

Food webs in Agroecosystems

Implications for Biological Control of Insect Pests

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Abstract

The management of insect pests in modern agriculture is dominated by chemical control, despite wide recognition of its detrimental impact on the environment and human health. As a sustainable alternative, the service of biological control of insect pests is provided by a diversity of natural enemies, such as ground dwelling carabids and spiders. A better understanding of natural enemy communities and the feeding relationship between natural enemies and their prey is therefore crucial to better conserve and promote the provisioning of biological control in agricultural fields. To this end, we quantitatively summarized published studies that addressed the relationship between increased natural enemy diversity and biological control and studied moderation by biotic and abiotic factors. The results of this meta-analysis support an overall positive effect of increased natural enemy diversity on herbivore suppression, and suggest this effect is lessened by an increase of prey diversity.

I then focused on communities of generalist, ground dwelling predators controlling aphids in cereal fields. I used recently developed DNA based molecular gut content analysis to study the feeding relationships between predators and their prey, i.e., food webs, and their implications for biological control. I investigated the effects and underlying mechanisms of increased predator diversity on aphid biological control in manipulative field cage experiments, and identified feeding interactions in relation to the availability of predators and prey during the growing season in field conditions. I showed that generalist predators appear to be functionally redundant in the provisioning of cereal aphid biological control, when considering short time periods. However, when the entire cropping season is considered the importance of different predators as aphid biological control agents varied, which suggests that high predator diversity may provide a more stable biological control service over time.

The findings of this thesis support the design of conservation strategies that promote predator diversity and high levels of non-pest extraguild prey in order to sustain generalist ground dwelling predators and secure their contribution to biological control services in agricultural fields.

Keywords: Natural enemies, Carabids, Spiders, Aphid, Cereal, Redundancy, Stability

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Näringsvävar i agroekosystem: Betydelse för biologisk bekämpning av skadeinsekter

Abstrakt

Hantering av skadeinsekter i det moderna jordbruket domineras av kemisk bekämpning, trots stort erkännande av dess skadliga inverkan på miljön och människors hälsa. Ett hållbart alternativ är ekosystemtjänsten biologisk bekämpning som tillhandahålls av en mångfald av naturliga fiender, såsom marklevande jordlöpare och spindlar. En bättre förståelse av naturliga fienders samhällen och förhållandet mellan naturliga fiender och deras byten är därför viktigt för att bättre kunna bevara och främja biologisk bekämpning i åkermark. Vi har kvantitativt sammanfattat publicerade studier som undersökt sambandet mellan ökad mångfald av naturliga fiender och biologisk kontroll och studerat påverkan av biotiska och abiotiska faktorer. Resultaten av denna metaanalys stödjer en positiv effekt av ökad mångfald bland naturliga fiender på begränsning av skadedjur, men denna effekt minskar genom en ökning av bytedjurens artmångfald.

Jag fokuserade sedan på samhällen av generalistiska, marklevande rovdjur som äter bladlöss i spannmålsfält. Jag använde nyligen utvecklad molekylär maginnehållsanalys för att studera förhållandet mellan rovdjur och deras bytesdjur, dvs näringsvävarna, och konsekvenser för biologisk bekämpning. Jag undersökte effekterna och bakomliggande mekanismer av ökad mångfald av rovdjur på biologisk bekämpning av bladlöss i manipulativa fältburexperiment, och identifierade interaktioner mellan rovdjur och bytesdjur i förhållande till tillgången på rovdjur och byten under växtsäsongen under fältförhållanden. Jag visade att många generalistiska rovdjur har likartade bytesval och därmed bidrar till bladlössens biologisk kontroll på samma sätt, när man överväger korta tidsperioder. Men över hela växtsäsongen varierar betydelsen av olika rovdjur för biologisk bekämpning av bladlöss, vilket tyder på att hög mångfald bland naturliga fiender kan ge en mer stabil biologisk bekämpningstjänst över tid.

Resultaten av denna avhandling ger stöd för bevarandestrategier som främjar en mångfald av naturliga fiender och stora mängder av alternativa bytesdjur för att gynna generalistiska marklevande rovdjur och säkra deras bidrag till biologisk bekämpning i åkermark.

Nyckelord: Naturliga fiender, jordlöpare, spindlar, bladlöss, spannmål, redundans, stabilitet

Réseaux trophiques dans les agroécosystèmes: Implications pour la lutte biologique des insectes ravageurs

Résumé

Dans l'agriculture d'aujourd'hui la lutte contre les insectes nuisibles se fait avant tout à travers l'usage d'insecticides, bien que leurs impacts néfastes sur l'environnement et la santé humaine soient reconnus. Néanmoins, une alternative durable existe: la lutte biologique par conservation. Cette dernière est principalement assurée par des auxiliaires de cultures qui consomment les ravageurs, tels que les carabes et les araignées qui consomment les pucerons en cultures céréalières. Pour renforcer l'efficacité de la lutte biologique, une meilleure compréhension du fonctionnement des communautés d'auxiliaires et des relations qui les lient avec leurs proies est nécessaire. À cette fin, nous avons fait une méta-analyse des études publiées qui traitent de la relation entre la diversité des auxiliaires et la suppression de ravageurs. Nous nous sommes intéressés aux facteurs biotiques et abiotiques qui peuvent moduler cette relation. Cette méta-analyse met en évidence un effet positif de la diversité des auxiliaires sur le contrôle des ravageurs. Nos résultats suggèrent cependant une réduction de cet effet lorsque la diversité des proies augmente. Suivant une démarche expérimentale, j'ai étudié les communautés d'auxiliaires généralistes (araignées et carabes) dans les cultures céréalières qui consomment, parmi leurs proies, les pucerons des céréales. J'ai utilisé des méthodes d'analyse moléculaire, basée sur l'ADN, pour étudier les contenus stomacaux des auxiliaires et définir les relations alimentaires entre les auxiliaires généralistes et leurs proies. J'ai étudié l'impact de la diversité des auxiliaires sur la lutte biologique des pucerons, et les mécanismes sous-jacents à cet impact. J'ai montré que les différentes espèces d'auxiliaires sont, sur une courte période, fonctionnellement redondants dans la lutte biologique. Toutefois, lorsque toute la saison de culture est considérée, mes résultats suggèrent que la diversité des espèces d'auxiliaires pourrait être bénéfique pour la stabilité de la lutte biologique. Les conclusions de ce travail sont favorables à l'élaboration de stratégies de conservation qui favorisent l'abondance et la diversité des auxiliaires prédateurs, tels que le maintien de niveaux élevés de proies alternatives, afin de garantir une meilleure contribution de ces auxiliaires aux services de lutte biologique dans les terres agricoles.

Mots clés: Auxiliaire de cultures, Carabes, Araignées, Pucerons, Cultures céréalières, Redondance, Stabilité

Dedication

À toi Mamie, à toi Raymond

Les insectes utiles sont ceux dont nous tirons quelque avantage dans nos arts et notre industrie ou dans notre état de maladie ou de santé, et ceux qui nous sont directement utiles en détruisant les espèces nuisibles.

Il y a quelques-uns de ces petits animaux qui nous rendent de très grands services [...]

Les insectes utiles à l'homme, C. Goureau (1872)

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List of Publications

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

- I** Kaartinen Riikka; Roubinet Eve, Jonsson Mattias (manuscript). Context-dependency of predator species richness effects on herbivore suppression - a meta-analysis
- II** Roubinet Eve, Straub Cory, Jonsson Tomas, Staudacher Karin, Traugott Michael, Ekbom Barbara, Jonsson Mattias (2015). Additive effects of predator diversity on pest control caused by few interactions among predator species. *Ecological Entomology* **40**, 362–371.
- III** Roubinet Eve, Birkhofer Klaus, Malsher Gerard, Staudacher Karin, Ekbom Barbara, Traugott Michael, Jonsson Mattias (manuscript). The diet of generalist predators reflects effects of cropping season and farming system on extra- and intraguild prey.
- IV** Roubinet Eve, Jonsson Tomas, Jonsson Mattias (manuscript). Low level of specialization and seasonal variation characterizes the predator-prey food web structure in agroecosystems.

Paper **II** is reproduced with the permission of the publisher.

The contribution of Eve Roubinet to the papers included in this thesis was as follows:

- I** Data base search, study selection. Participation in analysis. Significant contribution in writing.
- II** Main author, study design, data collection, design of molecular assay, laboratory work and data analysis. Writing with significant contribution of co-authors.
- III** Main author. Contributed to laboratory work with GM and KS. Data management and statistical analysis with significant contribution of second author. Writing with significant contribution of second author. MJ, BE and MT designed the experiment. MJ and GM collected the data. KS designed the molecular assays.
- IV** Main author. Statistical analysis. Writing with significant contribution of second author. Study design, data collection and molecular assays as in **III**.

1 Introduction

1.1 Biological control of agricultural pests

1.1.1 Agricultural pests and their natural enemies

Agricultural crops are attacked by a large variety of harmful organisms, such as insects. These organisms, often referred to as agricultural pests if exceeding a specific threshold, can cause significant economic losses and are generally targeted by prophylactic or curative control.

A large diversity of natural enemies, including birds, predatory arthropods, parasitoids, and pathogens can prey on pests, providing an ecosystem service: the biological control of agricultural pests. Biological control can be defined as “the use of an organism to reduce the population density of another organism and thus includes the control of animals” (Bale et al., 2008). In agriculture, it usually refers to four types of programs (Eilenberg et al., 2001):

- classical, with the introduction and support of exotic biological control agents to control invasive pest species,
- inoculation, with the release of natural enemies over a definite period, often the growing season, in controlled environments such as greenhouses,
- inundation, with the mass release of natural enemies, often parasitoids or micro-organisms, as a treatment to reduce already established pest populations
- conservation biological control, with the support of existing communities of natural enemies in agroecosystems.

In this thesis, I will focus on conservation biological control and for brevity, I will refer to it as “biological control”.

1.1.2 Conservation biological control in agroecosystems

Efficient biological control relies on the presence of natural enemies able to control pests, and biological control strategies aim to support populations of natural enemies. Such strategies were already used in ancient China, where farmers supported ant populations in citrus trees, and facilitated their movements between trees, to successfully control devastating caterpillars and boring beetles (DeBach and Rosen, 1991).

Most pests and their natural enemies do not spend their entire life cycle in agricultural fields. A good knowledge of their spatiotemporal distribution is needed to successfully promote biological control in agro-ecosystems. Particularly, natural enemies often rely on the availability of alternative habitats (e.g., permanent grassland, forests, alternative crops) and providing resources (e.g., plants, pollen or nectar, seeds, other arthropods) to complete their life-cycle. The existence of such habitats, and of connecting units between them, is vital to sustain natural enemy communities in agro-ecosystems. Their population dynamics can be influenced by management strategies at both local and landscape scales, which in turn, can influence the extent of biological control of agricultural pests (e.g., Rusch et al., 2010; Tschardt et al., 2007). The intensification of agriculture initiated in the past half-century is redefining agricultural landscape organization and field management, and thus the functioning of biological control.

1.2 Agricultural intensification and biological control

1.2.1 Historical setup

Agricultural intensification was initiated in the industrialized world in the 1950's and later followed in the developing world by the green revolution in the 1970's. It has resulted in a large increase of worldwide food production and transformed agricultural landscapes. In Europe, where more than 40% of the land area is dedicated to agriculture (Eurostat, 2014), it has resulted in a transition of land use, which has drastic effects on the rural landscape and thus on both social and ecological systems (Stoate et al., 2001). Since the 1950's, the number of agricultural holdings has been steadily falling, with some countries losing more than 40% of their agricultural holdings in the period 1975-1995 (Poiret, 1996). This trend is still topical, and the European countries have fewer agricultural holdings¹ and regular agricultural workers², while the average farm size has increased³ (Eurostat, 2014).

¹. -15% for the period 2005-2013, EU 18

Simultaneously, an intensification of farming practices has occurred. Integrated crop–livestock (“mixed”) and traditional, extensive livestock farming systems have become less profitable and less encouraged by agricultural policies and have thus decreased (Boschma et al., 1999). Oppositely, agricultural policies have encouraged the intensification of cereal farming systems, leading to an increase of agricultural areas specialized in cereal crops (Stoate et al., 2001). This has resulted in changes at both agricultural landscape and field scales. From a varied landscape, which included crops, meadows, livestock, forests, and other elements, the agricultural landscape has become more simple and specialized. At the field scale, external, synthetic inputs, i.e., chemical fertilizer, herbicides, insecticides, and fungicides have rapidly replaced the biological processes involved in crop production such as farm-nutrient recycling in mixed farming systems (green or animal manure) and biological management of weeds, insects, and diseases (Tschardt et al., 2005). Changes at local and landscape scales are often correlated, i.e., field management is more intensive in simple landscapes (i.e., Jonsson et al., 2012; Rusch et al., 2013a).

1.2.2 Pest management in intensified agriculture

Since agricultural intensification began, pest control has mostly relied on insecticide use, as prophylactic and/or curative treatment. An important milestone was the discovery of the dichlorodiphenyltrichloroethane (DDT), an organochloride molecule with insecticidal properties, which was at first celebrated⁴ and which initiated a “treadmill of chemical control” (Carson, 1962). Despite the promises that the use of insecticides and more recently of genetically modified organisms would diminish the losses to insect pests, they are still responsible for a 16-18% loss of agricultural yields (Oerke, 2005).

Impact on the Environment

The extensive changes in agricultural management in the past decades have initiated a global degradation of biodiversity (Matson, 1997; Moss, 2008; Potts et al., 2010). Management practices such as synthetic inputs, mechanization, and landscape simplification have had large negative impacts on ecosystems, and on the abundance and richness (number of species) of plants and animals,

². -12.5% for the period 2010-2013, EU 27

³. +12.2%, for the period 2010-2013, EU 27

⁴. Paul H. Müller was awarded the Nobel Prize in Physiology or Medicine for “his discovery of the high efficiency of DDT as a contact poison against several arthropods” (The Nobel Foundation, 1948).

i.e., biodiversity in general. (Fig.1) (Benton et al., 2002; Krebs et al., 1999; Stoate et al., 2001).

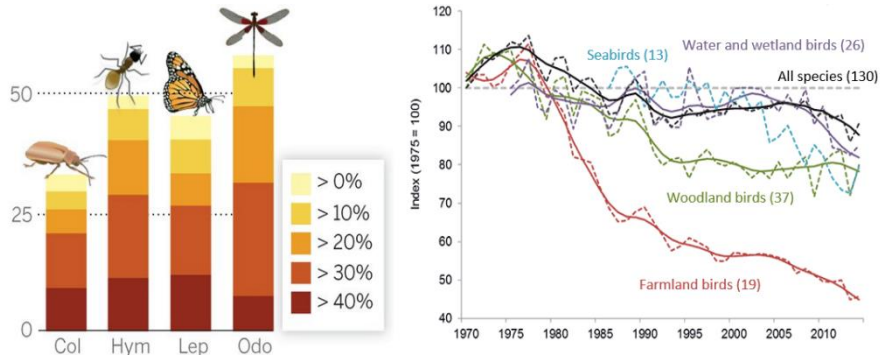


Figure 1. Trends of decrease among insects (A) and decline of overall abundance birds (B) in the UK. A. Colors indicate percent of decrease over 40 years (1970-2010) (Col= Coleoptera, Hym= Hymenoptera, Lep=Lepidoptera, Odo=Odonates). B. Variation of bird populations per habitat (Farmland, Woodland, Sea and Water and Wetland), in relation to abundances in 1975 (Index=100). Sources: (A) Dirzo et al. (2014) (B) UK Department for Environment, Food & Rural Affairs (2015). *Reproduced with the kind permission of the publishers.*

Impact on natural enemies and biological control

The extensive changes that occurred during the process of agricultural intensification have had repercussions on natural enemy communities both directly, through local management, and indirectly, through landscape modification (Chaplin-Kramer et al., 2011; Tuck et al., 2014).

The increased use of synthetic insecticides has had drastic impacts on arthropods, including natural enemies. Insecticides were initially used without control of their detrimental impacts on non-target organisms and on the environment. After the first realization of the ecological impacts of broad spectrum insecticides (Carson, 1962), insecticides have aimed to become more specific to the targeted pest, and to limit their negative side effects on non-target organisms (Stoate et al., 2001). More recently, insecticides are commonly used as preventive (i.e., prophylactic) measures against pests, e.g., through chemical treatment of seeds (also referred to as seed coating). As a result, outbreaks of pests targeted by insecticides have decreased, but pest resistance to insecticides and secondary pest outbreaks, i.e., harmful organisms that were otherwise not economically damaging, are now widespread (Wilby and Thomas, 2002).

Moreover, simultaneous changes in management practices, such as the adoption of synthetic fertilization and weed management, the simplification of crop rotation, and the intensive mechanization and its direct impact on soil

compaction, have reduced the abundance and richness of soil biota (Birkhofer et al., 2012). These organisms are important in nutrient recycling, and thus soil fertility (Birkhofer et al., 2012, 2008; Crowder and Jabbour, 2014). In addition, they provide additional resources to the above-ground system, and can sustain large communities of organisms, from microorganisms to arthropods, including natural enemies.

Simultaneously, the agricultural intensification process has led to a drastic simplification of the agricultural landscape due to the reduction of crop rotation and crop diversity, and the disappearance of connectivity between natural habitats. These extensive changes have seriously disturbed the habitat ranges of organisms. Some species have lost connections to vital habitats, while others, such as agricultural pests, have benefited from an expansion of their habitat. Many natural enemies, especially those relying on single resources or specialists, have reduced abundances or are threatened by local extinctions due to landscape simplification (Jonsson et al., 2012; Kruess and Tschardt, 1994)

1.3 Political awareness and measures

1.3.1 Biological control as an ecosystem service

In parallel to the observed degradation of biodiversity, a global degradation of the provisioning of the ecosystem services; i.e., the services provided by ecosystems; has been observed (Hooper et al., 2005; Millennium Ecosystem Assessment, 2005). These services have been classified into four types: regulating (e.g., water quality regulation, pollination, pest control), provisioning (e.g., food), cultural (e.g., recreation), and supporting (e.g., nutrient cycling) (Millennium Ecosystem Assessment, 2005). Agricultural fields and landscapes therefore not only provide provisional services, but also regulating and supporting ecosystem services such as pollination and biological control of agricultural pests, which should be preserved in order to not jeopardize the ultimate provisional service (Bommarco et al., 2013).

Policy makers were made aware of the risks incurred from a degrading ecosystem by valuating ecosystem services and therefore assigning them a monetary value. For example, the annual service of biological control has been valuated to be US\$ 4.5 billion in the United States (Losey and Vaughan, 2006). This calculation was based on the assumption that in the absence of insect natural enemies, harmful insects currently maintained below economic thresholds via biological control, would become pests for which farmers would need additional chemical control to reach the same yield levels. This valuation increased the awareness of policy makers on the necessity to protect the service of biological control in agricultural landscapes. Biological control has, since

then, been highlighted as a key ecosystem service indispensable for sustainable crop production (Bale et al., 2008).

1.3.2 Political awareness and agri-environmental schemes

Nearly three decades after the first public debate on environmental impacts of pesticides (Carson, 1962), agricultural policies first took into consideration the detrimental impacts of agriculture on ecosystems. In the European Union (EU 12), agricultural policies were adopted in the early 1990's to reduce the use of pesticides⁵ and to reduce the negative consequences of agricultural intensification on biodiversity⁶. To this aim, government programmes, or agri-environmental schemes, were "set up to help farmers manage their land in an environmentally-friendly way"⁷. More recently, the registration of new molecules for pesticides has become stricter and requires applicants to "identify the hazard arising, assess their significance and make a judgment as to the likely risks to humans, animals or the environment"⁸, making new registrations more complicated and expensive. In 2013, widely used insecticides were banned⁹ because of their potential negative impact on invertebrates and particularly pollinators (Bonmatin et al., 2015).

Organic farming is one of the agri-environmental schemes adopted in order to reduce biodiversity losses¹⁰. Organic crop production prohibits the use of inorganic inputs, largely synthetic insecticides, fungicides, herbicides, and fertilizers, and leaves to the farmers the decision on management strategies to be adopted in order to comply with this strict regulation. A large body of literature has emerged on the impact of organic farming systems on biodiversity by comparing organic versus conventional fields. An increased biodiversity in organic systems has been found (Bengtsson et al., 2005; Letourneau and Bothwell, 2008; Tuck et al., 2014), although some organisms can show different responses (Birkhofer et al., 2014). In addition, this positive effect of organic farming on biodiversity has been shown to decrease with increased landscape complexity, and no differences are observed in some regions located in particularly complex landscape settings (Winqvist et al., 2011).

⁵. Council Directive 91/414/EEC, European Commission, 1991

⁶. Council Directive 2078/92/EEC, European Commission, 1992

⁷. European Environmental Agency glossary

⁸. Regulation no. 546/2011, European Commission 2011

⁹. Regulation no. 485/2013, European Commission, 2013

¹⁰. Regulation no. 834/2007, European Commission 2010

The agri-environmental schemes adopted in the EU have been shown to benefit both natural enemy diversity and biological pest control services, still, the use of pesticides has been pointed out as one important factor responsible for the loss of biodiversity responsible for the loss of biodiversity and of biological control services throughout European farmlands (Geiger et al., 2010). According to Geiger et al. (2010), “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, a Europe-wide shift towards farming with minimal use of pesticides [especially insecticides and fungicides] over large areas is urgently needed”.

Simultaneously, the development of pest resistance is constantly challenging the efficacy of insecticidal molecules, of which more and more become unable to control pests (Huseeth et al., 2014; Nauen and Denholm, 2005). That, in addition to the increasing difficulty to synthesize new molecules and cost related to their registration ruled by strict regulation, might call into question the future of insecticides. The facilitation of biological control in agroecosystems is a way to reduce losses due to pests, without monetary and environmental costs or resistance risks. A better understanding of the service of biological control of agricultural pests and its mechanisms are thus needed to enhance the ecosystem service of biological control and reduce the environmental and human impacts of pesticides.

1.4 “In search of general laws”¹¹ driving biological control services in agroecosystems

The service of biological control in agroecosystem can be illustrated by a network of interacting species, or *food web*, where natural enemies (i.e., consumers) are linked to their prey[s] (i.e., resources).

1.4.1 Theories behind the relation between biodiversity and ecosystem services

Early observations of ecological systems presumed an increased stability with increased number of species (or species richness, referred to as diversity hereafter) (Elton, 1958, in McCann, 2000). This presumption was challenged by the theoretical observation of a negative relationship between diversity and

¹¹. In his opinion paper “Are there general laws in ecology”, Lawton (Lawton, 1999) calls for the study and identification of general patterns in natural systems. He highlights the need to focus on contingency, defined as “[what is] only true under particular or stated circumstances”, and on the identification of the rules of contingency in ecological research.

ecosystem stability in mathematical models of ecological networks (May, 1972). This result was based on the assumption of random interactions between consumer and resources, i.e., on randomly constructed networks. The differences between theoretical predictions and what was observed in empirical systems was later explained by the non-randomness of ecological systems (Yodzis, 1981). This non-randomness resulted from empirically determined links between interacting species. A manipulative experiment showed that the increase in plant species diversity increased the stability of plant communities (Tilman and Downing, 1994), which supported the early suppositions of increased stability with increased complexity. Extensive empirical and theoretical work in various ecosystems have corroborated this early finding and increased evidence pointing towards a positive relationship between diversity and ecosystem stability, productivity, multi-functionality, and protection against species invasion (Tilman et al., 2014). This positive relationship raises concerns on the impact of continuous loss of biodiversity on ecosystem services, including the loss of natural enemies on the biological control of agricultural pests.

1.4.2 Relation between predator biodiversity and biological control

Two recent meta-analyses by Letourneau et al. (2009) and Griffin et al. (2013) have found an overall positive impact of natural enemy species richness on prey suppression, but these studies have also detected large variation in the responses. This variability in the documented effects of predator richness on prey suppression suggests that they might be context dependent, or “only true under particular or stated circumstances” (Lawton, 1999). It highlights the need to better understand the mechanisms underlying this relationship, and to identify the sources of variability to improve our ability to make functional predictions of the extent of prey suppression in predator-prey communities.

Mechanisms involved in the service of biological control by diverse predator communities

Empirical studies have found different mechanistic pathways that can result in differing effects of predator diversity on prey suppression (Fig. 2). High predator diversity increases prey suppression when different predator species complement each other (“complementarity”, Cardinale et al., 2002; Snyder et al., 2006), for instance through spatially or temporally distinct predation on the prey population (Sih et al., 1998; Wilby and Thomas, 2002). A positive effect can also result from facilitation, when predators facilitate predation by other predators (Straub et al., 2008). Complementarity and facilitation should be distinguished, however, from a sampling effect, defined as the increasing

chance of having an efficient predator by increasing the number of predator species (Hooper et al., 2005). In addition, in a longer time frame, high predator diversity might insure the provisioning of biological control services against temporal and spatial fluctuation (Yachi and Loreau, 1999). On the other hand, high predator diversity can result in lower predation rates because of interference between predators. Predator interference comprises consumptive interference, when predators consume each other rather than the primary prey (termed *intraguild predation*; Finke and Denno, 2006; Polis et al., 1989), and behavioural interferences (Lang, 2003), when predators disturb each other from prey consumption. A neutral effect can also arise if predator species are redundant, i.e., they feed on the same pool of prey individuals. It could also occur if positive and negative interactions in the predator community are equally strong (Letourneau et al., 2009).

Empirical studies show that the effects and underlying mechanisms of increased natural enemy richness on prey suppression vary according to systems, and the traits of predators (such as mobility traits, Rosenheim et al., 2004), prey (such as prey mobility, Provost et al., 2006), and host plant (such as structural and chemical traits, Straub and Snyder, 2008). In systems combining predators, prey and host plants that contribute to various of the above mechanisms, an idiosyncratic response can be observed (Snyder and Tylianakis, 2012).

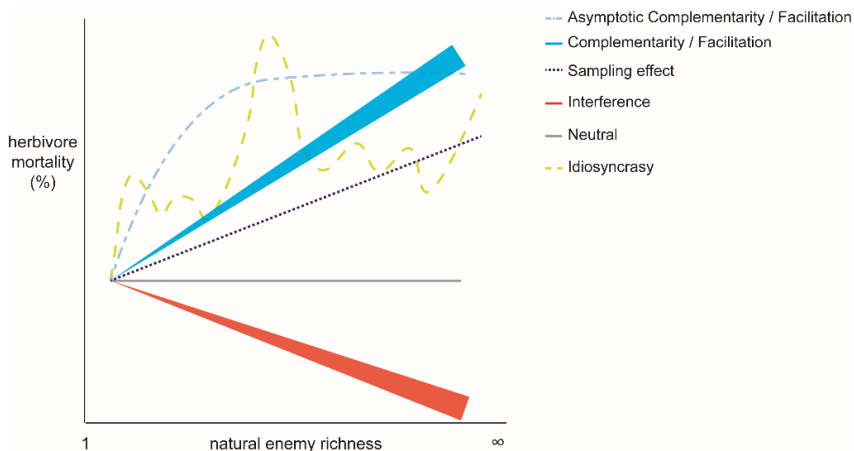


Figure 2. Potential mechanisms explaining the effect of increased natural enemy species richness on the strength of herbivore suppression. Interactions among natural enemy species lead to either positive (by complementarity, facilitation, or positive sampling effect), neutral (by minimal interaction or cancelling effects of positive and negative interactions), or antagonistic (via interference through intraguild predation or behavioural competition) effects on herbivore suppression. When the predator community includes species with varying positive and negative effects, the resulting effect on herbivore suppression is idiosyncratic. The relations are depicted as

linear, but which may be nonlinear (example of asymptotic additivity effect). Blue, red, grey and yellow colours refer to positive, negative, neutral, and idiosyncratic effects, respectively. Adapted from Letourneau *et al.* 2009 and Snyder and Tylianakis (2012).

Integration of the different components of agroecosystems in the relationship between predator diversity and biological control

Theory predicts that new properties emerge when individual components are combined into larger and more functional entities. This particularly applies to ecosystems as they “encapsulate successively smaller ones down to the level of the individual organisms [...], and [are] also part of an increasingly larger series” (Rowe, 1961). More specifically, agroecosystems are characterized by a varying richness and abundance of predators and prey in a field of variable attributes, under a given farming management, and integrated in a defined landscape. In such systems, a more complex response is expected compared to the added responses of individual, isolated components.

Alternative resources to natural enemies (i.e., alternative prey, or floral or seed resources from weeds) can interfere with the interactions between predators and their targeted prey directly, if natural enemies switch from consuming the targeted prey to alternative resources (Cardinale *et al.*, 2003; Madsen *et al.*, 2004), or indirectly, by altering inter- and intraspecific interactions among predators (Rickers and Scheu, 2005; Werling *et al.*, 2012). In the long term, it can also provide resources to natural enemies when targeted prey is scarce, and therefore support natural enemy communities and biological control (Snyder and Tylianakis, 2012). The structure of the system, modified for example by the presence of weeds, can similarly moderate the strength of biological control by providing additional spatial niches to natural enemies and their prey (Diehl *et al.*, 2013; Finke and Denno, 2006). In a larger spatiotemporal scale, landscape complexity can also benefit natural enemies and modify their contribution to biological control (Gagic *et al.*, 2011; Jonsson *et al.*, 2012; Rusch *et al.*, 2013b).

A good understanding of the feeding interactions between natural enemies and their food resources in relation to the various components of agroecosystems (diversity of predators and prey, field and landscape attributes) is therefore needed to better understand biological control in field conditions. The development of molecular methods has made it possible to identify predator-prey interactions with a resolution never rivaled before (e.g., Traugott *et al.*, 2013). Therefore, it opened up the possibility to better describe the network of feeding interactions between natural enemies and their prey in agroecosystems (Snyder and Tylianakis, 2012).

1.5 Knowledge gaps

1.5.1 Relationship between natural enemy diversity and biological control.

Many studies have tested empirically the relationship between arthropod natural enemy richness and biological control of agricultural pests, but its general outcome is unknown. The idiosyncrasy of the relationship between natural enemy species richness and prey suppression has been highlighted by recent meta-analyses, so that predictions are difficult to make (Griffin et al., 2013; Katano et al., 2015; Letourneau et al., 2009). These recent meta-analyses did not focus exclusively on arthropod natural enemies in agricultural systems, but also included studies with vertebrates predators (Letourneau et al., 2009), or studies from aquatic and terrestrial systems (Griffin et al., 2013; Katano et al., 2015). In agricultural systems, prey suppression by vertebrates might show different diversity responses due to the wider range of their habitat. It has also been shown that the outcomes of predator interactions on trophic cascades might differ in aquatic *versus* terrestrial systems (Halaj and Wise, 2002; Schmitz et al., 2000), so making a generalization for the diversity response from both systems might be difficult. So far, no meta-analyses have investigated the effect of the diversity of arthropod natural enemies on herbivore suppression in the context of biological control of agricultural pests.

In addition, a growing body of literature suggests that the idiosyncrasy observed could be explained by the traits of natural enemies, prey, and host plants. Therefore, it may be possible to predict better the outcome of the increase of predator species richness on prey suppression, by taking these traits into account (Griffin et al., 2013; Letourneau et al., 2009; Tylianakis and Romo, 2010). So far, the relationship between predatory arthropod biodiversity and biological control and its potential moderation by the traits of predators, prey, and host plants has not been investigated. Identifying the effects of predator biodiversity and biological control and its sources of variability would improve our understanding of the functionality of predatory arthropod diversity, and would help identify the mechanisms that drive this effect. This could, in turn, help improve the measures taken to promote biological control services in agricultural fields; and the predictions of biological control services.

1.5.2 Mechanisms driving the relation between predator diversity and biological control

The mechanisms underlying the positive, negative, or neutral effect of predator diversity on prey suppression are not well understood. The study of predator diversity effects has, so far, relied on indirect indicators, deduced from population count data (Finke and Denno, 2004; Griffiths et al., 2008; Straub

and Snyder, 2008, 2006; Wilby et al., 2005) or from behavioral observations (Straub and Snyder, 2008; Wilby et al., 2013) in microcosms of limited temporal duration. The mechanisms were thus only inferred. Newly developed molecular methods provide a tool to directly identify and better understand these mechanisms, including the occurrence of intraguild predation within the predator community, or the presence of facilitation among predators (Davey et al., 2013; Raso et al., 2014; Traugott et al., 2012).

1.5.3 Structure and temporal variability of agricultural food webs

In agricultural fields, predator-prey interactions are integrated in a complex and dynamic system. Simultaneous changes occur during the cropping season: both at a structural level, from bare soil to a more or less diverse community of plants of varying coverage and structural complexity, and at the arthropod community level, where herbivore abundances increase with increased resources and decrease when the crop matures and loses its nutritional interest for herbivores. Additionally, the intensity of farming practices can affect, both directly and indirectly, prey and predators in agricultural fields.

Studies of the complexity of arthropod food webs in agroecosystems has, so far, focused on host parasitoid systems (e.g., Gagic et al., 2011; Macfadyen et al., 2009). Much remains to be learned about the factors determining the contribution of the community of prey in the diet of diverse communities of generalist predators in agricultural systems. To date, the strength of predator-prey feeding interactions and its moderation by biotic and abiotic factors are little known. Molecular gut content analysis enables the direct investigation of trophic interactions between consumers and their prey, and thus provides a tool to investigate predator-prey food webs in agricultural fields. The study of predator-prey food web structure could help identify the drivers underlying the service of biological control of agricultural pests and its stability.

2 Aims

The goals of this thesis are to i) explore the service of biological control provided by ground dwelling arthropods in relation to their diversity, and to biotic and abiotic factors, and ii) describe the ground-dwelling arthropod food web in agricultural crops.

The specific aims are to:

1. Study the idiosyncratic effect of predator diversity on prey suppression in relation to predator, prey, and host plant traits using available literature (**I**)
2. Study the effect of predator diversity on biological control of cereal aphids in semi-field conditions and identify the mechanisms involved, with a particular focus on intraguild predation (**II**)
3. Examine the diet of generalist predators in agricultural fields according to crop growing season, predator and prey densities, and farming system (**III**)
4. Examine the temporal variability of predator-prey food web structure in agricultural fields according to the cropping season (**IV**)

3 Methods

Multiple types of methods have been used in the different studies presented in this thesis. The first study is the result of a large literature survey which resulted in a meta-analysis. In the other studies, we designed a manipulative field cage experiment (paper **II**) and a field survey (papers **III** & **IV**) to investigate the diet of predatory arthropods in natural conditions, using DNA-based gut content analyses. In this section, I will present motivations and reflections about these different methods, and the statistical tools used in the analyses.

3.1 Meta-analysis

3.1.1 Why a ([n] other) meta-analysis?

Meta-analysis is an objective and informative tool, that in contrast to other types of literature reviews, allows a quantitative summarization of results from individual studies that may have conflicting findings (Koricheva et al., 2013). Meta-analysis facilitates the identification of research gaps, and can be a powerful means of communicating a general message to stakeholders and policy makers to promote scientifically-based decisions. In the context of biological control, a meta-analysis could, for instance, provide scientific support for agricultural policies that target measures to support natural enemies.

Three meta-analyses have recently investigated the relationship between predator diversity and prey suppression (Griffin et al., 2013; Katano et al., 2015; Letourneau et al., 2009). These meta-analyses used different protocols for study selection and included a diversity of studies and systems that contributed to the variability observed in the results. In our meta-analysis, we aimed to address the relationship between the diversity of arthropod predators and herbivore suppression, to allow conclusions specifically interpretable in

the context of biological control in agroecosystems. Importantly, we also explicitly investigated the influence of predator, prey and, host plant traits, and study characteristics, on the relationship between predator species richness and herbivore suppression.

3.1.2 Procedure

A meta-analysis procedure is done in two stages: an initial stage, with the formulation of the question and the literature search, and a final stage, where data are extracted, analysed, interpreted and presented (Koricheva et al., 2013).

Defining the research question and protocol for study selection

We defined the research question inspired by the hypotheses stated by Tylianakis and Romo (2010) to explain the idiosyncrasy of the effects of predator diversity on pest suppression. The literature search protocol was defined by the search carried out by Letourneau et al. (2009), to which we added some criteria to set the focus on arthropod predators. The protocol for study selection is summarized in the material and methods in paper **I**.

Selection protocol for studies with several comparisons of predator diversity

Some of the selected studies had several predator treatments that could be compared to each other, so we had to define selection criteria. We decided on extracting a single comparison per independent experiment. This approach is more conservative than the one used by Letourneau et al. (2009) who used all possible comparisons of diversity levels in the selected studies. We chose this procedure because, although it leads to a smaller number of data points, it avoids pseudo-replication in the dataset. Griffin et al. (2013) used an alternative procedure: they took the comparison of the high diversity treatment to the mean low diversity treatment and, in a second analysis, to the best performing species. These two different analyses lead to different results (a positive effect of predator diversity on prey suppression, and no effect, respectively). To avoid any bias in our analysis, we opted to not do any a priori selection or average.

We decided to select the treatments with the highest and lowest predator species richness, or if there were several multi-species treatments with equal species richness, we selected one of them randomly. However, if a study presented comparisons from several independent experiments, we considered them as separate data points and included all of them in the analysis. The data selection and extraction are summarized in the material and methods in paper **I**.

Choice of the measure of effect size

Meta-analyses mainly use two common measures of standardized differences between two groups, or effect size: the standardized mean differences (SMD) or Hedges' d (Hedges and Olkin, 1985) and the log response ratio, calculated as the natural log of the ratio of the mean of the two groups (Hedges et al., 1999). For consistency with Letourneau et al. (2009), we used the measure of SMD, which is preferred in meta-analysis in ecology as it is robust against unequal sampling variance in the compared groups and includes a correction for small sample sizes (Koricheva et al., 2013).

Limitations

We acknowledge the potential publication bias in the studies selected in our meta-analysis. These biases can arise from failure to publish insignificant results, i.e., the “file drawer problem” according to which non-significant results would be less likely to get written than significant ones (Arnqvist and Wooster, 1995). This potential bias from underrepresented publication of non-significant results in our datasets was investigated (paper **I**). Additionally, publication bias can arise due to the “editorial love of controversy”, according to which the editor's search for novelty can prevent the accumulation of evidence of an already published pattern (Heleno, 2014). Such a bias could thus lead to the failure to assess whether or not there are effects of a factor on a process or variable in a meta-analysis.

3.2 Bird-cherry oat aphid on barley as the study system to investigate the relationship between predator diversity and biological control

In this thesis, we used spring-sown barley (*Hordeum vulgare* Linnaeus) in South-central Sweden, with *Rhopalosiphum padi* (L.), the bird-cherry oat aphid, as the study system (papers **II** & **III** & **IV**) (Fig. 3). Barley is one of the major crops grown in Sweden, with a production projected in 2013 of 1,814 million tons from 392,000 ha (Lyddon, 2013).

3.2.1 Aphids and their management in barley fields

Rhopalosiphum padi colonizes spring-sown barley fields early in the cropping season. Their population increases exponentially during stem elongation, until density peaks at heading (Fig. 4). Later in the season, another aphid, the grain aphid *Sitobion avenae* (Fabricius) also colonizes barley fields, but they usually remain at low densities in Swedish spring-sown cereal fields. *Rhopalosiphum*



Figure 3 *Rhopalosiphum padi* on barley. Photo Riikka Kaartinen.

padi can cause yield losses reaching as much as 50% some years in Sweden (Östman et al., 2003) and more generally in Europe (Leather et al., 1989). In recent years, however, *R. padi* densities have rarely exceeded economic thresholds, and insecticide treatments were rarely used. In Uppland, the region surrounding Uppsala, field management is of particular low intensity, with little (if not no) use of insecticides (Jordbruksverket & SCB, 2011). The control of aphids thus mostly relies on biological control.

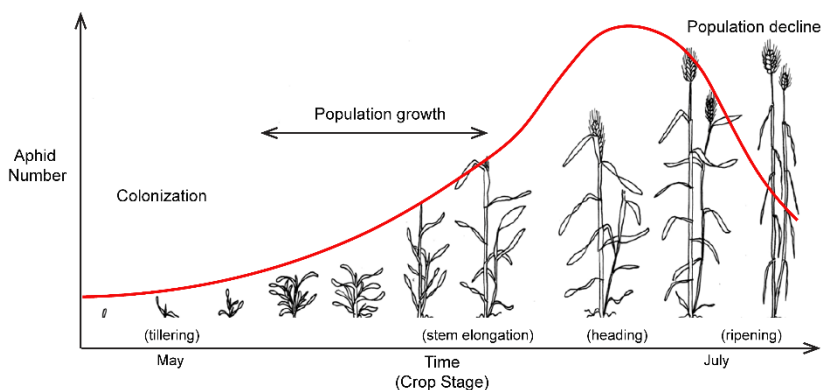


Figure 4. Population dynamic of *Rhopalosiphum padi* in relation to spring sown barley development stage in Sweden. Adapted from Chiverton (1987).

3.2.2 Natural enemies of cereal aphids

In cereal fields, a complex of natural enemies attacks aphids, including generalist, ground living predators, more specialized predators, and parasitoids. In South-central Sweden, aphid parasitism is rare, so the complex of aphid natural enemies mainly contains generalist predators such as spiders and carabids and more specialized predators such as larvae and adults of lady-beetles (Coleoptera: Coccinellidae), green lacewing larvae (Chrysopidae), and hoverfly larvae (Syrphidae).

The generalist predator community in the study region

In South central Sweden, the spider community is dominated by a few very abundant species of wolf spiders: *Pardosa agrestis* (Werling), *Trochosa ruricola* (De Geer) (family: Lycosidae) and web-building spiders: *Oedothorax apicatus* (Blackwall), *Agyneta rurestris* (Koch) (family: Linyphiidae). These spiders overwinter as adults in winter crops or grasslands and reproduce in spring/summer (Marc et al., 1999). The carabid community (Coleoptera: Carabidae) is dominated by *Pterostichus melanarius* (Illiger), *Poecilus cupreus* (L.), *Harpalus rufipes* (De Geer), *Bembidion lampros* (Herbst), *Trechus secalis* (Paykull), which are abundant carabids in many parts of Europe (Kromp, 1999; Thiele, 1977). *Poecilus cupreus* and *B. lampros* are spring breeders and overwinter as adults in nearby, uncultivated habitats (Wallin, 1989a, 1989b). The other carabids are autumn breeders, and overwinter as larvae in the field (Wallin, 1989a, 1989b). Carabids lay their eggs belowground, where larvae stay until pupation. Carabids are particularly susceptible to perturbations inherent to field management (e.g., seasonal harvesting, ploughing, sowing, Kromp, 1999).

Generalist predators colonize spring barley fields early after sowing, and can thus contribute to biological control of aphids as soon as aphids colonize the field (Birkhofer et al., 2008; Chiverton, 1988; Edwards et al., 1979; Öberg and Ekblom, 2006) when *R. padi* is mostly present on the stem base of the young barley plants (Wikteliuss, 1987, Fig. 3&4).

Feeding behaviour and biological control of aphids

In addition to aphid prey, generalist predators are characterized by their broad diet, and feed on prey from both the above- and belowground subsystems (Nyffeler and Benz, 1988; Toft and Bilde, 2002). Potential prey in the belowground subsystems includes annelids (earthworms) and arthropods such as Collembola and dipteran larvae. These organisms contribute to nutrient recycling in the soil through decomposition of dead or decaying organisms and are often referred to *decomposers*. Aboveground, pollinators such as

Hymenoptera and Diptera, and other herbivores such as Hemiptera (aphids, leafhoppers) and Thysanoptera are found in barley fields, and are thus potential prey for the generalist predators.

Additionally, intraguild predation (as opposed to “extraguild predation”, Wise, 2006) can occur among generalist predators, that may feed on each other, or even prey on conspecifics (i.e., “cannibalism”, Wise, 2006), at least for some spider species. Intraguild predation and cannibalism are also observed in the community of more specialized predators (e.g., Gardiner and Landis, 2007; Michaud, 2003; Michaud and Grant, 2003).

This generalistic feeding behaviour may have negative consequences for pest suppression as it may result in switching from consuming aphids to other extraguild prey such as decomposers or interference in the predator community due to intraguild predation (Lang, 2003; Snyder and Wise, 1999). The consumption of extraguild prey may, however, also promote biological control services as it provides critically important food resources to generalist predator populations when pest density is scarce (von Berg et al., 2010), for example at the beginning of the cropping season.

The extent of extra- and intraguild predation of these generalist predators is, however, difficult to assess directly, but the recent development of molecular methods has opened new prospects to the study of predators’ diet.

3.3 The use of molecular gut content analysis to study predators’ diet

3.3.1 Historical insights

Early studies of predators’ diet relied on direct observations and visual identifications of prey remains in dissected guts (Chiverton, 1987; Nyffeler and Benz, 1988; Sunderland and Vickerman, 1980), or, in webs for web-building spiders (Nyffeler and Benz, 1987). The resolution of prey identification was then coarse, and interactions that leave no identifiable prey remains in predators (e.g., fluid feeders, larval stages, eggs) could not be assessed. These limitations have been overcome by the development of molecular gut content analysis, which can detect existing trophic links between predators and their prey as long as specific prey molecules are detectable.

Early molecular work relied on the detection of protein markers using isoenzyme electrophoresis (Paill et al., 2002) or monoclonal antibodies in predatory arthropod guts (Ragsdale et al., 1981). Serological techniques (i.e., targeting antibodies) allowed the detection of stage-specific prey, and were for a long time favoured to screen large numbers of predators for a single prey species (Chiverton, 1987; Fournier et al., 2008). For instance, Chiverton (1987)

used serological techniques to investigate the predation of *R. padi* by 1350 ground dwelling generalist predators. However, the often long and costly development of individual specific antisera (Chen et al., 2000; Fournier et al., 2008; Greenstone, 1995) complicated the use of these methods for simultaneous multiple prey testing. Since the late 1990s, techniques based on deoxyribonucleic acid (DNA) using polymerase chain reaction (PCR) have been developed for the detection of prey in predators (Traugott et al., 2013). The first molecular assays targeted a single prey (“Singleplex-PCR”), but recent advances now allow a target of multi-prey species simultaneously (“Multiplex-PCR”).

3.3.2 Collection of live arthropods for molecular gut content analysis

Because DNA-based gut content analysis can detect minute amounts of prey DNA, it is crucial to avoid the contamination of samples during the predator collection. King et al. (2008) made recommendations on the best sampling methods for DNA-based gut content analysis (Table 1). Following the ‘best practices’ recommended, we collected predators using two non-invasive methods: hand collection and dry pitfall trapping, and used clay balls to serve as refuges for predators in order to prevent predation inside the traps. These methods considerably reduce the potential contamination of samples, which could be a significant source of error. We thus assumed that we avoided contamination as much as possible, and did not use any DNA decontamination treatments such as detergent to clean samples from external debris that could contain prey DNA. These treatments are primarily used when studying herbivores, which might contain plant DNA on their body parts (Matheson et al., 2008) or small organisms such as mites (Remén et al., 2010).

3.3.3 Molecular gut content analysis and the description of predator-prey interactions

Potential and limitations

Molecular gut content analysis can help to define predator-prey interactions both qualitatively (with the description of feeding links from a given predator species to a targeted prey) and quantitatively (with the rates of feeding interactions from a given predator species to a targeted prey). In agroecosystems, these analyses can be used to describe the predator community attacking a given pest and the contribution of predators to biological control. Predator-prey interactions can then be compared between different sites, to answer whether or not management practices or landscape features can influence these interactions (Szendrei et al., 2010).

Table 1. *Sampling methods listed in declining suitability for DNA-based gut content analysis. Methods in bold have been used in our studies. Adapted from King et al. (2008)*

Method	Principal targets	Issues	Potential solutions
Individual collection	plant dwelling predators,	Time consuming, Few individual collected	Possibility to use an aspirator for small insects To combine with population data
Dry pitfall trap	ground predators	Predation in receptacle,	mesh insert (to separate small individuals from larger ones), cover, refuges, frequent collection from the trap
Vacuum sampling	plant dwelling predators, ground predators	External contamination, Predation in receptacle	Low vacuum pressures, immediate contact with ice in the field, additional experiments to check for contamination
Sweep net	Flying insects, plant dwelling predators,	Contamination: regurgitate, wounded samples	
Wet pitfall trap	ground predators / flying insects	Contamination: regurgitates, DNA “soup”	

Molecular gut content analysis based on PCR does not, however, allow the detection of prey sharing the same targeted DNA fragment as its predator. Thus, cannibalism cannot be assessed. In addition, if gut contents are screened for prey at a taxonomic resolution above the species level (e.g., genus or family), prey that share the same taxonomic unit as the predator cannot be detected. These ‘forbidden links’ can underestimate the actual predation occurring in the field. Despite the rigorous methodological requirements and potential sources of errors, PCR-based molecular techniques are widely used to describe trophic interactions in agroecosystems (Chen et al., 2000; Davey et al., 2013; Eitzinger and Traugott, 2011; Greenstone et al., 2010; Kuusk et al., 2008; Kuusk and Ekbom, 2010; Traugott et al., 2012).

To conduct the molecular work presented in this thesis (papers **II** & **III** & **IV**), we used newly published or developed new multiplex-PCR assays to study predator-prey food webs in our study systems. We targeted the most abundant and, to our knowledge, most important prey available in the studied system, including herbivores, decomposers, and predators. The design of the specific multiplex-PCR assays are described in papers **II** & **III**.

Analyses of the molecular data

In this thesis, we analyzed the molecular gut content data using two different methods:

- (1) We compared the detection frequencies of the predator community to estimated abundances of prey. The aims were to reveal the mechanisms behind the effect of increased numbers of predator species on aphid suppression (paper **II**) and how seasonality, farming system, and weed abundance affect the extent of extra- vs intraguild predation by the community of arthropod predators in agricultural fields, and thus their potential for aphid biological control (paper **III**).
- (2) We studied the predator-prey food webs based on the detected predator-prey interactions and identified predator-prey interactions that appear to occur more and less frequently than expected by using comparisons of observed interactions to a null model based on bootstrapping the observed detection frequencies (paper **IV**).

3.4 Manipulative field cage experiments to identify the mechanisms involved in aphid suppression by diverse predator communities



Figure 5. Field cage experiment in a barley field. June 2012. Photo: Michael Traugott

To identify the mechanisms involved in aphid suppression by diverse predator communities and the potential interaction with the presence of weeds, we designed a field cage experiment where we manipulated predator diversity (Fig. 5, paper **II**). We aimed to design an experiment that mimics realistic field conditions at the time when aphid density peaks (at crop heading, Fig. 4), and limit perturbations to the system.

3.4.1 Choice of experimental design

The manipulation of predator diversity in diversity experiments can, according to the experimental design chosen, involve a simultaneous manipulation of predator abundances. The choice of the experimental design and the understanding of its limitations are thus crucial for interpreting the results of diversity experiments. Two experimental designs are generally recommended for diversity experiments: the substitutive design and the additive design. Substitutive designs ensure that total predator density (or potential consumption rate if that is used as a way of standardizing single predator treatments) is maintained constant across diversity treatments, while the additive design keeps individual predator species abundances constant across diversity treatments (Fig. 6). The latter is mostly used in diversity studies, and usually gives strong support to an overall positive effect of diverse predator communities on prey suppression (Letourneau et al., 2009) but confounds an increase of predator diversity with an increase in predator abundance, which influences the ratio of total predator to prey abundance. To avoid any confusion between the increase of predator richness and abundance, we used a substitutive design in our field cage experiment.

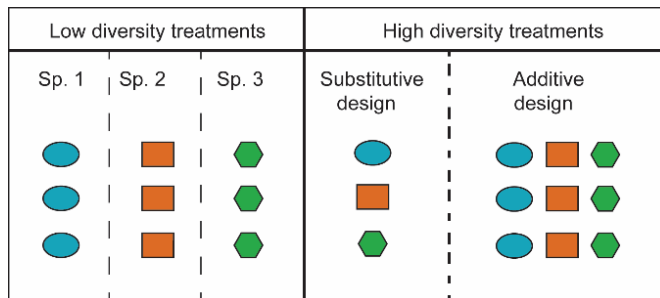


Figure 6. Schematic representation of experimental designs used to study the effect of predator diversity on prey suppression. Single symbol represent a standardized measure of individual species, e.g., number of individual, standardized consumption rates.

3.4.2 Selection of the organisms

The predators in the experiment were selected to represent a typical predator community attacking aphids at the time when aphid density peaks in spring barley. During this phase the predator community typically consists of both generalist ground dwelling predators and more specialized foliage dwelling aphid predators. Thus, we selected the ground dwelling carabid beetle *P. melanarius*, and the larvae of two more specialised predators, the lacewing *C. carnea*, and the lady beetle *C. septempunctata*.

3.4.3 Protocol

We investigated the effect of predators on aphid densities in the low diversity treatment (Fig. 6) and in the presence of the three predator species (high diversity treatment, Fig. 6). We further investigated the mechanisms involved using molecular gut content analysis. A more precise study design of this experiment is presented in paper **II**.

3.5 Field survey to unravel predator-prey food webs in agricultural fields

A large field survey was designed to study the diet of generalist predators in fields under organic and conventional management, during the barley growing season. The aim of this survey was to address the relationship between predator diet and predator and prey field abundances (paper **III**) and to study the structure of predator-prey food webs (paper **IV**), under field conditions.

3.5.1 Design of the study

The sampling was designed by Barbara Ekbom, Mattias Jonsson, Gerard Malsher, and Michael Traugott, and the field work was done during the summer of 2011.

Field selection

Ten spring barley fields were selected surrounding the city of Uppsala, in South-central Sweden (Fig. 7). Fields were located in pairs of one field that had been managed organically for more than 10 years and a conventionally managed field.

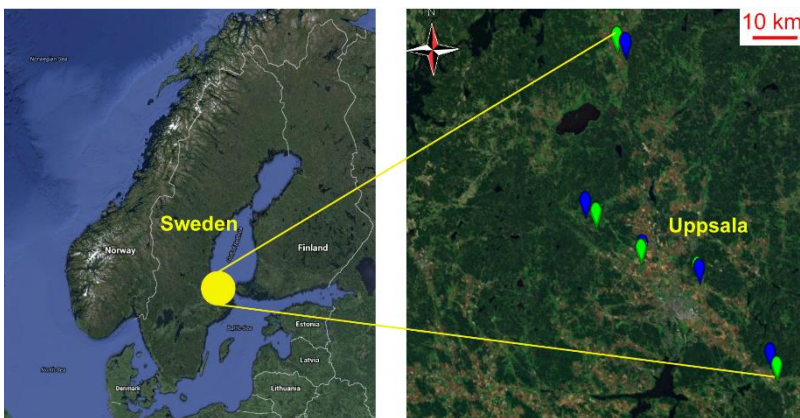


Figure 7. Distribution of the selected sites around Uppsala, Sweden. Blue and green dots denote conventional and organic fields, respectively.

Monitoring of the invertebrate community

Abundances of the ground dwelling predators and their potential invertebrate prey were monitored using different sampling methods (Fig. 8, described in paper **III**). We related these density estimates to the detection frequencies of different prey types in predator guts in paper **III**.



Fig. 8. Methods used to monitor the invertebrate community (from top to bottom and left to right): extraguild prey monitoring (to the left, in blue: thrips, Diptera, aphids; in orange: earthworms, Collembola, and thrips) and ground dwelling predator monitoring (to the right).

In addition to the ground dwelling predators and the invertebrates targeted by our molecular assays, a few other organisms were identified in the fields (Table 2). Their abundances were relatively low in relation to the targeted invertebrates sampled by the same methods, but we cannot exclude the fact that they might have been prey for the ground dwelling predator community.

Table 2. *Invertebrates not targeted by the molecular assays, but found in soil and sweepnet samples*

	Phylum	Class	Order	Family	Group of species
Soil Samples	Arthropoda	Arachnida			Acari
	Arthropoda	Diplopoda	Haplotaxida	Enchytraeidae	Enchytraeidae
	Arthropoda	Diplopoda			Diplopoda
	Arthropoda	Entognatha	Diplura		Diplura
	Arthropoda	Entognatha			Protura
	Arthropoda	Insecta	Coleoptera	Bruchidae	Bruchidae
	Arthropoda	Insecta	Coleoptera	Chrysomelidae	Chrysomelidae
	Arthropoda	Insecta	Coleoptera	Latridiidae	Latridiidae
	Arthropoda	Insecta	Coleoptera	Nitidulidae	Nitidulidae
	Arthropoda	Insecta	Hemiptera	Miridae	Miridae
	Arthropoda	Insecta	Hemiptera	Cicadellidae	Cicadellidae
	Arthropoda	Insecta	Hymenoptera		Apocrita
	Arthropoda	Symphyla			Symphyla
	Mollusca	Gastropoda			Troschidae
	Nematoda				Nematode
	Tardigrada				Tardigrada
Sweepnet	Arthropoda	Insecta	Coleoptera	Cantharidae	Cantharidae
	Arthropoda	Insecta	Coleoptera	Chrysomelidae	Chrysomelidae
	Arthropoda	Insecta	Heteroptera		Heteroptera (carnivorous)
	Arthropoda	Insecta	Heteroptera		Heteroptera (not carnivorous)
	Arthropoda	Insecta	Homoptera		Homoptera (other than aphids)
	Arthropoda	Insecta	Hymenoptera	Braconidae	Braconidae
	Arthropoda	Insecta	Hymenoptera	Ichneumonidae	Ichneumonidae
	Arthropoda	Insecta	Hymenoptera		Bees
	Arthropoda	Insecta	Hymenoptera		Sawflies
	Arthropoda	Insecta	Lepidoptera		Lepidoptera

3.6 Food web and statistical analyses

3.6.1 Food web analyses

Observed food web structure

Based on the detection of predator-prey interactions using molecular gut content analysis, we built predator-prey interaction metrics which characterized the predator-prey food web. The structure of food webs can be described by a number of metrics, at a network-level (describing the entire food web), at the guild level (e.g., predator or prey), and at the species level (describing the elements, e.g., predator species). We were particularly interested in food web metrics that took into consideration the strength of interactions (i.e., quantitative metrics), and that were robust to differences in sampling intensity ("distribution metrics", Kaiser-Bunbury and Blüthgen, 2015).

Comparisons to randomly generated food webs

To ensure the observed food webs metrics, and thus the food web structure, were not the results of chance alone, we compared the observed metrics with expectations from null models that randomly redistribute the observed feeding interactions of a prey among the allowable predators.

Patefield-generated null models (Patefield, 1981) are generally used for such comparisons (Dormann et al., 2008). These null models are generated assuming random interactions between species and constraining the total frequencies of detection of prey taxa and per predator species (i.e., equal to the ones in the observed interaction matrix). However, because of the limitations inherent to our molecular assays, we needed to specify “forbidden links”, i.e., the impossibility to detect intraguild prey of the same genus as the target predator for carabid predators and the same family/ order for spider predators. Additionally, we added a correction for the number of predators screened that differed according to predator species and field. Thus, the redistribution of observed feeding interactions among predators was done according to a multinomial distribution with probabilities proportional to the number of predator individuals analysed for the different predator species. As a result, in individual null model replicates, each predator species and each prey taxa was assigned the same number of total feeding interactions (prey items and predation events respectively) as observed in the empirical data (as in the Patefield-models), but with a variable distribution of detection frequencies among prey and predator species.

Identifications of favoured/avoided links

The comparison to null models can also be done for each predator-prey interaction, in order to identify specific interactions that deviate from random (Junker et al., 2010). The latter implies assessing the ‘temperature’ of trophic links by measuring how much the observed frequency of interactions deviate from null model expectations. Such deviations could potentially be driven by active choice of the predator and/or assortative microhabitat preferences of both species that affect prey availability (resulting in ‘warm links’), or active dismissal by predators and/or disassortative microhabitat preferences of both species that affect plant (or prey) availability (resulting in ‘cool links’).

3.6.2 Statistical analyses

In this thesis we used two major statistical approaches for the different studies, that can be broadly classified as univariate (papers **I** & **II** & **IV**) and multivariate analyses (paper **III**). In this section, I will motivate the use of these techniques and how they complement each other

Univariate analyses

In the studies where the response variables were univariate (papers **I** & **II** & **IV**), we used a linear approach. Linear models carry four main assumptions: the linear relationship between dependent and independent variables and the independence, equal variance, and normal distribution of errors. However, study design and data structure sometimes broke one or several of these assumptions such that we needed to adjust our statistical models:

- In the cage experiment presented in paper **II**, the repeated measurements in each cage implied a temporal autocorrelation of the measurements, which violated the assumption of independence. We therefore used generalized least squares models to account for such temporal correlation by allowing correlated errors (Crawley, 2007).
- In paper **II**, the data of presence/absence of prey DNA in predators' guts had a binomial structure violating the assumption of normality. We therefore used generalized linear models with a binomial family for the error structures.
- The study design in paper **IV** had a nested structure, which potentially violates the assumption of independence. Using a mixed model approach (i.e., including a random term), we controlled for the nested design such that our model tested general effects of the explanatory variables.
- The studies selected for the meta-analysis (paper **I**) were all different in their original designs in ways that could cause variation in the effect size between studies. We therefore used individual studies as a random factor in a random-effects model (Borenstein et al., 2007; Koricheva et al., 2013, pp. 89–107) to account for this potential variation in the test of the general effect.

Multivariate

Paper **III** included a multivariate response (i.e., the detection frequency of each prey by the generalist predator community). In addition, this study also had a nested study design. Thus, we used multivariate non-parametric mixed models, which specifically address the relationship between multivariate response variables and predictors (Legendre and Anderson, 1999). These models differ from linear approaches mainly in two ways:

- The response is multivariate, and not univariate
- There is no *a priori* assumption of the distribution of the errors.

4 Results and discussion

4.1 The relationship between predator species richness and herbivore suppression

4.1.1 Overall relationship and its moderation by predator, prey, and host traits

Overall effect

In paper **I**, we found a significant increase of herbivore suppression with increasing predator richness (average effect size 0.45 (\pm 0.27), ANOVA, $P=0.001$). Such a significant, positive increase was found in 47 out of 89 experiments (Fig. 9), while 22 experiments showed negative effects where increasing predator richness increased overall prey abundance, and 20 experiments showed non-significant effects, i.e., no difference in prey consumption between high and low predator species richness treatments. Thus there was a high variability among experiments in the effect of predator richness on herbivore suppression, suggesting context dependency, potentially due to predator, prey, and host traits and/or the study settings.

Moderation by predator, prey, and host plant traits

We found only limited support for predator, prey, and host traits moderating the effect of increased predator richness on herbivore suppression (paper **I**). Prey species richness was the only moderator that significantly influenced the diversity effect: we found that increasing prey species richness weakened predator richness effects (ANOVA, $P<0.001$). This result does not support our initial prediction that predator species richness would have a larger positive effect on herbivore suppression when herbivore species richness is higher. Instead, it suggests that predators may have switched to using alternative prey instead of feeding on the focal prey species: alternative prey may have been more easily available, more abundant or of better quality. However, all studies

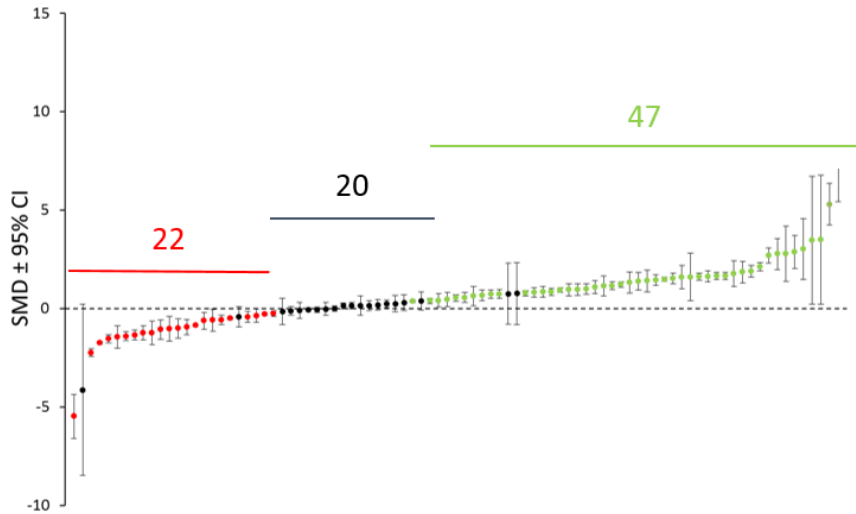


Figure 9. Study-specific effects sizes (SMD) with 95% confidence intervals. Positive values (green symbols) indicate studies where higher predator richness increased herbivore suppression, while negative values (red symbols) indicate studies where increased predator richness decreased herbivore suppression. Studies with black symbols showed no difference in predation between high and low predator richness treatments (as 95% CI overlapping with zero).

included in our meta-analysis focused on predation on a single prey species. A more positive effect of predator richness on herbivore suppression might have been likely if predation had been measured across multiple prey species. Additionally, we found a significant interaction between predator and prey species richness: when predator richness was more than doubled between low and high diversity treatments, herbivore suppression was significantly reduced when prey diversity was low. This could suggest the increase of negative interference (including intraguild predation) with increasing predator richness at low prey species richness. This result should, however, be interpreted with caution as the number of species in the low diversity treatment was, in most cases only one species, thus a more than two-fold increase still comprises only a few predator species.

In addition, we found a nearly significant increase in prey suppression when predators in the high richness treatment were more distantly related ($P=0.070$), although there was a lot of variation in the effect in relation to this moderator. This provides some support for the importance of a high diversity of predator traits for higher herbivore suppression, and concurs with a growing body of literature suggesting that predator functional trait diversity is usually a better predictor of prey suppression than predator species richness (Gagic et al., 2015; Rusch et al., 2015). The other moderators studied (prey patchiness, prey

density, host plant specialization, plant complexity) did not influence the effect of predator richness on prey suppression (paper I).

Moderation by the study settings

We found little influence on the effect of the increase of predator richness on prey suppression due to experimental settings. We found a nearly significant increase in prey suppression in studies with experimental study settings compared to observational ones ($P=0.070$). This result might relate to the lower variability in effects in experimental studies due to a better experimental standardization. The other settings-related moderators (study setting [laboratory vs field studies], study system [agricultural vs natural], temporal scale, spatial scale, and study design [additive vs. substitutive]) did not affect the effect of increased predator richness on herbivore suppression.

Limitation of the study

A large majority of the studies selected in our meta-analysis had focused on a limited number of species (of both predators and prey) and were carried out in controlled environments (laboratory and field cage manipulations). Although we found support for a positive effect of increased predator richness on prey suppression, studies using a broader range of prey taxa, host plants, and experiments with natural levels of complexity are needed to confirm this effect in complex agricultural and natural systems.

4.1.2 Case study: effect of predator diversity on aphid suppression in barley fields

In a controlled field-cage experiment, we combined count data and molecular gut content analyses to investigate the effect of increased predator richness on prey suppression, its potential moderation by the presence of weeds, and the possible mechanisms behind any such effect. We studied the effects when aphid populations peaks (paper II).

Effect of increased predator richness on aphid suppression

Using a substitutive design, we found no effect of an increase predator diversity on aphid suppression (T-test, $P=0.900$). Instead predators had an additive effect (paper II), implying that increasing predator abundances will increase herbivore suppression but that predator species richness has no effect.

Using molecular gut content analysis, we found no indication of facilitation of predation among predator species: the detection rates of aphids in *P. melanarius* and *C. septempunctata* did not differ depending on predator diversity (low vs. high predator diversity treatments, *P. melanarius*: $P=0.460$;

C. septempunctata: $P=0.410$). In addition, we found very little indication of intraguild predation between the predator species: *C. septempunctata* was detected at a low frequency (5.1%) in the gut of *P. melanarius* in the high predator diversity treatment, whereas *C. carnea* was not detected at all. Two of the 135 individuals of *C. septempunctata* collected in the high predator diversity treatment screened positive for *C. carnea* (1.5%).

These results suggest that the additive effect of predators on biological control was not a result of strong synergistic or antagonistic interactions, but instead was due to high redundancy within the predator community.

Influence of weeds

We expected weeds, by adding complexity and creating additional niches, to protect individuals from intraspecific or interspecific interactions, and strengthen aphid suppression (Finke and Denno, 2002). Contrary to our expectation, we found no effect of weeds in influencing aphid suppression (ANOVA, $P>0.05$). Additionally, we found no difference in the detection of intraguild prey in the presence or absence of weeds which suggests that there was no change in the frequency of intraguild predation in the presence of weeds. In our experiments, however, weeds mainly provided additional structural complexity as they did not supplement additional alternative prey. Additional effects of weeds may thus arise in a longer term, as the presence of alternative prey might provide additional resources to predators when pests are scarce.

4.2 Diet of generalist predators and aphid biological control

4.2.1 Diet of generalist predators and seasonal variation

The use of molecular gut content analysis made it possible to describe the diet of generalist predators to an extent never previously achieved (papers III & IV, Fig. 11). Out of the 15 prey taxa targeted by our molecular assays, all but the intraguild prey Lacewing and Pachygnatha spp. (spider family: Tetragnathidae) were detected. The use of this wide range of prey taxa confirms the previously described broad diet of ground-dwelling generalist predators in agroecosystems (Birkhofer et al., 2013; Nyffeler et al., 1994; Toft and Bilde, 2002).

The proportion of generalist predators that tested negative for any prey targeted by the multiplex assay (i.e., with “empty gut”) decreased from Early to Late season (ANOVA, $P<0.001$, Fig. 11, Venn diagrams). This is mainly driven by an increase in detection frequencies, from Early to Late season, of most extraguild prey for most predator species, while a similar trend could not be seen for intraguild prey (Fig. 11, Venn diagrams).

Extent of extraguild predation during the cropping season

Detection frequencies were generally higher for aphids and Collembola than for Diptera, thrips, and earthworm prey (Fig. 11a&b). The detection frequencies of aphids increased on average 4.4 fold from Early to Late season in all generalist predator species (Fig. 11a&b). A similar pattern was observed for Collembola, but only in carabids: detection frequencies remained fairly constant in spiders throughout the cropping season (Fig. 11). Earthworms were generally only detected in carabids: none was detected in Linyphiids while a few *P.agrestis* tested positive for earthworms (range: 0-13% per field per season, Fig. 11).

The diet of generalist predators in terms of extraguild prey differs between carabids and spiders (PERMANOVA, $P=0.002$) and from early to late season (PERMANOVA, $P=0.001$). Aphids is the prey taxa contributing most (21.6%) to the seasonal variation (Fig. 10).

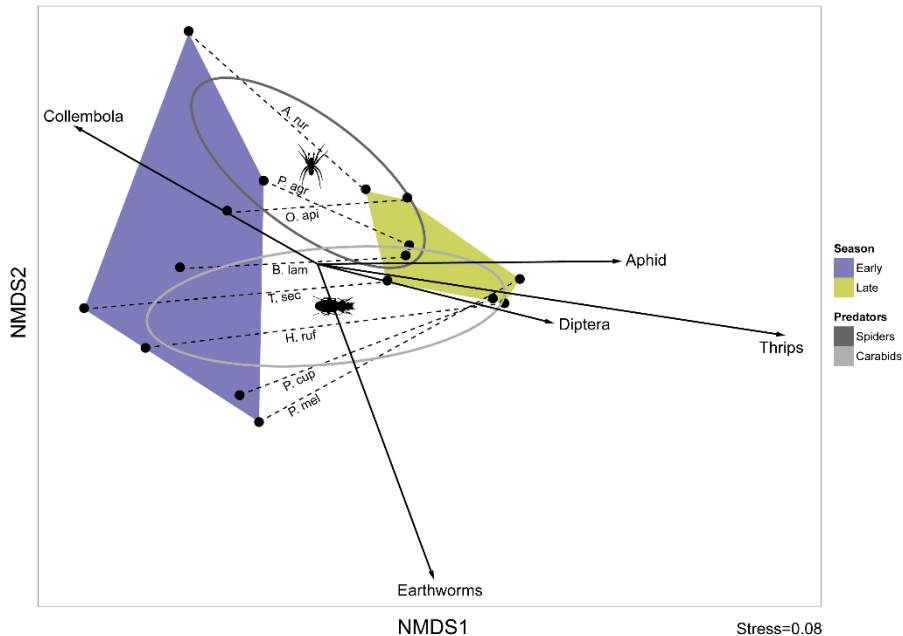


Figure 10. Overlap in predator diets in terms of extraguild prey (aphid, Diptera, Collembola, thrips, and earthworms) visualized using non metric multidimensional scaling (NMDS) using Bray-Curtis ordination of the extraguild prey community. Extraguild prey scores have been added to the final NMDS plot as weighted averages, based on their relative detection frequency. Proximity of predator species (carabids: *Pterostichus melanarius*, *Poecilus cupreus*, *Harpalus rufipes*, *Bembidion lampros*, *Trechus secalis* and spiders: *Agyreta rurestris* (family: Linyphiidae), *Oedothorax apicatus* (family: Linyphiidae) and *Pardosa agrestis* (family: Lycosidae) within the ordination plot indicates that the prey communities detected in their diet are similar.

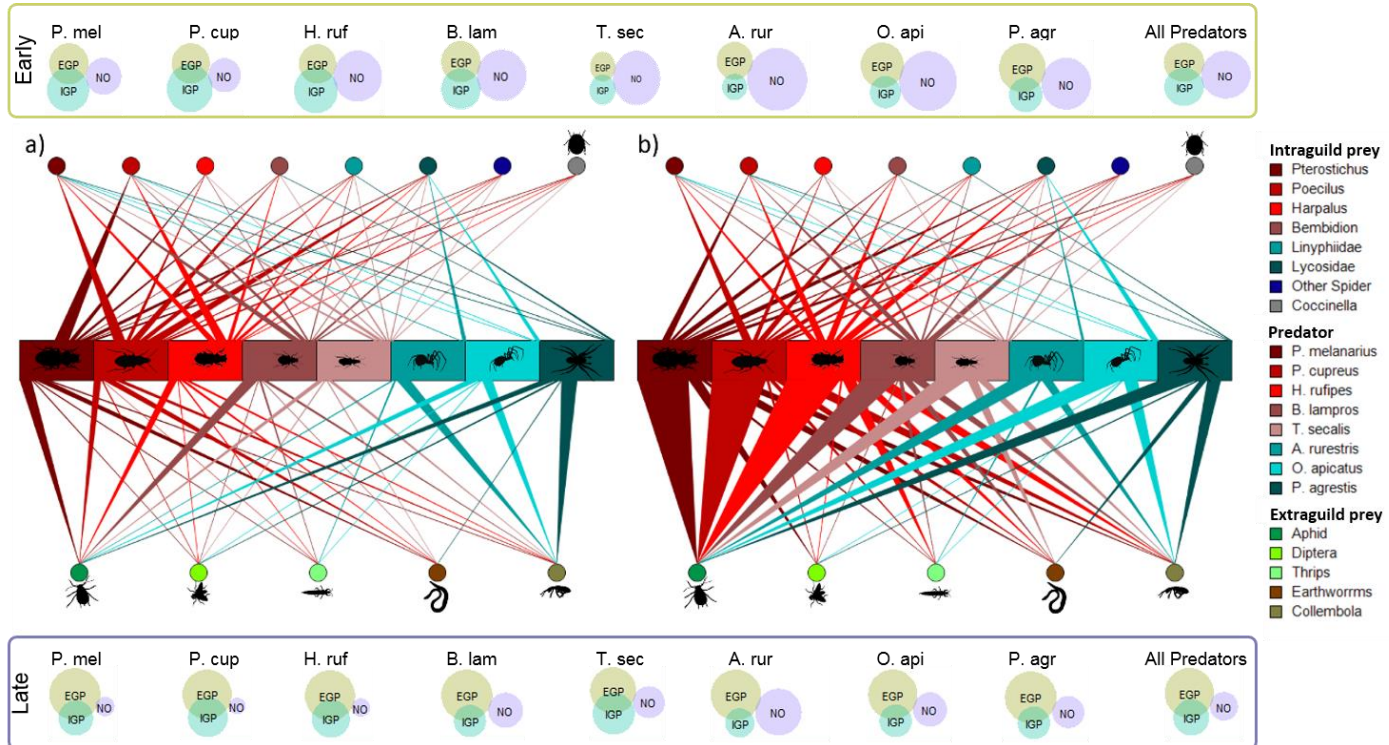


Figure 11. Predator-prey food web in a) Early and b) Late season. The figure shows the proportion of predators screened across all fields that were positive for a) extraguild prey (bottom taxa: Aphid, Diptera, Thrips, Earthworms, Collembola) and b) intraguild prey (top taxa: Pterostichus, Poecilus, Harpalus, Bembidion, Linyphiidae, Lycosidae, Other spiders, Coccinella) detected in eight generalist predator species (Middle taxa: carabids: *Pterostichus melanarius*, *Poecilus cupreus*, *Harpalus rufipes*, *Bembidion lampros*, *Trechus secalis* and spiders: *Agyneta rurestris* (Linyphiidae), *Oedothorax apicatus* (Linyphiidae) and *Pardosa agrestis* (Lycosidae). The Venn diagrams (above and below the food web) represent the amplitude of detection frequencies per prey type, i.e., the proportion of predators that tested positive for extraguild prey (at least one extraguild prey detected, “EGP”), intraguild prey (at least one intraguild prey detected, “IGP”), and that tested negative for all prey (“NO”) targeted by the multiplex assay, in Early (top) and Late (bottom) season. Figure realized with ‘Food Web Designer’ (Sint and Traugott, 2015) and the package ‘venndiagram’ in R (Chen, 2015)

Intraguild predation

Intraguild predation was more often observed in carabids than in spiders (Fig. 11). On average, less than 1% of the spiders tested positive for carabid intraguild prey across study sites (range 0-5%). No spider tested positive for prey from the carabid genus *Harpalus*, even though this potential prey group was present in all fields. Linyphiidae spiders were found to feed on Lycosidae (range 0-25%), and *Pardosa agrestis* fed on Linyphiidae (range 0-25%, Fig. 11). These results concur with other studies showing that spiders rarely prey on carabids (Davey et al., 2013; Dinter, 1998; Raso et al., 2014), and is likely to reflect spiders' avoidance of carabid prey due to difficulties, and potentially high risks, in attacking them (Davey et al., 2013), as spiders would need to penetrate the chitinous exoskeleton of carabids before ingestion. On the other hand, our work confirms that spiders frequently prey on other spiders (Birkhofer and Wolters, 2012; Raso et al., 2014; Rypstra and Samu, 2005).

In contrast, on average more than 16% of the carabids tested positive for spider intraguild prey across study sites (overall range 0-55%, with 0-16% for Linyphiidae, 0-31% for Lycosidae, and 0-9% for other spider prey). Carabids also fed on each other at varying frequencies (Fig. 11): *P. melanarius* had the highest detection frequencies for carabid intraguild prey (range 0-44% for *Bembidion*, 0-20% for *Harpalus*, and 0-33% for *Poecilus*).

Intraguild predation was thus unidirectional with carabids feeding on spiders but spiders rarely feeding on carabids. However, spiders frequently preyed on other spiders, and carabids preyed on other carabids. We most likely underestimated the frequency of intraguild predation due to the limited targets of our multiplex assay, and the impossibility to detect prey from the same family (for spiders) or genus (for carabids). Given the relatively common intraguild predation by carabids on spider prey, high densities of spiders that colonize cereal fields early in the cropping season (Birkhofer et al., 2013; Bishop and Riechert, 1990) may contribute to attracting carabid populations to cereal fields (Östman, 2004).

The overall frequency of intraguild predation observed in our field study (papers III & IV, Fig. 11) is higher than the one observed in our manipulative, field cage experiment (~5% of *C. septempunctata* [larvae] detected in *P. melanarius*). The detection frequency of *Coccinella spp.* in *P. melanarius* was higher in the field survey (Early season: 7.97%, Late season: 12.93%), which might indicate that 1) intraguild predation among the ground dwelling predator community is higher than between ground- and foliage-dwelling predators and 2) that *P. melanarius* consumes other life stages than larvae in the field.

4.2.2 Detection of aphids in predators' guts and contribution of generalist predators to biological control of aphids

All predators studied were positive for aphids, at various detection frequencies (Fig. 11&12). The detection frequencies of aphids were higher than those reported using gut dissection (Sunderland, 1975) or serological techniques (Chiverton, 1987) (Fig. 12), which highlights the high sensitivity of molecular methods. The molecular assays used in papers II & III & IV were able to detect between 125 and 1000 copies of targeted DNA fragments. Prey DNA can thus most likely be detected for a longer period than prey proteins in ELISA (8.5 hours for *B. lampros*, Chiverton 1987).

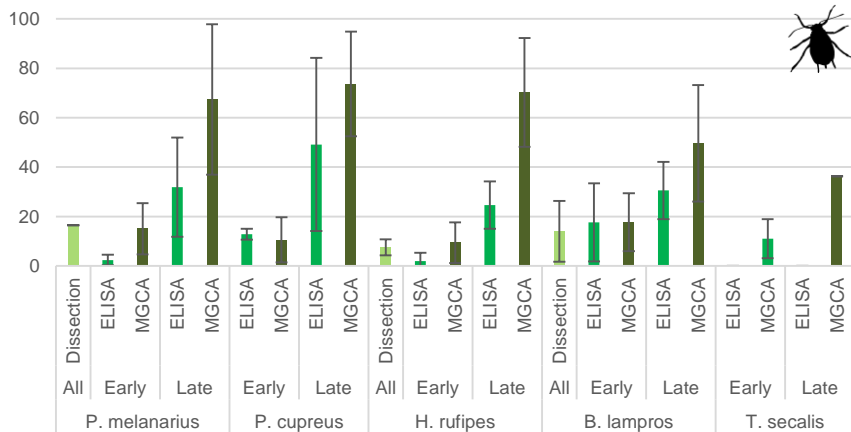


Figure 12. Proportion of carabid predators positive for aphids (\pm standard deviation) recorded in published studies using visual gut dissection (Dissection, Sunderland, 1975) and serological antibodies (ELISA, Chiverton, 1987) and in paper IV using DNA-based molecular gut content analysis (MGCA). The carabid predators (*Pterostichus melanarius*, *Poecilus cupreus*, *Harpalus rufipes*, *Bembidion lampros*, *Trechus secalis*) were included in the calculation if the number of individuals >9/year (dissection), /season/year (ELISA), /field/season (MGCA).

Although we could not directly relate aphid predation rates to the contribution of generalist predators to biological control in paper III and IV (a study of biological control potential using exclusion cages was conducted in parallel, but the methodology failed), generalist predators have been shown to lower aphid densities in cereal fields, particularly early in the cropping season (Östman et al., 2003). In addition, we showed in the manipulative cage experiment (paper II) that generalist predators can lower aphid population growth in late cropping season (paper II, Fig. 13).

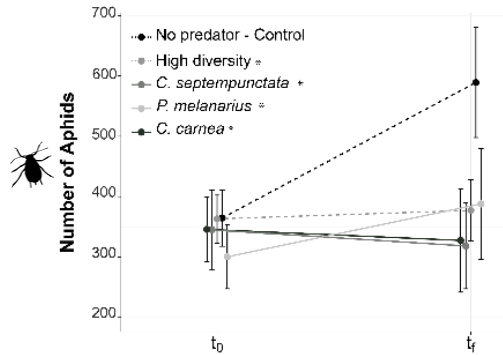


Figure 13. Number of *Rhopalosiphum padi* (mean numbers per 20 tillers \pm SE) at predator introduction (t_0) and at the end of the experiment (t_1) (paper II). Predator treatments were: no-predator control, high diversity, *Coccinella septempunctata*, *Pterostichus melanarius*, and *Chrysoperla carnea*; * after the legend denotes a significant difference in the aphid number with the no-predator control at $\alpha=0.05$.

4.2.3 Factors affecting the diet composition of generalist predators

In paper III, we studied the effect of season, farming system, prey and predator composition, and weed abundance on the diet composition of generalist predators.

Predation on extraguild prey

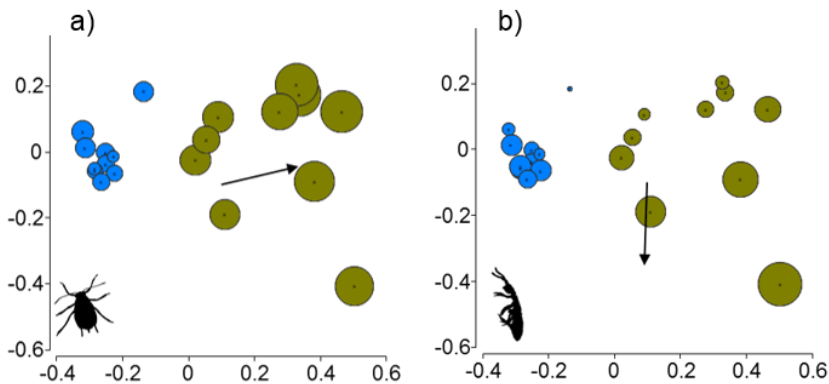


Figure 14. Ordination of the distance-based redundancy analysis as visualization of the distance-based linear model relating the abundance of extraguild prey (represented by vectors) to the detection frequency (represented by bubbles) in generalist predators for a) aphids (abundances range from 0.00 to 16.21 per tiller; bubble sizes range from 1-87% of positively tested predator individuals), b) Collembola (0.00 to 23.5 per soil sample; 0.01-69%). An increase of bubble size towards the direction of a vector suggests that the number of predators that tested positive for a prey group increases with the abundance of that prey group. The first axis explains 76.9% of the total variation in diet composition and the second axis explains an additional 18.2%. Blue bubbles stand for Early season sampling, dark yellow for Late season sampling.

We found that the field composition of extraguild prey explained 26% of the variation of their detection frequencies in generalist predators ($P=0.014$). More specifically, DNA detection rates of the two most common extraguild prey groups (aphids and Collembola, size of the bubbles, Fig. 14a&b) were positively related to their abundances (direction of the vector, Fig. 14a&b). For aphid prey, density and detection frequencies were only positively related in Late season, as illustrated by an increasing size of the bubbles along the vector in Late season (Fig. 14a), whereas Collembola abundances and DNA detection frequencies were positively related during both seasons (Fig. 14b). The detection frequencies of Diptera, thrips, and earthworms showed no density dependence (paper III).

Aboveground herbivores (aphids) and decomposers (Collembola) were both important prey for generalist predators early in the cropping season, while the importance of aphid prey increased with increasing aphid densities later in the cropping season. Collembola predation, in contrast, showed this positive relationship to prey abundance in both cropping seasons.

Predation on intraguild prey

Because of the low frequencies of carabids detected in spiders, we only analyzed the composition of spider prey in carabid predators. We found a significant effect of farming system (organic vs conventional) in the composition of spider intraguild prey in carabid diets ($P=0.005$), but not by season ($P=0.872$). DNA detection frequencies for *Linyphiidae* ($+3.7\% \pm 2.54\%$, mean \pm SD per field pair) and *Lycosidae* ($+7.85\% \pm 7.54\%$) prey in carabids were slightly higher in fields under organic farming management (Fig. 15a). However, neither spider prey composition (distLM¹², $P=0.117$), carabid predator composition ($P=0.285$), nor weed cover (distLM, $P=0.225$) significantly explained the variation in the intraguild spider prey detection frequencies in carabids. There was, however, some graphical support for higher detection of *Lycosidae* and *Lyniphiidae* according to their field densities (Fig. 15b, larger bubbles in the direction of the density vectors). Organically managed barley fields may thus have higher generalist predator numbers (Bengtsson et al., 2005), but also higher levels of intraguild predation by carabids on spiders, which could negatively affect aphid biological control. More studies are therefore needed to address the net effect of intraguild predation (in field conditions) on aphid biological control.

¹² Distance based linear model

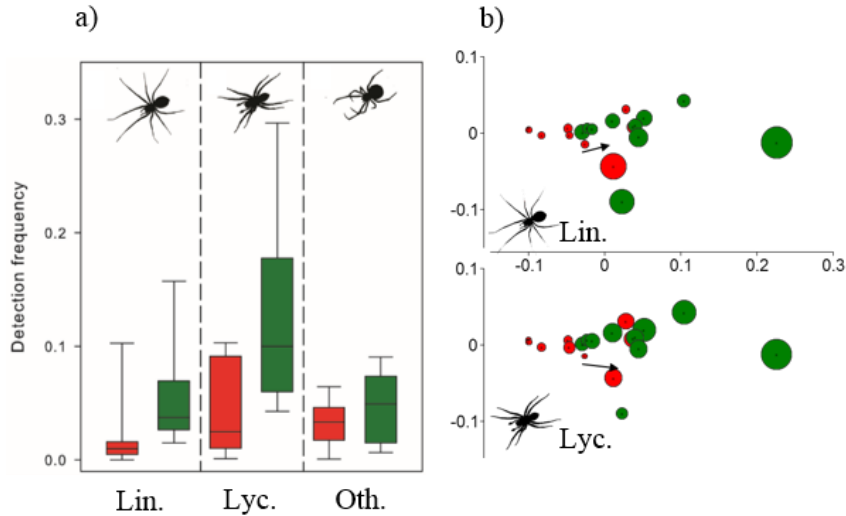


Figure 15. a) Effect of farming system on detection frequencies of intraguild prey in carabid communities per field and b) ordination of the distance-based redundancy analysis as visualization of the most important predictor (farming system) in the full model relating the composition of intraguild (spider) prey (represented by vectors) to the diet composition (represented by bubbles) of carabids for *Linyphiidae* (Lin., abundances range from 0.07 to 1.49 per pitfall trap/day ; bubble size range from 0-16% of positively tested predator individuals), *Lycosidae* (Lyc., 0.00 to 3.50; 0-31%) and other spider (Oth.) prey in conventionally (red) and organically (green) managed fields. An increase of bubble size towards the direction of a vector suggests that the number of predators that were tested positive for a prey group increases with the abundance of that prey group. The first axis explains 82.6% of the total variation in diet composition and the second axis explains an additional 10.1%. Boxplots in a) show medians (horizontal line), 25th and 75th percentiles (upper and lower box limits), extreme observations (bars).

4.2.4 Effect of farming systems

Apart from the small increase of spider prey detected in carabids, we found little support for an effect of farming system on the diet of generalist predators in agricultural fields. The difference in terms of predator and prey community composition and weed abundance between organically and conventionally managed field was, however, very small (Table 3), which confirms the low intensity of conventional cereal management in the study region already reported in published studies (Östman et al., 2001; Weibull et al., 2000). There were no differences in abundance and evenness of the predator community and coverage of weeds. Among the extraguild prey targeted by our assay, only Diptera had higher densities in organically managed fields (Table 3).

Table 3. ANOVA table of linear mixed models testing variation of extraguild prey abundance, predator abundance and evenness, and weed coverage according to season (Season) and farming system (System). Seasonal and spatial autocorrelations were accounted for in the random factor. Factors in **bold** are significant at $\alpha=0.05$.

	Response	Factors	Sum Sq.	Num DF	Den DF	F	P
Extraguild prey	Earthworms	System	9.71	1	8	2.19	0.177
		Season	0.15	1	8	0.03	0.857
		System:Season	0.03	1	8	0.01	0.938
	Aphids	System	32.22	1	8	2.49	0.153
		Season	131.77	1	8	10.20	0.013
		System:Season	31.94	1	8	2.47	0.155
	Collembola	System	23.73	1	8	1.28	0.291
		Season	2.33	1	8	0.13	0.732
		System:Season	1.17	1	8	0.06	0.808
	Diptera (log+1)	System	23.17	1	16	36.67	<0.001
		Season	4.75	1	16	7.52	0.014
		System:Season	1.05	1	16	1.66	0.216
	Thrips	System	1.67	1	8	2.40	0.160
		Season	12.8	1	8	18.41	0.003
		System:Season	1.25	1	8	1.8	0.219
Ground dwelling predators	Abundance	System	0.09	1	8	0.70	0.428
		Season	0.19	1	8	1.59	0.243
		System:Season	0.02	1	8	0.13	0.731
	Evenness	System	0.01	1	8	0.74	0.414
		Season	0.03	1	8	2.18	0.178
		System:Season	0.02	1	8	1.32	0.283
Weeds	Coverage	System	0.43	1	4	2.23	0.210
		Season	14.82	1	8	76.57	<0.001
		System:Season	0.20	1	8	1.02	0.343

4.3 Predator-prey food webs

In paper **IV**, we studied the structure of predator-prey food webs (Fig. 16), whether the interactions deviated from randomness, and identified predator-prey interactions that particularly deviated from what would be expected by chance. Given the biotic and abiotic changes occurring during the cropping season identified in paper **III**, we hypothesized that there will be seasonal differences in predator-prey food web structure, that the structure would be more random early in the cropping season, as a result of predators being able to make fewer active choices when prey is scarce, so that predators make more active choices later in the cropping season. I focus here on the specialization metrics as characteristics of the food web structure. Additional metrics are analysed in paper **IV**

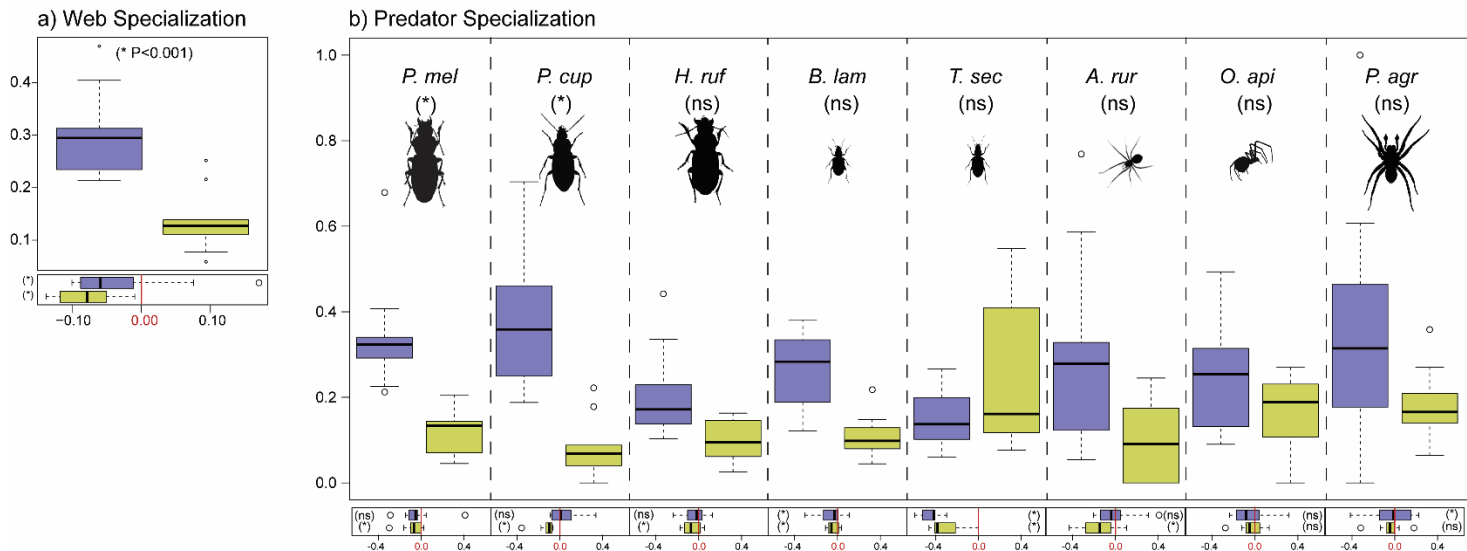


Figure 16. Seasonal variation in predator-prey food web specialization at a) the network level and b) the species level (upper boxplot), and the deviations in observed metrics from null model expectations (lower boxplot) in Early and Late season (light and dark grey boxes respectively). Boxplots show medians (horizontal line), 25th and 75th percentiles (upper and lower box limits), extreme observations (bars) and data identified as outliers (dots). * and ns denote whether there was a significant difference (*) or not (ns) in the (i) seasonal variation, at $\alpha=0.05$, in the observed food web metric (reported in parenthesis inside the upper boxplot), and (ii) deviation from null model expectation of the observed food web metric (reported in parenthesis inside the lower boxplot). No significant seasonal variation was observed in the deviation from null model.

4.3.1 Seasonal variation in the structure of predator-prey food webs in agricultural fields

In paper **IV**, we show that predator-prey food webs were characterized by low levels of specialization both at the network ($H_2' = 0.22 \pm 0.02$, across-season mean \pm SEM) (Fig. 16a), and species-level (Fig. 16b). There was a decrease in the degree of specialization from low to extremely low at network ($P < 0.001$) and species-level ($P < 0.001$), with variation in the seasonal decrease depending on predator species ($P = 0.003$, Fig. 16b). The seasonal decrease was, in general, larger for carabids (except for *T. secalis*) than for spider species. The seasonal variations in network metrics are likely explained by changes in prey availability, as herbivore abundances increased from early to late in the cropping season (paper **III**).

The observed low levels of specialization suggest a high functional redundancy of the generalist predators in agricultural fields (Kaiser-Bunbury and Blüthgen, 2015), particularly later in the cropping season. Whereas high functional redundancy might reduce the potential for pest control at a specific point in time, it could provide stability to the network, and thus insurance against perturbation (i.e., stability).

The specialization of the predator-prey food webs differed from random expectation (Binomial test, $P < 0.001$). At the species-levels, predator specialization did not deviate from random in Early season (Fig. 16b, lower boxplots, Binomial test, $P > 0.050$ for all predator species, except for *T. secalis* & *P. agrestis*: $P < 0.001$). In contrast, in Late season specialization of all carabids was significantly lower than expected by chance (Fig. 16b, lower boxplots, Binomial test, $P < 0.050$). The significant difference in specialization observed at the network-level but not at predator species level might be explained by a larger sample size in the former analysis. The network structure thus appears not to be primarily driven by random processes, but rather by prey preferences and phenological or spatial mismatches (Blüthgen et al., 2008), as often observed in agricultural systems (Birkhofer et al., 2011).

4.3.2 Favored and avoided links

We identified warm links (i.e., links more observed than expected by chance) to extraguild prey that reflect predator feeding preferences already suggested in previous studies: we found that spiders had warm links to Collembola (see e.g., Kuusk and Ekbom, 2010), and large carabids had warm links to earthworms (King et al., 2010) (paper **IV**). Link temperature between predators and aphids was particularly dependent on predator species and season. We show that links between aphids and spiders and between aphids

and small carabid species (*B. lampros* and *T. secalis*) are warm during times when cereal aphids colonize fields, while links between aphids and large carabids (*P. cupreus* and *H. rufipes*) are warm once aphid populations had been established. This suggests a seasonal change in the importance of different predator species as aphid biological agents, and a complementarity of the predator community across the cropping season

5 Conclusions and Future Directions

This thesis supports an overall positive effect of increased predator diversity on herbivore suppression. In a meta-analysis, we show that this effect is lessened by the increase of prey diversity (paper **I**). Using molecular gut content analysis, we were then able to identify the mechanisms underlying the relationship between predator species richness and biological control in a manipulative field cage experiment (paper **II**) and to quantify the importance of extraguild and intraguild prey in the diet of generalist, ground-dwelling arthropods in field conditions (papers **III** & **IV**).

We demonstrated:

- The important functional role of generalist predators as aphid natural enemies in manipulated field cage experiments (paper **II**) and in field conditions (papers **III** & **IV**)
- No effect of predator species richness in a community consisting of both generalist ground dwelling and more specialized foliage dwelling predators, due to very low frequencies of positive and negative interactions among predators, and no support for any change in the impact of predator diversity on biological control services by habitat complexity (paper **II**)
- Little support for the potential switch of predation from aphids to alternative prey (here non-aphid, extraguild prey and intraguild prey) in communities of generalist predators.
- A density dependent predation on aphids independent from predation on alternative extraguild prey (paper **III**),
- A high redundancy in the diet of generalist predators (papers **II** & **IV**),
- A seasonal complementarity in the choices of specific predators towards aphids (paper **IV**).

Thus, a general conclusion from this work is that there is a high functional redundancy among generalist predators in terms of cereal aphid biological control (papers **II** & **III** & **IV**), when considering short time periods. However, when the entire cropping season is considered we found that the importance of different predators as aphid biological control agents varied (papers **III** & **IV**). This suggests that high predator diversity may provide a more stable biological control service over the cropping season.

The recent development of new molecular methods based on DNA barcoding (e.g., “next generation sequencing”) offers the possibility to identify the complete predator diet by simultaneously amplifying and sequencing DNA from all organisms present in a sample (assuming their DNA sequence is known; e.g., Wirta et al., 2015a, 2015b). The use of such techniques in the agroecosystem could be a valuable tool to assess the importance of arthropod diversity in the structure and function of predator-prey food webs.

Additionally, conservation strategies promoting biological control in agroecosystems would benefit from future studies that would:

- 1) address, under field conditions and at a biologically relevant time scale, the net effect of predator diet, and particularly extraguild and intraguild predation, on generalist predator population dynamics and aphid biological control;
- 2) assess the strength and stability of biological control services by linking the structure of predator-prey food webs to the provision of biological control;
- 3) investigate the functional importance of predator traits in the provisioning of biological control.

These future studies would expand upon the findings of this thesis, and aid the design of conservation strategies that promote predator diversity and high levels of non-pest extraguild prey in order to sustain generalist ground dwelling predators and secure their contribution to biological control services in agricultural fields.

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