

# **Landscape and Farm Management Influence Generalist Predators**

**Effects on condition, abundance and biological control**

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## Abstract

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Chemical pest control is currently the dominant form of pest management against insect pests in agroecosystems, but has negative side effects. Biological control by specialist predators has been successful in greenhouses, but has not been successfully applied in agroecosystems. Generalist predators have features constraining them as control agents, but have one advantage: they can survive when pests are absent by feeding on alternative prey. In this thesis I have studied the influence of landscape structures and farm management on generalist predators and their predation on an aphid pest on cereals, *Rhopalosiphum padi*.

In accordance with theoretical predictions, predation on establishing aphids in spring was more important for the total aphid attack than predation during the aphid population growth phase. Predation on establishing aphids was higher on organic than conventional farms and highest in landscapes with abundant field margins and perennial crops. Predation during the population growth phase was, surprisingly, highest in simple landscapes, with no differences between organic and conventional farms.

The presence of alternative prey can result in decreasing predation of generalist predators on pests, and I show that this effect is scale-dependent. On a field scale, generalist predators were aggregated at high prey densities, and predator abundance was more important for predation on aphids than alternative prey abundance. Thus, the effect of alternative prey was larger on the generalist predator abundance than on the predators' diet. However, higher alternative prey abundance in complex landscapes may still have resulted in the observed lower predation rates on aphids in these landscapes during aphid population growth.

Condition of generalist predators, which often is food-limited, was better on organic farms and in landscapes with abundant field margins in a non-aphid year. Possibly because of an aphid outbreak, condition changed asynchronously between farms over three study years. The temporal and spatial environmental variation affected the condition of different species differently, which can be explained by the species' diet and habitat selectivity.

This thesis provides further evidence for earlier suggestions that more field margins and perennial crops in relation to annual crops increase alternative prey abundance and overwintering sites for the generalist predators and thereby their abundance, which can enhance biological control of cereal aphids.

*Keywords:* bird cherry-oat aphid, *Carabidae*, *Nabidae*, fitness, natural enemies, patch choice, selectivity, spatial-temporal variation.

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# Landskap och odlingssystem påverkar naturliga fiender till bladlöss

## Effekter på kondition, täthet och biologisk bekämpning

Idag används mestadels kemisk bekämpning, med negativa bieffekter, mot insektsangrepp i jordbruket. Biologisk bekämpning av naturliga fiender som är specialiserade på att äta endast en typ av skadeinsekt har varit framgångsrikt i växthus, men inte fungerat så bra i jordbruket. Naturliga fiender som inte är specialiserade på en typ av skadeinsekt, s.k. generalister, har flera egenskaper som begränsar deras möjligheter att bekämpa skadeinsekter, men de har en betydande fördel: de kan överleva även när skadeinsekten är borta genom att livnära sig på andra byten. De kan därför finnas i fälten när skadeinsekten kommer, och därmed hindra att populationen av skadeinsekten byggs upp. I denna avhandling har jag studerat hur landskapets utformning och olika odlingssystem (ekologiskt-konventionellt) påverkar generalistiska naturliga fiender och deras predation på havrebladlöss i korn.

Predationen på nyanlända bladlöss påverkade omfattningen av bladlusattacken i korn mer än predationen under bladlössens tillväxtfas. Predationen på nyanlända bladlöss var större på ekologiska gårdar än konventionella gårdar, och oberoende av odlingssystemet, högre i landskap där det fanns mycket åkerkanter och vallar. Under bladlössens tillväxtfas var predationen, förvånande nog, större i enkla landskap, och det var heller ingen skillnad i predation mellan odlingssystemen.

Att generalistiska naturliga fiender har alternativa byten till bladlöss kan orsaka en minskad predation på bladlössen, och jag visar att denna effekt beror på den rumsliga skalan. På fältskalan ansamlades de generalistiska naturliga fienderna där det sammanlagt fanns mest byten, men tätheten av generalistiska naturliga fiender var av större betydelse för predationen på bladlöss än mängden alternativa byten. Dock kan den större mängd alternativa byten som fanns i mosaikartade landskap orsakat den lägre predationen på bladlöss i dessa landskap under bladlössens tillväxtfas.

Konditionen av enskilda naturliga fiender, som antas vara födobegränsad (dvs. de skulle må bättre om det fanns mer föda), var högre på ekologiska gårdar och i landskap med mycket åkerkanter under ett år utan bladlöss. Men under ett år med mycket bladlöss så ändrades konditionen asynkront (olika) mellan gårdarna. Den tidsmässiga och rumsliga variationen i föda påverkade olika arter av naturliga fiender på olika sätt, vilket delvis kan förklaras med arternas olika födo- och platsval.

För att få en bättre biologisk bekämpning av havrebladlöss är det viktigt att det finns gott om alternativa byten och platser för övervintring åt de naturliga fienderna. Åkerkanter, vallar, och åkerholmar är exempel på platser där det finns mycket alternativa byten och där naturliga fiender kan övervintra. Användande av stallgödsel eller grüngödsling istället för konstgödsling samt avsaknad av kemiska bekämpningsmedel gynnar också de naturliga fienderna.

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# Appendix

## Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Östman, Ö. Ekbom, B. & Bengtsson, J. 2001. Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology* 2: 365-371.
- II. Östman, Ö. The relative effects of natural enemy abundance and alternative prey abundance on aphid predation rates in ephemeral agricultural habitats. (Submitted).
- III. Östman, Ö. & Ives, A.R. Scale-dependent interactions between two prey through a shared predator. (Submitted).
- IV. Östman, Ö. Ekbom, B. Bengtsson, J. & Weibull, A. 2001. Landscape complexity and farming practice influence the condition of polyphagous carabid beetles. *Ecological Applications* 11: 480-488.
- V. Östman, Ö. Spatial and temporal variation in condition and fecundity of two carabid species in agricultural landscapes in Sweden. (Manuscript).

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## Introduction

After the Second World War there have been large structural changes in agriculture in the developed world. Pesticides and inorganic fertilisers are used to increase the yields, and there have been substantial changes in landscape structure. Non-cropping habitats (*e.g.* island habitat, ditches) have been erased, and fields have become larger (Krebs *et al.*, 1999; Chamberlain *et al.*, 2000), which has transformed the agricultural landscape into a homogeneous landscape where only a few monoculture crops are grown. But these management and landscape changes have had negative effects such as nutrient leaching, pesticide contamination, species extinction, and evolution of pesticide resistance because of continuous use of pesticides (*e.g.* French-Constant *et al.*, 2000).

During the last decades both consumers and politicians have called for food produced in an environmentally sound manner. Among the requirements is the reduction of insecticides, which implies that farmers must rely more on natural enemies for control of insect pests. Natural enemies have successfully been introduced into greenhouses to control pests since the 1970's (*e.g.* van Lenteren & Woets, 1988), but biological control has not been incorporated into pest management strategies in open agricultural ecosystems to the same extent. The basic problem is a lack of knowledge about the factors determining the efficacy of biological control agents (Lewis *et al.*, 1997).

The successful biological control management in greenhouses predominantly relies on specialist predators and parasitoids. Generalist predators have several life-history traits constraining their efficiency as biological control agents. They often produce few offspring per pest consumed and their development time from egg to adult is long, they often have low maximum predation rates, and may eat prey other than the pest (*i.e.* alternative prey). Thus, their numerical response to the pest is weak and slow, each predator consumes few pests, and they may be unable to aggregate to areas of high pest densities. All these constraints act to decouple their population dynamics from the pest, and they usually cannot control pests at a constant low level (Sabelis, 1992, but see Symondson *et al.*, 2002a).

Generalist natural enemies, however, have an advantage that specialist natural enemies lack: generalist natural enemy abundance can be sustained when there are no pests, by consumption of alternative prey. Hence, generalist natural enemies can be present and predate on the pests also at low numbers of pests, thereby preventing the pest from establishing (Cheng & Kareiva, 1999; Symondson *et al.*, 2002b). This can be especially important in agroecosystems where much of the land is ephemeral, which disrupts the action of specialist natural enemies. Generalist natural enemies, on the other hand, can be present in the fields before pests appear. In different agroecosystems, generalist predators have been shown to have an impact on the pest abundance (Ekbohm *et al.*, 1992; Settle *et al.*, 1996; Symondson *et al.*, 2002a, b), preventing or delaying an attack.

Because of the low capacity of generalist predators for behavioural and numerical responses to a single prey, it is important for biological control that generalist natural enemy abundance is high when the first pests appear in crop

habitats. This can be ensured by rapid colonisation into the crop after a disturbance (such as tillage, mowing) (Wissingner, 1997), or a high alternative prey abundance when the pest is absent (Settle *et al.*, 1996). Natural enemy abundance in cropping habitats, of both generalists and specialists, has been shown to be dependent on the quality of the field margins (Thomas *et al.*, 1991, 1992; Corbett & Rosenheim, 1996; Denys & Tschardtke, 2001), as well as the configuration, composition and structure of non-cropping habitats in the landscape (Lys *et al.*, 1994; Marino & Landis, 1996; Thies & Tschardtke, 1999; Kruess & Tschardtke, 2000; Landis *et al.*, 2000). Different farming practices have been shown to affect generalist (and specialist) natural enemy abundance within the cropping habitats. Insecticides can kill natural enemies, or affect the abundance or quality of their prey (*e.g.* Wallin *et al.*, 1992). Herbicides affect vegetation structure in the crops and thereby prey diversity (Samu *et al.*, 1999). The use of manure or inorganic fertilisers affects the abundance of alternative prey (Settle *et al.*, 1996; Samu *et al.*, 1999; Kromp, 1999). Tillage regimes affect the overwintering survival of ground-living predators (Caracamo *et al.*, 1995; Clark *et al.*, 1997; Kromp, 1999; Samu *et al.*, 1999). In organic farming pesticides are abandoned and manure is used instead of inorganic fertilisers. In general, organically managed fields have densities and diversities of generalist natural enemies higher than conventional managed fields (Kromp, 1989; Moreby *et al.*, 1994; Drinkwater *et al.*, 1995; Moreby & Sotherton, 1997). Thus, adopting a landscape- and farm management perspective for biological control schemes in agroecosystems may influence generalist natural enemies and enhance biological control by generalist natural enemies.

For more efficient biological control by generalist predators it is relevant to ask what factors generally regulate the population density of such predators. Many studies suggest that adult arthropods that are generalist predators are food-limited, *i.e.* survival or fecundity is enhanced with experimentally added food (Wise, 1975; Lenski, 1984; Pearson & Knisely, 1985; Juliano, 1986; Ernsting *et al.*, 1992; Bommarco, 1998a; Bilde & Toft, 1998). Increased food abundance does not necessarily lead to increased population density, but higher population growth rates with increasing food abundance has been observed (Wise, 1975; Lenski, 1984; Symondson *et al.*, 2002a). For several generalist predator species there is spatial variation in the degree of food limitation; fecundity, condition, or survival of individuals differs between sites (Pearson & Knisely, 1985; Juliano, 1986; Ernsting *et al.*, 1992; Bommarco, 1998b, 1999). This suggests that habitat quality and landscape complexity is important for the value of fitness-related traits, and thereby possibly also population dynamics.

## **Aims of the thesis**

Earlier experiments have shown that generalist predators decrease the peak abundance of *Rhopalosiphum padi* in cereals (Chiverton, 1986), and negative correlations between generalist predator abundance and *R. padi* peak abundance have been found among fields (Ekbohm & Wikteliu, 1985). Theoretical analyses of the *R. padi* - cereal system have suggested that it is the predation on aphids at the

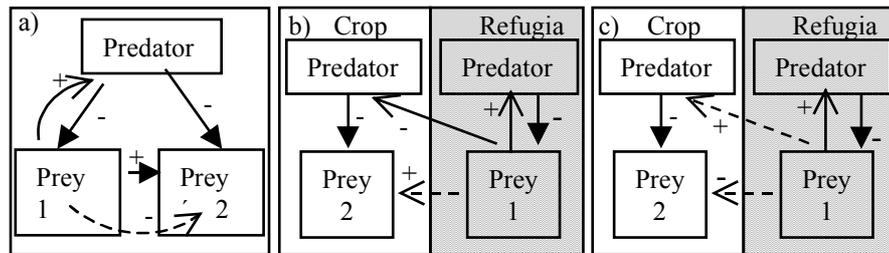
onset of an attack that is important for decreasing the total attack (Ekbohm *et al.*, 1992). There is, however, no empirical evidence that generalist predators actually cause the spatial variation in peak aphid abundance, or that the early predation is more important than the predation later on. Bommarco (1998b) showed that fecundity and condition of a generalist predator were higher on organic farms in complex landscapes, but could not separate the effects of landscape and farming system. This thesis aims to study the effect of landscape and farm management on condition of individual generalist predators, their abundance and importance as biological agents. I have specifically asked:

1. Do generalist natural predators have an impact on *R. padi* in cereal fields, and can the action of generalist predators explain differences in *R. padi* abundance among sites? This was examined in a field experiment with predator enclosures on farms in different landscapes. (*Paper I*)
2. How do landscape features surrounding the crop fields and farm management influence the natural enemies' predation rates on *R. padi* in cereals? This was examined by correlating predation rates on aphids with landscape parameters and farm management (*Papers I, II*)
3. Does the abundance of alternative prey species affect the predation rate of generalist predators on aphids (the pest)? Is there an indirect interaction between prey species confounding the putative positive relationship between generalist natural enemy abundance and pest predation rate? (*Papers II, III*)
4. How does habitat selection by generalist predators affect predation rates? Do indirect interactions between pest and alternative prey depend on spatial scale, and what effects do non-crop habitats and differences in farm managements have on generalist predator abundance in crop fields? Question 3 and 4 were examined by studying predation rates on aphids at different abundances of alternative prey, and by studying how predator abundance changed with different prey densities, and along landscape gradients and between farm managements (*Papers II, III*)
5. Does the degree of food-limitation of carabids, common generalist predators, depend on both landscape features and farm management, and is the degree of food-limitation constant, or does it change between farms over time? (*Paper IV, V*)
6. Is the degree of food-limitation correlated between species among farms, *i.e.* do species respond similarly to temporal and spatial variation in the environment? Question 5 and 6 were examined by measuring condition and fecundity of different generalist predator species at farms with different landscape structure and farm management over three years (*Paper IV, V*)

These topics range from the level of individuals to the level of ecological guilds, but they all fall within the framework of landscape ecology. The subsequent analyses of these questions show to what extent a landscape- and farm management perspective can be used to understand the applied problem of pest management, and hopefully bring it closer to a sustainable solution.

## Theoretical background

In open agroecosystems the distribution of alternative prey and refugia is important for the predation on pests by generalist predators (Wissinger, 1997; Cheng & Kareiva, 1999; Symondson *et al.*, 2002b), as well as reproduction and survival of individual predators.



*Fig. 1.* Indirect interactions from changes in abundance of one prey species (Prey 1) on a second prey species (Prey 2) that are equally profitable in three different scenarios. The signs indicate the sign of the interaction, solid lines represent direct interactions, whereas hatched lines represents indirect interactions. A compact arrow indicates an interaction on a short time scale, whereas a simple arrow indicates a longer time scale (*i.e.* for numerical and aggregate responses to occur). (a) Two prey species and a predator in one patch: an increase in Prey 1 temporarily results in lower predation on Prey 2 (substitution). In a longer run predator abundance increases because of increased reproduction or immigration, which increases predation on Prey 2 (*i.e.* apparent competition). (b) Prey species are divided in space: an increase in Prey 1 causes predators to aggregate in that patch, resulting in a lower predation on Prey 2 in the other patch. (c) As in (b) but an increase in Prey 1 increases the predator abundance in that patch through reproduction, which also increases predator dispersal to the patches adjacent to patch 1, resulting in increased predation on Prey 2.

### Alternative prey

The abundance of alternative prey affects the diet selection of generalist predators in the short run, and in the long run generalist predator density. Depending on the profitability of different prey (nutrient or energy intake per handling time), the probability of an attack on one prey species changes with the abundance of the more profitable prey (Murdoch & Oaten, 1975; Krebs *et al.*, 1977; Stephens & Krebs, 1986). Unless a prey is very profitable, an increase in the abundance of a second prey species can increase the predators' total handling time of the second prey, thereby decreasing time available for searching for the first prey. This can decrease predation rates on the first prey (substitution), or the predators may even exclude it from the diet (switching; this only occurs if the second prey is more profitable than the first). This behavioural response to variation in the abundance of different prey can result in a positive indirect interaction between prey species in the short run, *i.e.* an increase in one prey has a positive effect on the others (Fig. 1a; Murdoch & Oaten, 1975; Krebs *et al.*, 1977; Stephens & Krebs, 1986; Crawley, 1992). The increase in abundance of one prey species may, in a longer perspective, increase predator reproduction (numerical response), which is likely to result in increased predation on other prey sharing the predators. This results in a negative indirect interaction between the prey species (*i.e.* apparent competition;

Fig. 1a; Holt, 1977; Holt & Lawton, 1994). Moreover, on an intermediate time scale the increase in abundance of one prey may also attract more predators (aggregate response). Again, this may cause a negative indirect interaction between the prey species (Fig. 1a; Holt and Lawton, 1994; Evans & England, 1996).

## Refugia

Animals may select diets (prey species) within habitats on a short time scale, but select habitats on a landscape scale on an intermediate time scale (Brown & Morgan, 1995). If predators select habitat according to prey abundance, *i.e.* they aggregate at high prey densities, an increase in abundance of one prey in a patch may cause predators to aggregate in this patch. As mentioned in the previous section this can result in a negative indirect interaction between prey species within a patch (Fig. 1a), but it also results in decreasing predator abundance and predation rates in other patches. Thus, there can be a positive indirect interaction between prey species among patches (Fig. 1b; Holt & Lawton, 1994, Brown & Morgan, 1995, Morgan *et al.*, 1997).

Although predator density is usually higher at high prey densities, there can be a net dispersal of predators from patches with high prey densities to patches with lower densities because of factors other than prey abundance. This results in higher predator densities than expected from the prey abundance alone and also higher predation rates in the adjacent habitats. Thus, in this case there is a negative indirect interaction between prey species among patches (Fig. 1c; Pulliam, 1988; Polis *et al.*, 1997). Factors other than prey abundance that may affect predator abundance can be related to predator survival if they cannot survive in one habitat only. For example, the predator abundance in an annual crop may be dependent on the amount of refugia as a source of immigration, *i.e.* there is source-sink dynamics (Pulliam, 1988; Wissinger, 1997) over the season.

## Spatial variation in food-limitation of generalist predators

According to the theory of ideal free distribution (Fretwell & Lucas, 1970; Rosenzweig, 1991) spatial differences in fitness (reproduction success and survival) of individuals should not be persistent over time. At sites where individuals have high fecundity and survival, and hence population growth rate is high, more individuals would share the resources over time. This would reduce individual fecundity and survival, and population growth rate, and the fecundity and survival would be equal for all individuals in the long run. That is, the differences in the degree of food-limitation will disappear between sites.

There are several possible reasons why there is spatial variation in fitness-related traits. Population regulation may occur during the larval stage, or population density is limited by predation or habitats (*e.g.* refugia) (Lövei & Sunderland, 1996; Holland, 2002). Hence, an increased food supply for adult individuals does not necessarily lead to increased population densities, or has a very small effect on the density-dependence on the adults, and the spatial variation in the degree of food-limitation can remain. This implies that the degree of food-limitation only reflects local resource availability. There may also be net dispersal from areas with

high fitness to areas with lower fitness, *i.e.* similar to a source-sink population structure (Pulliam, 1988). The net dispersal from high quality areas could be because of interference between predators or because predators cannot recognise high quality areas (Ranta *et al.*, 2000). Another possibility is asynchronous temporal variation in fitness-related traits between sites. That is, a year could be relatively good at one site and relatively bad at another site, but the next year the situation may be reversed because of asynchronous changes in the environment or asynchronous changes in population densities.

## Study organisms

### *Rhopalosiphum padi* (L.) (bird cherry-oat aphid) (Paper I)

In Sweden, and throughout Europe, *R. padi* is an important pest species in cereal fields. It primarily infests spring cereals in Sweden, but also winter cereals in other parts of Europe (Leather *et al.*, 1989). If not treated with insecticides, *R. padi* causes up to a 15% decrease in yield (Leather *et al.*, 1989, Hallqvist, 1991; Hansen, 2000).

The life cycle of *R. padi* in Sweden is shown in Fig. 2. The magnitude of the spring migration from the winter host to cereal fields is the most important factor affecting *R. padi* abundance in cereal fields (Wikteliu, 1987; Ekbom *et al.*, 1992). The abundance of *R. padi* in cereals is highly variable between years, at least in Northern Europe. The reasons for these fluctuations are not known, but high abundances seldom occur in subsequent years (Wikteliu *et al.*, 1990).

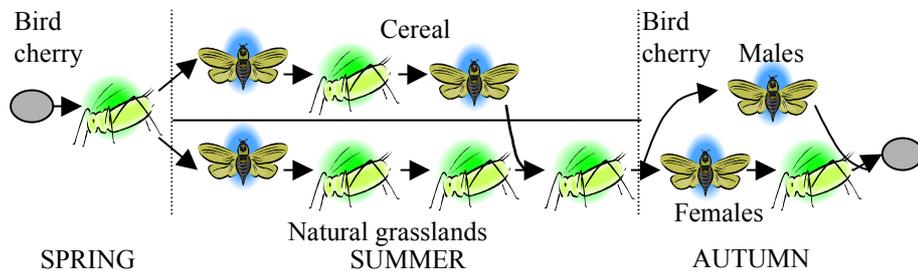


Fig. 2. The life cycle of *Rhopalosiphum padi* in Sweden, adapted from Wikteliu *et al.* (1990). *R. padi* overwinters as eggs on bird cherry trees (*Prunus padus*). The eggs hatch in May, and after some non-winged parthenogenetic generations, winged *R. padi* develop, which migrate to cereal fields and other grasslands. The winged *R. padi* then begin to produce non-winged aphids parthenogenetically. In cereal fields, *R. padi* populations collapse when the crop matures, and winged aphids migrate into natural grasslands. In autumn, winged *R. padi* develop in the grasslands, and now males also develop. Sexual reproduction occurs on bird cherry trees, where eggs are laid for overwintering.

### Generalist natural enemies

In *Papers I* and *II*, I studied predation on aphids by a guild of generalist natural enemies (mostly spiders, carabids, and rove beetles). The various generalist predator species differ in many life-history and behavioural traits, but they are

generally mobile and move between several habitats during their lifetime (Baars, 1979; Wallin, 1985, 1988; Samu *et al.*, 1999). Although generalist predators can show selectivity (higher predation on a prey species than expected from its relative abundance) for aphids, they often do not prefer aphids (Eubanks & Denno, 2000; Lang & Gsodl, 2001).

I chose to study carabids for spatial and temporal variation in fitness of individual generalist predators (*Paper IV, V*). They are common in agricultural landscapes, easy to sample and handle, mobile, and feed on *R. padi* (Chiverton, 1987a; Wallin *et al.*, 1992). Moreover, their biology is relatively well known, and there are differences in life-history, diet- and habitat selectivity between species (Wallin, 1985).

### **Pea aphids, potato leafhoppers and nabids (Paper III)**

To study scale dependent indirect interactions between prey species (*Paper III*) I chose to study pea aphids (*Acyrtosiphon pisum* (Harris)) and potato leafhoppers (*Empoasca fabae* (Harris)), which are both pests in alfalfa in the US (Blackman & Eastop, 1984; Hoffman & Hogg, 1991). They were chosen because their relative abundances were likely to differ between three different harvest treatments: conventional harvest (control), harvest + insecticides, and strip management (Fig. 4 in *Paper III*). Potato leafhoppers are more mobile, adults are winged (Al'Dawood *et al.*, 1996; Roda *et al.*, 1997), than pea aphids, and leafhopper abundance was therefore expected to be less negatively affected by insecticides and less dependent on strips for recolonization after harvesting than pea aphids. I used nabids as a shared predator because they feed on both prey species (Flinn *et al.*, 1985; Evans & Youssef, 1992), and are mobile. Adults are winged and commonly found in aerial traps (Lattin, 1989), and therefore have the potential to show both diet- and patch-selectivity.

## **Farms, farm management, and landscape parameters**

The field studies, except in *Paper III*, were conducted on the same ten farms around Uppsala (59°51'N, 17°41'E), Central East Sweden. Five farms were managed organically, *i.e.* without pesticides and inorganic fertilisers, and five were managed conventionally, *i.e.* regular use of pesticides (however, not always insecticides (*Paper IV*)) and inorganic fertilisers. The ten farms were divided into five pairs matching one organic and one conventional farm, based on land use, size, and location. Details on the pairing are presented in Weibull *et al.* (2000). By pairing conventional and organic farms, the risk of having the conventional farms clustered at one end of a landscape gradient and the organic farms at the other end of the gradient was minimised. The Swedish agricultural landscape is generally more heterogeneous compared to many other developed countries. Mean farm size in Sweden is 35 ha (Statistiska centralbyrån, 2001) compared with 230 ha in the

United States (USDA, 2002), and many Swedish farms in this region also have livestock or forestry production.

I have used seven different landscape parameters to quantify the landscapes (Table 1). Some landscape parameters (3 – 7 in Table 1) were not constant between years because of crop rotation and because the sampling sites on the farm changed between years. Even though the different landscape parameters are not dependent on each other, they can be correlated to each other (*e.g.* Table 1 in *Papers I, II*). To increase the interpretability I transformed them into principal components in *Papers I* and *II* to piece them apart. The principal components describe landscapes along statistical gradients and are not directly translated into real landscape features. In *Paper IV* there were no correlations between landscape parameters and I chose not to transform them into principal components.

*Table 1.* Description of the landscape parameters used, and in which studies they are used . Because of correlations between parameters, and to reduce the number of independent variables in the analyses, all landscape parameters have not been used in all studies

Parameter	Description	Used in Paper
1. Large-scale landscape heterogeneity	Shannon habitat* diversity index over 25 km <sup>2</sup> centered at the farm	I,II
2. Small-scale landscape heterogeneity	Mean Shannon habitat <sup>†</sup> diversity index from four 400×400 m squares from the farm	I,II,IV
3. Perimeter-to-area ratio	Mean perimeter-to-area ratio of cultivated fields within 400 m radius of sampling site	I,II,IV
4. Cultivated perimeter-to-area ratio	Like 3. but only including perimeter bordering other cultivated areas	IV
5. Percentage perennial crop	Percentage perennial crops of total cultivated area within 400 m radius from sampling site	I,II,IV
6. Percentage perennial and winter crops	Percentage perennial and winter crops of total cultivated area within 400 m radius from sampling site	II
7. Crop diversity	Shannon crop <sup>‡</sup> diversity index of cultivated fields within 400 m radius from sampling site	I,II,IV

\*) Habitat categories were: arable land, other open land, mixed forests including clear-cuts, deciduous forests, water and built-up areas.

†) Habitat categories were: arable land, other open land, mixed forests, clear-cuts, habitat islands, water and built-up areas.

‡) Crop categories were: cereal, ley (including improved pastures), semi-natural pasture, fallow, and other crops.

## Sampling

I estimated the abundance of *R. padi* (*Paper I*) and alternative prey (*Paper II*) with D-vac sampling (Southwood & Henderson, 2000). Because aphid damage to the crop depends on both duration and magnitude of aphid attack, I calculated aphid abundance as the cumulative number of aphid-days (see Methods in *Paper I*) during the season in the cereals. The impact of ground-living predators on aphid population growth rate was estimated by comparing aphid abundances inside and outside predator exclusion barriers. Aphid predation rates in *Paper II* were estimated by experimentally adding aphids on self-adhesive papers, and counting the ones remaining after 24 h, hereafter referred to as "aphid removal rates", I use "aphid predation rates" for predation on naturally occurring *R. padi*. The abundance of foliage-living predators in *Paper II* was estimated with D-vac sampling, whereas the ground-living predators were trapped with pitfall traps containing water and detergent. I pooled the numbers of these two predator groups by adding their standardised abundances (distribution mean was scaled to zero and variance to one) at each site. I used pitfall traps to trap living carabids for the estimation of fitness (*Paper IV, V*). In *Paper III* predation rates in the greenhouse were estimated by visual counting, and field abundances were estimated with sweep netting.

Condition of individual carabids (*Papers IV, V*) was estimated as the body mass in relation to body length. In *Paper V*, the condition estimate was complemented with extraction of fat content, and fecundity was estimated using the number of eggs females laid using resources obtained before capture.

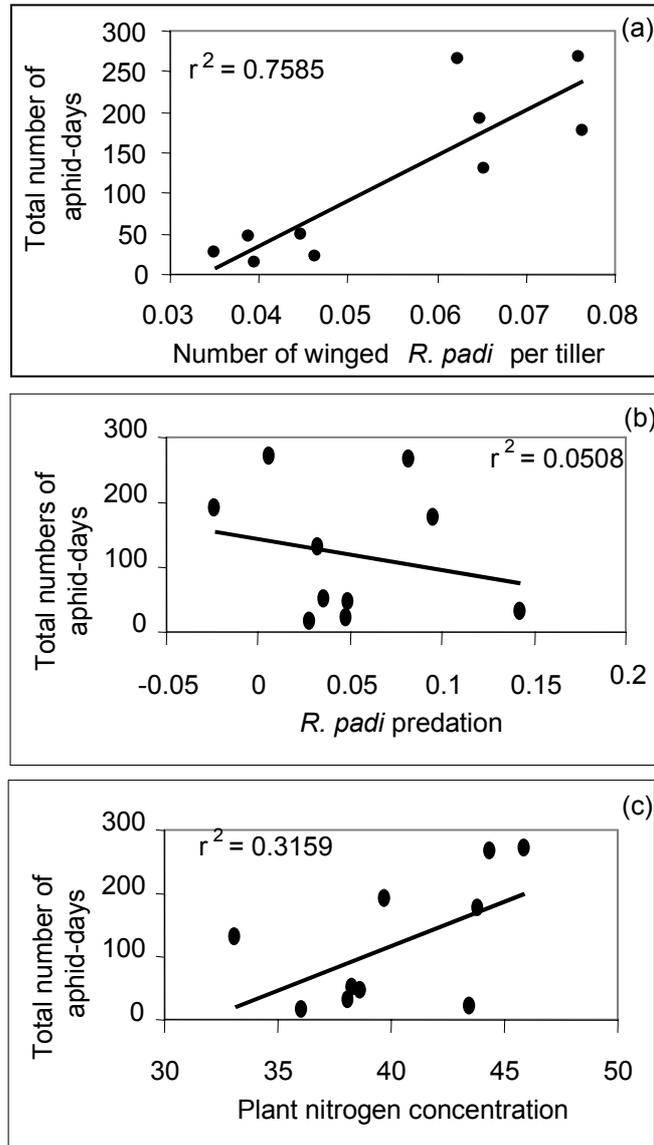
## Results and Discussion

### Generalist predators as biological control agents

There were, on average, twice as many aphid-days in the predator free exclusion barriers compared to where generalist predators were present (*Paper I*; Östman *et al.*, 2001), suggesting a substantial increase in yield because of the action of generalist natural enemies (cf. Hansen, 2000). The number of winged *R. padi* establishing in the spring crop was more important for the total number of aphid-days in the crops than the effect of predators on the aphid population growth rate after colonisation, and also more important than the plant nitrogen concentration (Fig. 3; *Paper I*). This confirms the importance of generalist natural enemies on *R. padi* abundance, and the importance of achieving an early control of pest numbers for efficient biological control by generalist natural enemies. These results confirm predictions from theoretical analyses of this predator-aphid system (Ekbohm *et al.*, 1992), as well as from other systems (Settle *et al.*, 1996; Sunderland, 1999; Symondson *et al.*, 2002b).

The number of winged *R. padi* establishing in a field depends both on the number of aphids arriving into the fields and on predation on the arriving aphids

(Wiktelius *et al.*, 1990). The removal rate of experimentally added aphids was negatively correlated with the number of establishing aphids among farms (compare Fig. 4a and b; *Paper I*), suggesting that predation by natural enemies affects the number of winged *R. padi* establishing in a field. This also suggests that the negative correlation between generalist predator abundance and peak *R. padi* abundance among farms (Ekblom & Wiktelius, 1985) represents a causality.



*Fig. 3.* The total number of aphid-days in spring barley fields was best explained by the number of winged aphids established (a). There was a considerably lower influence of (b) the impact of ground-living generalist predators on the *R. padi* population growth rate, and (c) plant nitrogen concentration on the total number of aphid-days in spring barley.

Although generalist predators decreased *R. padi* abundance in the study year, yield losses were still substantial (Östman *et al.*, 2001), hence the biological control was not really successful. In a year with less extensive spring migration of *R. padi*, the predation of generalist predators on *R. padi* is likely to prevent pest outbreaks (Ekbom *et al.*, 1992) in cereals. Wiktelius *et al.*, (1990) suggested that the *R. padi* population density between years is regulated between summer and autumn migration (see Fig. 2). Hence, generalist predators in cereal fields have little impact on the *R. padi* population dynamics between years, but decrease aphid abundance in cereal fields.

### **The effect of farm management and landscape on aphid predation**

Fewer winged *R. padi* established on organic farms and, irrespective of farm management, fewer established in landscapes with high field perimeter-to-area ratio (Fig. 4a; *Paper I*) and high percentage perennial crop (*Paper I*). Data from 1979 to 1982 (Ekbom & Wiktelius, 1985) also showed a positive correlation between field size (correlated to the perimeter-to-area ratio) and peak *R. padi* abundance. The results on removal rates of experimentally added aphids further confirmed that the predation on winged *R. padi* colonising the fields was higher in landscapes with high perimeter-to-area ratio of the fields, and higher on organic farms (Fig. 4b, *Paper II*).

The decrease in *R. padi* population growth rate because of predation by ground-living natural enemies was largest in landscapes with low habitat heterogeneity at the farm scale (*i.e.* landscapes with much arable land), whereas there was no effect of farm management (Fig. 4c; *Paper I*). Predation on experimentally added aphids during the corresponding period showed different results: aphid removal rates increased with habitat heterogeneity on the multiple farm scale (*Paper II*). After the crop had matured (naturally occurring *R. padi* had left the crop, but other aphids occur, *e.g.* *Sitobion avenae*) the predation on experimentally added aphids decreased with habitat heterogeneity on a multiple farm scale, and was higher on organic farms (*Paper II*).

In conclusion, the relative predation rate on *R. padi* on farms varies over the course of one season, and also between years. During the, for biological control, important aphid colonisation phase the results were consistent over the two years; predation was higher on organic farms and in landscapes with abundant field margins and perennial crops.

### **Diet selectivity, generalist predator abundance, and predation rates**

Under most natural prey densities, generalist predators did not show any major changes in diet selectivity as the abundance of different prey changed (*Paper II, III*). The effect of alternative prey abundance on aphid removal rate was generally low (Fig. 5a; *Paper II*). That is, generalist predators (as a guild) substituted the poor quality aphids (Wallin *et al.*, 1992; Toft, 1995) for alternative prey species to only a small extent. It should be noted that the aphids (in *Paper II*) were sessile

(but alive) and on a non-natural background perhaps making them more prone to attack, diminishing the effect of alternative prey abundance on aphid removal rate. There was, however, a tendency towards a negative correlation between alternative prey abundance and aphid removal rate during the aphid population growth phase in cereals (*Paper II*), *i.e.* a positive indirect interaction of the alternative prey abundance on aphids. This positive indirect interaction was probably an effect of that predators had an increased handling time with increased alternative prey abundance, resulting in decreased searching time, and hence fewer experimentally added aphids attacked.

Individual nabids showed selectivity for pea aphids compared to potato leafhoppers, but the selectivity did not change much with changing prey ratios (*Paper III*). In another study of nabids, pea aphids, and potato leafhoppers, using higher prey densities, Flinn *et al.* (1985) found that the nabids' diet selectivity changed with the prey ratio. Thus, nabids seem to forage opportunistically at low to normal prey densities, but at higher densities they make a diet choice.

From the two experiments (*Paper II, III*) there was no indication that generalist natural enemies showed any active diet choice, *i.e.* changes in selectivity, as long as the abundances of alternative prey and pest were low to moderate. Hence, the indirect interactions between prey species were small in the short run.

In contrast to alternative prey abundance, generalist predator abundance was important for the aphid removal rates (*Paper II*). Generalist predator abundance was positively correlated with aphid removal rates among fields (Fig. 5b), and moreover, nabid abundance was negatively correlated with growth rate of leafhoppers (*Paper III*). Generalist predator abundance was positively correlated with alternative prey abundance (*Paper II*), and nabid abundance was mainly correlated with pea aphid abundance (*Paper III*). Thus, there was a negative indirect effect of alternative prey on aphids, causing a positive correlation between alternative prey and aphid removal rates among samples (Fig. 5c; *Paper II*). The indirect interaction of pea aphids on potato leafhoppers was positive when the prey species were subdivided on different plants, because pea aphids attracted nabids away from plants with leafhoppers. Among fields there was a negative indirect interaction of pea aphids on leafhoppers because pea aphids attracted nabids or caused a higher nabid reproduction (*Paper III*). Thus, there were indirect interactions between prey species among patches, but the sign depended on the spatial scale. On a field scale, there were negative indirect interactions.

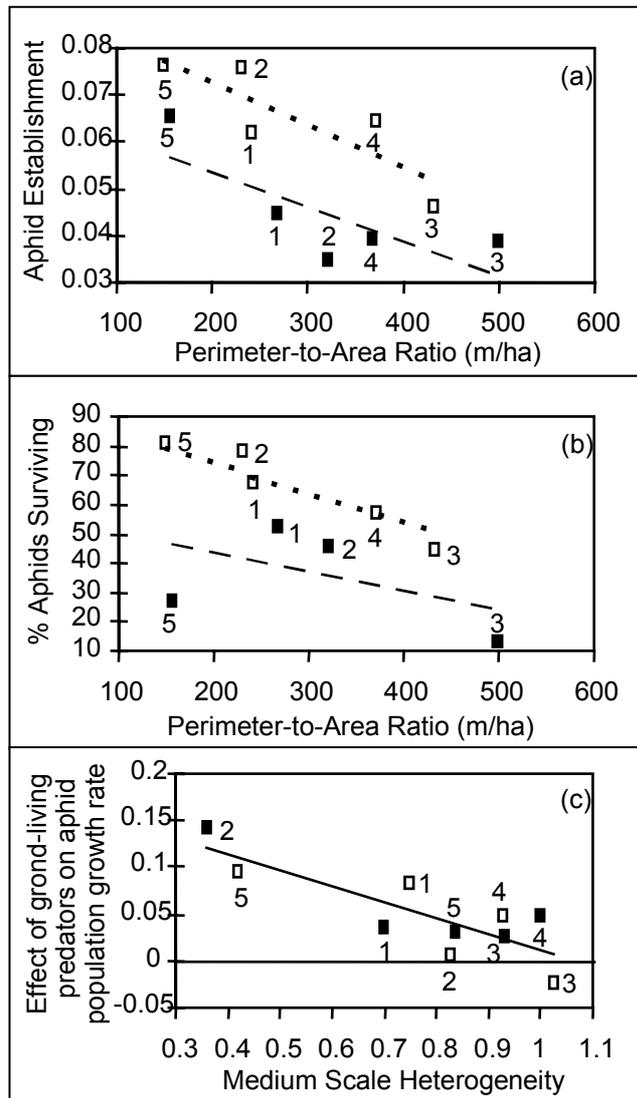


Fig. 4. (a) The number of winged *R. padi* per tiller during the establishment phase was lower on organic farms than on conventional farms and decreased with mean field perimeter-to-area ratio. (b) The proportion of experimentally added aphids surviving during the establishment phase was lower on organic farms than on conventional farms and decreased with mean field perimeter-to-area ratio. Because of crop rotation, aphid survival could not be measured on the organic farm in pair 4. (c) The difference in *R. padi* population growth rate between inside and outside the exclusion barriers decreased with habitat heterogeneity on a farm scale, and there was no effect of farming system. Filled squares are organic farms, and open squares are conventional farms. Farms with the same number are paired.

There are several explanations for the positive correlation between alternative prey abundance and generalist predator abundance among fields: 1) There could be a behavioural response, *i.e.* predators aggregate at high prey densities. 2) Predators

could increase their reproduction with increasing prey densities, *i.e.* numerical response, which assumes that alternative prey abundance is repeatable between years because the densities of some predator species are likely to depend on prey abundance previous years. 3) Alternative prey abundance and predator abundance could both be correlated to a third uncontrolled factor. For example, field margins may act as sources for both alternative prey and predators. This would mean that interactions in crop habitats are not important for the population dynamics for either alternative prey or predators. Hence, the negative indirect effect of alternative prey on aphids occurs not in the crops but in non-crop habitats, or the indirect interaction is spurious (alternative prey abundance has no effect on predator abundance). None of these explanations is likely to be exclusive, on the contrary, they are likely to act in concordance, and my experimental set-up cannot be used to estimate their relative importance.

In conclusion, the generalist predators investigated did not seem to do any active diet choice, at least not up to moderate prey densities. Generalist predator distribution matched prey distribution to some extent. This resulted in negative interaction between prey species in some cases, but when the alternative prey abundance became high they tended to have a positive indirect effect on aphids (*i.e.* decreased predation on aphids).

### **Effects of farm management and landscape on the condition and fecundity of carabids**

There was spatial variation in condition and fecundity of carabid beetles among farms. In late summer of a year with no aphids, the condition of four predatory carabids was higher on organic farms than on conventional farms, and irrespective of farm management higher in landscapes with abundant field margins (Fig. 1, 2 in *Paper IV*). This was in agreement with an earlier study of a smaller number of farms. Bommarco (1998b) found that individuals of a carabid species, *Pterostichus cupreus* (L.), were in better conditions and had higher fecundity on organic farms that were situated in complex landscapes.

A more comprehensive study of condition, fat content and fecundity of two carabid species, *P. cupreus* and *P. melanarius* (Ill.), over two more years showed a more complicated picture. All investigated traits showed asynchronous temporal variation between farms, *i.e.* the changes in the fitness-related traits over time were not similar between farms (*Paper V*). On farms where individuals of *P. cupreus* had the highest levels of fat content and fecundity in one generation/year, individuals had the lowest levels in the next generation (fat content) or year (fecundity) (*Paper V*). These results can explain why fitness-related traits for generalist predators show spatial variation, even if they are food limited. However, I do not know what limits the population density of these species. Results from Bommarco (1998b) and *Paper IV* show that the levels of fitness-related traits increased with food supply, but that does not necessarily mean that the population density is food limited for the adult carabids. Even if food is not the limiting factor regulating the populations, these traits can have positive short-term effects on population abundance, *e.g.* by increasing overwintering survival (Petersen, 1999), which is important for the control of colonising winged *R. padi* in spring (*Paper I*).

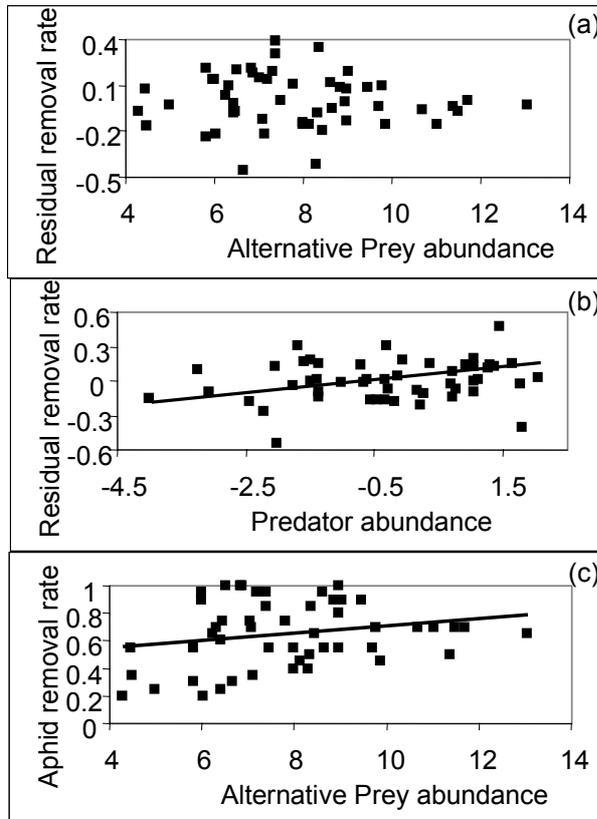


Fig. 5. Correlations between aphid removal rates (percentage aphids removed), and abundance of natural enemy or alternative prey in spring barley. (a) There was no correlation between aphid removal rate and alternative prey abundance when adjusted for predator abundance (residual removal rate) among all samples. (b) If removal rates were not adjusted for predator abundance, there was a positive correlation between aphid removal rate and alternative prey abundance among samples. (c) There was a positive correlation between aphid removal rate and predator abundances among samples when adjusted for alternative prey abundance.

My study of fitness-related traits only spanned over three years, which is too short time to determine what drives the changes in the fitness-related traits. For both species, the year effect explained most of the variation in the traits, which suggests that the changes are mainly driven by temporal environmental variation over large areas (e.g. weather, aphid outbreaks). For both species most traits showed higher values in 1999 (sunny, aphid outbreak) than in 2000 (rainy, no aphids). The asynchronous changes in the traits between farms could be explained in two ways: 1) The temporal variation over large areas could affect environmental conditions on a smaller scale differently, for example, cereal fields may be advantageous during an aphid outbreak but be the opposite if there are no aphids. This implies that it is the environmental conditions that are important for the fitness-related traits, and not the population density, *i.e.* the traits are density-independently food-limited. 2) Population density changes are not synchronised between farms, because of random events (for example in recruitment rates) or

different degrees of density dependence. In this case, the environmental conditions in relation to the population density are important for the fitness-related traits, *i.e.* the traits are density-dependently food-limited. I cannot conclusively test if any of these two explanations is insignificant, but I believe the negative correlation in relative fat content and fecundity between sites over time for *P. cupreus* suggests that density-dependence has some effect on the traits of individual *P. cupreus* (Fig. 4 in *Paper V*), supporting the second explanation.

The *R. padi* outbreak in 1999 may be one reason why the earlier consistent results from Bommarco (1998b) and *Paper IV*, that condition, fat content, and reproduction of *P. cupreus* and *P. melanarius* in general are higher in complex landscapes and on organic farms, were not repeated in *Paper V*. Although a single diet is not optimal for generalist predators (Wallin *et al.*, 1992; Toft, 1999), the aphids were likely to increase food abundance substantially. An aphid outbreak, which happens every 3-5 years, may dramatically change environmental conditions for the carabids and increase reproduction. I suggest that the aphid outbreak increased the population densities so much that density-dependence became important, especially for *P. cupreus*, which has a more restricted diet than *P. melanarius*. The higher values of the fitness-related traits at some sites in the years between aphid outbreaks may then reflect variation in local food abundance.

The different traits were positively correlated to each other among individuals, *i.e.* an individual with high condition had high fat content or laid many eggs (Fig. 6). For *P. cupreus* there were positive correlations among populations, *i.e.* populations with high population means of condition had high population means of fat content or number of eggs laid (*Paper V*). This was not the case for *P. melanarius*. This suggests that *P. cupreus* allocates increased resources between traits, for example fat content and fecundity, in a similar way between populations. However, for *P. cupreus* there was a clear change in resource allocation between the two years (Fig. 6; *Paper V*). Individuals allocated relatively more resources to egg production during 1999 than in 2000.

The positive correlation in condition between species in 1998 (*Paper IV*) could not be found in the following years (*Paper V*). That is, the two species did not respond similarly to the environmental temporal variation (*e.g.* the aphid outbreak in 1999) although they have overlapping food resources (Wallin, 1985). The species differ in other traits, *e.g.* *P. melanarius* has a broader diet, and is less restricted to arable land than *P. cupreus* (Wallin, 1985; Chiverton, 1987a). Further, *P. melanarius* spend their first winter as larvae, whereas *P. cupreus* has its larval stage during the summer (Wallin, 1985). These differences could explain why the two species responded differently to temporal and spatial variation.

In conclusion, individual generalist predatory carabids may often be favoured by organic farming and by perennial habitats (field margins, perennial crops) in the landscape. But some environmental variation over large areas (*e.g.* weather, aphid outbreaks) seems to affect the individual carabids on different farms in different ways, causing asynchronous temporal variation in the fitness-related traits between sites. Life-history, diet breadth and habitat affinity of different species influence the individuals' responses to environmental variation. This means that the relative

importance of single generalist predator species as biological control agents changes between years and sites.

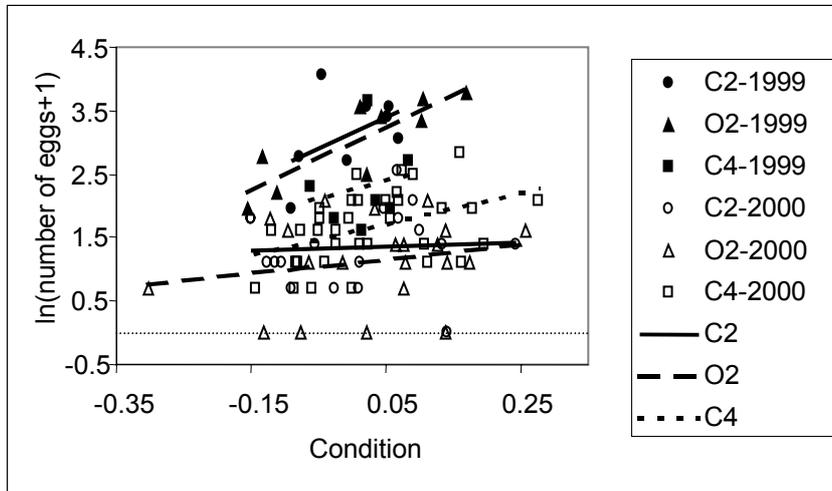


Fig. 6. Within years and sites there was a positive correlation between condition and the number of eggs ( $\log_e$ -transformed) female *P. cupreus* laid at three sites during two years. There was a clear year effect, on all sites fecundity in relation to condition was higher in 1999 than 2000. Moreover, the rank order of mean number of eggs per females changed between the two years. In the figure only data from three sites is presented to better illustrate the relationships.

## Landscape, farm management, and abundances of generalist predators and alternative prey – a synthesis for enhanced biological control

Predation on aphids was higher in landscapes with abundant field margins and perennial crops during the colonisation phase of *R. padi* in spring cereal. During this period, predator abundance determined aphid removal rates. Predator abundance also tended to be higher in these landscapes ( $F_{1,15} = 3.5$ ;  $P = 0.08$ ). Field margins and perennial crops are important both as overwintering sites and as food-rich habitats for many generalist predators, thus improving their prospects for survival and reproduction (Wallin, 1985; Zangger *et al.*, 1994; Bommarco, 1999; Landis *et al.*, 2000; Sunderland & Samu, 2000). In the autumn prior to the study of naturally occurring *R. padi*, the condition of individual carabids was higher on farms with a high perimeter-to-area ratio of the fields, and they were in better condition on organic farms than on conventional farms. Although predator condition does not give any information about abundance, better condition may have affected winter survival positively (*e.g.* Petersen, 1999). Thus, in landscapes with abundant field margins and perennial crops there is likely to be a large dispersal of generalist predators from non-cereal habitats (source of immigration) into cereal fields in the spring (Fig. 7).

In 1999 with high aphid densities, the impact of predators on aphid population growth rate decreased with habitat heterogeneity on a farm scale. During the corresponding period the following year there were low aphid densities; aphid removal rate increased with habitat heterogeneity on a multiple farm scale and the amount of perennial crops, and aphid removal rate tended to decrease with alternative prey abundance, whereas there was no significant effect of predator abundance. The contrasting results between the two years may have been a result of the large difference in aphid abundance.

Aphid-only diets are not optimal for many generalist predators (Wallin *et al.*, 1992, Toft, 1995), but predators can show selectivity toward aphids because of their high vulnerability (Eubanks & Denno, 2000; Lang & Gsodl, 2001). How the selectivity of generalist predators for *R. padi* changes with changes in relative or total abundance of *R. padi* is not known, but predators may reject them as prey more often when *R. padi* is very abundant. Moreover, Wallin (1985) found that carabids often left the cereal fields after reproduction. In landscapes with a high proportion of non-arable habitats it may be easier for generalist predators to find other prey species as the season progresses, either because of higher alternative prey abundances in cereal fields in these landscapes, or because predators more easily can find non-cereal habitats (Fig. 7).

Lower numbers of winged *R. padi* established on organic farms than on conventional farms, and there was also higher aphid removal rate during aphid establishment in spring. Predator abundance was important for aphid removal rates, and there were higher predator abundances on organic farms ( $F_{1,97} = 8.3$ ;  $P = 0.005$ ). Several other studies have shown that organic farming enhances generalist predator abundance (Kromp, 1989, 1999; Moreby *et al.*, 1994; Drinkwater *et al.*, 1995). The alternative prey abundance was also higher on organic farms ( $F_{1,97} = 4.0$ ;  $P = 0.05$ ), increasing the possibility for generalist predators to substitute alternative prey for *R. padi*, which could explain why the predator impact during exponential growth was not larger on organic farms compared to conventional farms.

Manure instead of inorganic fertilisers enhances soil organism abundance (Yeates *et al.*, 1993; Moreby *et al.*, 1994), and abandoning herbicides also increases the abundance and diversity of alternative prey (Chiverton & Sotherton, 1991; Samu *et al.*, 1999). The effect of insecticide use is more complicated. Insecticides affect predators negatively, both by directly harming them and by decreasing food abundance and quality (Wallin *et al.*, 1992). However, in this area of Sweden, insecticides are not used regularly on all conventional farms, and are not applied to all crops. Hence, there is no year-long constant insecticide pressure and there are many refugia in the landscape, compared with large-scale intensely managed agricultural areas in Western Europe and US (Statistiska centralbyrån, 2001; USDA, 2002). The long-term effects of insecticides on the predator populations may be low at the studied farms.

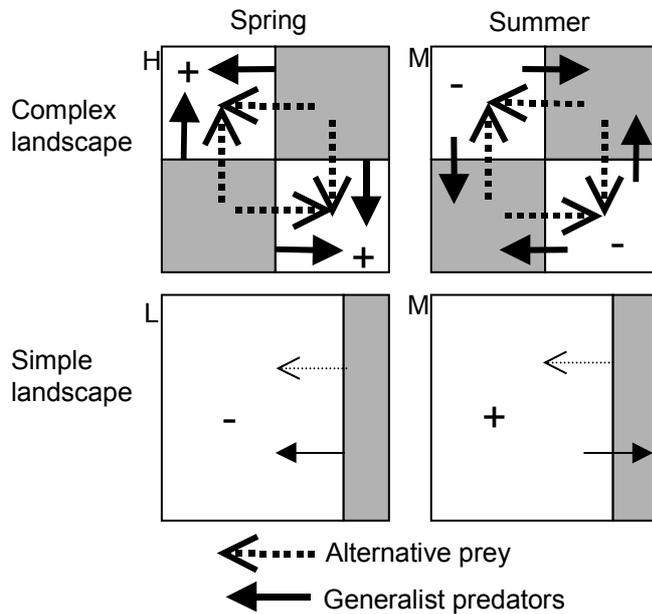


Fig. 7. Simplified figure of generalist predator movements (solid lines) and alternative prey movements (dotted lines) over a season with an outbreak of *R. padi* in a complex landscape (high perimeter-to-area ratio, many non-cereal habitats) and a simple landscape (low perimeter-to-area ratio, few non-cereal habitats), and the resulting effects on predation of *R. padi*. A thick arrow indicates relatively high net migration, + denotes higher, and - denotes lower predation on *R. padi* relative the other landscape. In spring, there is a large net migration of generalist predators and alternative prey into the cereal fields in the complex landscape relative to the simple landscape. Because alternative prey abundance is still moderate the generalist predator abundance is more important for the predation on *R. padi* than alternative prey abundance. Predator abundance is high (H) in the complex landscape and low (L) in the simple landscape, thereby predation by generalist predators on aphids is higher in the complex landscape. In summer, alternative prey abundance in cereals is higher in the complex landscape and generalist predators decrease their predation on aphids to feed on alternative prey. Generalist predators may also leave the cereal fields, which is easier in complex landscapes, resulting in medium (M) densities in both landscapes. This results in lower predation on *R. padi* in the complex landscape compared to the simple.

In conclusion, during, for the biological control important, aphid establishment, a high generalist predator abundance was important for decreasing aphid numbers and crop damage. Predator abundance and predation rates were higher, and the number of winged aphids that established was lower, on organic farms and, irrespective of farm management, in landscapes with abundant field margins and perennial crops. Later, during the *R. padi* population growth phase, few alternative prey in the crop and few qualitatively different habitats in the surroundings increased predation by generalist natural enemies on *R. padi*.

## Concluding remarks

This thesis has demonstrated that generalist natural enemies to the pest *R. padi* had a major impact on the abundance of *R. padi* in spring barley. The predators decreased *R. padi* abundance so much that an increase in yield is likely. Although predation by generalist predators on *R. padi* decreased the yield losses, generalist natural enemies were not able to hold *R. padi* abundance below the economic threshold, where insecticide treatment is profitable, in a year with massive spring migration. This shows that the action of generalist natural enemies in some years has to be complemented with other inputs, such as specialist predators, plant resistance, or pest antagonists (*e.g.* fungi) for successful biological control in all years.

## Recommendations for changes in landscape features and farm management

The landscape features surrounding crop habitats and farm management both influenced the predation rates on *R. padi* by affecting both alternative prey abundance and generalist predator abundance. Generalist predators did not show any major changes in prey selectivity at moderate prey abundance. This suggests that high generalist natural enemy abundance is the most important factor for enhancing biological control efficacy by generalist natural enemies. Having many refugia for overwintering and an alternative food supply, for example available in field margins and perennial crops, in the vicinity of the cereal fields resulted in increased generalist predator immigration into cereal fields, and thus in enhanced predation on *R. padi*.

Landscape features and farm management influenced fitness-related traits of individual generalist predators, carabids, but the temporal variation over large areas (*e.g.* weather, pest outbreaks) was most important for the absolute levels of the fitness-related traits. This study and others suggests that the fitness-related traits of carabids often are higher on organic farms and in complex landscapes. However, there was asynchronous temporal variation in the fitness-related traits among sites, *i.e.* fitness-related traits was not consistently higher on some farms, but changed over time. I believe this was because the aphid outbreak caused asynchronously population changes resulting in different degrees of density-dependence among farms. Moreover, different predator species responded differently to the temporal and spatial variation in environment.

Based on the comparative studies, the recommendations to farmers for increasing the efficacy of biological control would be the following: 1) To have more field margins (*e.g.* strip management) and perennial crops in relation to annual crops. 2) To increase organic matter in soil, *e.g.* use manure, but not necessarily halt inorganic fertilisers. 3) Careful use of pesticides, both of insecticides and herbicides. These recommendations are, however, far from new (*e.g.* Chiverton, 1987b; Wallin, 1987; Thomas *et al.*, 1991, 1992). The reasons they have not been incorporated into pest management schemes are partly because productive land would have to be taken out of production, and there would be more obstacles to

cultivation. Moreover, biological control is not as efficient as chemical control, unless pests are developing resistance, causing lower yields some years, *i.e.* abandoning insecticides would increase the uncertainty of farmer's profit from yield. Another important factor why these recommendations have not been implemented is that they are difficult to generalise into universal practices, forcing recommendations to be rather site specific.

Currently (autumn 2002), there is a debate about the subsidies to farmers in the European Union. If the production subsidies are decreased, the marginal profit of the yield will decrease, and the decrease in yield losses from the changes in land-use and farm management suggested here will become lower. That is, the changes in land-use and farm management will be relatively cheaper than at present. On the benefit side for the society is that species richness could be expected to increase in more heterogeneous landscapes (*e.g.* Weibull, 2002), less pesticide residues remain in the environment, and the agricultural landscape become more accessible for recreation.

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