Biodiversity and Biological Control

Effects of Agricultural Intensity at the Farm and Landscape Scale

Camilla Winqvist
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Uppsala

Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2011

Acta Universitatis agriculturae Sueciae
2011:40

Cover: Landscape with Green Corn by Vincent van Gogh.

ISSN 1652-6880
ISBN 978-91-576-7584-2
© 2011 Camilla Winqvist, Uppsala
Print: SLU Service/Repro, Uppsala 2011

Biodiversity and Biological Control. Effects of Agricultural Intensity at the Farm and Landscape Scale

Abstract

Agricultural intensity on the local field or farm scale and on the regional landscape scale affects the organisms utilizing the arable landscape, and may affect ecosystem services and functions.

This thesis examines how plants, birds, community composition of ground beetles, and biological control of cereal aphids are affected by local agricultural intensity, organic farming and the surrounding landscape in Sweden and across Europe. The contribution of naturally occurring predator groups to the control of cereal aphid populations in complex and simple arable landscapes is also examined.

Overall, an increase in yield or pesticide use decreased species richness of all studied organisms, and reduced the biological control potential. Organic farming was beneficial to plants, whereas the effect on ground beetles and birds differed between studies. Organic farming enhanced biological control potential in heterogeneous landscapes only. On conventional farms the biological control was similarly high in all landscapes. Plants and birds were more abundant and species rich in heterogeneous landscapes, whereas ground beetles, especially omnivores, were more abundant in homogeneous landscapes. Ground-dwelling and flying predators reduced both the density and population growth rate of cereal aphids.

This thesis will improve the understanding of effects of agricultural intensity on biodiversity and biological control of cereal aphids across Europe. Although results vary among taxa and trait groups, they show that a shift towards farming with minimal pesticide use over large areas would affect biodiversity positively. The thesis also shows that naturally occurring predators are able to suppress cereal aphids and thereby reduce the need for insecticide applications. Finally, local management and landscape complexity need to be considered when developing future agri-environment schemes.

Keywords: Aphids, birds, ground beetles, landscape complexity, natural enemies, organic farming, pesticides, plants, traits, yield

Author's address: Camilla Winqvist, SLU, Department of Ecology,
P.O. Box 7044, 750 07 Uppsala, Sweden
E-mail: Camilla.Winqvist@slu.se

"Om man inte drömmer blir man galen. Men mitt i drömmen väcks man av förståndet, som beställer en traditionell engelsk frukost. Man får gå halvgalen en dag till."

Werner Aspenström

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
Geiger, F., Bengtsson, J., Berendse F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., **Winqvist, C.**, Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., and Inchausti, P. (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, 11, 97-105.

II
Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Pärt, T., Thies, C., Tscharntke, T., Weisser, W.W. and Bommarco, R. (2011) Mixed effects of organic farming and landscape complexity on farmland biodiversity and biocontrol potential. *Journal of Applied Ecology*, DOI: 10.1111/j.1365-2664.2010.01950.x

III
Winqvist, C., Bengtsson, J., Öckinger, E., Aavik, T., Berendse, F., Clement, L.W., Fischer, C., Flohre, A., Geiger, F., Liira, J., Thies, C., Tscharntke, T., Weisser, W.W. and Bommarco, R. Traits influence ground beetle responses to farm and landscape level agricultural intensification across Europe (manuscript).

IV
Winqvist, C., Bommarco, R. and Bengtsson, J. Flying and ground-dwelling natural enemies provide effective biological control of cereal aphids across landscapes (manuscript).

Paper I and II are reproduced with the permission of the publishers.

1 Introduction

As the human population grows, so does the demand for food, fiber and energy. Landscapes are simplified as new land is claimed for agriculture, and yields grow through increased inputs of pesticides and fertilizers and the use of new cultivars. Through such agricultural intensification cereal yields in Europe have almost tripled from 1960 to 2000 (Robinson and Sutherland, 2002; Donald *et al.*, 2001). The total tilled area has increased by 20%, and the area of fallows and permanent grassland has decreased over a 30 year period in the UK (Benton *et al.*, 2003). This intensification affects the organisms living in the arable landscape. In Europe, farmland biodiversity, for instance birds (Wretenberg *et al.*, 2006; Fuller *et al.*, 2005; Donald *et al.*, 2001), plants (Biesmeijer *et al.*, 2006; Wilson *et al.*, 1999;) and insects (Biesmeijer *et al.*, 2006; Kotze and O'Hara, 2003; Benton *et al.*, 2002; Wilson *et al.*, 1999) have declined dramatically, supposedly as a result of this agricultural intensification (Wilson *et al.*, 1999). As species with different traits will be affected in different ways, agricultural intensification may also lead to changes in species composition. For instance, lower intensity of farming may favor insect feeding birds like grey partridges (*Perdix perdix*), whereas skylarks (*Alauda arvensis*) benefit from high cereal production (Benton *et al.*, 2002).

In order to counteract negative effects of agriculture, the European Union has implemented agri-environment schemes, such as organic farming. The effects of agri-environment schemes vary between taxa (Kleijn and Sutherland, 2003), but organic farming systems usually have higher species richness of birds, insects and plants (Bengtsson *et al.*, 2005). The effectiveness of organic farming for enhancing biodiversity differs depending on for instance the organism under study and on the landscape context (Bengtsson *et al.*, 2005).

Other than affecting biodiversity, agricultural intensification may also have consequences for the functioning of ecosystems and services provided (MEA, 2003). An ecosystem service is a service provided to humankind by organisms in an ecosystem (MEA, 2003). In the arable ecosystem, pollination of crops and pest control by naturally occurring enemies are two important services. Cereal pests such as aphids may benefit from high levels of agricultural intensification, especially increased applications of nitrogen fertilizers in combination with growth regulators and fungicides that increases host plant quality and quantity (Honek, 1991), but also by losses of natural enemies (Tscharntke *et al.*, 2007; Bianchi *et al.*, 2006). Studies of how ecosystem services are affected by agricultural intensification are still rare (but see Flohre *et al.*, 2011; Diekötter *et al.*, 2005).

It is now becoming clear that it is important to include both local and regional aspects of agricultural management when studying effects on biodiversity, functions and services. In my thesis I have studied how farmland biodiversity and the ecosystem service of biological control of cereal aphids are affected by local agricultural intensity and landscape complexity, and if organic farming may counteract negative effects of agricultural intensity.

2 The aims of the thesis

The overall aim of this thesis is to understand how local and regional effects of agricultural intensity affect biodiversity (species richness, abundance and community composition) and the biological control of a pest by naturally occurring predators in the agricultural ecosystem.

The specific aims are to:

- Identify the most important local and regional components of agricultural intensity affecting biodiversity and biological control in farms across Europe (Paper I)

- Examine if biodiversity and biological control potential are affected by an interaction between local and landscape level agricultural intensity in organic and conventional farms in Europe (Paper II)

- Explore if agricultural policies (such as organic farming) in Europe have counteracted possible negative effects of intensive farming on biodiversity and biological pest control (Paper I and II)

- Examine if the trait composition of ground beetle assemblages changes because of local and regional intensity in organic and conventional farms across Europe (Paper III)

- Examine if the relative contribution of different guilds of predator change with landscape complexity and how that ultimately affects the biological control of aphids (Paper IV)

3 Agricultural intensification

3.1 Landscape complexity

The appearance of a landscape is shaped by interactions between society and the environment, integrating history, culture, techniques and environmental parameters (Baudry *et al.*, 2000). The arable landscape of today is the result of a historic process, where, in order to gain land for cultivation, perennial habitats (for instance grassland and forest) have been transformed into arable fields, and lakes and wetlands have been drained. To create larger and more easily managed fields, smaller fields have been merged and field boundaries with perennial vegetation, stone walls, hedges, ditches, clearance cairns and field islands are removed (Tscharntke *et al.*, 2005).

In current heterogeneous arable landscapes these changes have been smaller, and a high diversity of natural and semi-natural habitats are still present alongside arable fields. Heterogeneous arable landscapes often harbor a higher biodiversity than homogeneous arable landscapes since semi-natural and natural habitats provide more diverse food sources, shelter from disturbances by agricultural practices, overwintering sites, and alternative hosts or prey (Bianchi *et al.*, 2006; Tscharntke *et al.*, 2005). There is a spill-over from nearby uncultivated habitats that may increase the biodiversity on arable fields in heterogeneous landscapes. Biological control by ladybirds has been shown to be greater in diverse landscapes (Gardiner *et al.*, 2009) and Thies *et al.* (2003) found higher rates of parasitism in areas with a higher percentage non-crop habitat.

Homogeneous arable landscapes on the other hand are dominated by arable crops and natural and semi-natural habitats are highly fragmented, minute remnants. Organisms that are well adapted to disturbed habitats or can disperse well between suitable habitat patches may thrive, or at least cope, in homogeneous arable landscapes (Thiele, 1977). The mass occurrence of crops in monocultures may benefit for instance certain bumble bees that are positively affected by large oilseed rape fields (Westphal *et al.*, 2003). Biological control may also be positively affected; Östman *et al.* (2001) found an increased pest control by ground-dwelling predators in homogeneous landscapes.

3.2 Farming intensity and organic farming

In order to increase yields on the field or farm scale, farmers use shorter crop rotation with fewer crops, higher yielding or more resistant cultivars, irrigation, heavier fertilization and mechanical weed control or more pesticides (Tscharntke *et al.*, 2005). Many of these management actions work in concert and are hard to disentangle (Chamberlain *et al.*, 2000). Cereal yield can be used as a proxy of local intensification level, because it has been shown to correlate with for instance fertilizer use and numbers of tractors per worker (Donald *et al.*, 2001).

Agri-environment schemes in Europe differ between countries, but the objectives underlying them are the same in all the EU-countries. The effectiveness of these agri-environmental schemes has been critically evaluated (Kleijn and Sutherland, 2003). Organic farming "combines best environmental practices, a high level of biodiversity, the preservation of natural resources, the application of high animal welfare standards and a production method in line with the preference of certain consumers for products produced using natural substances and processes" (Council Regulation (EC) No 834/2007).

The effectiveness of organic farming on biodiversity differs depending on for instance the organism under study (Bengtsson *et al.*, 2005; Hole *et al.*, 2005) and on the landscape context. The effect of organic farming has been shown to depend on the surrounding landscape for weeds (Roschewitz *et al.*, 2005), bees (Holzschuh *et al.*, 2007), decomposers (Diekötter *et al.*, 2010) and microorganisms and earthworms (Flohre *et al.*, 2011). Rundlöf and Smith (2006) studied the effects of organic and conventional farming in landscapes with different proportions of arable fields, and concluded that organic farming only increased species richness and abundance of butterflies in homogeneous landscapes. The effect of interactions between the local management and the surrounding landscape on ecosystem services and functions is not well studied (but see Flohre *et al.*, 2011; Diekötter *et al.*, 2010).

4 Farmland biodiversity

Most people appreciate skylarks singing in fields in the spring and most of us marvel at cereal fields coloured by cornflowers, poppies or thistles later in the season. However, many more bird and plant species can be found in cereal fields in Europe. The not so conspicuous organisms that are common on arable land are different arthropods, for instance spiders, beetles and bugs. Bees, butterflies and bumblebees may also be found looking for flowers in cereal fields. Some of these insects are pests that feed on crops and reduce yields or lower the quality, whereas others are beneficial, feeding on pest species. Most of them we do not know very much about yet. The farmland biodiversity that I have studied in my thesis are ground beetles, plants and ground-nesting birds.

4.1 Ground beetles

One of the most well studied groups of ground-dwelling arthropods in the arable landscape are ground beetles (Coleoptera: Carabidae). Some ground beetles are well adapted to disturbed, open habitats such as cereal fields (Thiele, 1977), and species such as *Pterostichus melanarius* (Figure 1), can be very numerous on arable land. Ground beetles display a number of "life styles"; some are small, winged and day active; others are wingless, large and nocturnal. Many ground beetles are predators or omnivores, most of them generalists feeding on a wide range of prey. Some ground beetles feed on pest such as aphids (Chiverton, 1987), thereby being potential biological control agents. Studies have shown that the more species of predators there are in a system, the better the biological control (Snyder *et al.*, 2006). But ground beetles may feed on other predators such spiders (Lang, 2003), a phenomenon called intra-guild predation, which may reduce the biological control potential of pests (Finke and Denno, 2005). Apart from being natural enemies of crop pests, a few ground beetles are pests themselves, feeding on for instance crop seeds (Thiele, 1977). Ground beetles, and other arthropods, are also part of the diet for birds (Benton *et al.*, 2002; Blake *et al.*, 1994).

Figure 1 The ground beetle *Pterostichus melanarius. Photo:* Vitezslav Manak

Even though many ground beetles in the arable landscape overwinter in the field (Holland *et al.*, 2009), some ground beetles need semi-natural habitats such as hedgerows or field margins for overwintering. These habitats are also used for shelter, breeding and dispersal (Holland and Luff, 2000). In England, the Entry Level Stewardship Scheme (an agri-environment scheme (AES)) enables farmers to create or maintain grass ridges in their fields, so called beetle banks (Natural England, 2010), thereby providing habitat for insects, birds and small mammals. Organic farming is another AES aiming at enhancing biodiversity, but species richness and abundance of ground beetles are not always increased by organic farming (Bengtsson *et al.*, 2005; Purtauf *et al.*, 2005). Kromp (1989) found more phytophagous ground beetle species in biologically managed farms, presumably because of their higher weediness and absence of pesticides. Organic fertilization has also been shown to enhance ground beetles (Holland and Luff, 2000). Pesticide can have both direct and indirect negative effects on ground beetles, but results are so study- and species-specific that generalizations are hard to make (Holland

and Luff, 2000). It seems as if ground beetles as a group are quite unaffected by farm management actions (Kromp, 1999).

4.2 Plants

Farmers often spend a lot of time and money on reducing the amounts of wild plants in the fields (a.k.a. weeds). They have been very successful, so much so, that some of the weeds are even locally red listed. The Forking Larkspur (*Consolida regalis*) in Figure 2 is using cereal fields as its habitat and has the status Near Threatened in Sweden due to pesticides and competition from today's dense crops (Gärdenfors, 2010).

Figure 2 The Forking Larkspur (*Consolida regalis*) is a red listed plant that you can find in cereal fields in Sweden. If you are lucky!

Despite competing with the crops and potentially reducing yields, weeds fulfill many important roles in the arable ecosystem, for instance as food for birds and pollinators. Plants are also important for natural enemies of pests, directly by providing food resources, and indirectly by increasing prey availability or by affecting the microclimate (Landis *et al.*, 2005). Some weeds even reduce the likelihood of pests settling on crops (Ninkovic *et al.*, 2009).

Plants often increase in species richness or abundance on organic farms (Bengtsson *et al.*, 2005; Fuller *et al.*, 2005), as a direct result of the absence of herbicides. High nature-value species (Aavik and Liira, 2010), or plants pollinated by insects (Gabriel and Tscharntke, 2007) are particularly benefited. The surrounding landscape may affect the biodiversity of plants more than the local field management (Aavik and Liira, 2010). Roschewitz *et al.* (2005) found that the diversity of arable weed species was similar between organic and conventional farms in complex landscapes, but higher in organic than conventional farms in simple landscapes. Clearly, both local and regional scale intensity affect the biodiversity of plants (Roschewitz *et al.*, 2005).

4.3 Birds

Birds are well-known by the public and easy to survey, and effects of farming practices and agricultural intensification on birds have gained a lot of scientific interest. Apart from singing beautifully, birds are important parts of the agricultural ecosystem since they feed on weeds and pest insects (Wilson *et al.*, 1999), even though some birds feed on crops too (Wilson *et al.*, 1999). Farmers are often well aware of the bird species on their farms (Ahnström, 2009) and have noticed changes in bird diversity over the years. The decline in bird biodiversity has been very dramatic in Europe over the last 60 years (Benton *et al.*, 2003; Chamberlain *et al.*, 2000), most likely due to agricultural intensification and changes in food diversity (Wilson *et al.*, 1999). The negative effect of pesticides on birds was brought to public attention by Rachel Carson book *Silent spring* in 1962. More indirect changes, such as the timing of cultivation events, have also affected some bird species. Eggers *et al.* (2011) found that both species richness and territory abundance of ground-foraging species were lower in autumn-sown than in spring-sown cereal.

Some AESs are specifically aimed at reducing the negative impact of agricultural intensification on birds. Examples are skylark plots and vegetation strips sown with seed mixtures designed to provide food for birds (Natural England, 2010). Birds are often benefited by organic farming and will increase both in numbers and species richness (Bengtsson *et al.*, 2005), but birds with different traits may respond in different ways. Dänhardt *et al.* (2009) found that invertebrate feeders were more abundant on organic fields, whereas omnivores had higher densities in homogeneous landscapes. Sometimes only species nesting and feeding in the crops, such as skylarks and lapwings (*Vanellus vanellus*), respond positively to organic farming (Piha *et al.*, 2007).

5 Biological control

Herbivores may cause severe damage to crops, but naturally occurring enemies that prey on the herbivores can suppress them and reduce yield loss (Bianchi *et al.*, 2006; Larsson, 2005; Östman *et al.*, 2001), thereby reducing the need for chemical control. Biological control of pests in arable fields is an important ecosystem service provided by enemy communities (Thies *et al.*, 2005; Tscharntke *et al.*, 2005; Östman *et al.*, 2001).

The species richness, abundance and life-history traits of predators, as well as the community composition, all affect the efficiency of biological control, and positive, negative or counterbalancing interactions between predators may take place. Increased predator diversity should in theory lead to improved biological control (Colfer and Rosenheim, 2001), but that is far from always the case. It is still not concluded whether more diverse communities of natural enemies will suppress pest populations better than poorer ones (Straub *et al.*, 2008). Simplified natural enemy communities have been shown to control pests equally well, or even better, than complex communities (Finke and Denno, 2004). Negative interactions between predators such as intraguild predation, cannibalism and hyper parasitism may disrupt the biological control (Straub *et al.*, 2008). Finke and Denno (2005) showed that when more strict predator species were added to a system, the biological control increased, but adding intra-guild predators reduced biological control.

The effect of different predator groups can also be larger when they act in concert than on their own (Straub *et al.*, 2008; Schmidt *et al.*, 2003; Colfer and Rosenheim, 2001). This may happen through resource partitioning, for instance when different predators are active at different parts of the season and therefore can predate the pest during a longer time period (Straub *et al.*, 2008). Another case is facilitation when one enemy species enables a second enemy to kill more prey than it would on its own (Straub *et al.*, 2008). This may happen when flying predators cause aphids to drop from the plant to avoid attack, and are eaten by ground-dwelling predators instead.

Neutral effects of increased predators may occur when enemies are redundant or compete for prey (Straub *et al.*, 2008). The abundance and diversity of so called alternative prey may also affect the biological control, either disrupting it (Koss and Snyder, 2005) or have only small effects (Östman, 2004).

Other factors may also come into play, such as weather and abiotic conditions, the local management and the complexity of the surrounding landscape. Herbicides have been shown to have negative effects on both weeds, non-target arthropods and predatory arthropods (Chiverton and Sotherton, 1991), thereby potentially affecting the biological control. Organic farms have been shown to have lower abundances of aphids, but not higher parasitism rate (Roschewitz *et al.*, 2005). Östman *et al.* (2001) showed that prey had a lower establishment and survival on organic farms and farms with small fields and more perennial crops. Both these two latter studies have also found effects of the surrounding landscape. In a review by Bianchi *et al.*, (2006) it was concluded that "diversified small-scale landscapes therefore provide better conditions for effective pest control by natural enemies than do large-scale landscapes". This statement is both (indirectly) supported (Gardiner *et al.*, 2009; Thies *et al.*, 2003) and not (Roschewitz *et al.*, 2005; Thies *et al.*, 2005). Some studies have even found a better pest control in simple landscapes (Östman *et al.*, 2001).

All in all, the role of natural enemies in pest control is not sufficiently understood to predict and suppress pest outbreaks, especially not when multiple predator groups are involved, and at different levels of agricultural intensity.

5.1 Cereal pests: Aphids

In this thesis cereal aphids (Homoptera: Aphididae) are the target pest. The bird cherry-oat aphid *Rhopalosiphum padi*, the grain aphid *Sitobion avenae* and the rose grain aphid *Metopolophium dirhodum* are common cereal pests in Europe. In Sweden *R. padi* is most common (Figure 3), especially in spring sown crops (Wiktelius and Ekbom, 1985). Aphids can multiply quickly once they have colonized a field, since they reproduce asexually during the summer. Adult bird cherry-oat aphids can produce ca 2.5 offspring per day, and the young can start producing offspring of their own after only about five days (Taheri *et al.*, 2010).

Figure 3. An adult bird cherry-oat aphid *Rhopalosiphum padi* and her offspring on the base of spring barley.

In Sweden, *R. padi* colonizes the cereals in the middle of May to early June and reach peak densities in the first half of July (Chiverton, 1986). The typical population development involves an initial slow build-up in the cereals, a rapid multiplication phase, and then the population increase will slow down and eventually stagnate. *R. padi* are often situated close to the base of cereals, or even below the soil surface, in the early stages of crop growth. Later in the season they may even be active on the soil surface (Wiktelius and Ekbom, 1985; personal observation). Finally, normally in late July, aphid populations in cereals will decrease rapidly as crops mature (Chiverton, 1986). Winged individuals migrate first to grasslands and later on to bird cherry trees (*Prunus padus*) which is the winter host. High densities during the summer will result in large numbers of aphids migrating to the winter host laying eggs (Wiktelius, 1984). Migration to cereal fields the following year is larger and earlier if aphids are abundant on the winter host (Wiktelius, 1984). If aphid numbers can be reduced in cereal fields, and subsequently on bird cherry trees, the impact of aphids may be reduced.

5.2 Generalist and specialist aphid predators

There are a number of naturally occurring predators that are potential enemies of aphids (Chiverton, 1987). Unfortunately, for most of these organisms we do not know their true potential. Predators can be broadly divided into generalists and specialists, depending on their level of diet specialization (Symondson *et al.*, 2002).

Generalistic predators are for instance ground beetles, spiders (Araneae) and rove beetles (Coleoptera: Staphylinidae). Under lab conditions, adult ground beetles have been found to devour up to 30 aphids per day (Bilde and Toft, 1997), and when dissecting ground beetles caught in fields in Sweden, Chiverton (1987) found that 18% of the beetles had been feeding on aphids. Since generalists can feed on a number of prey species, or even plant material, they may be present in the cereal fields early in the season, which gives them a head start when aphids colonize. Generalists have been found to be able to suppress aphid numbers and growth rates in the early stages of aphid development (Lang, 2003; Chiverton, 1986).

Specialist such as some parasitic wasps (Hymenoptera) and ladybirds (Coleoptera: Coccinellidae) are specialized on aphids. Specialists are able to respond numerically to aphid abundances and have been shown to reduce aphid population growth later in the season (Snyder and Ives, 2003). Common aphid parasitoids can parasitize up to 500 aphids in a season (Snyder and Ives, 2003), and ladybirds have been shown to feed on up to 33 aphids per day (Colfer and Rosenheim, 2001).

The relative importance of generalist and specialist predators for biological control of cereal aphids is not well known. Even less understood is if the relative importance differs between landscapes. It is also interesting to see whether the two groups will interact in a positive or negative way when biological control is regarded.

6 Methods

6.1 Farm and field selection

The field work for paper I in this thesis was conducted in collaboration with my coauthors on 30 farms per region in nine regions in Europe: Sweden, Estonia, Poland, Göttingen and Jena in Germany, Ireland, the Netherlands, France and Spain in May to July 2007. In order to separate effect of local and regional agricultural intensification, we selected farms with different yields (as a proxy of intensity) along a landscape complexity gradient. To be able to compare our data we used a standardized protocol and performed surveys and experiments at standardized times, using the growth stage of cereals as a time reference. Winter wheat (*Triticum aestivum*) was the main crop in 2007. For paper II and III data from the five regions with data both from organic and conventional farms were used: Sweden, Estonia, Göttingen and Jena in Germany and the Netherlands. Apart from using fewer regions, the same fields and methods as in paper I was used.

In paper IV data from the counties of Uppland and Skåne in Sweden was used. Eight conventional farms per region, four farms in heterogeneous landscapes and four farms in homogeneous landscapes, were used. One spring barley (*Hordeum vulgare*) field per farm was studied in June to July 2008.

6.2 Landscape measures and farm management

The effect on biodiversity or ecosystem functions of landscape composition can be studied using the degree of fragmentation or connectivity of habitat patches, the distance between patches or the area of that habitat in the landscape (Ewers and Didham, 2006). Other commonly used measures are for instance diversity indices, the percentage of semi-natural grasslands, and the mean field size or perimeter to area-ratio. These measures are often highly correlated (Holzschuh *et al.*, 2007; Roschewitz *et al.*, 2005). The percentage of arable land in the landscape is another common measure (Holzschuh *et al.*, 2007) of landscape heterogeneity.

The relevant scale at which to study the landscape is determined by the movement and dispersal capacity of the studied organisms. The arable landscapes in Europe have been studied at various scales often represented by a circle with a radius ranging from a 0.25-3 km from the field or farm of interest. Aphids have been found to respond to the surrounding landscape at radius of 1-3 km (Roschewitz *et al.*, 2005), ground beetles at 1.5 km (Purtauf *et al.*, 2005), parasitoids at 0.5-2 km (Thies *et al.*, 2005), plants at 0.25 km-1 km (Aavik and Liira, 2010; Roschewitz *et al.*, 2005) and open land birds at 0.5 km (Fischer *et al.*, 2011). Landscape measures at multiple spatial scales are often highly correlated (Tscharntke *et al.*, 2005).

In paper I the percentage of arable land and the mean field size in a 0.5 km radius landscape surrounding the farm was used as a measure of landscape complexity. In the following three papers a 1 km radius was used for all landscape analyses. In paper II and III the percentage of arable land was used as a landscape measure. In paper IV farms were situated in "complex" or "simple" landscapes as defined by the percentage arable land in the surrounding landscape, and in that study the percentage grasslands was also included as a landscape variable.

Information about farm management was collected by means of a questionnaire to the farmers. We collected data on for instance yield per hectare, farm size, amount of fertilizers and pesticides used and whether farms were organic or conventional (see Paper I, Appendix 1, Table 4).

6.3 Biodiversity sampling 2007

In paper I and II five sampling points per farm were used for assessing plant and ground beetle biodiversity, and one field per farm was used for a bird survey (Figure 4). Sampling points were situated along a vegetated field margin, 10 m into the field. Plants were recorded in three 2 x 2 m plots per sampling point. All plants with at least the first two leaves (after the cotyledon) were identified to species and the total cover of wild plants was estimated. Ground beetles were collected using roofed pitfall traps, two per sampling point. These were placed one each in the outermost vegetation sampling plots. Pitfall traps were open for one week at the time, two times during the season. All ground beetles were identified to species and counted. The ground beetle data was also used in Paper III.

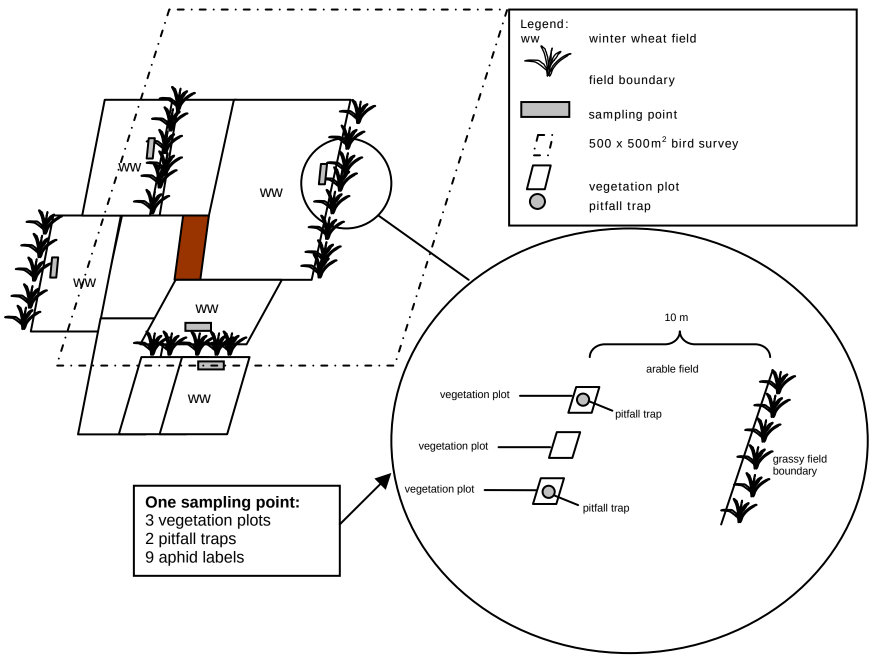

Figure 4. The design of the biodiversity sampling and experiment with glued aphids in 2007.

The largest field on each farm was used for a bird survey. Birds were monitored three times according to a modified version of the British Trust for Ornithology's Common Bird Census (Bibby *et al.*, 1992). All bird individuals were identified to species, and behaviour and nesting sites were noted on maps. Using bird behaviour observed on the three survey rounds the number of breeding bird territories was determined.

6.4 Biological control experiments

6.4.1 Study with glued aphids in 2007

One way of comparing the biological control potential between areas is exposing prey in the field and survey the removal of prey (Östman, 2004). This approach will not tell us which predator that actually ate the prey, but can help us estimate the relative potential biological control between for instance conventional and organic farms. For the experiment used in Paper I and II we glued live pea aphids (*Acyrthosiphon pisum*) to plastic labels (Figure

5) and placed them in cereal fields for 24 h. Three of the five sampling points per farm were used. Three labels were placed in each vegetation plot, one central and two at diagonal corners, so that there were 27 labels with 81 aphids in total at each farm. We checked how many aphids were still present every 6^{th} hour for 24 h, and repeated the experiment twice. The median survival time and the percentage of aphids remaining after 24 h were used as measures of the biological control potential.

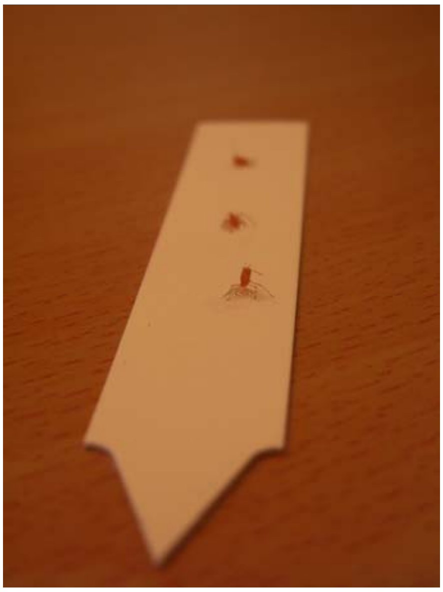

Figure 5. Pea aphids glued to plastic labels prior to placing in the field for 24 h.

6.4.2 Cages and barriers study in 2008

To study potential differences between predator groups and to get better estimates of the impact of predators, exclusion techniques can be used. Exclusion methods were used already in 1942 (Chambers *et al.* 1983), and since then different cages and barrier have been used in a number of studies (Gardiner *et al.*, 2009; Schmidt *et al.*, 2003; Östman *et al.*, 2001). For the experiment in paper IV we used circular plastic barriers (Figure 6 top) to exclude ground-dwelling predators, metal cages (Figure 6 bottom) sprayed with glue to exclude flying predators, and a combination of both to exclude all predators. Control plots were accessible to all naturally occurring predators. The four experimental plots were replicated twice per field. We counted the number of aphids on 100 barley shoots per experimental plot twice. Once when aphids had just colonized the fields, and again later in the season when aphids had reached their peak densities.

Figure 6. Barriers for exclusion of ground-dwelling predators (top) and cages for exclusion of flying predators (bottom) being fitted.

6.5 Traits of ground beetles

Traits are interesting to study since they reveal so much more about how organisms are adapted to their environment than pure abundance and species richness do. To better understand how ground beetle communities are affected by agricultural intensification, I studied how the species richness and abundance of ground beetles with different body size, diet and wing morphology responded to changes in intensity. Ground beetles traits were gathered using the literature and via collaboration with researchers holding unpublished databases.

7 Results and discussion

7.1 Negative effects on biodiversity and biological control of increased yield and pesticide use

As cereal yields increased, the overall species richness of wild plants (weeds), ground beetles and ground nesting farmland birds in nine regions in Europe decreased (Paper I, Table 1, and Figure 7 A-C). On average, an increased cereal yield from four to eight ton/ha resulted in the loss of five of nine plant species, two of seven ground beetle species and one of three bird species. Yield is correlated to a number of farm actions and can therefore be used as a proxy of intensity (Tilman *et al.*, 2002). With the increase in human population and increasing demand for food, cereal yields are believed to increase in the future. Extrapolating our results to higher yields would suggest further declines in species richness of farmland biodiversity.

An increase in yield also resulted in a longer survival time of the aphids glued to labels, indicating a reduced biological control (Figure 7D). Ground beetles, being one of the most abundant groups of ground-dwelling generalist predators, were found to decrease with increased yield. If other predators decrease in numbers too, this may explain the reduced biological control. Another explanation may be that alternative prey is more abundant in more productive fields with higher yield (Flohre *et al.*, 2011), thereby reducing the predation of the glued aphids.

Pesticide application or amount of active ingredient showed the most pronounced negative effects on biodiversity of the 13 studied components of intensification. All studied organisms responded negatively to pesticide use. Modern pesticides are highly effective, but yet the amount of pesticide use has increased over the past 50 years (Tilman *et al.*, 2002) and larger areas are being sprayed each year (Robinson and Sutherland, 2002).

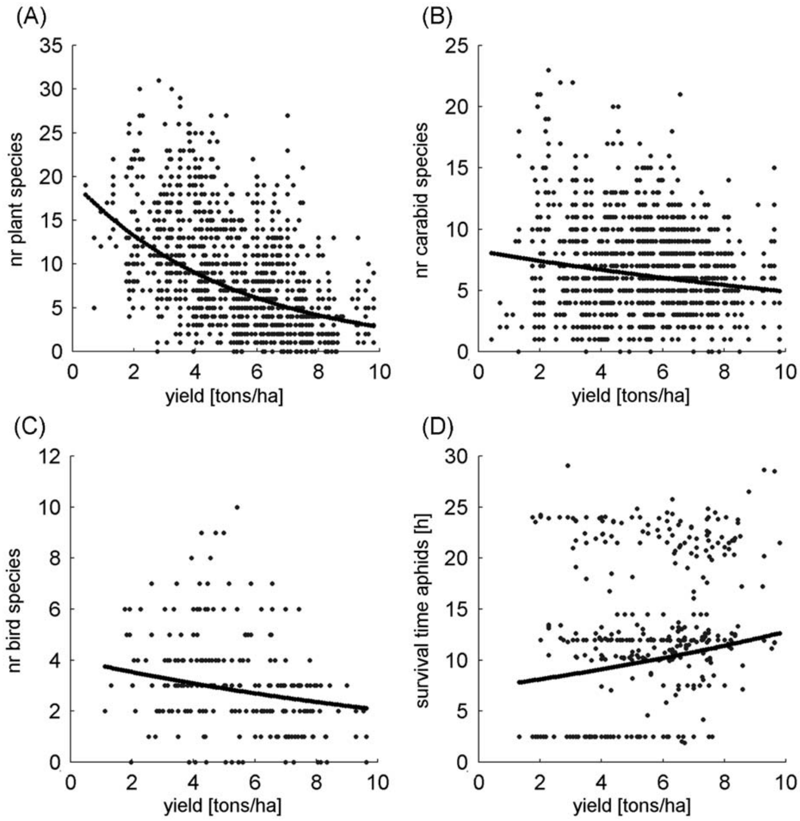

Figure 7. Effects of cereal yield (ton/ha) on: (A) the number of wild plant species per sampling point (in 3 plots of $4m^2$), (B) the number of carabid species per sampling point (per trap during 2 sampling periods), (C) the number of ground-nesting bird species per farm (one survey plot of $500^{x}500$m), and (D) the median survival time of aphids (h). Trend lines were calculated using GLMM including the two surrounding landscape variables as covariates and field, farm and study area as nested random effects.

Despite several decades of implementing a Europe-wide policy intended to considerably reduce the amount of chemicals applied on arable land, pesticides are still having disastrous consequences for wild plant and animal species on European farmland. Reasons for this may be that negative effects of pesticides spread into the landscape, outside of farms that use pesticides, and that there may be a lag of recovery.

The amount of active ingredients of insecticides applied correlated negatively with the biological control potential. Ground beetles were found to decrease with the amount of active ingredients of insecticides too. The conclusion from this may be very simple: If you use insecticides, naturally occurring arthropod predators die, and the biological control potential is reduced. But, insecticides kill aphids too, so the farmer will benefit from using them, at least on a short time basis. Since aphids are able to reproduce rapidly, aphid populations may build up very quickly again after spraying (Langhof *et al*, 2003). Add to this the fact that aphids may become resistant to insecticides and the benefits of biological control become apparent.

Since a recommendation to reduce the yield is not very fruitful in times when yields need to be increased, we therefore conclude that reducing pesticide use is vital for the conservation of farmland biodiversity and biological control.

7.1.1 Predators not affected by increased yields

When effects on ground beetles with shared trait were studied, we found that omnivorous and phytophagous species richness was negatively affected by increased yields (Paper III). Predatory ground beetles were not affected; they were just as species rich in low and high yield farms. This may imply that predator may be relatively more species rich if yields increase more, hopefully resulting in better biological control of arable pests. The potential effect of increased predator diversity on biological control is still debated, since more predators may lead to increased intra-guild predation, thereby reducing the biological control of pests (Finke and Denno, 2005).

The abundances of all trait categories decreased with increased yield, except for wingless beetles, and small and middle sized beetles which were not affected at all. If agricultural intensification continues and yields increase further, small beetles will be relatively more common, something that could affect intra-guild predation (Prasad and Snyder, 2006), biological control potential (Costamanga and Landis, 2006) and ground beetles role as food for birds (in Blake *et al.* 1994).

We have not yet analyzed the potential impacts of changes in relative diversity of ground beetles with different traits on the biological control or other ecosystem functions. That will be next on the to-do-list!

7.2 Mixed benefits from organic farming

We have tested the effect of organic farming in two papers. In paper I all nine regions in Europe were used. The results showed that organic farms harbored a higher species richness of plants and ground beetles (Paper I, Table 1). An increase in the percentage of land under any AES also increased the species richness of plants and ground beetles, and increased the biological control potential.

In paper II, only the countries having data on both organic and conventional farms were included. In that case we found that the species richness and abundance of birds and plants were higher on organic farms (Paper II, Table 2). For ground beetles on the other hand, we found the same species richness and abundance on organic and conventional farms. Many studies have found positive effects of organic farming on plants (Bengtsson *et al.*, 2005; Hole *et al.*, 2005), so it should be safe to state that organic farming is beneficial to plants, which most likely is because of the absence of herbicides. Even if that statement makes environmentalists happy, not all farmers will be as thrilled…

A problem with comparing organic and conventional farming is that these two farming systems are overlapping in a number of practices. For instance, conventional farms may use inorganic fertilizers, but farms with animal production often use organic fertilizers, just like organic farms. Besides, many conventional farms do not apply any pesticides even though they may and organic farmers can successfully reduce weeds with non-chemical methods. This may be some of the reasons why expected differences between organic and conventional farms sometimes cannot be found, and why results differ between studies (Ahnström, 2009).

In paper I no effect of organic farming was found for birds, whereas in paper II both the abundance and species richness was higher on organic farms. A possible explanation for this discrepancy could be that data from Poland and Spain was used in paper I. These two regions are characterized by high species richness on conventional farms, and no organic farms were studied there. In paper II only countries with data from both organic and conventional farms were used.

We conclude that plants benefit directly from organic farming, whereas the effects on birds and ground beetles are more indirect, and therefore vary between studies.

7.2.1 No traits affected by organic farming

Even though organic farming did not affect the species richness or abundance of ground beetles in paper II, the traits composition might have been affected. However, none of the studied traits of ground beetles differed in abundance or species richness on organic and conventional farms (Paper III). Maybe the different types of management, for instance inorganic pesticides contra mechanical weed control, affect the ground beetles just as much. The nature of the disturbances can be different on organic and conventional farms, but they may still be similar enough not to affect ground beetles with different traits in different ways.

Maybe other traits are affected by organic farming? Or maybe Purtauf *et al.*, (2005) were right when they found that spring breeding ground beetles only had a higher density on organic farms in landscapes with a larger proportion of grassland, and therefore concluded that the surrounding landscape was more important than organic farming for ground beetle diversity.

We conclude that if shifts in ground beetle community composition occur because of an intensification to increase yields, organic farming can not be used to reverse such changes, since no trait was affected by organic farming.

7.3 Plants and birds more diverse in heterogeneous landscapes

In paper I, we found fewer plant species in landscapes with larger fields, when measured at a 500 m radius. Field size was not correlated to yield, so an increase in yield can not be the explanation to this finding (Paper I, Appendix 1, Table 6).

When looking at the larger landscape scale of 1000 m radius in paper II, we found that both the abundance and species richness of plants and ground-nesting birds decreased with a higher percentage arable land in the landscape (Figure 8 and 9). These results are supported by a number of studies showing that plants and birds are more diverse in landscapes with more semi-natural and natural habitats (e.g. Piha *et al.* 2007; Roschewitz *et al.* 2005). That bird species richness was not affected by the landscape at 500 m radius, but at 1000 m, may be an indication that this is the scale of the landscape that birds respond to.

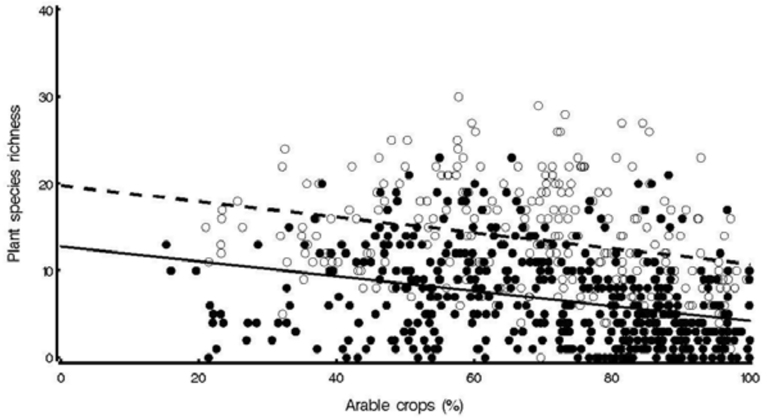

Figure 8. Plant species richness on organic and conventional farms plotted against landscape complexity (percentage of arable crops in a buffer zone with 1000 m radius). Organic fields: open circles and dotted line. Conventional fields: filled circles and solid line.

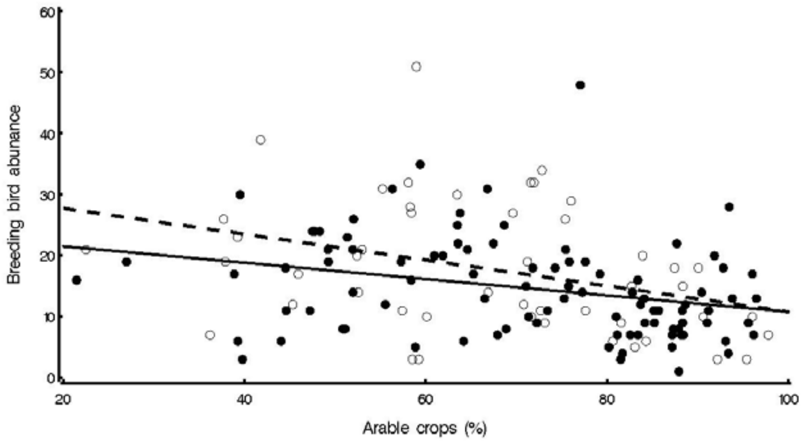

Figure 9. The abundance of breeding birds on organic and conventional farms plotted against landscape complexity (percentage of arable crops in a buffer zone with 1000 m radius). Organic fields: open circles and dotted line. Conventional fields: filled circles and solid line.

7.4 Ground beetles are more abundant in homogeneous landscapes

Ground beetles increased in abundance in homogeneous landscapes, whereas the species richness was unaffected by landscape complexity. Östman (2005) found that for ground beetles, temporal variation in the landscape is more important than spatial variation. This may explain why we found more ground beetles in homogeneous landscapes: crops may vary temporally more than for instance grasslands or forests. Another possible reason is that resources are more abundant in homogeneous landscapes (Tscharntke *et al.* 2005). One important aspect here is also that many ground beetles have the arable fields as their habitat (Thiele, 1977), and increasing the area of habitat will then increase their numbers.

We conclude that heterogeneous landscapes enhance the biodiversity of plants and ground-nesting birds, whereas ground beetles are more abundant in homogeneous landscapes.

7.4.1 Omnivores more abundant in homogeneous landscapes

Omnivorous beetles increased in abundance as landscapes became more homogeneous, whereas both phytophages and predators were unaffected by landscape complexity. Omnivores will then be relatively more abundant in more simple landscapes. Increasing the number of omnivores in a community could result either in reduced biological control (if they eat other prey than pests) or increased biological control (if they can survive periods with low pest numbers on other types of prey). More information is need on the impact on ecosystem services and functions of changes in the relative abundance of species with different traits.

We also found that the species richness of wingless beetles were higher in simple landscapes. This finding opposes a number of studies (Tscharntke *et al.*, 2005), and theory (Ewers and Didham, 2006) announcing that high mobility is advantageous in fragmented, agricultural landscapes. But once again, don't forget that to many ground beetles the cereal fields are the habitat! A heterogeneous landscape is also fragmented, especially if the resources you want are in cereal fields.

We conclude that omnivores are affected in opposite ways by the local management (yield) and the landscape complexity, which makes predictions for the future hard, since increased yield and landscape simplification may go hand in hand.

7.5 Biological control potential greatest on organic farms in heterogeneous landscapes

The highest biological control potential was found on organic farms in heterogeneous landscapes, and the lowest in organic farms in homogeneous landscapes (Figure 10). On conventional farms the biological control potential was the same in all landscapes, when generalizing across five European regions. This interaction shows us that we can not assume that ecosystem services are affected by organic farming in the same way in all landscapes. Landscape dependent effects of organic farming have previously been shown for arable weeds (Roschewitz *et al.*, 2005), bees (Holzschuh *et al.*, 2007) and butterflies (Rundlöf and Smith, 2006). An interaction was also found for respiration by Flohre *et al.* (2011).

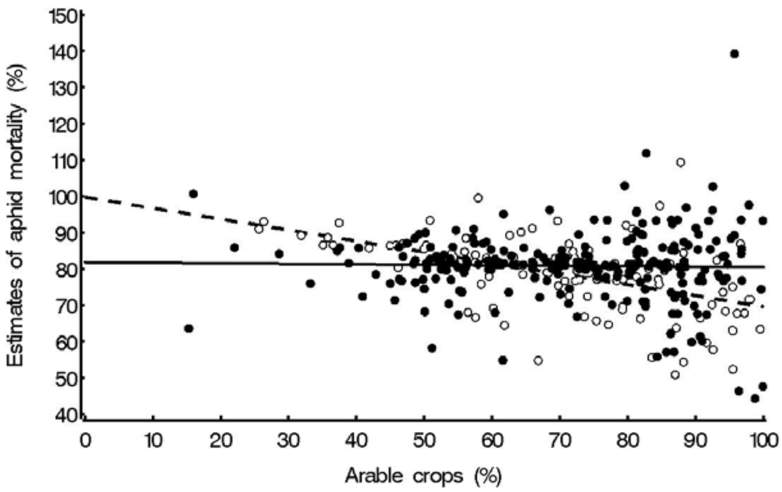

Figure 10. Percentage of eaten aphid model estimates and residuals plotted against landscape complexity (percentage of arable crops in a buffer zone with 1000 m radius). Organic fields: open circles and dotted line. Conventional fields: filled circles and solid line.

Unfortunately, our studies of ground beetles traits (paper III) give us no clues either, since no trait was affected by organic farming. The abundance of omnivores increased in homogeneous landscapes, but why that should lead to a reduction in biological control in organic farms only remains a mystery.

Another explanation for the difference in biological control between organic and conventional farms may be that the amount of naturally occurring aphids differs between landscapes or farming practices (e.g. Roschewitz *et al.* 2005). If naturally occurring aphids are abundant, then our "take away" aphids are less interesting as food. On the other hand, a galore of aphids may attract more predators, hopefully increasing biological control potential.

The biological control potential may also be affected by for instance the occurrence of alternative prey (Koss and Snyder, 2005). Herbicides have been shown to have negative effects on weeds, non-target arthropods and predatory arthropods. In herbicide treated plots, more individuals of a ground beetle had fed on aphids than in untreated plots, where they instead fed on bugs, spiders and springtails (Chiverton and Sotherton 1991). On the other hand, Östman (2004) found no negative effect of alternative prey on biological control.

Another explanation, that is currently under study by Thies *et al.*, (in press), is whether naturally occurring predators may also be affected differently by local management (for instance organic farming) and landscape complexity, so that the predator community differs, resulting in different biological control potential.

We conclude that it is important to keep both local management and regional landscape structure in mind when trying to promote or preserve biological control. Our finding of an interaction suggests that the effect of local management may differ between landscapes for other ecosystem functions and services too.

7.6 Functional groups and biological control

Aphid densities and population growth rates increased in the absence of naturally occurring predators (Paper IV). In Skåne the total exclusion of predators resulted in approximately 14 times more aphids in plots were predators were excluded than in open plots. We also found that the combined effect of both ground-dwelling generalists and flying specialist were greater than the contribution of generalist and specialist predators each on their own (Figure 11). This finding supports the results of several earlier studies (Snyder *et al.*, 2006; Schmidt *et al.*, 2003; Colfer and Rosenheim, 2001). Different groups of predators may interact, for instance may flying predators such as ladybirds cause aphids to drop from the plants, thereby increasing their risk of being eaten by ground-dwelling predators.

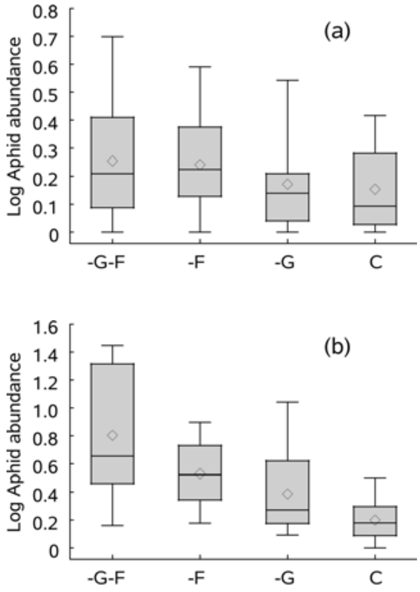

Figure 11. Boxplot of final aphid densities (log10(x+1) in (a) Uppland and (b) Skåne separated per treatment. -G, -F: cages and barriers excluding all predator; –F: cages with flying predators excluded, G: barriers with ground-dwelling predators excluded, C: open control plot where all predators have access. Dots=mean, midline=median, boxes= 25th and 75th percentile, whiskers=minimum and maximum values.

We did not find any differences in biological control in complex or simple landscapes in this study that could explain the results found in (Winqvist *et al.*, 2011). Neither were the total biological control greater in any landscape, nor did the relative contribution of different predator groups differ between landscapes. Caballero López (2009) conducted a similar study in Skåne but using organic farms instead of conventional, and found that even although both specialist and generalist predators were affected by the surrounding landscape, there was no effect of landscape on final aphid densities. Parasitism rate has been shown to be higher in complex landscapes than in simple landscapes, but greater abundances of aphids have also been noted in complex landscapes, thereby cancelling out each other (Roschewitz *et al.*, 2005; Thies *et al.*, 2005).

Final aphid densities in our study are well below the economical threshold of 5.5 bird cherry-oat aphids per tiller in barley (Plant Protection Centre, Swedish Board of Agriculture). Even so, naturally occurring enemies help farmers reducing their yield loss due to aphids. In Skåne, the mean density of aphids in the full exclusion reached ca 9.5 aphids per tiller in the final count. Spraying the crops at an earlier stage equivalent to that density would have resulted in approximately 100 kg/ha higher yield (Hallqvist, 1991). In plots where naturally occurring predators can reduce aphids to as low numbers, yield loss is negligible and there is no need for pesticide applications.

We conclude that naturally occurring predators, both flying specialist and ground-dwelling generalists are important in reducing aphid densities and population growth rates to levels where pesticide use is not economically valid.

8 Conclusions and implications

(Paper I)
In a Europe-wide study in eight West and East European countries, we found important negative effects of agricultural intensification on wild plant, ground beetle and bird species diversity and on the potential for biological pest control of aphids. The use of pesticides had consistent negative effects on biodiversity, and insecticides also reduced the biological control potential of aphids. We conclude that despite decades of European policy to limit the use of pesticides, the negative effects of pesticides on wild plant and animal species persist, at the same time reducing the opportunities for biological pest control. If biodiversity is to be restored in Europe and opportunities are to be created for crop production utilizing biodiversity based ecosystem services such as biological pest control, there must be a Europe-wide shift towards farming with minimal use of pesticides over large areas.

(Paper II)
Using five regions in Europe we showed that organic farming enhanced the biodiversity of plants and birds in all landscapes, but only improved the potential for biological control in heterogeneous landscapes. These mixed results stress the importance of taking both local management and regional landscape complexity into consideration when developing future agri-environment schemes, and suggest that local-regional interactions may affect other ecosystem services and functions. This study also shows that it is not enough to design and monitor agri-environment schemes on the basis of biodiversity, but that ecosystem services should be considered too.

Paper III)
In the study of ground beetles traits, both the local scale intensity, with yield as a proxy, and the regional scale landscape complexity influenced the species richness and abundance of species with different traits. It is especially

noteworthy that landscape simplification and agricultural intensification affected the same trait category, omnivores, in different directions. Contradictory findings like this, if common, will make it hard to predict the future changes in community composition under agricultural intensification, because landscape simplification and increased yields often go hand in hand. According to our results, organic farming does not compensate for changes in ground beetle trait composition related to landscape changes or agricultural intensification, since no trait group was affected by farming practice. Besides, no trait category was promoted by heterogeneous landscapes, which stands in contrast to a number of earlier studies. Changes in community composition may potentially have effects on ecosystem functions and services. This implies that not only species richness or abundance, but also the trait composition of the communities delivering ecosystem services, may need to be taken into account in management and conservation of arable ecosystems under intensification.

(Paper IV)
The landscape study of the impact of flying specialist and ground-dwelling generalist predators is one of the first studies to assess if and how the relative impact of different predator groups vary in simple and complex arable landscapes across regions. We found that both flying and ground-dwelling predators reduce aphid densities and population growth rate in Skåne, resulting in approximately 14 times more aphids in plots where predators were excluded than in open plots. We also found that the combined effect of both predator groups were greater than the contribution of generalist and specialist predators each on their own. We did not find any differences in biological control in simple or complex landscapes, indicating that in our study system, intra-guild interactions (positive or negative) are not affected by landscape complexity. If naturally occurring predators can reduce aphids to as low numbers as we have shown in our study, yield loss is negligible and there is no need for pesticide applications.

9 Future challenges

An issue of intensification that would be interesting to investigate is the timing and frequency of disturbances in cereal fields. The disturbance regime will affect the time when certain habitats or resources are available to organisms, and at what life-stage organisms are affected. Studying these disturbances in more detail can help us understand which species or groups that are likely to increase or decline in agricultural landscapes.

It would also be useful to combine different methods to get a better overall picture. It would for instance be interesting to combine studies using molecular methods of prey detection in predators with biological control experiments, to get a better understanding of which predators are actually doing the job.

Much more work on intraguild interactions and predation in particular is needed. Food webs, even in such simplified ecosystem as cereal fields, are still almost unexplored. Information on intra-guild interactions could help explaining some of the differences in pest control efficiency between farming systems and landscapes and allow us to predict the outcome of management actions.

Finally, studying the variation in traits between organic and conventional farms, or in contrasting landscapes, could help us reach a better understanding of arable communities. It would for instance be interesting to know if the percentage of winged individuals of dimorphic species is higher in more disturbed fields, and what implication that would have for us studying conservation and ecosystem services.

> "I must detain you no longer, there is much to be done"
> (Southwood, 1977).

References

Aavik, T. and Liira, J. (2010). Quantifying the effects of organic farming, field boundary type and landscape structure on the vegetation of field boundaries. *Agriculture, Ecosystems and Environment* 135: 178-186.

Ahnström, J. (2009) *Farmland biodiversity- in the hands and minds of farmers. Effects of landscape structure, management and the farmer's interest in nature.* Doctoral thesis, Swedish University of Agricultural Sciences.

Baudry, J., Burel, F., Thenail, C. and Le Coeur, D. (2000) A holistic landscape ecology study of the interactions between farming activities and ecological patterns in Brittany, France. *Landscape and Urban Planning* 50: 119-128.

Bengtsson, J., Ahnström, J. and Weibull, A-C. (2005) The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* 42: 261-269.

Benton, T.G., Bryant, D.M., Cole, L. and Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* 39: 673-687.

Benton, T.G., Vickery, J.A. and Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182-188.

Bianchi, F.J.J.A., Booij, C.J.H. and Tscharntke, T. (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society Series B.* 273: 1715-1727.

Bibby, C.J., Burgess, N.D. and Hill, D.A. (1992) *Bird Census Techniques*. Academic Press Limited, London.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards. M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. and Kunin, W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313: 351-354.

Bilde, T. and Toft, S. (1997) Consumption by carabid beetles of three cereal aphid species relative to other prey types. *Entomophaga* 42: 21-32.

Blake, S., Foster, G.N., Eyre, M.D. and Luff, M.L. (1994) Effects of habitat type and grassland management on the size distribution of carabid beetles. *Pedobiologia* 38: 502-512.

Caballero López, B. (2009) *Arthropod diversity in agro-ecosystems: the effects of landscape, management and assembly of weed communities*. Doctoral thesis. Universitat de Barcelona.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. and Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology* 37: 771-788.

Chambers, R.J., Sunderland, K.D., Wyatt, I.J. and Vickerman, G.P. (1983) The effects of predator exclusion and caging on cereal aphids in winter wheat. *Journal of Applied Ecology* 20: 209-224.

Chiverton, P.A. (1986) Predator density manipulation and its effects on populations of *Rhopalosiphum padi* (Hom.: Aphididae) in spring barley. *Annals of Applied Biology* 109: 49-60.

Chiverton, P.A. (1987) Predation of *Rhopalosiphum padi* (Homoptera: Aphididae) by polyphagous predatory arthropods during the aphids' pre-peak period in spring barley. *Annals of Applied Biology* 111: 257-269.

Chiverton, P.A. and Sotherton, N.W. (1991) The effect of beneficial arthropods of the exclusion of herbicides from cereal crop edges. *Journal of Applied Ecology* 28: 1027-1039.

Colfer, R.G. and Rosenheim, J.A. (2001) Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* 126: 292-304.

Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M. and Chaney, K. (2002) Influence of beetle banks on cereal aphid predation in winter wheat. *Agriculture, Ecosystems and Environment* 93: 337-350.

Costamanga, A.C. and Landis, D.A. (2006) Predators excert top-down control of soybean aphid across a gradient of agricultural management systems. Ecological Applications 16: 1619-1628.

Counsil Regulation (EC) No 834/2007.

Ewers, R.M and Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81: 117-142.

Diekötter, T., Wamser, S., Wolters, V. and Birkhofer, K. (2010) Landscape and management effects on structure and function of soil arthropod communities in winter wheat. *Agriculture, Ecosystems and Environment* 137: 108-112.

Donald, P.F., Green, R.E. and Heath M.F. (2001) Agricultural intensification and the collapse of Europe's farmland bird population. *Proceedings of the Royal Society Series B* 268: 25-29.

Dänhardt, J., Green, M., Lindström, Å., Rundlöf, M. and Smith, H.G. (2009) Farmland as stopover habitat for migrating birds-effects of organic farming and landscape structure. *Oikos* 119: 1114-1125.

Eggers, S., Unell, M. and Pärt, T. (2011) Autumn-sowing of cereals reduces breeding bird numbers in heterogeneous agricultural landscapes. *Biological conservation* 144: 1137-1144.

Fischer, C., Flohre, A., Clement, L.W., Batáry, P., Weisser, W.W., Tscharntke, T. and Thies, C. (2011) Mixed effects of landscape structure and farming practice on bird diversity. *Agriculture, Ecosystems and Environment* 141: 119-125.

Finke, D.L. and Denno, R.F. (2004) Predator diversity dampens trophic cascades. *Nature* 429: 407-410.

Finke, D.L. and Denno, R.F. (2005) Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8: 1299-1306.

Flohre, A., Rudnick, M., Traser, G., Tscharntke, T and Eggers, T. (2011) Does soil biota benefit from organic farming in complex vs. simple landscapes? *Agriculture, Ecosystems and Environment* 141: 210-214.

Fuller, R.J., Norton, L.R., Feber, R.E., Johnson, P.J., Chamberlain, D.E., Joys, A.C., Mathews, F., Stuart, R.C., Townsend, M.C., Manley, W.J., Wolfe, M.S., Macdonald, D.W. and Firbank, L.G. (2005) Benefits of organic farming to biodiversity vary among taxa. *Biology Letters* 1: 431-434.

Gabriel, D. and Tscharntke, T. (2007) Insect pollinated plants benefit from organic farming. *Agriculture, Environment and Ecosystems* 118: 43-48.

Gardiner, M.M., Landis, D.A., Gratton, C., DiFonzo, C.D., O'Neal, M., Chacon, J.M., Wayo, M.T., Schmidt, N.P., Mueller, E.E. and Heimpel, G.E. (2009) Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecological Applications* 19: 143-154.

Gärdenfors, U. (eds) (2010) *The 2010 red list of Swedish species*. Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Hallqvist, H. (1991) Bekämpningströsklar för havrebladlus (Rhopalosiphum padi) i vårsäd-resultat från mellansverige. *32nd Swedish Crop Protection Conference*. Swedish University of Agricultural Sciences. (Summary in English)

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V. and Evans, A.D. (2005) Does organic farming benefit biodiversity? *Biological conservation* 122: 113-130.

Holland, J.M. and Luff, M.L. (2000) The effects of agricultural practices on Carabidae in temperate agroecosystems. *Integrated Pest Management Reviews* 5: 109-129.

Holland, J.M. and Reynolds, C.J.M. (2003) The impact of soil cultivation on arthropod emergence on arable land. *Pedobiologia* 47: 181-191.

Holland, J.M., Birkett, T. and Southway, S. (2009) Contrasting the farm-scale spatio-temporal dynamics of boundary and field overwintering predatory beetles in arable crops. *BioControl* 54: 19-33.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. and Tscharntke, T. (2007) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology* 44: 41-49.

Honek, A. (1991) Environment stress, plant quality and abundance of cereal aphids (Hom., Aphididae) on winter wheat. *Journal of Applied Entomology* 112: 65-70.

Kleijn, D. and Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40: 947-969.

Koss, A.M. and Snyder, W.E. (2005) Alternative prey disrupt biological control by a guild of generalist predators. *Biological Control* 32: 243-251.

Kotze, D.J. and O'Hara, R.B. (2003) Species decline-but why? Explanations of carabid beetles (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135: 138-148.

Kromp, B. (1989) Carabid beetle communities (Carabidae, Coleoptera) in biologically and conventionally farmed agroecosystems. *Agriculture, Ecosystems and Environment* 27: 241-251.

Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficiency, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment* 74: 187-228.

Landis, D.A., Menalled, F.D., Costamanga, A.C. and Wilkinson, T.K. (2005) Manipulating plant resources to enhance beneficial artropods in agricultural landscapes. *Weed Science* 53: 902-908.

Lang, A. (2003) Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. *Oecologia* 134: 144-153.

Langfof, M., Gathmann, A., Poehling, H-M. and Meyhöfer, R. (2003) Impact of insecticide drift on aphids and their parasitoids; residual toxicity, persistence and recolonization. *Agriculture, Ecosystems and Environment* 94: 265-274.

Larsson, H. (2005) A crop loss model and economic threshold for the grain aphid, Sitobion avenae (F.), in winter wheat in southern Sweden. *Crop protection* 24: 397-405.

Millennium Ecosystem Assessment (2003) *Ecosystems and human well-being: current state and trends assessment*. Island Press, Washington D.C., USA.

Natural England. (2010) *ELS handbook 3rd edition*. http://www.naturalengland.org.uk

Ninkovic, V., Glinwood, R. and Dahlin, I. (2009) Weed-barley interactions affect plant acceptance by aphids in laboratory and field experiment. *Entomologia Experimentalis et Applicata* 133: 38-45.

Östman, Ö., Ekbom, B. and Bengtsson, J. (2001) Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology* 2: 365-371.

Östman, Ö. (2004) The relative effects of natural enemy abundance and alternative prey abundance on aphid predation rates. *Biological Control* 30: 281-287.

Östman, Ö. (2005) Asymchronous temporal variation among sites in condition of two carabid species. *Ecological Entomology* 30: 63-69.

Plant Protection Centre. Swedish Board of Agriculture http://www.sjv.se/vsc

Prasad, R. and Snyder, W.E. (2006) Polyphagy complicates conservation biological control that targets generalist predators.Journal of Applied Ecology 43: 343-352.

Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharntke, T. and Wolters, V. (2005) Landscape context of organic and conventional farms: Influence on carabid beetle diversity. *Agriculture, Ecosystems and Environment* 108: 165-174.

Piha, M., Tiainen, J., Holopainen, J. and Vepsäläinen, V. (2007). Effects of land-use and landscape characteristics on avian diversity and abundance in a boreal agricultural landscape with organic and conventional farms. *Biological Conservation* 140: 50-61.

Robinson, R. and Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39: 157-176.

Roschewitz, I., Gabriel, D., Tscharntke, T. and Thies, C. (2005) The effects of landscape complexity on arable wed species diversity in organic and conventional farming. *Journal of Applied Ecology* 42: 873-882.

Rundlöf, M. and Smith, H.G. (2006) The effect of organic farming on butterfly diversity depends on landscape context. *Journal of Applied Ecology* 43: 1121-1127.

Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. and Tscharntke, T. (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of London Series B* 270: 1905-1909.

Snyder, W.E. and Ives, A.R. (2003) Interactions between specialist and generalist enemies: parasitoids, predators and pea aphid biocontrol. *Ecology* 84: 91-107.

Snyder, W.E., Snyder, G.B., Finke, D.L. and Straub, C.S. (2006) Predator biodiversity strengthens herbivore suppression. *Ecology Letters* 9: 789-796.

Southwood, T.R.E. (1977) Habitat, the template for ecological strategies? *Journal of Animal Ecology* 46: 337-365.

Straub, C.S., Finke, D.L. and Snyder, W.E. (2008) Are the conservation of natural enemy diversity and biological control compatible goals? *Biological Control* 45: 225-237.

Symondson, W.O.C., Sunderland, K.D. and Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47: 561-94.

Taheri, S., Razmjou, J. and Rastegari, N. (2010) Fecundity and development rate of the bird cherry-oat aphids (Rhopalosiphum padi (L) (Hom: Aphididae) on six wheat cultivars. *Plant Protection Science* 46: 72-78.

Thiele, H.-U. (1977) *Carabid beetles in their environments. A study on habitat selection by adaptations in the physiology and behavior.* Springer-Verlag, Berlin and New York.

Thies, C., Steffan-Dewenter, I. and Tscharntke, T. (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101: 18-25.

Thies, C., Roschewitz, I. and Tscharntke, T. (2005) The landscape context of cereal aphid-parasitoid interactions. *Proceedings of the Royal Society Series B.* 272: 203-210.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. and Polansky, S. (2002) Agricultural sustainability and intensive production practices. *Nature* 418: 671-676.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. and Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity- ecosystem service management. *Ecology Letters* 8: 857-874.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhous, S. and Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control* 43: 294-309.

Westphal, C., Steffan-Dewenter, I. and Tscharntke, T. (2003) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology* 46: 187-193.

Wiktelius, S. (1984) Studies on population development on the primary host and spring migration of Rhopalosiphum padi (L.) (Hom., Aphididae). *Zeitschrift für Angewandte Entomologie* 97: 217-222.

Wiktelius, S. and Ekbom, B.S. (1985) Aphids in spring sown cereals in central Sweden. Abundance and distribution 1980-1983. *Zeitschrift für Angewandte Entomologie* 100: 8-16.

Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C. and Bradbyry, R.B. (1999) A review of the abundance and diversity of invertebrate and plants foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems and Environment* 75: 13-30.

Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T. and Pärt, T. (2006) Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. *Journal of Applied Ecology* 43: 1110-1120.

Acknowledgements

Tack!

Riccardo för dina insikter om insekter, statistik, jordlöpare, burförsök och allt annat mellan himmel och jord. Vi tycker olika om det mesta, men vi tycker ju något i alla fall och det är väl det viktigaste? Tack för att du lärt mig så mycket om hur forskningsvärlden fungerar och vikten av samarbeten och nätverk, och för att du är otroligt strukturerad och vet hur man ska skriva en publicerbar artikel. Och tack för att du inte blivit frustrerad på mig när jag varit frustrerad på mig, och dig… Tack också för att du har gett mig en massa döda rävar, kastat måsar och hjälpt mig att träna hunden. Tack för att du vågar blanda allvar och skoj, privatliv och forskning så man blir helt yr i huvudet. Jag känner att jag nu börjar få lite ordning på dig så att jag tryggt kan lämna dig vidare till nästa kull doktorander!

Janne för din stora obotliga optimism, stora kunskap om landskapen och metasamhällena! Du visar upp en perfekt kombination av hardcore forskning och kreativitet (men jag måste väl erkänna att jag aldrig fattat vad det är som är så himla intressant med vattenloppor?). Tack för att du faktiskt pratar lika mycket och minst lika förvirrat som jag! Tack för alla uppmuntrande ord, sms och bilder på nallen Blixa… Och tack för erbjudandet om choklad vid mitt första seminarium, du vet hur man tar hand om en nervös doktorand! Tack för alla musikfiler du har skickat under åren och för sällskapet på EN på Berns. Tack också för att det är så roligt och givande att diskutera med dig, speciellt på någon pub i Europa med lite rödvin som sällskap.

Mina handledare är yin-yang, bad cop- good cop, varsin sida av samma mynt, den mjuka och den hårda, den kategoriska och den visionära, och ofta tvärt om… Och bevisar sanningen i ”om två personer tycker samma sak är en av dem överflödig"! Ni är outtröttliga, outbytliga och omåttligt omtyckta!

Mina doktorandvänner och ex-doktorandvänner

Tack alla för diskussioner vid litteraturseminarium, kurser, workshops, pubar, fikor och luncher.

Erik Ö för att du aldrig blir arg när jag kommer och avbryter dig med alla mina frågor. Och för att du alltid ställer jobbiga frågor tillbaka. För att du alltid tar dig tid att hjälpa mig med allt mellan himmel och jord, och för att du alltid ler när du gör det, i alla fall på ytan... För att du kan förklara det som mina handledare misslyckas med att förklara. Du har varit som min tredje handledare, och jag hoppas att jag någongång kan återgälda allt du gjort för mig.

Jens Å för att du orkar lyssna på mina långa förvirrade utläggningar och nästan kontinuerliga gnällande, att jag "får" komma in på ditt rum och beklaga mig i 10 min med jämna mellanrum… För att du håller mig uppdaterad på de senaste rönen inom hundpsykologin… Och för att du slog mig i 100-armhävningar på ett förträffligt sätt. Men jag har inte gett upp än…

Johan A för att du vet när jag behöver en klapp på armen när du möter mig i korridoren, eller en kram om det är riktigt allvarligt, och för att du tar dig tid att prata med mig när jag behöver prata. Det är alltid så roligt att prata med dig! Och tack för hjälpen nu i slutspurten, det hade inte gått utan dig!

Cecilia R för att du pratar hundar och kampsport med mig, och att jag får sno dina SAS/R-koder. För att du alltid är så lugn och arg. Tack för sällskapet och samtalen på Argentinaresan!

Ola L för att du är så himla lugn och smart och alltid säger tvärt om vad jag vill att du ska säga. Utom när du säger precis rätt saker, som jag då önskar att jag vore smart nog att komma på själv. Min avhandling hade blivit klar mycket snabbare om jag fått åka tåg till Trondheim med dig några gånger till! Tusen tack för all hjälp, jag är skyldig dig många öl nu…

Matt H för att vi är så bra på att snacka skit och gnälla av oss ihop! Och för att dina modeller får mina statistikproblem att kännas försvinnande små…

Anna-Karin K för stödet under slutspurten och med papper 3! Och för att du gjort en så fin avhandling som verkligen inspirerat mig.

Karna H för allt stöd och pepp nu under slutspurten! För att du alltid är så lugn och analytisk. Och för sällskapet till trädgårdsmässan, Richard är i chock fortfarande…

Karin A för att du tar dig tid att hjälpa mig med att alltifrån att låna ut nycklar när jag låst mig ute till att svara på "Ska det vara såhär?". Och tack för hjälpen med kappan!
Dennis J för hjälpen på sluttampen och under resans gång.
Freddy M thanks for sharing the room with me, and being one step ahead of me now at the end, making me work harder.
Georg A för sällskap på MODS-möten och i framförallt för alla promenader, middagar och låånga workshopstimmar i Göttingen, och för att du är så himla rolig och cool! Jag önskar att det inte var så långt till Lund….
Maj R för att du är så snäll och alltid hjälper mig, med SAS eller med att piffa håret. För att du hjälpt mig när mina handledare varit jobbiga mot mig, för att dom lyssnar på dig när jag gett upp!
Martin K för att du pratar minst lika fort och mycket som jag och om minst lika konstiga saker. För att du alltid sänker nivån på alla samtal så att t.o.m. jag fattar…
Sandra Ö för att du alltid tar dig tid att hjälpa mig och för att du artbestämt mina spindlar. Du var den första doktorand jag träffade när jag sökte jobbet, och det fick mig att vara extra säker på att jag ville ha tjänsten!
Martin P for spending so much time helping me with statistics and parasitoid rearing, and for never saying no thanks to a beer. I miss you!
Karin H för att du alltid säger konstigare saker än jag, och för att du hjälper mig att ta tag i saker och få struktur på mina förvirrade tankar. Och för att du hjälper mig piffa när det är panik!
Alla övriga med-doktorander, ingen nämnd, ingen glömd. Lycka till nu alla ni andra doktorander som har ert roliga kvar!

Övriga kollegor!
För alla roliga samtal och fester.
Robert G för alla pratstunder, mail, drömtydningar, självsförsvars-diskussioner, bildidéer och konsertsällskap. Och på det mer vetenskapliga planet, tack för privatlektionerna i både bladlusanatomi och parasitoidekologi.
Tomas R för att du orka svara på alla mina frågor och inte blir galen av mitt babblande. ("Jag har fått den information jag behöver"). Jag fattar inte hur man kan se så glad ut jämt som du gör! Och tack för att du en gång trodde att jag var med i en paradorkester, det var en av de underligaste kommentarer jag någonsin fått! Tack också för alla gånger du slagit mig i badminton, det är ett rent nöje att se dig vinna!
Tomas P för kreativa samtal och visa ord. Och onödigt prat om musik förstås.

Ben W for always starting weird conversations, and for helping me with the "Monet"…
Sönke E för att du alltid hjälper mig och tar dig tid och lär mig en massa saker om fåglarnas liv och leverne.
Peter T för de trevliga medarbetarsamtalen och för att du bryr det om hur det går för oss doktorander.
Anna L för att du bidrar med en massa kunskap om hur man hanterar manuskript och annat som är livsnödvändig för en doktorand att veta. Och för att du så öppenhjärtigt berättar om ditt liv och höjer taket på jobbet avsevärt.
Helena B för trevliga pratstunder och möten i forskarskolan.
Barbara E för att du utan pardon säger vad du tycker är dåligt med vad man gör, eller bra för den delen om man nu faktiskt skulle ha fått till nåt sånt. Och tack för litteraturlistan jag fick första tiden som doktorand, den var till stor hjälp! Och för den väldigt lärorika kursen om parasitoider!
Göran N, Martin S och **Mats J** för att ni orkar med mina smått imbecilla småkrypsfrågor.
Åke L som varit den som fått små "presenter" att artbestämma med jämna mellanrum. Jag hoppas jag blir lika lärd/skadad som du någon dag! Tack också för det förträffliga nedsågandet av granar. Och tack för samarbetet med halensis-artikeln!
Lena L, **Hillevi S** och **Berit L** för all hjälp med alla papper.
Bladlusgänget för alla trevliga fikaraster och luncher och för att ni orkat med mina frågor och hjälpt mig med praktiska detaljer.
Det är så skönt att jobba i Ekologishuset, man känner sig alltid omgiven av vänner!

My dear friends in AGRIPOPES
For endless conversations at pubs, at meetings all over Europe or via email.
Sebastian H for taking care of me in Göttingen, for showing me the secret place by the pond, and for trusting me to be you friend.
Flavia G for being very patient with me and always giving me quick answers to my many questions, and for teaching me how to play Regenworms…
Chris D for the patience with me on the traits-matter, for supporting emails and for trait discussions. And for beating me in snooker in an underground metal pub in Göttingen.
Lars W for endless support and for designing a wonderful t-shirt motif.
Viola H for nice parasitoid collaboration.

The "elderly" gentlemen in Agripopes for support and discussions, especially **Carsten T**, **Teja T**, **Jaan L** and **András B**.

Mina fält- och labassistenter och exjobbare

Sandra L för hjälpen med fältarbetet 2007 och för ditt fina exjobb. Och för all hjälp med artiklarna! Lycka till med ditt eget doktorerande!
Johan B för att du jobbat och slitigt åt mig i två år. Det jag inte har koll på har du full koll på, tack!
Frida H, Pelle B och **Henrik C** för allt slit fältsäsongen 2008.
Linnea B och **Anders J** för exjobben 2009.
Carol H och **Solveig** för att ni lärt mig så mycket om jordlöpare och andra kryp.
Joel H för all hjälp med de många tusen skalbaggarna, de många tusen frågorna och halensis-artikeln.
Ola B och **Sophie H** för insektssortering och artbestämning.
Maya J för hjälpen med att slutföra arbetet med traitsen och för räknandet av skalbaggar.
Ged M för hjälpen med spindlarna, och andra småkryp som jag hittar.

Mina nära och kära.

Peter för att du är min bäste vän och för att du alltid orkar lyssna på mitt gnäll. Och för att du ger mig glass när jag är ute i fält, och rödvin när jag kommer in igen. För att du säger åt mig att ta det lugnt, med ganska arg röst ibland… Jag undrar hur många mil vi åkt bil ihop och hur många mil vi gått tillsammans?
Marit, du är den roligaste och smartaste person jag känner! Och jag saknar dig.
Peter & Anna för alla middagar, hundvakter, fester och livet i Solgläntan.
Sara & Jörgen för alla roliga fester, middagar och utflykter.
Morgan & Elin för alla dödade fåglar och mysiga frukostar.
Jari & Lisen för trevliga fikor och sångstunder.
Sara U för allt hund-, hus-, bäbis- och doktorandprat.
Sophie G för alla uppmuntrande ord och långa promenader, och för att du visat att man kan mer än vad man själv tror.
Jhonny & Marie för alla fikor & underliga filmer.
Toni H för all djurskräckfilmstips!
Fredrik S för peppningarna i slutspurten! Jag hoppas att vi kan träffas och dricka whisky snart!
Mamma & pappa för att ni inte tycker att jag är alltför konstig som kommer hem och mest bara sover på bryggan… För att jag får låna stugan

och ta det lugnt eller jobba ostört. För att ni inte klagar på att jag inte har ett riktigt jobb… Jag har skrivit kappan så att du ska förstå mamma, så nu hoppas jag verkligen att du läser den!
Therése, Stefan, Marie, Ola och **Mats** för att ni ger mig perspektiv på tillvaron. För att ni finns där för lite småprat om allt och inget. Och tack Tirre för läsningen av kappan!
Tuva, Vilmer och **Daisy** (och bullen i ugnen också), mina syskonbarn som är djupt imponerade över mina fantastiska insektskunskaper och som ger mig tusen kramar och pussar och förkylningar varje gång vi ses. Jag är så stolt över er!
Blixa för att du tvingar ut mig på långa promenader när jag kan öva på föreläsningar, lösa problem, och komma på nya brillianta idéer…
Ulf för att du orkar med mig under de perioder jag är stressad och jobbigt. För att du ger mig prestationsångest över att jag tränar för lite, äter för onyttigt och är för okulturell. För att du inte bangar en fika eller hundpromenad. Och för att du är nog den enda person jag känner som aldrig sagt till mig att jag pratar för mycket. Tack för att du alltid är där i andra änden av telefonen.
Världens bästa **Alice och Paddy**, för att jag får låna er när jag behöver gosa lite eller vill gå på skogspromenad och dricka varm choklad. Tack för att ni får mig att aldrig glömma bort att livet är det som händer en helt vanlig onsdagskväll.
Richard! Du har gett mig allt stöd och all den uppmuntran jag behöver, och mer därtill! Du har låtit mig vara stressad, sur och frustrerad och gjort ditt bästa för att få mig i balans igen (Ett glas rött? Choklad? Ska vi såga ner ett träd?). Och du har gjort ditt bästa för att få mig att fokusera på avhandlingen när jag istället tänkt sätta igång att gräva ännu en rabatt eller städa en garderob. Tuysen puysar.

Kram till er alla!

Ett speciellt tack också till **Bo W S** för att du är den enda lärare som svurit och skrikit åt mig i samma mening ("Det ser du väl för i helvete att det inte är några grävarben!!") men som också gett mig en guldängel i gips och den finaste ekologikomplimang jag någonsin fått!

Och ett sista tack går till **Tommy L** som en gång sa att jag ställer frågor han inte trodde fanns, vilket jag ännu idag inte vet om det var menat som någonting bra eller dåligt. Men hur som helst tänker jag fortsätta med det länge till!