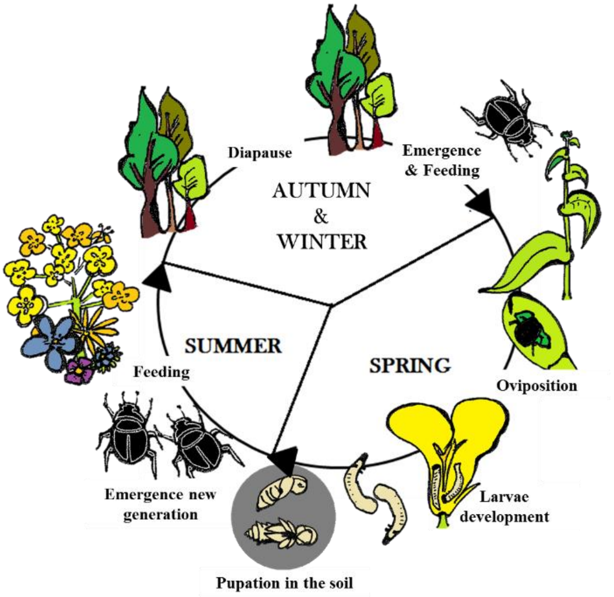

***Figure 2**: Life-cycle of the pollen beetle Meligethes aeneus on oilseed rape.*

3.3 Pesticide resistance a landscape perspective (Paper I)

3.3.1 The role of landscape in insect resistance management

Research concerning the role of landscape in insect resistance management has primarily focused on the role of abundance and distribution of refuge habitats in delaying the evolution of resistance to Bt crops (Onstad and Carrière 2014). Spatially explicit models show that temporal and spatial variation in abundance of Bt and non-Bt crops determines the pattern for resistance evolution (Onstad and Carrière 2014). The effect of landscape composition on the occurrence of insecticide resistance has rarely been investigated. We can expect that in landscapes with uniform and prolonged insecticide application, resistant individuals might be strongly selected for, whereas where the insecticide application is intermittent or low, susceptible individuals will persist. Thus, the proportion of host crop and non-host crop habitat (as a proxy for insecticide application) defines landscapes with varying levels of selection pressure for insecticide resistance. While efforts have been made to monitor spatial variation in insect pest resistance (Tabashnik et al 1990, Nauen 2007), few attempts have been made to link this variation to land-use features, such as host crop area, across spatial and temporal scales (Carrière et al. 2012).

3.3.2 Background: Pesticide resistance in pollen beetle

For almost two decades in Sweden, pollen beetle populations were effectively controlled with pyrethroid insecticides, which act on the insect central nervous system (Slater et al. 2011). However, the lack of insecticides with different modes of action and the widespread use of pyrethroids for other pests, such as stem weevils, has resulted in selection for resistance in pollen beetles. As a result, resistance to pyrethroids is now widespread among European pollen beetles, with the first records in France in 1997 and in Sweden in 2000 (Detourne et al. 2008, Zimmer and Nauen 2011a b, Slater et al. 2011).

Several separate mechanisms are involved in pesticide resistance in pollen beetles. Regional differences in levels of **metabolic resistance** (i.e. alteration of the toxin by enzymes such that it no longer binds to its target site) have been identified across Europe with higher proportion of resistant individuals in Nordic populations of pollen beetles. **Target-site resistance** (i.e. *kdr*) involves the mutation of one or a group of genes and confers strong resistance to virtually all pyrethroids. This has hitherto only been detected in populations from Denmark and Sweden (Zimmer et al. 2014). The situation in Sweden is particularly interesting because resistant *kdr* genotypes have only been detected in the far south, and not in more northern parts of Sweden where OSR is also grown. This suggests a spatial component in the occurrence of resistance in pollen beetles in Sweden.

High pesticide resistance in Nordic countries can be attributed to several factors. Firstly, between 1985 and 2001, pyrethroid insecticides were exclusively used against pests in OSR. This precarious practice was further undermined by low spraying thresholds in Nordic countries leading to more and earlier pesticide sprayings (Sweden thresholds: 2-3 beetles per plant in winter OSR; 0.5-2 beetles per plant in spring OSR, Williams 2010). Secondly, cultivation of spring OSR in Nordic countries means that there is a mixture of spring and winter OSR cultivation in the landscape leading to a greater number of pesticide applications throughout the growing season, first against beetles in winter OSR and subsequently in spring OSR fields.

3.3.3 Goals and methods of Paper I

While the connection between pyrethroid application and resistance in pollen beetles has been documented, how landscape and regional features might modify the incidence of resistance over time has not been investigated. For pollen beetles, insecticide pressure can be expected to be highest not only in landscapes with a high proportion of OSR but, in particular, in areas where both winter and spring forms of OSR are grown in similar proportions.

We analysed trends in pyrethroid resistance in *M. aeneus* adults from 180 sites across 10 regions in Sweden over 7 years between 2003 and 2014. We first hypothesized that resistance in pollen beetles would be highest in areas with a high proportion of OSR cover and in areas with an even mixture of winter and spring OSR. This was examined for both landscape (3 km radius around the field) and regional spatial scales and over short (2 years) and longer (4 years) temporal scales.

3.3.4 Results and conclusions (Paper I)

We confirm the hypothesis that pesticide resistance in pollen beetles is greater when there is a high proportion of OSR in the landscape. However, this effect was visible only at the regional spatial scales over short temporal scales. Furthermore, we found a positive effect of mixture of winter–spring OSR both in the short- and in the long-term, but only at the regional spatial scale. The better fit of the long-term models (4 years) suggests a legacy effect of past regional landscape factors on current pest resistance.

This paper is a first step in understanding how interactions of land-use features over time and space affect the distribution of pesticide resistance, and highlights the importance of regional-scale management and land-use legacy effects for the improvement of pesticide resistance management programmes for *M. aeneus*.

3.4 Biological pest control a landscape perspective (Paper II)

3.4.1 The role of landscape in natural pest control

When the ecological foundations of IPM were being formulated, a critical idea was that modern agroecosystems were too simplified and therefore lacked the ability to regulate pest populations. Many researchers accordingly envisioned the diversification of agricultural systems as a desirable goal (Rabb and Guthrie 1970, Pimentel and Goodman 1978).

Most species, be they pests or their natural enemies, require more than one habitat over their life-cycle for food, reproduction or overwintering. It is generally accepted that semi-natural or natural habitats (i.e. forests, meadows) are more stable habitats than cultivated areas and therefore these habitats should support higher abundances of predators (Landis et al. 2000, Denys and Tscharntke 2002). As shown in several recent reviews, natural enemy populations are on average higher and pest pressure can be lower in complex, heterogeneous landscapes versus simple, homogeneous landscapes, leading to enhanced pest suppression and reduced yield loss (Bianchi et al. 2006, Tscharntke et al. 2007, Chaplin-Kramer et al. 2011, Rusch et al. 2016). For example, it has been shown that pollen beetles in landscapes with large amounts of natural habitat exhibit higher parasitism rates and cause less damage to OSR in Germany (Thies and Tscharntke 1999); and higher biocontrol of cereal aphids in complex landscapes has been demonstrated across Europe (Thies et al. 2011, Rusch et al. 2013a). Despite the general evidence of the benefits of natural habitat to sustaining biological pest control in agricultural landscapes, variability is high and there is also some evidence for the reverse. That is, natural habitat can have no, or even a negative, effect on natural enemies and on biological control (Bianchi et al. 2006).

Variation in landscape effects on pests and natural enemy abundances and ultimately on biological control, may arise for several reasons (Tscharntke et al. 2016). In particular it has been hypothesized that within-field management will modulate the outcome of landscape complexity, with enhanced biodiversity and ecosystem services in fields with increased local field diversity in less complex landscapes – the “intermediate landscape-complexity” hypothesis (Tscharntke et al. 2012). In addition, the outcome of biological control depends on interactions among predator functional guilds, through facilitation, intraguild predation, or behavioural interference (Straub et al. 2008, Letourneau et al. 2009, Martin et al. 2013). There is increasing evidence that abundance, species richness, and community evenness of different taxa of biological control agents respond differently to landscape complexity with implications for pest control services (Gardiner et al. 2010, Woodcock et al. 2010, Rusch et al. 2014). However, different natural enemy groups have rarely been examined simultaneously.

3.4.2 Background: Landscape effects on pollen beetle and their natural enemies

Landscape composition influences abundance of pollen beetles directly, by affecting their dispersal and mortality (Zaller et al. 2008b, Rusch et al. 2013b, Schneider et al. 2015) and indirectly, by affecting parasitism rates (Thies and Tscharntke 1999, Thies et al. 2003, 2008, Zaller et al. 2009, Rusch et al. 2011, Beduschi et al. 2015, Schneider et al. 2015) (Figure 3). Generally, increasing cover of semi-natural habitat in the landscape has a positive effect on both pollen beetle abundances and parasitism rates in oilseed rape crops (Figure 3). Generalist natural enemies have been suggested to be important pollen beetle predators (Büchi 2002, Öberg et al. 2011, Haschek et al. 2012), but little is known about their actual impact on pollen beetle population dynamics or how they respond in OSR to within-field and landscape complexity.

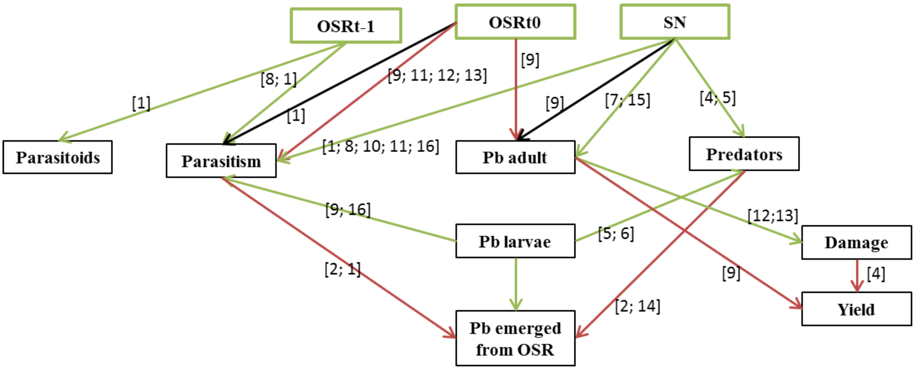

Figure 3*: Schematic summary illustrating published effects of landscape on pollen beetle control in OSR systems. Black arrows correspond to no effects, red arrows to negative effects and green arrows to positive effects. Numbers in [#] refer to references: 1. Beduschi et al. 2015; 2. Büchi 2002; 3. Drapela et al. 2008; 4. Gagic et al. 2016; 5. Öberg et al. 2011 Rusch et al. 2013b 7. Rusch et al. 2011; 8. Schneider et al. 2015; 9. Thies and Tscharntke 1999 10. Thies et al. 2003; 11. Thies et al. 2008; 12. Valantin-Morison et al. 2007; 13. Zaller et al. 2008b; 14. Zaller et al. 2008c; 15. Zaller et al. 2008a; 16. Zaller et al. 2009.*

3.4.3 Goals and methods of Paper II

While much research has been performed on how single taxa of natural enemies interact with landscape, few studies have encompassed the impact of both field and landscape scale management on the wider community of generalist and specialist natural enemies, and their impact on pollen beetle suppression. In this thesis we investigated how pest mortality in OSR was affected by natural enemy communities, and how characteristics at the local and landscape scale in combination influenced the pest and its natural enemies (Figure 4). The study was carried out in 2013 in 15 conventionally managed winter OSR fields in the Swedish province of Västra Götaland.

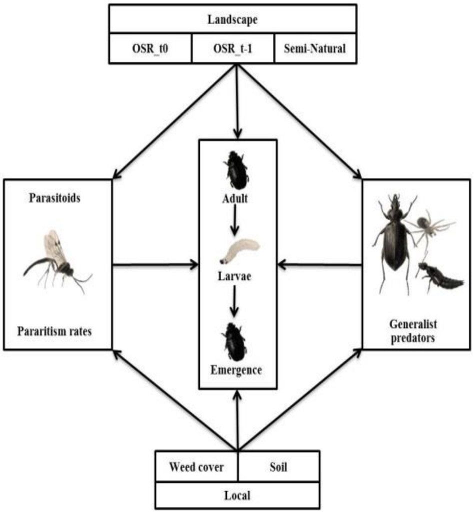

Figure 4*: Diagram illustrating the tested hypotheses. Abbreviations: OSR$_{t0}$ - present year OSR, and OSR$_{t-1}$ - past year OSR.*

3.4.4 Results and conclusions (Paper II)

We found that pest abundance increased with increasing OSR in the landscape while parasitism rates declined, indicating a lower pest control by specialist natural enemies in landscapes with a high proportion of OSR (Figure 5). Increasing proportion of semi-natural habitat in the landscape did not enhance local pest or natural enemy abundances. Contrary to the intermediate landscape-complexity hypothesis, more even communities of generalist predators were found in landscapes with a low proportion of semi-natural habitats and low local weed cover. This suggests that the generalist predator communities do not depend on the species pool provided in semi-natural habitats. Finally, we show that pollen beetle mortality increased when overall abundance of ground-dwelling generalist predators was high and when soil clay content was high. In contrast, we found no effect of parasitism rates on net pollen beetle mortality.

Our results suggest that increasing OSR in the landscape has the potential to undermine biological control of pollen beetles by specialist natural enemies and corroborates previous studies (see Figure 3). However, overall generalist predator abundances in OSR crops were not affected by landscape context, suggesting that they are well adapted to arable habitats, at least within the gradient investigated. Therefore, predation by generalist ground-dwelling predators could offset the detrimental effects of increasing OSR in the landscape on specialist pest control. Parasitism rates did not affect pest mortality, which is interesting as parasitoids have been considered major control agents in OSR (Nilsson 1987, Hokkanen 2008). Furthermore, restricting planting of OSR to soils with high clay content, where available, may improve pollen beetle control.

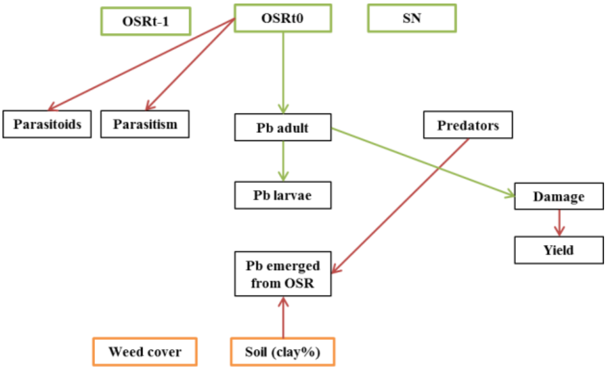

***Figure 5**: Schematic summary illustrating results of landscape and local scale effects on pest control in Sweden oilseed rape systems. Red arrows correspond to negative effects and green arrows to positive effects.*

The key messages from this study are:

- Generalist predator communities appear to be well adapted to crop landscapes at the scale of complexity investigated.
- Generalist predator abundances rather than species diversity (richness) appear to be an important factor for biological control of pollen beetles.
- Specialist natural enemies appear to be more dependent on landscape composition, with strong dilution effects occurring in landscapes with increasing host-crop.
- Local soil characteristics may play an important role on pollen beetle larval mortality.

These results suggest that promoting generalist predators for the control of pollen beetle in OSR does not require maintaining or restoring semi-natural habitats in the landscape at the investigated scales. Local scale management such as planting of hedge-rows, reducing pesticide applications, and/or decreasing tillage may adequately improve local pest management. However, landscapes should be investigated for multiple ecosystem services, as promoting one service can undermine others. What is needed is to balance all these potentially conflicting ecosystem services, and this will require further investigation into how ecosystem services interact (Tamburini 2015).

4 Local scale perspective

4.1 Local crop management

4.1.1 Economic injury thresholds

An important area of pest management research has been to investigate the relationship between pest intensity, damage and yield loss for selected pests. While this research has greatly increased our knowledge of the effects of pests in solitary infestations and allowed the development of economic injury thresholds, much less effort has been directed toward studying the effect caused by infestations of combinations of pests. Yet these have important implications for crop damage and yields and therefore for the formulation of realistic thresholds for a given pest.

There are three possible outcomes of combined pest infestations on crop yield: 1) no interactions, 2) additive (synergistic) interactions, and 3) less than additive or compensatory (antagonistic) interactions (Figure 6) (Lidicker 1979). Synergistic interactions are important because the economic injury threshold for each pest can be lowered by the presence of the interacting pest. On the other hand, antagonistic interactions raise the threshold of a pest, given the presence of the interacting pest. Evidence for both additive and compensatory effects of multiple herbivores species on plant communities have been found in grasslands. The interaction outcome depended on which factor limited production in the system (i.e. light, water or nutrients, Ritchie and Olff 1999). However, these interactions have largely been overlooked in agroecosystems where herbivores feed on the same plant species.

In this thesis we investigated how four major herbivores interactively affected yield in an oilseed rape system (Paper III).

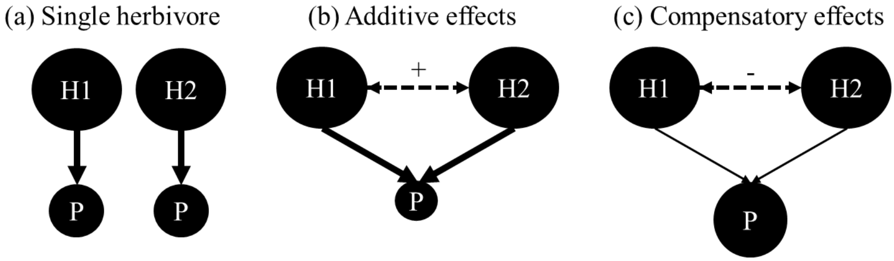

Figure 6: *Hypothetical effects of herbivore (H) diversity on plant (P) productivity. Dashed lines indicate indirect effects.*

4.1.2 Farming practices

Agricultural land uses consist of a mix of high and low input systems with varying potentials to degrade the environment. To achieve ecological sustainability, all of the land uses in a region must be able to meet reasonable soil, water, and air quality criteria. Sustainable management, including pest control measures, begins at the smallest operating unit of agriculture, the fields in which crops are grown. Populations of both pests and their natural enemies may depend on arable fields as a source of potential hosts or prey, pollen and nectar resources, and diapause or overwintering areas. This dependence is particularly strong when the proportion of semi-natural habitats in the landscape is low (Tscharntke et al. 2012). In this case, natural enemies are highly susceptible to the effects of crop management at the field scale.

Key local scale management practices that have been shown to influence the effectiveness of pest management and natural pest control are: within-crop diversity, host plant resistance, fertilisation, soil tillage, sowing and harvesting date, plant density, crop rotation, and, of course, pesticide use (Table 1). While much work has been done on the effect of local management practices directly on herbivore populations, knowledge of their effects on natural enemy populations, and ultimately on biological control, is lagging behind.

In this thesis we focused on one local management practice, namely mineral and organic fertilisation, and its effect on pest management (Papers IV and V).

***Table 1**: Local scale management practices and their expected effects on pest densities (Abbreviations: - for negative, + for positive effects).*

Management practice	Hypotheses	Effect on pest density	References	Description
Within crop diversity	Enemy Hypothesis	-	Pimentel 1961, Root 1973	Intercropped fields will decrease herbivore abundances due to the attractiveness of the intercrop promoting natural enemies abundances, due to increased availability of resources and habitats compared to monocultures.
	Trap Crop Hypothesis	-	Vandermeer 1992	High herbivore densities on the trap crop will lower the incidence of herbivores on the main crop.
Host plant resistance		-	Vanemden 1991, Sharma and Ortiz 2002	Insect-resistant crop varieties will be less susceptible to pest damage.
Mineral fertilisation	Plant Stress Hypothesis	+	White 1984	Physiologically stressed plants are more susceptible to pest attacks due to diminished investment in resistance mechanisms.
	Plant Vigour Hypothesis	+	Price 1991	Herbivores will preferentially feed on vigorous plants, because they provide a better source of food.
Soil tillage		- ?	Altieri 1999	Soil tillage has been shown to reduce the abundance of various natural enemies.
Crop rotation		- ?	Büchs et al. 1997	Rotation of annual crops will decrease pest pressure.
Pesticide use		-		Pesticides are toxic to the pest.
		+	Onstad 2014, Geiger et al. 2010	Pesticide resistance in the pest, leading to recovery of pest populations and detrimental effects on natural enemies.
Plant density	Resource Concentration Hypothesis	+	Tahvanainen and Root 1972, Root 1973	Predicts an increase in herbivore density per host plant with increasing plant density.
	Resource Dilution Hypothesis	-	Rhainds and English-Loeb 2003, Otway et al. 2005	Predicts a decrease in herbivore density per host plant with increasing plant density.

4.2 Pest damage and oilseed rape yield (Paper III)

4.2.1 Background: OSR herbivores complex

OSR is a crop that attracts several insect herbivores. Together with the pollen beetle, the most common insect pests on winter OSR in Nordic countries are the seed weevil (*Ceutorhynchus obstrictus* (Marsham)[1], Curculionidae, Coleoptera), the cabbage stem weevil (*C. pallidactylus* Marsh.) and the pod midge (*Dasineura brassicae* Winn., Cecidomyiidae, Diptera) (Figure 7). These four

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[1] Alternatively referred to as *C. assimili* Payk.

species attack either different plant parts or during different stages of the plant's development (Alford et al. 2003). The magnitude of the negative effects of these four pest species on crop yield differs greatly, with pollen beetles being the major pest in OSR, while stem weevils rarely cause serious economic losses in northern Europe[2] (Alford et al. 2003). Pest infestations can trigger compensation mechanisms in oilseed rape (Free and Williams 1978, 1979). However, the interactive effects of plant damage caused by these four herbivores on OSR yield have not been investigated.

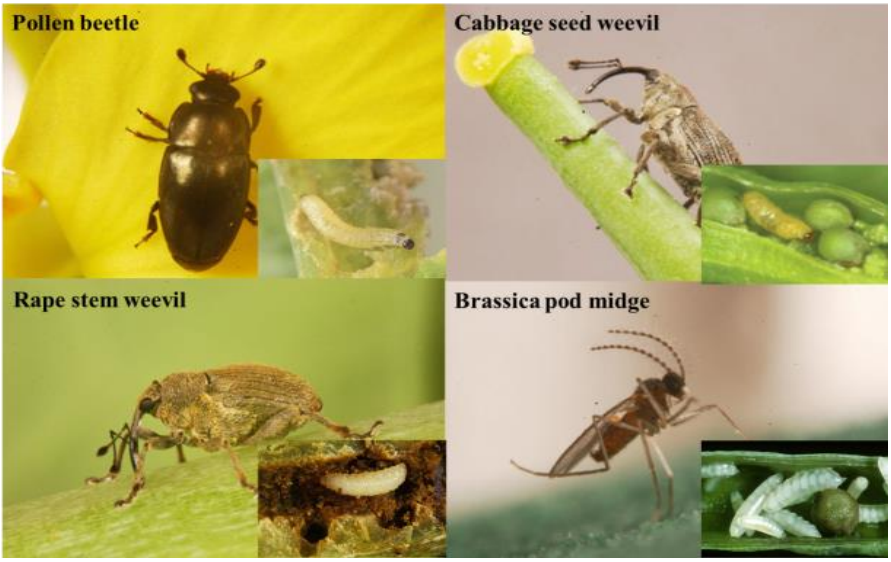

Figure 7*: Photos of the four major pests in OSR in their adult and larvae form* (©Rothamsted Institute).

4.2.2 Goals and methods of Paper III

Loss in yield due to simultaneous attacks by multiple herbivores is not necessarily additive, as demonstrated in studies on grassland plant communities. However, it is not clear how this transfers to crop plants. We used 15 oilseed rape fields to investigate how plant damage caused by four insect pest species (brassica pod midge, seed weevil, stem weevil, and pollen beetle) in concert affect oilseed rape seed yield.

4.2.3 Results and conclusions (Paper III)

Although OSR damage and yield varied considerably among fields, pollen beetles substantially reduced seed yield. We also found that, although neither stem weevil nor seed weevil individually influenced seed yield, they jointly had a positive impact, presumably due to plant overcompensation following insect

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[2] But in some areas, particularly centre Europe, stem weevil (e.g. *C. napi*) can be among the major pests (Derron et al. 2015).

attack. **When stem and seed weevils both attacked the plant, the seed yield increased more than two fold, mainly via an increase in pod number.** Pod midge damage had little effect on yield.

Hence, attacks by several pests can modify the impact on OSR yield of individual pest species. Increasing our knowledge about how multiple pest–plant interactions (i.e. insect pests, diseases) may interact to increase yield can reduce the level of pesticide input, via the implementation of more accurate pest thresholds. Future research investigating multi-pest effects in OSR will require controlled field experiments investigating a range of pest intensities, and factorial arrangements for creating different pest infestation levels.

4.3 Long-term organic and mineral fertilisation affects soil community composition and associations (Paper IV)

4.3.1 Background: Soil fertility

Healthy soil is the foundation of our food system. Recognizing this, the 68th UN General Assembly declared 2015 the International Year of Soils. The aim was to increase awareness and understanding of the importance of soil for food security and essential ecosystem functions. Farming systems have historically tended to mine the soil for nutrients and to reduce soil organic matter levels through repetitive harvesting of crops alongside inadequate efforts to replenish nutrients and restore soil quality.

There are alternative management practices that enhance soil health while allowing sustained agricultural productivity. Maintenance of soil fertility for plants typically requires the addition of nitrogen, phosphorus, and potassium in the form of mineral fertilisers. However, some have criticized the use of mineral fertilisers, claiming that the water-soluble nitrogen does not provide for the long-term needs of the plant and pollutes waterways (FAO 1972, Ren et al. 2014). Application of organic fertilisers (i.e. manure, compost), tend to increase the organic matter budgets of soils (Bot and Benites 2005). The FAO recognizes that addition of organic matter can make an important contribution to the agriculture sector through its enhancement of soil quality (Bot and Benites 2005). While adding organic or mineral fertilisation to a crop is a pervasive practice in agriculture, its effects on above- and below-ground communities and ultimately on pest management have seldom been investigated.

4.3.2 Goals and methods of Paper IV

Mineral and organic fertilisation has been shown to affect individual soil organism groups. However, little is known about how fertilisers affect the composition of the entire soil community, in particular under long-term application. To investigate long-term effects of different fertilisers on soil biota across trophic levels, we used a 17 year old fertilisation experiment. We sampled six fertilisation treatments: three organic matter treatments (compost, manure, and hay), two mineral nitrogen fertilisers (calcium nitrate and ammonium sulfate), and one unfertilised treatment.

4.3.3 Results and conclusions (Paper IV)

We expected organic fertilisers to enhance soil biota compared to mineral fertilisers. However, no differences in taxonomic richness or abundance of soil biota were found between these treatments. Overall, organic fertilisation enhanced primary decomposers compared to no fertilisation but there was limited evidence of a bottom-up effect of primary decomposers on secondary decomposers and predators. In general, long-term fertilisation enhanced abundance of most soil biota groups compared to no fertilisation. Co-occurrence analyses showed differences in network associations among soil fauna between all treatments. This indicates different ecological processes underlying soil community assembly in each treatment that would warrant further research. **Altogether, our results suggest that in intensively managed agricultural systems, biennial organic fertilisation may be insufficient to promote soil communities in the long-term.**

4.4 Fertilisation quality mediates the direction of trophic cascades in an agroecosystem (Paper V)

4.4.1 Background: Fertilisation and tri-trophic interactions

Mineral nitrogen fertilisation has been shown to play an important role in the population dynamics and performances of herbivores by affecting plant resistance, host selection mechanisms and the ability of plants to recover from the damage inflicted by herbivores (White 1984, Price 1991). Generally, addition of mineral fertilisers enhances plant growth, which in turn increases pest damage (Scriber 1984, Altieri and Nicholls 2003). Mineral fertilisation has been shown also to affect natural enemies. For instance, *Diadegma insulare,* a parasitoid of the pest *Plutella xylostella* (Diamondback moth) in cabbage, performed better on plants grown with high levels of mineral fertiliser (Sarfraz et al. 2009). Investigations of the bottom-up effects of nitrogen fertilisation on tritrophic interactions are important for integrated pest management. However, effects of mineral fertilisation on generalist predators in agroecosystems have received little attention.

Organic fertilisation was suggested as a management practice to increase the functioning of generalist predators as control agents of plant herbivores via its positive effect on soil fauna abundances (Holt and Lawton 1994, Polis and Strong 1996). Indeed, various types of organic matter have been shown to have a positive impact on abundances of polyphagous predators, including carabids, staphylinids and spiders (Halaj and Wise 2002, Bell et al. 2008, von Berg et al. 2010). Each of these groups is known to rely on food resources from the below-ground system (Settle et al. 1996). Maintaining an abundant community of soil organisms enables such predators to persist in fields outside the season when the pest is present. Conversely, adding organic matter could be detrimental to effective pest control if it fosters a surplus of alternative prey, potentially causing predators to switch away from the pest. In addition, organic matter varies in properties important to the soil fauna, for example, high quality manure (labile, i.e. easily decomposed) and low quality hay (recalcitrant, i.e. resistant to decomposition), with unknown effects on above-ground pest control.

4.4.2 Goals and methods of Paper V

We tested the hypothesis that organic and mineral inputs will strengthen the regulation of the aphid pest *Rhopalosiphum padi* (L, Homoptera, Aphididae) via an increase in either top-down (predator) or bottom-up (resources) forces. We also test the idea that the magnitude and the direction of these forces will depend on which compartment of the food-web receives the subsidy (i.e. mineral fertilisation that subsidises the plant, or organic fertilisation that subsidises the soil fauna) and on the quality of the subsidy (i.e. decomposability of the organic matter) to the relevant trophic level. We tested this in an above- below-ground tri-trophic cereal system using large cage mesocosms in a long-term fertilisation experiment (Figure 8).

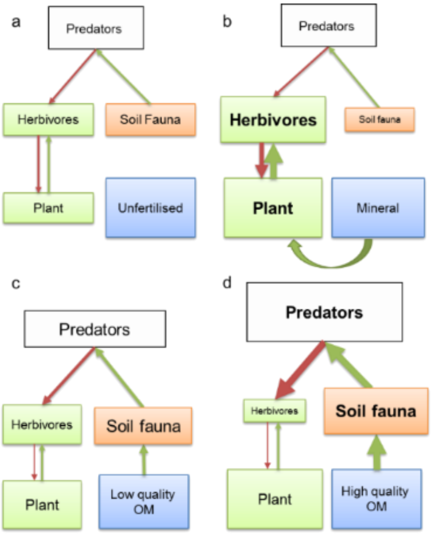

Figure 8: *Hypothesized direction and magnitude of controls in a tri-trophic system under four fertilisation regimes: a. no fertiliser; b. mineral fertiliser; c. addition of recalcitrant organic matter and d. addition of labile organic matter. Arrow colour: red - negative effect; green - positive effect; black - neutral. Width of the arrow: interaction strength relative to no fertilisation. Width of the text: increase in biomass relative to the no fertilisation treatment.*

4.4.3 Results and conclusions (Paper V)

Our results provide empirical support for the subsidy hypothesis (Lindeman 1942, Leroux and Loreau, 2008), that adding subsidy will strengthen top-down or bottom-up regulation of herbivores in the receiving food-web. We found that the direction and strength of these forces will vary with utilization and quality of the subsidy. In particular, we found that top-down control dominated in food webs where the detrital compartment was subsidized (organic fertilisation), while bottom-up controls were stronger when the green compartment received the subsidy (mineral fertilisation). Furthermore, our results indicate that high quality subsidy (i.e. manure) propagated through the food chain faster than low quality subsidy (i.e. hay).

These results have potentially important implications for biological control in agro-ecosystems. Firstly, we found an overriding positive effect of organic matter on coleopteran predator emergence. Secondly, negative effects of predators on aphid densities were detected in the manure treatment. Thirdly, a strong positive effect on aphid abundances was detected in the mineral treatment. **Overall, the results suggest that, generalist predators benefited from high quality organic fertilisation in the long-term, which in turn exerted top-down control on the aphid pest**.

5 Materials and methods

5.1 Notes on experimental design

Multiple methods, from field sampling to semi-controlled cage experiments, were used in this thesis. The pollen beetle resistance study is based on compilation of long-term data collections of pollen beetle resistance across Sweden (**Paper I**). In the other OSR studies, we designed a large scale field survey along a gradient of landscape complexity (**Paper II & III**). To investigate the impact of local scale management practices on biological control, we used manipulative field cage experiments within a long-term field experiment (**Paper IV & V**).

The use of a variety of field and experimental methods in ecology allows us to answer questions at different scales and at different levels of complexity. **Field surveys** are routinely used to investigate whether patterns exists, e.g. between abundances of organisms and landscape complexity. However, these are often too crude to provide the causal understanding needed for extrapolation and prediction. Instead, **cage experiments** offer the control required to isolate particular combinations of factors and derive a better understanding of interaction mechanisms among them. However, the applicability of such insights to predicting whole ecosystem function remains a challenge. Acknowledging the limitations and advantages of each method is essential for the correct interpretation of the results.

Another point to note is that different crops were used in this thesis: oilseed rape, winter barley, and spring wheat. These are all important crops in Northern Europe. As such, their cultivation is under strong pressure to deliver high yields, which has often led to a loss of natural services in these systems. Therefore these crops are all pertinent to the objectives of this thesis. In the parts of this thesis where OSR is the study system, the focus is on investigating the interactions between local and landscape scale management effects on pest resistance, pest abundances, and biological control. To investigate local scale management more closely, it was desirable to take a more mechanistic approach to what drives variation in biological control and therefore to design a more controlled set up, using cages. To this end, we identified long-term experimental plots where fertilisation treatments had been applied at regular intervals. This offered a unique framework in which to investigate the local effect of long-term fertilisation management on soil organisms and biological control. The crops grown on these plots were cereals.

5.2 Experimental design

5.2.1 Field surveys

Large field surveys were designed to study (i) the local interactive effects of pest densities on OSR yield (**Paper III**), (ii) the interactive effect of local and landscape scale complexity on biological control of pollen beetle in OSR crops, (**Paper II**) and (iii) the large scale effect of OSR in the landscape on pollen beetle pesticide resistance (**Paper I**).

For **Paper I**, data on pollen beetle resistance was compiled from field collections and bioassay tests conducted between 1998 and 2014. Landscape composition data around each sampling point were assembled from the sampled field coordinates, and matched with historic land-use data obtained from the Integrated Administrative and Control System (IACS) database and interpreted using MATLAB R2012b.

For **Papers II** and **III**, 15 winter OSR fields were selected in the province of Västra Götaland in 2013. To ensure variation in landscape composition among fields, they were chosen along a gradient of agricultural intensity, measured as percentage arable land in a circular landscape sector of 1.5 km diameter encompassing the field (Zaller et al. 2008c). Within each field, we selected a plot, 40 x 70 m, of unsprayed area located at the edge of the field. Observations of invertebrates and weed coverage were made along two transects parallel to the field edge 3 and 30 m into the field.

5.2.2 Long-term field experiments

Long-term field experiments have proven to be a useful resource when assessing the impact of different management practices on, for example soil structure and soil fertility. To investigate the effect of local management, namely fertilisation, on soil fauna and biological control (**Papers IV** and **V**) we selected one of the long-term experiments maintained at Lanna agricultural research station in Västra Götaland. This experiment had been previously used to investigate the effects of fertilisers on plant yield, microbial communities, soil structure and organic matter budgets (Börjesson et al. 2013, Kätterer et al. 2014).

The experiment included nine treatments in a randomized block design with four repeats, i.e. a total of 36 plots, each with an area of 112 m^2. Over the course of two years we sampled six treatments comprising: three separate organic matter treatments (compost, manure, and hay), two mineral nitrogen fertilisers (calcium nitrate and ammonium sulfate), and one unfertilised treatment. The organic amendments were applied after harvest and before ploughing in the fall every second year from 1996 onwards. Only cereals were grown over the 19 year period. In 2014 the crop was winter wheat and in 2015, spring barley.

The particularity of this experimental set-up was that all organic amendments received similar amounts of carbon inputs. Therefore this set up allowed us to investigate the role of carbon quality, as defined by its lability/accessibility to decomposers, independent of carbon quantity. In terms of practical implications, the levels of fertilisers applied in this long-term study corresponded to the levels recommended when the experiment started in 1996. Notably, the carbon amount added with compost and manure are about twice as high as those generally applied in Swedish agriculture nowadays (Kätterer et al. 2014). Therefore, care should be taken when extrapolating these results to current field conditions.

5.2.3 Manipulative cage experiments

To determine whether fertilisation management caused significant variation in the level of biological control and plant biomass (**Paper V**), we designed a field cage experiment where we manipulated the type of fertiliser applied to the plot and the presence/absence of predators (Figure 9). We aimed to design an experiment that mimicked realistic field conditions at the time of early aphid colonization in the field (tillering stage), while limiting perturbation to the system.

The setup of a cage experiment requires several decisions as to what degree of initial heterogeneity among treatments is permissible, and regarding the extent to which one should attempt to regulate environmental conditions during the experiment. These decisions are all a matter of subjective judgment and can affect the interpretation of the results. Firstly, to minimize the variation due to climate, landscape composition and local management - other than fertilisation treatment - we designed the study in a controlled long-term field experiment as described above. This allowed us to effectively disentangle the effect of fertilisation from other management practices as well as keeping climatic variables constant between treatments. Secondly, the most delicate decisions were those pertaining to predator selection, and initial abundances of aphids and predators to introduce into the cages. Wolf spiders, Lycosidae, were selected to be the key predator for several reasons: they are common predators in Swedish agricultural landscapes, they are known predators of aphids, and finally they are not able to dig and hide in the soil, as do ground beetles. The latter point was an essential consideration for the successful recapture of the predators at the end of the experiment. Densities of predators and prey were based on field densities but subsequently adjusted on account of the wet and cold weather that kept aphid population growth rates very low.

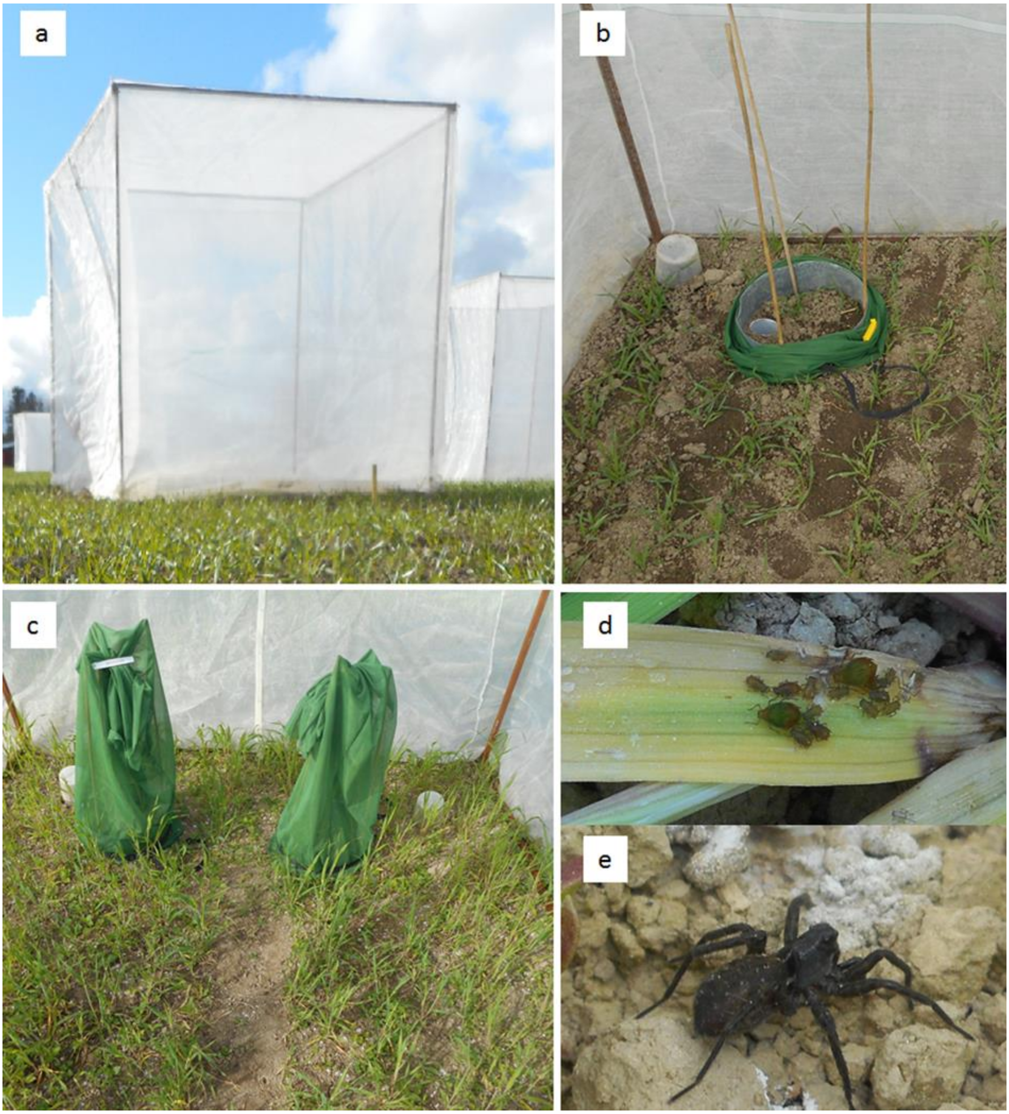

Figure 9*: Field cage experiment: Cage (a), barrier for predator and herbivore exclusion (b-c), R.padi on barley (d) and wolf spider (e).*

5.3 Experimental execution: sampling and identification

A diversity of established sampling techniques were used to sample insect herbivores, arthropod natural enemies, micro- and meso- soil fauna, microbes, and plant material throughout this thesis. A thorough description of each method can be found in each Paper. In this section I discuss only the use of one of the more technical methods, namely **quantitative PCR** (qPCR).

While most organisms were identified morphologically, soil microbes required the use of molecular techniques for quantification to be possible. For quantification of soil fungi and bacteria (**Paper IV**) we used real-time qPCR methods adapted for soil samples. PCR technology is widely used to aid in quantifying DNA because the amplification of the target sequence allows for greater sensitivity of detection. In a PCR reaction, the target quantity will approximately double during each amplification cycle. In qPCR, the amount of amplified product is linked to fluorescence intensity using a fluorescent reporter molecule. Real-time qPCR measures the fluorescence at each cycle as amplification progresses. With each amplification cycle, the increase in fluorescence intensity is proportional to the increase in amplicon concentration. In a nut shell, these methods measure the number of copies of DNA present in a gram of soil sample and have been widely used in soil microbiology as a proxy for microbial biomass.

These techniques have several pitfalls. Firstly, the fungal and bacterial primers used are not universal, that is they will not amplify all groups of fungi or bacteria with equal success (Bellemain et al. 2010). Secondly, amplification of non-active microbes could lead to over-estimation of the abundances of microbes in the soil. However, we were interested in the relative abundances of microbes between fertilisation treatments, and assuming that these issues were consistent between treatments, we were able to compare biomass of bacterial and fungal DNA in soils treated with different fertilisers.

5.4 Statistical methods

In this thesis we used two major statistical methods for the different studies. These can broadly be classified as univariate (**Papers I - V**) and co-occurrence (**Paper IV**) methods. Within univariate methods, several different approaches have been used to draw inferences. Namely, we used the traditional null hypothesis testing method (**Paper I, IV & V**), and the more recent information theoretic approach that examines several competing hypotheses simultaneously to identify the best set of models (**Paper II & III**) (Burnham and Anderson 2004). In this section I will motivate the use of these techniques and explain how they complement each other.

5.4.1 Univariate methods

In all studies the response variables tested were univariate, therefore we used a linear approach. Linear models carry four main assumptions: a linear relationship between dependent and independent variables, and the independence, equal variance and normal distribution of errors. Where study design and data structure broke one or more of these assumptions, we adjusted our models either by adding spatio-temporal autocorrelation structures and applying generalized least square models to account for temporal correlation in the data (**Paper I**); or by transforming the response variables using logarithmic or square root transformation to normalize the data (**Paper I - V**). All experimental designs had a nested structure, which potentially violates the assumption of independence. Using a mixed model approach (i.e. including a random term), we controlled for the nested design in all studies.

- Null hypothesis testing or frequentist approach

For much of the past century, Fisherian or ‘frequentist’ statistical approaches based on null-hypothesis testing have been a central paradigm guiding analysis in ecological research and many other sciences. The result of a frequentist approach is either a "true or false" conclusion from a significance test (i.e. the probability that it is a real effect rather than a sampling artefact). This framework is robust when testing clearly formulated hypotheses, particularly under experimental set-ups where the design is controlled so that only certain factors vary (**Paper IV** & **V**). This analysis is also helpful when there are strong *a priori* grounds to suspect that the selected factors will explain an effect (**Paper I**).

- Multi-model inference or information–theoretic model comparison

In the last decade, information–theoretic model comparison has been suggested as an alternative paradigm for statistical analysis (Burnham and Anderson 2004). Model-selection approaches are powerful tools where multiple hypotheses are plausible or multiple predictors are considered in combination (Johnson and Omland 2004). Under this framework, several models can be ranked and weighted to provide a measure of relative support for each hypothesis. Several parameters were investigated in **Paper II** and **III**, and the aim in these papers was to select the combination of variables that best explained the observed variation in the investigated factor. In these cases, we did not have strong *a priori* expectations and therefore selected the multimodel inference approach, allowing us to test multiple hypotheses and weight factors by their relative importance.

5.4.2 Co-occurrence analyses and network inference

An important aspect of investigating how local scale management affects communities is to consider changes in potential interactions among trophic groups. However, interactions can be difficult to observe and quantify, in particular in below-ground systems (Pocock et al. 2012). An approach that can provide insights into potential soil food-web structures is similarity-based network inference analyses based on co-occurrences, i.e. correlations, between abundances of organism groups (Faust and Raes 2012, Creamer et al. 2016). Similarity-based network inference assesses the co-occurrence and/or mutual exclusion pattern of two species over multiple samples using a measure that quantifies the similarity of two species distributions (e.g. Spearman correlations). In a second step, the significance of the similarity score is assessed (usually with a null distribution generated by permuting the data set in question). After assessing all possible combinations of species in a given abundance data set, all significant pairwise relationships are then combined to construct a network.

Inferring relationships between organisms using these methods is based on the premise that strongly non-random distribution patterns are mostly attributable to ecological reasons (Faust and Raes 2012). Nevertheless, it is important to keep in mind that most network inference approaches cannot distinguish between true ecological interactions and other non-random processes (for example, cross-feeding vs. niche overlap). We acknowledge that these methods have a number of pitfalls (well described in: Faust and Raes 2012) and it is dangerous to draw any solid conclusion about organismal relationships from isolated case studies. We argue that replication of such analyses in similar systems will allow us to characterize key relationships, both direct and indirect, in soil systems and to build sound and testable hypotheses.

6 Conclusions and remarks

In this thesis, various aspects of IPM, namely pest resistance, pest damage, and biological control, have been investigated across spatial scales and cropping systems. This thesis contributes to increasing the current knowledge of the effects of interactions between landscape and local scale management practices, and between above- and below-ground compartments on pest management in agro-ecosystems. Although a wide array of topics were touched upon in this thesis, nevertheless several broader conclusions can be drawn.

The **importance of the soil compartment** for sustainable pest management emerges as an important conclusion (**Papers II, IV** and **V**). Soil texture can play an important role in influencing coleopteran pest mortality during the pupation stage in the soil. We found a positive correlation between pollen beetle mortality and clay content in the soil that would deserve further investigation into its driving mechanisms (e.g. entomopathogens) (**Paper II**). Furthermore, there was a positive effect of soil organic matter on coleopteran emergence, showing that under similar management conditions soils amended with organic matter can increase the abundance and/or survival of overwintering natural enemies (**Paper V**). Finally, long-term fertilisation management in intensive agro-ecosystems influences soil community composition, with consequent effects on natural pest control via alternative prey availability (**Papers IV** and **V**). All these results show the ubiquitous influence of soils in aboveground ecosystem services such as pest control. However, major challenges impede the progress in our understanding of the relationship between soil and ecosystem services. These challenges involve quantifying and qualifying soil communities and linking biotic interactions to soil biogeochemical properties (e.g. texture, pH, and soil organic matter).

A greater knowledge is required of (1) the functions and traits of the great majority of soil organisms, (2) how interactions among soil organisms and/or soil properties impact ecosystem functions (e.g. pest mortality), and (3) the spatial and temporal variability of soil organisms and biogeochemical properties. At present it is difficult to sample this variability representatively, and it is unclear how it affects the functions we want to promote. Recent advances in molecular techniques (e.g. next-generation sequencing) and micro-analytical methods (e.g. X-ray tomography, X-ray microscopy, NanoSIMS. Herrmann et al. 2007; Templeton & Knowles 2009; Helliwella et al. 2013) provide insights into the structure and function of soil and its key role in regulating ecosystem services (Wall et al. 2012). Sustained efforts in using these technologies to unravel structures and interactions in the soil will help to shed light on the mechanisms behind the patterns observed in this thesis. Furthermore, long-term experiments are needed to understand how chronic disturbances (e.g. soil management) affect the physical and biotic properties of soil and in turn how these will influence aboveground services such as pest management.

Second, another topic that spans several papers is that of **resource quality and quantity** (**Papers I, II, IV** and **V)**. Resource quality was defined in different ways and at different scales depending on the ecology of the organism investigated (refuge, habitat provision, or nutritional quality). We tested whether the abundance of resources at the landscape scale (habitat provision) and /or local scale (within-crop plant diversity) influenced the abundance of pollen beetles, the abundance of their natural enemies, and the incidence of pesticide resistance. We found that increasing host-crop resources in the landscape had a positive effect on pest abundance and pesticide resistance but a detrimental effect on specialist natural enemies, with no effect of resource quantity on generalist predators at either scale (**Papers I** and **II**). Manipulating fertilisation (i.e. resources to plant and soil biota) led to complex feedbacks on the structure of soil communities and above-ground interactions in the long-term (**Papers IV** and **V**). We found that high quality, easily decomposable organic matter increased the strength of top-down trophic cascades. Positive effects of predators on barley biomass were found in manure, but not in hay treatments.

Further research is required to: (1) disentangle the energetic and non-energetic effects of resource quality (nutritional *versus* refuge) and quantity on trophic interactions; (2) understand which resources limit specific herbivores and their natural enemies at different spatial scales; and (3) identify potential trade-offs between resource quantity (i.e. patch size of a certain habitat in the landscape or amount of prey to a predator) and quality (i.e. type of habitat or prey for a certain predator). Progress in this vast field of research could be fostered by a common research framework starting with a shared terminology on how to define and quantify resource quality for both nutritional and habitat resources. One existing framework to better understand the mechanistic links between food resource quantity / quality and ecosystem processes is stoichiometry (Yu et al. 2010). Integrating stoichiometry into current studies of population dynamics of pests and their natural enemies is one way towards an increased understanding of what the limiting resources for beneficial arthropods are.

Finally, in this thesis we focused on specific groups of pests and natural enemies. A complementary approach would be to investigate functional traits and **link traits to services and disservices in agro-ecosystems**. A quantitative review has revealed that functional trait-based indices of animal diversity consistently provided greater explanatory power than species richness or abundance in predicting various ecosystem functions including pest control (Gagic et al. 2015). A question seldom investigated is the effect of functional traits of multiple pests or pest communities and their impact on damage to plants/crops (**Paper III**). Therefore, it might be interesting in the future to compare traits of pests with those of their natural enemies in order to understand which natural enemy communities have the best chance of controlling a particular set of pests. In addition, if the functional traits that determine sensitivity to environmental change (response traits) are those that also influence ecosystem processes such as natural pest control or herbivory (effect traits), then understanding how functional-trait diversity is affected by land-use change is critical for predicting changes in community functioning (Lavorel and Garnier 2002).

7 References

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8 Acknowledgements

This thesis owes a lot to numerous people.

Thank you to all my supervisors. **Riccardo**, thank you for your support, for walking me through this unique experience and your contagious enthusiasm in science in moments of insecurity. Thank you **Barbara,** for sharing your knowledge and experiences, for your availability and your feedbacks that were always friendly and constructive. Thank you **Vesna** for your invaluable help at the beginning of the PhD, your good humour and critical thinking were an inspiration and a driver when I was confused. I am also grateful for your prompt and constructive advices while being oceans away. **Adrien**, thank you for giving me a unique opportunity to work with you in France and for guiding me through the discipline of landscape ecology. **Astrid**, thanks for your support and wise advice throughout the PhD.

Ged, thanks for introducing me to Sweden, for your unique company in the field, for your help ("YES WE CAN!") and sharing hours of music and brainless activity…I would have gone crazy and bland without your wise company. Thank you **Carol** for your hands-on magic when it all seemed so complicated. **Milda** thank you for being a friend and a great field assistant and for making a field season a unique adventure.

Francesca, no words are needed (*tacci tua*!). Thank you for being by my side over the last four years, for sharing spaces and thoughts, always true to yourself, an inspiration. **Pernilla**, my partner in crime, thanks for all the laughs, for bringing some healthy silliness to this PhD life and for dancing through my mood swings. **Eve**, I would probably not be writing all this if you had not been here on my first day. Merci pour ton énergie et tes convictions, une source d'inspiration et de motivation sans faille. To all the ladies, **Anna**, **Preeti**, **Laia** and **Kati**, who enriched and coloured my life in Uppsala in so many ways and made it a home. Thanks **Caro**, **Mel**, **Micia**, **Marthe** and **Rudi**, for being my pillars in a constantly changing environment.

Thanks to all the PhD students, postdocs and people at the Ecology Department and VPE who made my time here such an enjoyable experience.

Finally, I would like to thank my family: **Lea**, **Maman**, **Papa** et **Mamie** merci pour votre soutien et vos encouragements qui m'ont permis de mener à terme ce travail!