ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

DOCTORAL THESIS NO. 2021:61
FACULTY OF NATURAL RESOURCES AND AGRICULTURAL SCIENCES

Weed seed predation

A promising ecosystem service in agriculture

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SCIENCES

DOCTORAL THESIS
Uppsala 2021

Acta Universitatis Agriculturae Sueciae
2021:61

Cover: Illustration of the weed community and weed seed predators in agricultural landscapes.
(Illustration: Eirini Daouti)

ISSN 1652-6880
ISBN (print version) 978-91-7760-799-1
ISBN (electronic version) 978-91-7760-800-4

Uppsala
Print: SLU Service/Repro, Uppsala 2021

Weed seed predation. A promising ecosystem service in agriculture

Abstract

Enhancing biodiversity and promoting vital ecosystem services can reduce the global dependence on anthropogenic inputs in agriculture while securing crop yield. Weed infestation can severely reduce crop yield but the dominance of herbicides for weed control can impair human health, beneficial organisms and ecosystem service delivery. Thus, it is essential to identify more sustainable alternatives for weed control. Using data from four European countries, this thesis examined whether the ecosystem service of weed seed predation in cereal fields can be a viable alternative for regulation of weeds. The impact of agricultural intensity on weed seed predation, weed regulation and functional redundancy in predation was investigated, as well as the role of seed and alternative prey availability. The results showed that through weed seed predation, regulation of weeds at population and community level is achievable. Weed seed availability increased predators' potential for weed seed predation, but higher alternative prey biomass reduced seed consumption. Functional diversity in predation increased the spatial stability of weed seed predation. Agricultural intensity decreased weed seed predation and functional redundancy in predation estimates, via increased disturbances at field level, reduced diversity of crops sown in rotation and reduced landscape heterogeneity. These findings confirm the potential of weed seed predation for sustainable weed control and suggest that to support weed seed predators and the service they provide we need to reduce field management intensity and diversify cropping systems at both field and landscape scale.

Keywords: Carabid beetles, arable plants, agricultural intensification, *Alopecurus myosuroides*, trophic interactions, ecosystem functioning

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Predation av ogräsfrön. En lovande ekosystemtjänst inom jordbruket

Sammanfattning

Genom att öka den biologiska mångfalden och främja viktiga ekosystemtjänster kan vi minska vårt beroende av insatsmedel i jordbruket samtidigt som vi säkrar skördarna. Ogräs kan minska skördarna, men den intensiva användningen av herbicider för ogräsbekämpning hotar människors hälsa, nyttoorganismer och ekosystemtjänster. Det är därför viktigt att hitta mer hållbara alternativ för ogräsbekämpning. Med hjälp av data från fyra europeiska länder undersöktes i denna avhandling om ekosystemtjänsten predation av ogräsfrön i spannmålsfält kan vara ett alternativ för reglering av ogräs. Jordbruksintensitetens inverkan på predation av ogräsfrön, reglering av ogräs och funktionell redundans av predation undersöktes, liksom betydelsen av tillgången på frön och alternativa bytesdjur. Resultaten visade att det är möjligt att reglera ogräs på populations- och samhällsnivå genom predation av ogräsfrön. Tillgången på ogräsfrön ökade rovdjurens potential för predation av ogräsfrön, men högre biomassa av alternativa bytesdjur minskade fröpredationen. Funktionell redundans i predation ökade den rumsliga stabiliteten hos predation av ogräsfrön. Jordbruksintensitet minskade predationen av ogräsfrön, och predationens funktionella redundans, via ökade störningar på fältnivå, minskad mångfald av grödor som sås i växelbruk och minskad heterogenitet i landskapet. Dessa resultat bekräftar att predation av ogräsfrön kan bidra till hållbar ogräsbekämpning. För att stödja predatorer av ogräsfrön och de tjänster de tillhandahåller behöver vi minska jordbruksmetodernas intensitet och diversifiera odlingssystemen på både fält- och landskapsnivå.

Nyckelord: Jordlöpare, ogräs, intensifiering av jordbruket, *Alopecurus myosuroides*, trofiska interaktioner, ekosystem funktioner

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Dedication

To my grandfather, who instilled a land ethic in me.

> *We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect.*
>
> Aldo Leopold ~ A Sand County Almanac

Contents

List of publications

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

I. Daouti, E., Jonsson, M., Vico, G. & Menegat, A. Seed predation is key to prevent population growth of annual weeds (accepted in Journal of Applied Ecology)

II. Carbonne, B., Petit, S., Neidel, V., Foffová, H., Daouti, E., Frei, B., Skuhrovec, J., Řezáč, M., Saska, P., Wallinger, C., Traugott, M. & Bohan, D.A. (2020). The resilience of weed seedbank regulation by carabid beetles, at continental scales, to alternative prey*. Scientific Reports* 10, 19315

III. Daouti, E., Bommarco, R., Feit, B., van der Werf, W., Carbonne, B., Neidel, V., Foffová, H., Saska, P., Skuhrovec, J., Wallinger, C., Rubbmark, O.R., Traugott, M., Petit, S., Bohan, D.A. & Jonsson, M. Intensified agriculture reduces weed seedbank regulation by seed predators (manuscript)

IV. Daouti, E., Feit, B. & Jonsson, M. Effects of management intensity and habitat refugia on the strength of weed seed predation (manuscript)

V. Daouti, E., Bommarco, R., Feit, B., van der Werf, W., Carbonne, B., Neidel, V., Foffová, H., Vasconcelos, S., Saska, P., Skuhrovec, J., Wallinger, C., Traugott, M., Petit, S., Bohan, D.A. & Jonsson, M. Functional redundancy enhances spatial stability of weed seed predation but is reduced by intensified agriculture (manuscript)

The contribution of Eirini-Lamprini Daouti to the papers included in this thesis was as follows:

I. Main author. Designed with contributions from other co-authors the weed seed predation experiment, collected the weed seed predation data, contributed to the analysis (led by AM), wrote with AM the first version of the manuscript, reviewed and edited the final version of the manuscript.

II. Co-author. Planned and designed the experiment with the other co-authors. Collected data with contributions from the other co-authors, contributed to analysis ideas (analysis led by BC), reviewed and edited the final version of the manuscript with all co-authors.

III. Main author. Planned and designed the experiment with the other co-authors. Collected data with contributions from the other co-authors, performed the data analysis, and wrote the first version of the manuscript. Reviewed and edited the final version of the manuscript with support from the co-authors.

IV. Main author. Planned and designed the experiment with other co-authors. Collected the data, performed the data analysis, wrote the first version of the manuscript. Reviewed and edited the final version of the manuscript with support from co-authors.

V. Main author. Planned and designed the experiment with the other co-authors. Collected the data with contributions from the other co-authors, performed the data analysis and wrote the first version of the manuscript. Reviewed and edited the final version of the manuscript with support from co-authors.

Abbreviations

FAOSTAT	Food and Agriculture Organisation of the United Nations Statistics
HMSC	Hierarchical Modelling of Species Communities
HTS	High Throughput Sequencing
iSNH	Interface between crops and Semi-Natural Habitat
MGCA	Molecular Gut Content Analysis
PCR	Polymerase Chain Reaction
RFU	Relative Fluorescent Units
SNH	Semi-Natural Habitat

1. Introduction

1.1. From agricultural intensification to ecological intensification

Agricultural intensification, a process that accelerated during the Green Revolution, in the 1950s, which was characterised by agronomic advances, large-scale land-use conversion and intensive use of fertilisers and pesticides has increased food production per unit area (Matson *et al*., 1997; Godfray et al. 2010). However, this remarkable progress came with a heavy toll on the environment and biodiversity (Tilman, 1999; Donald *et al*., 2001; Hörnfeldt, 2004). Rachel Carson's book *Silent Spring*, published in 1962, was among the first to highlight the cost of increased of pesticides, such as DDT, to biodiversity and human health and raised concerns over the danger of a "silent" future without birdsongs and whirring cicadas. It stimulated a movement to shift to ecological alternatives for agricultural production and, partly in response to the Green Revolution, the concept of agroecology emerged, referring to the application of ecological methods for agronomic research. Although the concept had existed since 1928, through the 1960-1970s there was a gradual increase in application of ecological principles in crop production systems (Altieri *et al*., 2012; Gallardo-López *et al*., 2018). During the same period, Integrated Pest Management (Stern *et al*., 1959) was established as an approach that sought to rely more on natural pest control mechanisms for the regulation of weeds, pathogens, arthropods and non-arthropod animals. In early 2000, new qualifiers of the term intensification appeared in the scientific literature, such as "sustainable intensification" (Pretty *et al*., 2011) and "ecological intensification" (Cassman, 1999; Doré *et al*., 2011; Bommarco *et al*., 2013). Based on the new paradigms of agricultural intensification, ecological intensification supported the idea of a type of intensification that relies on ecosystem services, instead of chemical inputs, to meet food production demands.

Ecological intensification, as an alternative approach to agricultural intensification, suggests a type of crop production that replaces anthropogenic inputs, such as pesticides and fertilisers, with regulating and yield-supporting ecosystem services provided by beneficial organisms (Bommarco *et al.*, 2013). Effective use of ecological intensification for crop production depends on a land-use design that supports beneficial organisms by increasing their habitat at the landscape level and reduces environmental stressors at the local field level. That design should support the numerical growth of beneficial organisms, increase their services and reduce the need for external inputs to sustain crop yields (Bommarco *et al.*, 2013; Kleijn *et al.*, 2019).

1.2. Ecosystem functions and services

The biological foundation of ecosystem services consists of a set of ecosystem functions, such as decomposition of organic matter, pollination and pest predation, that determine the supply of vital ecosystem services (*e.g.* soil generation and fertility, climate stability, crop pollination) (Kremen, 2005; Oliver *et al.*, 2015). According to the Millennium Ecosystem Assessment (2005), ecosystem services can be categorised into four groups: provisioning (e.g. food, water), regulating (*e.g.* climate and pest regulation), cultural (*e.g.* recreation) and supporting (*e.g.* soil formation). All of these depend on biodiversity, so drivers that directly or indirectly reduce biodiversity also decrease ecosystem service levels and ecosystem functioning (Cardinale *et al.*, 2012). Kremen (2005) suggested that successful management of ecosystem services depends on bridging the gap between ecosystem service research and ecological research. For regulating ecosystem services such as pollination and pest control, an extensive amount of research has used ecological theory, such as meta-community dynamics or food web theory, to understand the mechanisms by which pollinators and natural enemies contributes to these ecosystem services (*e.g.* Memmott, 1999; Hoehn *et al.*, 2008; Lami *et al.*, 2021). However, for other ecosystem services such as weed seed predation, less research has been conducted to understand the role of seed predators to ecosystem service supply. The potential of weed seed predation for weed control has been raised in the academic literature during the past two decades (Westerman *et al*., 2003a,b, 2005; Bohan *et al*., 2011). However, compared with other regulating ecosystem services, weed seed predation research still seems to be in its infancy.

1.2.1 Weeds and weed seed predation

In agricultural fields, weeds can have opposing effects, a detrimental effect that can lead to yield loss via crop-weed plant competition and a beneficial effect that supports several ecosystem services. Potential crop losses due to weeds can reach an average of 23%, which is a higher rate of crop loss caused by any animal pest or plant pathogen (Oerke, 2006). On the other hand, weeds provide food resources for several functional groups of arthropods, such as pollinators, earthworms and natural enemies, but also farmland birds and mammals (Petit *et al*., 2011). As a result, weeds support, directly or indirectly, several ecosystem services like pollination, pest control, soil quality and weed seed predation. To reduce weed densities in crops, conventional weed management relies on herbicides and mechanical practices (Green, 2018). In the European Union, herbicides comprise over 40% of the total pesticide usage, which equates to an annual mean of 179,798 tonnes of herbicides (FAOSTAT 2021). Rising concerns about negative impacts of herbicides on human health (Zhang *et al*., 2019), beneficial organisms and the environment (Druille *et al*., 2013; Van Bruggen *et al*., 2018; Straw *et al*., 2021) question common methods of weed control with countries to apply stricter rules in herbicide use (Reuters 2021). However, weed control is necessary to protect yield thus research on sustainable alternatives is essential.

Predation of newly shed weed seeds (or post-dispersal weed seed predation) is a regulating ecosystem service that has the potential to support weed regulation. It has been shown that seed predators can decrease seed density by on average 50% (Davis *et al*., 2011) which could potentially lead to a reduction in population growth of weed species. For example, it has been shown that 40% of cumulative seed losses due to predation can reduce the population density of the weed species *Abutilon theophrasti* (velvetleaf) (Westerman *et al*., 2005). In addition, high abundance of carabid seed predators has been found to correlate negatively with weed seedbank change over the cropping season, indicating that seed predators can regulate the weed seedbank (Bohan *et al.*, 2011). Consequently, weed seed predation can be used for weed control, reducing the current reliance on herbicides to minimise weed-related crop losses. However, one obstacle to utilisation of weed seed predation in agriculture and targeted use in weed management strategies has been high variability in observed predation rates between studies (Menalled *et al.*, 2007; Saska *et al.*, 2008; Davis & Raghu, 2010). For broader application of weed seed predation, it is important to know whether variation in predation rates cascades down to weed species population dynamics and weed seedbank regulation.

1.3. Beneficial organisms as ecosystem service providers

In agroecosystems, ecosystem services depend on phylogenetically distant species, for example birds and beetles that prey on arthropod pests, bees and flies that pollinate crop flowers, earthworms and nematodes that maintain soil quality and mycorrhizal fungi that improve nitrogen acquisition (Foley *et al.*, 2011). All act at different spatial and temporal scales, but all are vital for crop production. As a result of agricultural intensification and associated environmental degradation, the diversity and abundance of birds, pollinators and pest predators has declined considerably (Fried *et al.*, 2009; Grab *et al.*, 2019; Sánchez-Bayo & Wyckhuys, 2019; Şekercioğlu *et al.*, 2019). The world is now witnessing what is often referred to as “Insect Armageddon” (Hallmann *et al.*, 2017). Globally, studies report an overall 45% decline in the majority of insect populations over the past few decades (Dirzo *et al.*, 2014). In Germany, insect biomass in protected areas has suffered a decline of more than 75% (Hallmann *et al.*, 2017). However, it should be noted that not all insects are experiencing drastic declines. A recent meta-analysis of 166 long-term surveys showed declines for terrestrial insects, but not freshwater insects (Klink *et al.*, 2020).

For every species or insect population lost, important ecosystem services such as pollination or pest control are also reduced. Bigger communities of beneficial organisms is more likely to contain a combination of species that complement each other in service provision, implying a positive effect of beneficial organisms on ecosystem service supply (Fründ *et al.*, 2013; Dainese *et al.*, 2017). In contrast, smaller and less diverse communities of beneficial organisms are becoming more fragile to environmental change, with associated negative effects on their services (Oliver *et al.*, 2015;

Donohue *et al*., 2016). A recent analysis of 89 studies showed that greater diversity of pollinators and natural enemies increases pollination and pest control services, with cumulative positive effects on crop production (Dainese *et al*., 2019). Over the past decades, policies addressing reduced abundances and biodiversity loss in agroecosystems have improved and agri-environmental schemes started to emerge to conserve farmland species (Batáry et al. 2015). Surprisingly, for some species even technological fixes has been suggested to replace reduced diversity. Pollinating robots have been proposed to replace lost diversity of wild pollinators (Chechetka *et al.*, 2017). However economic, ecological and ethical arguments show that technological fixes are non-viable solutions for addressing lost biodiversity (Potts *et al*., 2018) and is important to develop more existing measures to protect and increase abundances of beneficial organisms (Pe'er *et al.,* 2020) and thus improve and maintain ecosystem services such as pollination and pest control.

1.3.1 Weed seed predators

In weed seed predation, the spectrum of organisms that feed on weed seeds is impressively broad and quite diverse. Seed predators can consume seeds before seed shedding (pre-dispersal seed predators) and/or after seed shedding (post-dispersal seed predators) (Sarabi, 2019). The pre-dispersal group includes specialist insects that prey on seeds of a specific plant species or family and vertebrate species (*e.g*. birds) (Hulme, 2002; Crawley, 2013). The post-dispersal seed predators can be divided into those that prey on seeds scattered on the soil surface and seeds buried in the soil seedbank (*e.g*. earthworms). In this thesis work, the focus was on the post-dispersal seed predators that feed on weed seeds scattered on the soil surface.

Post-dispersal seed predators in temperate ecosystems are generally divided into two functional groups, vertebrates (small rodents and birds) and invertebrate species (carabid beetles, crickets and ants) (Janzen, 1971; Fischer *et al*., 2011; Honek *et al*., 2013). These two groups of seed predators exhibit fundamental differences in size, dispersal ability and activity patterns that ultimately result in seasonal variations in their weed seed intake (Westerman *et al*., 2003a; Holmes & Froud-Williams, 2005; Westerman *et al*., 2011; Berl *et al*., 2017). In temperate agroecosystems, invertebrate species prey on seeds from early spring to late autumn, when they are active, whereas vertebrates prey on seeds all year. In addition, larger seeds seem to be more likely to be preyed upon by vertebrates compared with invertebrate predators, which appear to prefer smaller seeds (Abramsky, 1983; Brust & House, 1988; Harrison *et al.*, 2003; Booman *et al*., 2009). Based on previous findings, it can be concluded that the relative importance of the two functional groups of post-dispersal seed predators for weed control is context-dependent. For instance, Westerman *et al*. (2003a) found that vertebrates accounted for a larger proportion of seed predation compared with invertebrates, which exhibited lower and more variable predation rates. In contrast, others have found that invertebrates exhibit higher predation rates than vertebrates (Brust & House, 1988; Cromar *et al*., 1999; Gallandt *et al*., 2005). To evaluate their relative importance, it is essential to determine the impact of each group's predation levels on weed population dynamics.

Among the invertebrates, carabid beetles are the most important seed predators in temperate agroecosystems (Honek *et al*., 2013). Carabid beetle diets have been a subject of investigation for decades (Thiele, 1977; Holland, 2002). Based on field and laboratory 'cafeteria' experiments (Hagley *et al*., 1982; Alignier *et al*., 2008; Saska *et al*., 2008; Petit *et al*., 2014; Lami *et al*., 2020), dissections of carabid gut contents (Dawson, 1965) and, more recently, molecular gut content analysis (MGCA) (Wallinger *et al*., 2015; Frei *et al*., 2019), it is known that many carabid predators consume both plant (*e.g*. seeds) and animal (*e.g*. aphids, collembolans) prey. Based on their dietary preferences, carabid beetles are divided into three trophic guilds, granivorous (plant-based diet), carnivorous (animal-based diet) and omnivorous (mixed animal- plant diet) (Lindroth, 1985). However, recent results from MGCA of three common omnivorous species suggest that weed seed consumption is more common than originally hypothesised, as more than 70% of all carabid individuals examined tested positive for plant DNA, compared with 21.6% for collembolans and 4.2% for aphids (Frei *et al*., 2019).

According to the alternative prey hypothesis, abundances of alternative prey can either increase or decrease weed seed predation levels, via apparent mutualism or apparent competition, respectively (Chailleux *et al*., 2014). Since other studies have demonstrated the potential of alternative prey to disrupt biological pest control (Prasad & Snyder, 2006; Symondson *et al*., 2006; von Berg *et al*., 2009), it is important to identify the direction in which variations in prey availability impact weed seed predation. In addition, in order to assess how seed predators impact weed seed density, it is important to understand how seed availability affects the response of predators towards their prey. For instance, weed populations can be regulated when seed predators respond to weed seed abundance in a density-dependent manner through increased population growth, aggregation or food-switching as seed availability increases (Westerman *et al*., 2008;Baraibar *et al*., 2012; Gray *et al*., 2021). However, as a result of agricultural intensification, weeds have declined (Fried *et al*., 2009; Meyer *et al*., 2013), which can reduce the ability of predators to respond to weed seed availability. To understand the ecological mechanisms that explain the variation in weed seed predation estimates, and thus support stronger weed control, it is essential to consider the impact of both alternative prey and seed availability on weed seed predation. Further, since seed availability is susceptible to agricultural intensity, it is essential to consider the indirect effect of management intensity via weed seed availability on weed seed predation and weed regulation.

1.4. Ecological intensification at local and landscape level

Ecological intensification depends on beneficial organisms and in order to utilise ecological intensification in crop production, it is necessary to design cropping systems at both local and landscape scale that support beneficial organisms and their services (Bommarco *et al*., 2013). During their life cycle, most beneficial organisms use both crop and natural habitat to secure food resources, overwintering and nesting sites (Chaplin-Kramer *et al*., 2011; Schellhorn *et al*., 2015). Their population dynamics are shaped by complex ecological processes that are significantly affected by field and landscape management (Karp *et al*., 2018; Dainese *et al*., 2019; Tamburini *et al*., 2020).

Within fields, agro technical operations such pesticide usage and tillage can directly and indirectly affect beneficial organisms (Bianchi *et al*., 2006; Sirami *et al*., 2019; Gagic *et al*., 2021). Directly, tillage and pesticide application can increase the mortality rate of beneficial organisms such as ground dwelling predators and reduce their population size (Chan, 2001; Thorbek & Bilde, 2004; Goulson *et al*., 2015). Indirectly, herbicide applications by reducing weed communities and altering the field’s microclimate can limit resource continuity for pollinators and natural enemies and thus indirectly limit their population increase (Marshall & Moonen, 2002; Storkey & Neve, 2018). At the landscape scale, as the percentage of crop area increases, crop fields are more likely to border other crops, rather than natural habitat (Chaplin-Kramer *et al*., 2011; Landis, 2017). Consequently, the agricultural mosaic becomes more uniform, with reduced connectivity between remaining natural habitat and the crop. Recent research findings has shown that beneficial organisms traits, such as dietary requirements, dispersal ability and overwintering habitat preferences, reflect their responses to increasing landscape heterogeneity (Martin *et al*., 2019). Simplified landscapes promote species with good dispersal ability between crop and natural habitat and generalists in food choice. In contrast, they reduce the diversity of more specialised species with limited dispersal ability that depend on a short distance between the crop and natural habitat to meet their resource needs (Chaplin-Kramer *et al*., 2011; Chisté *et al*., 2018). Both specialist and generalist are essential for high ecosystem service delivery (Peralta *et al*., 2020).

Consequently, to support more abundant and diverse communities of beneficial organisms such as pollinators and natural enemies and obtain higher levels of their services (Thies & Tscharntke, 1999; Redlich *et al*., 2018, 2021; Sirami *et al*., 2019; Aguilera *et al*., 2020) is essential to reduce field management disturbances and diversify cropping methods at both local and landscape scale. Additionally, to rely on ecological intensification instead of agricultural intensification to maintain crop yield, it is necessary to determine whether the same measures simultaneously enhance the levels of several ecosystem services.

1.4.1 Ways to increase weed seed predation at local and landscape level

Many weed seed predators are well adapted to agroecosystems, but their abundance can be reduced by agricultural intensity, with cascading effects on the level of weed seed predation. At the local field level, increased field management intensity through increased pesticide application and intensive soil cultivation has been found to have negative effects on weed seed predators and weed seed predation levels (Menalled *et al*., 2007; Trichard *et al*., 2013). Among the intensive soil cultivation practices employed, tillage can reduce the temporal availability of seeds on the soil surface (Cardina *et al*., 2002) and directly kill both invertebrate and vertebrate seed predators (Holland & Luff, 2000; Thorbek & Bilde, 2004; Blubaugh & Kaplan, 2015) or alter their nesting habitats (Witmer *et al*., 2007; Baraibar *et al*., 2009). Consequently, reduced tillage or no-till has been found to favour weed seed predation in several studies (Menalled *et al*., 2007; Baraibar *et al*., 2009; Petit *et al*., 2017). Using a higher diversity of crops in rotation has also been shown to increase weed seed predation levels, *e.g*. Westerman *et al*. (2005) found that weed seed predation increased in more diverse crop rotations. By increasing the diversity of the crops sown in rotation and increasing the diversity of agrotechnical operations (*e.g*. tillage and herbicide choice), diversified habitats and weed communities are formed, which can favour seed predators and weed suppression (Heggenstaller *et al*., 2006). Cover crops also seem to benefit seed predators and favour weed seed predation, by providing more dense vegetation with better microclimatic conditions and more food resources (Meiss *et al*., 2010; Birthisel *et al*., 2015; Blubaugh *et al*., 2016).

Weed seed predators are mobile and many species need to use both crop and non-crop habitat for complementary resources, as a refuge from disturbances and as overwintering habitats (Thiele, 1977; Holland, 2002). Consequently, the composition and configuration of habitats at the landscape level can influence seed predator abundance and weed seed predation. It has been suggested that increasing landscape heterogeneity, with an increasing amount of semi-natural habitat, increases seed predator abundance and their services (Tscharntke *et al*., 2012; Landis, 2017). However, seed predators are well adapted to agroecosystems and some species even spend their whole life cycle within arable fields (Aguilera *et al*., 2020). Weed seed predation has been found to both increase (Trichard *et al*., 2013) and decrease (Jonason *et al*., 2013) with landscape diversity. In some cases, landscape heterogeneity enhances weed seed predation by supporting predator abundance, while in other cases the crop field can provide more suitable resources than natural habitat (Tscharntke *et al*., 2016). Overall, however, it can be can concluded that agricultural intensification in the form of increased pesticide application, intensive soil cultivation and simplified crop rotations reduces weed seed predation levels, while the impact of landscape heterogeneity is more context-dependent. To increase weed seed predation and sustainably control weeds, a detailed understanding is needed of direct and indirect mechanisms by which local and landscape aspects affect weed seed predation and whether those effects ultimately result in weed regulation.

1.5. Why biodiversity matters

A wide diversity of genes, species and functional traits support a multitude of ecosystem services, such as decomposition of organic matter, pollination and pest control, on which human well-being is dependent (Cardinale *et al*., 2012). Biodiversity, by supporting several ecosystem services, is increasingly being recognised as a major determinant of ecosystem functioning (Naeem *et al.*, 2012; Tilman *et al*., 2014), stability, and resilience as the capacity to respond to and recover from disturbances (Tilman *et al*., 1994; Oliver *et al*., 2015). The positive effect of biodiversity on ecosystem services has been linked with several mechanisms that can operate in combination (Hooper *et al*., 2005). For instance, diverse communities are more likely to have multiple species that contribute to an ecosystem service due to statistical selection. Through the sampling effect or the selection probability effect, high biodiversity ensures that among many, some species will have a dominant effect on a service (Hooper *et al*., 2005). In addition, communities with many species may include combinations of species that complement and facilitate each other in resource use or resource accumulation (Loreau & Hector, 2001; Ives *et al*., 2005). These mechanisms indicate a positive effect of biodiversity on ecosystem functioning, which has indeed been observed as positive effects of biodiversity on the level of ecosystem services such as pollination and pest control (Dainese *et al*., 2019). It is well established that species richness generally enhances the magnitude of supply of several ecosystem services (Hooper *et al*., 2005; Dainese *et al*., 2019), but the effect of species richness on their stability has been less well explored (Peralta *et al*., 2014; Larsen & Noack 2021).

In addition to ecosystem functioning, greater species diversity can also be expected to increase ecosystem stability. Based on early observations in ecological systems, ecologists came to believe that an increased number of species can increase the stability of ecological systems (MacArthur, 1955; Elton, 1958; McCann, 2000). Although this relationship has been challenged (*e.g*. May, 1973; Pimm & Lawton, 1978), long-term manipulative experiments by David Tilman and co-workers (Tilman *et al*., 1994, 1996), along with theoretical and experimental work, have provided supporting evidence that high species diversity increases ecosystem stability.

Functional redundancy, i.e., the diversity of functionally equivalent species is one of the underlying mechanisms by which biodiversity is hypothesised to stabilise ecosystems functioning and thus ecosystem service provisioning (Cardinale *et al.*, 2012; Loreau & Mazancourt, 2013). According to the insurance hypothesis or portfolio effect, redundancy in species resource use in combination with diversity in species response to environmental fluctuations ensures that some species will conserve an ecosystem service when others are lost or cannot contribute (Yachi & Loreau, 1999; Schindler *et al.*, 2015). For example, farmers want stable pest control services, despite the variability in field temperatures, and higher diversity of pest predators means higher diversity of predator temperature activity niches (Feit *et al.*, 2019, 2021). In the case of an extreme temperature event, diversity expressed through redundancy (or overlap) in pest predator climatic niches ensures that at least one species will feed on the pest when others cannot. While understanding of the importance of biodiversity for ecosystem service provisioning is increasing, there is still a lack of evidence regarding the importance of biodiversity for ecosystem service stability in agroecosystems.

1.5.1 Importance of biodiversity for the stability of weed seed predation

For weed seed predation, the diversity of species that contribute to weed seed predation have been well studied (Janzen, 1971; Crawley, 2013; Honek *et al.*, 2013), but the effects of predator diversity on weed seed predation levels and weed seed predation stability are less well understood. The relationship between diversity and weed seed predation levels has been explored in a few studies within weed seed predation research, with the results indicating that higher seed predator diversity increases predation rates (Jonason *et al.*, 2013). By inferring networks between carabid seed predators, weed seeds and alternative prey, Gray *et al.* (2021) recently showed that a higher number of trophic links between predators and prey supports higher weed regulation. Regarding the relationship between diversity and weed seed predation stability, it is known that diverse communities of small seed predators, but not large seed predators, reduce the variability of weed seed predation (Lami *et al.*, 2020). Cafeteria experiments also suggest that seed predators prefer specific weed seed taxa, with a considerable overlap between species (Saska *et al.*, 2008; Petit *et al.*, 2014). Consequently, it can be hypothesised that higher diversity of predators can lead to high redundancy in weed seed choice, which according to the insurance hypothesis, can increase weed seed predation stability.

Determining the contribution of several species of predators to predation of numerous weed seed taxa under field conditions would be logistically difficult, limiting the ability of researchers to explore how greater diversity of seed predators ensures stable weed seed predation. However, with recent developments in molecular gut content analysis (MGCA), it has become easier to quantify redundancy in resource use between seed predators (*e.g.* Feit *et al.*, 2019). Using DNA-based methods, it is now possible to explore whether functional redundancy supports more reliable weed seed predation. At the same time, agricultural intensity is likely to impact predator diversity, resource use and availability, and diversity of prey (Geiger *et al.*, 2010; Sanguankeo & León, 2011; Batáry *et al.*, 2012). The majority of investigations performed to date on the impacts of agricultural intensity on weed seed predation have focused on the immediate effects of agricultural intensity on predation levels. To make predictions on how the stability of weed seed predation and other biodiversity driven ecosystem services can be enhanced, it is essential to understand how agricultural intensity affects ecosystem service provisioning.

2. Aims

The overarching aim in the work described in this thesis was to improve understanding of the ecosystem service of weed seed predation and explore the relationships between regulation of weeds, seed predator diversity and agricultural intensity. Specific objectives of the thesis were to:

- Quantify the extent to which weed seed predation by two functional groups of seed predators affects the population dynamics of annual weeds (**Paper I**).
- Assess whether weed seed predation can lead to community-level regulation of weeds via changes in the weed seedbank (**Papers II & III**)
- Investigate the role of alternative prey and weed seed availability in weed seed predation and weed regulation (**Papers II, III & IV**).
- Examine how agricultural intensity affects weed seed regulation through altering seed availability and seed predation strength (**Paper III**)
- Explore the effects of field-level disturbances and landscape-level availability of habitat refugia on weed seed predation rates (**Paper IV**)
- Investigate how agricultural intensity moderates the functional redundancy of seed predator communities and test whether functional redundancy can ensure stability of weed seed predation (**Paper V**)

3. Methods

3.1. Wheat crop

Wheat (*Triticum aestivum*) is one of the foundation crops in Western agriculture (Figure 1). Although its historical origin is debated (Peng *et al*., 2011), archaeological evidence from the Southern and Northern Levant regions suggest that it appeared in prehistoric habitations of humans at around 8000 BC (Araus *et al*., 2007). Today, wheat is one of the most important crops worldwide and a major source of calories and protein in the human diet (Mondal *et al*., 2016). The Green Revolution, characterised by agronomic advances, large-scale land-use conversion and intensive use of fertilisers and pesticides, stimulated an increase in wheat production. Global wheat yield increased from 10 889 (hg/ha) in 1961 to 35 468 (hg/ha) in 2019 (FAOSTAT 2021). In recent years, global population growth and income growth, along with changes in eating habits, have triggered an increase in demand for wheat (Iizumi *et al*., 2021). For instance, in sub-Saharan Africa increasingly affluent consumers are diversifying their diets to include higher-value products such as wheat. Thus global wheat demand is growing rapidly, while global wheat production is struggling to keep pace with the demand (Mason *et al*., 2015). According to predictions, a yield increase of an additional 1 ton/ha of wheat grain will be needed by 2050 to meet global demand (Alexandratos & Bruinsma, 2012). Biotic and abiotic stressors, such as climate change and pests, can compromise the ability of global agriculture to meet wheat production goals (Iizumi *et al*., 2021). Among all the pests affecting wheat, weeds can cause the greatest yield reductions, with losses in wheat yield of 18-29% (Oerke, 2006). Excessive use of herbicides over decades, along with reliance on glyphosate-resistant wheat crops (Green, 2018), has reduced weed diversity (Storkey & Neve, 2018) and has placed extraordinary selection pressure on remaining weed species to develop resistance. The emergence of herbicide-resistant weed species (Heap, 2014) and changing policies on herbicide use (Kudsk & Mathiassen, 2020) are now forcing farmers to change their weed management and integrate other non-chemical measures for weed management into wheat production systems. Against this background, wheat was selected as an appropriate crop in this thesis for addressing questions regarding the importance of weed seed predation as a tool for sustainable weed control.

Figure 1. Wheat field at (a-c) different stages of crop growth and (d) after harvest. In this thesis, weed seed predation experiments were conducted at all different stages of wheat growth and post-harvest. Photos: Eirini Daouti

3.2. Plot experiment

To explore the relationship between weed seed predation by two functional groups of seed predators and assess whether it affects the population dynamics of annual weeds, a plot experiment was conducted in two long-term experimental fields in Skåne, Sweden, in 2019 (Paper I). This work was part of a study over three to six wheat cropping seasons by researchers at the Department of Crop Production Ecology, SLU, to study the impact of weed management on the population dynamics of *Alopecurus myosuroides* (blackgrass) (Figure 2). *Alopecurus myosuroides* is an annual grass native to Eurasia with a life cycle very well adapted to agroecosystems. Its resistance to several herbicides (Moss, 2017), combined with short primary dormancy and a long germination period (from late summer until late spring), allows it to bypass soil management in autumn and weed control measures in spring. This makes *A. myosuroides* one of the most damaging weeds in Western Europe in terms of yield losses in cereal production (Moss *et al.*, 2007). A recent study estimated annual wheat losses in England of about 0.8 million tons due to insufficiently controlled blackgrass populations (Varah *et al.*, 2020). Given the importance of *A. myosuroides* for wheat production, a field experiment was conducted to estimate the mortality of *A. myosuroides* seeds through weed seed predation by both vertebrate and invertebrate seed predators (Paper I).

In each of the two field experiments, sampling was performed along 12-24 m long transects every four weeks from mid-May (*i.e.* early growth) to August (*i.e.* post-harvest) to cover all the developmental stages of the life cycle of *A. myosuroides*. To estimate predation on *A. myosuroides* seeds, non-woven waterproof sanding pads (112 mm × 42 mm × 8 mm), each with 30 seeds of *A. myosuroides* (Menalled *et al.*, 2000; Davis *et al.*, 2003), were used. The number of seeds per pad was set to replicate the seed density already documented in the experimental fields. On each transect, two sampling points (at 8 m and 16 m) with one treatment only for invertebrates were established, using a metal net cage to exclude vertebrates (mesh size 1 cm^2). After four days of exposure, the pads were collected and the remaining seeds were counted to quantify *A. myosuroides* seed survival.

3.2.1. Analysis of Paper I

To investigate the impact of weed seed predation on population growth of *A. myosuroides*, seed survival estimates from the weed seed predation experiment were used to parameterise a population model of *A. myosuroides*. The population model, a stage-classified stochastic matrix model developed by Alexander Menegat (co-author, Paper I), was designed to represent the life cycle of annual grass weeds in temperate agroecosystems and was parameterised with empirical demographic data on different life stages of *A.*

myosuroides. These data included field estimates of weed seed predation (for both invertebrate and vertebrate seed predators), together with data on *A. myosuroides* plant survival, fecundity and seed dormancy measured at the experimental plots over three to six winter wheat cropping seasons. To investigate the implications of seed predation for population growth rate of *A. myosuroides*, seed predation rate before or after crop harvest was varied stepwise from zero to one. The full weed life cycle was simulated with 10^4 iterations, each time with all other parameters sampled according to their distribution. By varying the level of weed seed predation, it was possible to determine the stochastic growth rate of *A. myosuroides*, its sensitivity and its elasticity. Sensitivity was defined as the sensitivity of population growth rate (λ) to a small change in a generic vital rate, while elasticity is defined as the proportional sensitivity of λ, *i.e*. the ratio between the change of λ and the imposed change in the parameter.

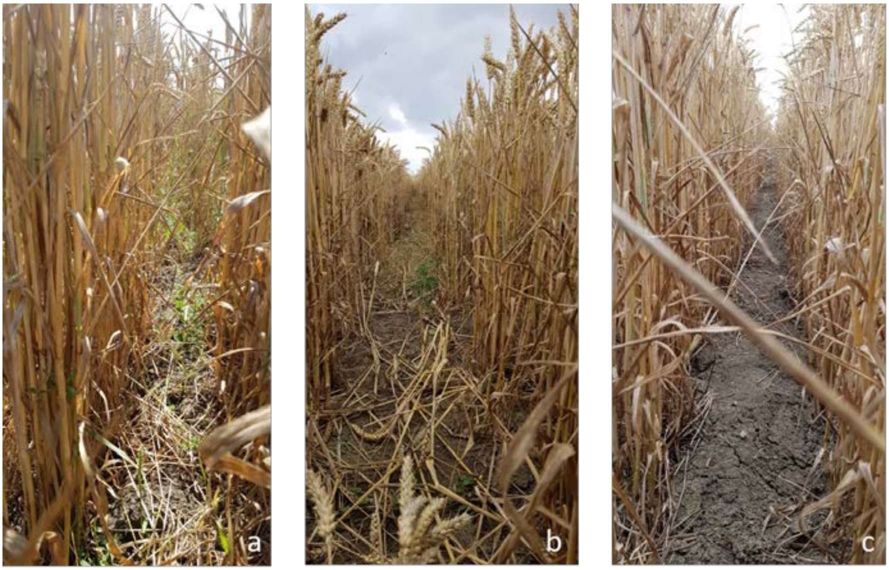


Figure 2. Long-term experimental field plots cropped with wheat and with (a) high, (b) intermediate and (c) low density of *Alopecurus myosuroides* (blackgrass). Photos: Eirini Daouti.

3.3. BioAWARE experiment

To explore the relationships between agricultural intensity, weed seed predation, seed predator diversity and weed seed bank regulation, a large-scale landscape study was conducted between 2017 and 2018 (Papers II-V). That study formed part of the European project BioAWARE, the aim of which was to investigate whether high richness and abundance of weed seed predators can ensure natural weed control. To reach this aim, 60 cereal fields (winter wheat and barley) were selected across Sweden, France, Austria and Czech Republic. These fields were selected along a landscape gradient ranging from 5% to 95% of arable land within a 565 m radius. Field size ranged from 0.55 to 20.73 ha (5.58 ±3.85 ha). Fields in Sweden, Czech Republic and France were within landscapes characterised by high-input cropping systems dominated by cereals and cruciferous crops, while landscapes in Austria were characterised by a combination of permanent grassland, rural settlements and arable land. To control pests, fields in France, Austria and the Czech Republic were managed with herbicides, insecticides and fungicides, whereas fields in Austria were not treated with insecticides and fungicides. The experimental design was based on four transects running into the field, with sampling points at 4, 8, 16 and 32 m from the field edge (Figure 3). In each country, sampling was conducted during four sampling sessions at the beginning and late stage of crop growth. In addition, before crop sowing and after the crop harvest, soil samples were taken from each field to evaluate weed seedbank change.

As part of the project, 15 Swedish fields located in Skåne, the southernmost province of Sweden, were selected. The province is a predominately agricultural, with 38.6% of land used for agricultural production (Swedish Board of Agriculture, 2021), and was thus suitable for addressing the thesis aims. Sampling was performed from mid-June to late July 2018, while soil sampling took place in September 2017 and August 2018.

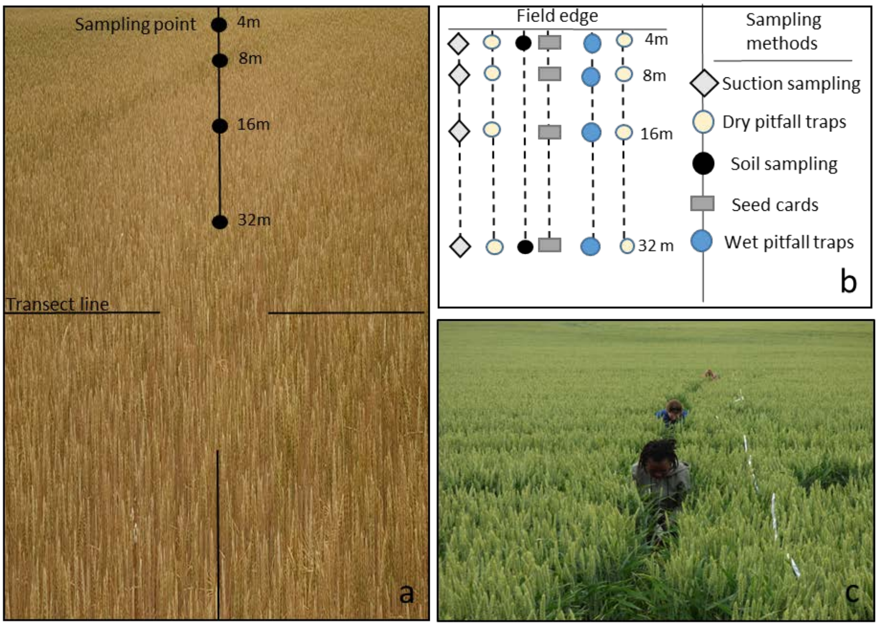


Figure 3. Experimental design in the BioAWARE project fields. Each field was sampled along four 32 m long transects (a & c), with (b) sampling points at 4, 8, 16 and 32 m along virtual transects (dashed lines) from the field edge. Photos Eirini Daouti

3.3.1. Sampling methods

The sampling methods used in the BioAWARE project were soil sampling for evaluation of the seedbank, seed cards for estimation of weed seed predation, suction sampling for estimation of availability of weed seeds and animal prey and wet pitfall traps for estimation of carabid seed predator activity density. In addition, dry pitfall traps were used for collection of carabid beetles for MGCA (Figure 3). All sampling methods used in the thesis and methods that were part of the BioAWARE project are described in detail below. For a summary of the data used for each paper, see Box 1.

Weed seed predation

Weed seed predation was estimated using seed cards with attached seeds of the weed *Poa annua* (annual meadow grass). Seed cards are a common method for measuring weed seed predation in agricultural fields and have been used in several studies of weed seed predation (Westerman *et al.*, 2003b; Daedlow *et al.*, 2014). *Poa annua* was selected as a study species based on a geographical distribution that includes all four participating countries in the BioAWARE project and because it is targeted by several species of carabid predators (Saska *et al*., 2008). On each seed card (95 mm x 40 mm sandpaper sheet with grain size 60), 50 seeds of *P. annua* were attached. Weed seed predation for invertebrate predators was estimated using one exclusion treatment with a metallic cage (mesh size 1 cm^2) (Figure 4f). After seven days of exposure, seed cards were collected and the remaining weed seeds were counted.

Weed seedbank regulation

Weed seed bank regulation was estimated using soil sampling before crop sowing and after harvest to estimate the seedbank change over the cropping year. Specifically, in each field, soil samples were taken at two sampling points on each transect (Figure 3b) before crop sowing in 2017 and after harvest in 2018. At each sampling point, five soil cores (0-20 cm deep, 5 cm diameter) were extracted (Figure 4a), and seedbank composition was determined using the seedling emergence method (Thompson & Grime, 1979). The samples were placed in the greenhouse (12-h photoperiod and 18 ^{o}C day and 15 ^{o}C night temperature) and emerging seedlings were counted (Figure 4b).

Carabid seed predators

Carabid seed predator activity density was estimated using wet pitfall traps filled with approximately 100 mL of a preservative solution of soap (to reduce surface tension) and saltwater and placed at four sampling points on each transect (Figure 3b). Each trap was composed of a plastic cup (7 cm diameter, 7 cm depth) placed inside a polypropylene pipe buried in the soil. Above each trap, a cover was installed to avoid the risk of rain inundation (Figure 4e). Traps were set up at four sampling points on each transect (Figure 3b) and after seven days of exposure, the contents of the trap were collected. In the laboratory, collected carabid beetles were identified to species level and counted. For Papers II and IV, carabid species were assigned to a trophic guild (carnivore, omnivore, granivore) based on Lindroth (1985) and Homburg *et al*. (2014).

Weed seed availability and alternative prey

Weed seed availability and alternative prey were assessed using suction sampling (Figure 4c). Sampling was conducted at four sampling points on each transect (Figure 3b) during days with no rain and low wind when the temperature was above 15 °C and arthropods were active. For each sample, counts were made of the total number of seeds and the abundance of three animal groups (aphids, arachnids and collembolans) known to be consumed by carabid beetles (Roubinet *et al.*, 2018; Frei *et al.*, 2019).

3.3.2. Molecular characterisation of carabid predators trophic interactions

Molecular characterisation of the trophic interactions among carabid predators was performed using molecular gut content analysis (MGCA). First, carabid beetles were collected using dry pitfall traps with the same dimensions as the wet pitfall traps. The traps contained wood chips as hiding places (Figure 4g), and thus reduced the risk of intraguild predation (King *et al.*, 2008). The traps were set up at four sampling points on each transect (Figure 3b) and emptied after 24 hours. Collected carabids were placed in reaction tubes and taken to the laboratory, where they were identified to species level and stimulated to regurgitate (Figure 4d), as described by Wallinger *et al.* (2015). All regurgitate samples were sent to the Department of Zoology, University of Innsbruck, for diagnostic multiplex polymerase chain reaction (PCR) analysis.

The methodology used for PCR analysis was that described by Frei *et al.* (2019). The regurgitate extracts were tested for the presence of DNA of five invertebrate prey taxa using a QIAxcel Advanced System (Qiagen, Hilden, Germany). The prey taxa selected for screening were three aphid species (*Metopolophium dirhodum*, *Rhopalosiphum padi* and *Sitobion avenae*), earthworms, collembolans and plants (Roubinet *et al.*, 2018; Frei *et al.*, 2019). Screened samples were considered positive for animal prey if the signal strength exceeded a threshold of 0.07 relative fluorescent units (RFU) (Rennstam Rubbmark *et al.*, 2019). For plant prey, signal strength was set to 0.3 RFU to reduce signals from environmental DNA and ensure that positive interactions were feeding interactions.

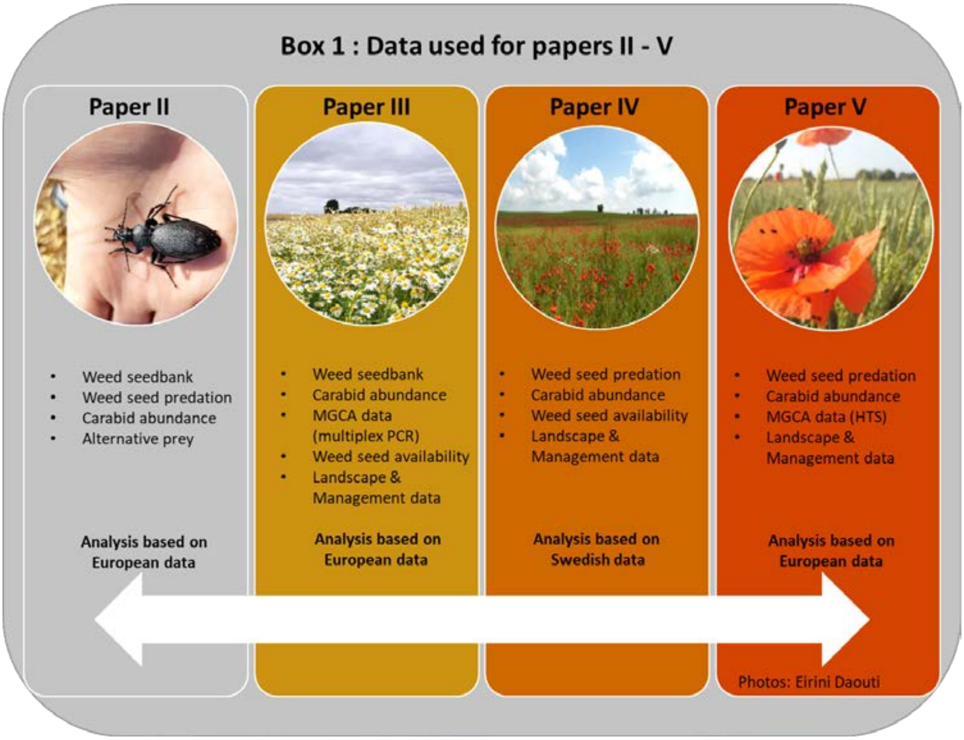
From all 10 088 collected regurgitate samples, a subsample of 5 738 samples was selected for high throughput sequencing (HTS), which made it possible to identify the specific weed choice for each collected carabid predator. The plant primer UniplantR (Moorhouse-Gann *et al.*, 2018) was modified for better performance of the PCR analyses and samples were tested for the presence of weed species using the Nextera XT DNA library preparation system (Illumina Inc., San Diego, CA). Libraries were prepared in the laboratories of Sinsoma (Innsbruck, Austria) and sequenced at Vienna Biocenter Core Facilities (VBCF) (Vienna, Austria). After consultation with a botanist, the positive plant detections were linked to individual weed species or to higher taxonomic levels of weeds when detection to the species level was not possible.

Figure 4. Sampling methods used Papers II-V. (a) Sampling for seedbank analysis using soil cores. (b) Seedbank size and composition were evaluated by the seedling emergence method (Thompson & Grime, 1979). (c) Weed seed availability and alternative prey were estimated by suction sampling. Carabid predators were collected in (e) wet and (f) dry pitfall traps. Wet pitfall traps were used to estimate carabid beetle activity density and dry pitfall traps for collection of beetles for MGCA (d). Photos: Pavel Saska (a), Kateřina Křížová (b), Benjamin Carbonne (c), Veronika Neidel (d), Eirini Daouti (e-g).

3.3.3. Estimation of management and landscape variables

To investigate the impact of agricultural intensity imposed via landscape-level and local effects on weed regulation (Paper III), and functional redundancy of weed seed predation (Paper V), management and landscape data from all 60 fields in the BioAWARE project were evaluated. To learn more about the management of the fields, questionnaires were sent to all participating farmers. The responses to these questionnaires made it possible to estimate the field management intensity of each field and the crop rotation simplification, where field management intensity was calculated as total number of field visits by the farmer to conduct operations, while crop rotation simplification was calculated as number of cereal crops (or cereal frequency) grown in the fields from 2013 to 2017. The range of field management intensity for all fields was 4-18 field visits, while crop rotation simplification range was 0-5 cereal crops sown in rotation. To quantify landscape heterogeneity, circular polygons within a 564 m radius from field centres were created in ArcMap software (ESRI, v.10.4.1). A 564 m radius was chosen since it is known to have an impact on carabid species (Rusch *et al.*, 2016). In the next step, a rasterised map was created in the software CHLOE 4.0 (Boussard & Baudry, 2017), to calculate several variables that represent the configuration and diversity of the landscape surrounding each field. The extracted variables were the length of the interface between crops and semi-natural habitat (iSNH), the proportion of cover of cereal crops (pCereal) and the proportion of cover of semi-natural habitat (pSNH). The value of pCereal in the landscape was found to range between 0.01 and 0.89, pSNH between 0.01 and 0.74 and iSNH between 0.27 and 13.06 km.

To explore the effect of availability of crop and non-crop habitat as disturbance refugia on predators and weed seed predation (Paper IV), an additional landscape analysis was performed using only the 15 Swedish fields. Landscape data were obtained from the Integrated Administration and Control System (IACS) managed by the Swedish Board of Agriculture (Jordbruksverket). Within a radius of 200 m from the centre of each field's transect, circular polygons were created. This scale was chosen as it corresponds to short-term movements of carabid seed predators (Firle *et al.*, 1998). Proportion of cover of semi-natural habitat (SNH) and proportion of cover of annual crops were estimated as potential habitat refugia in which predators could shelter after a disturbance event. The range of crop refugia was 0-0.74 and that of SNH refugia was 0-0.43, while field management intensity for the Swedish fields ranged from five to 13 field visits.



3.3.4. Analysis of Paper II

To explore the relationship between weed seedbank regulation and weed seed predation with carabid abundance and alternative prey biomass, data from all four participating countries in the BioAWARE project were used (Box 1). To estimate the efficiency of individual carabids for predation on seeds and assess their response to availability of alternative prey, combined seed predation and carabid data were used to estimate per capita seed consumption for carabids, calculated as number of seeds consumed divided by number of carabids captured. To explore the relationship between weed seedbank regulation and seed consumption with the availability of alternative prey, counts of alternative prey were converted into biomass (mg). Biomass estimates were based on allometric equations for arachnids (Pey *et al*., 2014; Penell *et al*., 2018; Nentwig *et al*., 2019) or indirect estimates for aphids and collembolans (Caballero *et al*., 2004; Migui & Lamb, 2006). The statistical tools selected to explore the relationships between weed seedbank regulation and weed seed predation with carabid abundance and alternative prey biomass were a combination of linear (LM), mixed linear (LMM) and generalised mixed linear models (GLMM).

3.3.5. Analysis of Paper III

To explore how agricultural intensity effects cascaded down to weed seedbank regulation via effects on seed availability and carabid predators, data from all four participating countries in the BioAWARE project were used (Box 1). To establish a direct link between the potential of the carabid community for predation on seeds and weed regulation, a metric of seed predation strength R_i was developed using data derived from realised feeding interactions. This metric, which approximates the potential of a carabid species *i* for predation on weed seeds, is a function of three variables: carabid plant diet specialisation d_i (which was based on MGCA data), carabid species abundance A_i, and a scaling factor of the metabolic rate of each species I_i as an approximation of its feeding rate.

$$R_i = d_i \times A_i \times I_i \quad \text{(eq. 1)}$$

To estimate the plant specialisation index d_i for each carabid species *i* in each field, presence/absence of animal or plant DNA in the MGCA results was used to calculate Blüthgen’s *d'*, which represents the degree of interaction specialisation for each species (Blüthgen *et al.*, 2006). The value of Blüthgen’s *d'* ranges between 0 and 1, representing low to high interaction specialisation, but does not indicate the prey type (plant or animal) in which the predators are more specialised. To estimate for each predator its plant diet specialisation strength, the total number of feeding interactions for each predator at each field was calculated. When plants were detected at a higher frequency than animals, d_i was calculated as: $d_i = 1 + d_i'$. When detections of animal prey were higher than detections of plants, d' was calculated as: $d_i = 1 - d_i'$. The values of d_i obtained ranged from 0.69 to 1.49, representing lower to higher specialisation in plant prey. Each predator’s abundance was estimated by the activity density of each species from wet pitfall trap catches. Since the frequency of predation events depends on the energy requirements of each species (Brose *et al.*, 2008), the potential feeding rate of each species was approximated using a similar methodology as in Feit *et al.* (2019). Specifically, the feeding rate was based on metabolic rate, which scales according to species body mass M_i, and consumer feeding rates follow the same mass-dependent relationship (Brown *et al.*, 2004). The body mass of each carabid species body was estimated based on the allometric function of Jarošík (1989). Finally, the seed predation strength for the carabid community was calculated by summarising the predation strength by all carabid predators in each field.

The statistical tool selected for the analysis in Paper III was piecewise structural equation models (pSEM) (Lefcheck, 2015; Shipley, 2016). Piecewise SEMs have recently begun to be used as statistical tools in ecology (Gagic *et al.*, 2017; Peralta *et al.*, 2020). Compared with classical SEMs, pSEM have smaller sample size requirements and allow for nested and non-normally distributed data. This methodology made it possible to discriminate between the impact of direct and indirect effects of agricultural intensity on weed seedbank regulation via weed seed availability and seed predation strength.

3.3.6. Analysis of Paper IV

To study the effect of agricultural intensity and habitat refugia on weed seed predation via seed predation strength and weed seed availability, data from Sweden were used (Box 1). To approximate the potential of each carabid species for predation on *Poa annua* weed seeds, which was the selected weed species on the seed cards, a metric that approximates the risk of *P. annua* predation R_i was developed. This metric is a function of the likelihood of granivory L_i, seed preference P_i and abundance A_i of each carabid species and a scaling factor I_i of the metabolic rate of each species as an approximation of its feeding rate:

$$R_i = L_i \times P_i \times A_i \times I_i \quad \text{(eq. 2)}$$

To approximate the likelihood of granivory, carabid species found in the fields were divided into trophic guilds (carnivorous, omnivorous and granivorous) and assigned a likelihood of granivory of 0.1 for carnivorous species, 0.5 for omnivorous species and 0.9 for granivorous carabid species. Based on feeding experiments described by Saska *et al.* (2008), a preference index P_i for *P. annua* seeds was created. Abundance and feeding rate of each carabid species were estimated as described in the analysis of Paper III (see section 3.3.5). Community strength of seed predation was estimated by summarising the predation risk by all carabid predators in each field.

The statistical tool selected for the analysis in Paper IV was piecewise structural equation models (pSEM) (Lefcheck, 2015; Shipley, 2016), as used in Paper III. This methodology allowed discrimination between direct and indirect effects of agricultural intensity and habitat refugia on weed seed predation.

3.3.7. Analysis of Paper V

To investigate how agricultural intensity moderates the functional redundancy of seed predator communities and whether functional redundancy can enhance stability of weed seed predation, data from all four participating countries of the project BioAWARE were used (Box 1). Based on molecular dietary analysis of 5 738 field-sampled carabid predators, functional redundancy of the predation of each weed genus was calculated using the methodology described by Feit *et al.* (2019). Functional redundancy refers to the redundancy in the mortality risk of each weed genus by the functional group of carabid seed predators. It is expressed as the exponential Shannon diversity of each carabid species predation pressure $R_{i,j}$ on each weed genus:

$$e^{H'j} = \exp(-\sum R_{i,j} \times \ln(R_{i,j})) \quad \text{(eq. 3)}$$

Species-specific predation pressure $R_{i,j}$ was estimated based on the probability of each carabid predator i feeding on each weed genus j. Functional redundancy was calculated for 65 weed species that were found in the field and over 10 feeding interactions detected by MGCA and HTS. Species-specific predation pressure $R_{i,j}$ was calculated based on the probability $p_{i,j}$ of a specific weed genus being preyed upon, predator abundance A_i and predator feeding rate I_i:

$$R_{i,j} = p_{i,j} \times A_i \times I_i \quad \text{(eq. 4)}$$

Predation probability $p_{i,j}$ for each weed genus by each predator in each field was derived from the presence-absence data from the HTS

To explore how different aspects of agricultural intensity affect the potential for stability of weed seed predation, the statistical tool Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskaine *et al.* 2017) was selected. This methodology was used to relate animal community responses to environmental covariates and account for random effects related to sampling design. Using HMSC, it was possible to link functional redundancy with the three aspects of agricultural intensity and assess in detail how agricultural intensity affected functional redundancy for all weed genera and each individual genus. The statistical tool used to test whether high functional redundancy of *P. annua* seeds was linked with the spatial variability of field-sampled *P. annua* predation estimates was a generalised linear model (GLM).

4. Results and Discussion

The results of this thesis provided clear evidence that weed seed predation is a promising ecosystem service in agriculture. The results showed that, via weed seed predation, it is possible to achieve regulation of weeds at both population and community level. However, agricultural intensity at local and landscape scale was found to reduce the potential for higher weed control and the stability of this ecosystem service. Specifically, weed seed predation by both invertebrate and vertebrate seed predators reduced population growth of the herbicide-resistant weed species *Alopecurus myosuroides* (blackgrass) (Paper I). Increased abundance of carabid predators and increased seed predation strength enhanced regulation of the weed seedbank (Papers II & III), but effective regulation depended on high weed seed availability and low availability of alternative prey (Papers II & III). Functional redundancy increased the spatial stability on field estimates of weed seed predation, confirming the importance of the diversity of functionally equivalent species (i.e. functional redundancy) to ensure stability in ecosystem functioning (Paper V). Agricultural intensity via an increased level of disturbances, simplified crop rotations at the field level and reduced landscape heterogeneity, reduced weed regulation (Paper III) and functional redundancy of predation (Paper V). To support weed seed predators and enhance weed seed predation, there is thus a need to reduce field management intensity (Paper IV) and design more diversified cropping systems at both field and landscape level (Papers III -V) (Figure 5).

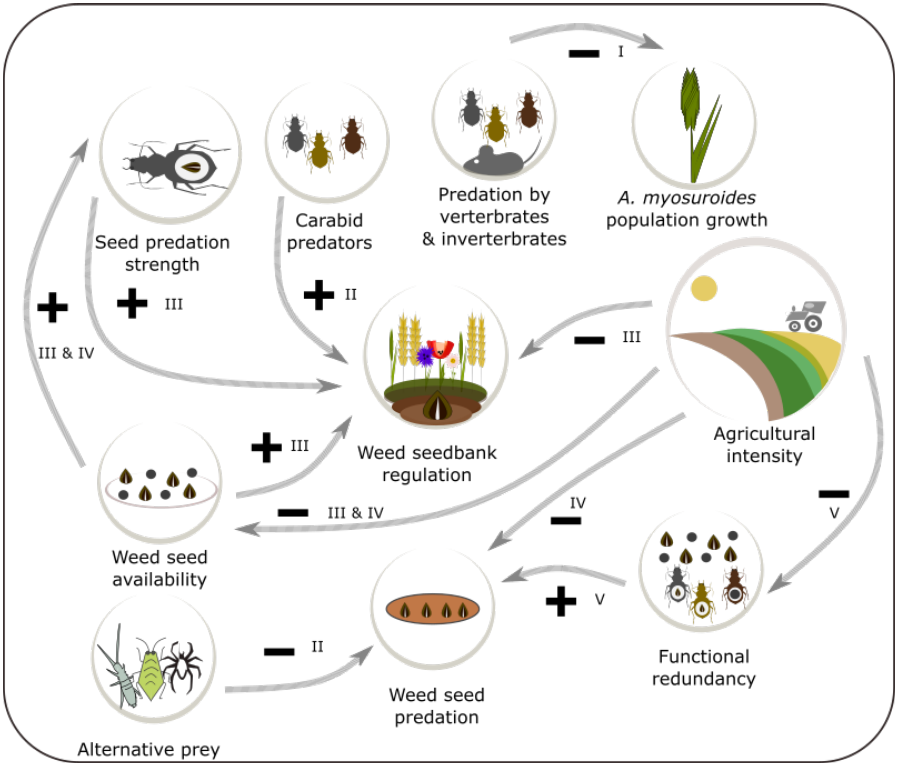


Figure 5. Graphical summary of key findings in Papers I-V in this thesis. Predation on weed seeds by vertebrate and invertebrate seed predators reduced the population growth of blackgrass (*Alopecurus myosuroides*) (Paper I) and enhanced weed seedbank regulation (Papers II & III). Weed seed availability enhanced seed predation strength by carabid beetles, while higher biomass of alternative prey reduced weed seed predation levels (Paper II). Higher functional redundancy in predation increased the spatial stability of weed seed predation, but was reduced by three different components of agricultural intensity (Paper V). One aspect of agricultural intensity, field management intensity, reduced weed seed availability and weed seed predation (Paper IV), with cascading negative effects on seed predation strength (Papers III & IV) and weed seedbank regulation (Paper III). Crop rotation simplification and landscape heterogeneity reduced seed predation strength and, indirectly, seedbank regulation. Latin numbers next to each arrow indicate the Paper number.

4.1. Impact of weed seed predation on regulation of weeds

4.1.1. Regulation at population level

In agroecosystems, weed seed predation by both vertebrate and invertebrate seed predators reduced the growth rate of the annual weed *Alopecurus myosuroides* (Paper I). It was found that, to reduce *A. myosuroides* growth rate below 1, seed losses due to predation needed to reach at least 78% at the peak of weed seed shedding (Figure 6). Field-measured predation by both invertebrate and vertebrate seed predators reached an estimated average of 89% in July, which exceeded the suppression threshold, indicating that weed seed predation can reduce population growth of *A. myosuroides*. Vertebrates were more important seed predators in July (average predation rate 73%, compared with 16% for invertebrates), but invertebrates were more important after crop harvest (average predation rate 61% and 1% for invertebrates and vertebrates, respectively).

Use of population modelling as a tool to explore the impact of weed seed predation on population growth of weeds has been examined in a few previous studies. For example, Westerman *et al.* (2005) showed that estimated seed predation of *Abutilon theophrasti* must be 86% in diverse crop rotations to ensure regulation. The relative contribution of vertebrates and invertebrates to weed seed predation has been a subject of debate, with previous studies showing higher predation rates by invertebrates (Harrison *et al.*, 2003; Mauchline *et al.*, 2005) or by vertebrates (Westerman *et al.*, 2003b; Tschumi *et al.*, 2018). This thesis contributes to the existing research by demonstrating that combined predation by both groups of seed predators is essential to suppress the population growth of annual weeds such as *A. myosuroides*. Since seed losses due to predation must reach 78% at the peak of seed shedding to ensure weed population regulation, weed seed demand must overlap with high seed availability.

4.1.2. Regulation at community level

Carabid seed predators contribute to regulation of weeds at weed community level by reducing the size of the annual weed seedbank. Analysis of data from four European countries revealed that carabid predator abundance (Paper II) and estimated seed predation strength (Paper III) increased seedbank regulation, meaning that the predators reduced the size of the annual seedbank at the end of the crop year. The same relationship between carabid predator abundance and reduction in weed seedbank has been demonstrated previously at national scale in the UK, using data from 257 conventionally managed fields (Bohan *et al*., 2011). This thesis demonstrated that a similar relationship exists at continental (European) scale (Papers II & III). In Paper III, a direct link was found between the estimated seed predation by a carabid community (seed predation strength) and weed regulation, using data derived by MGCA.

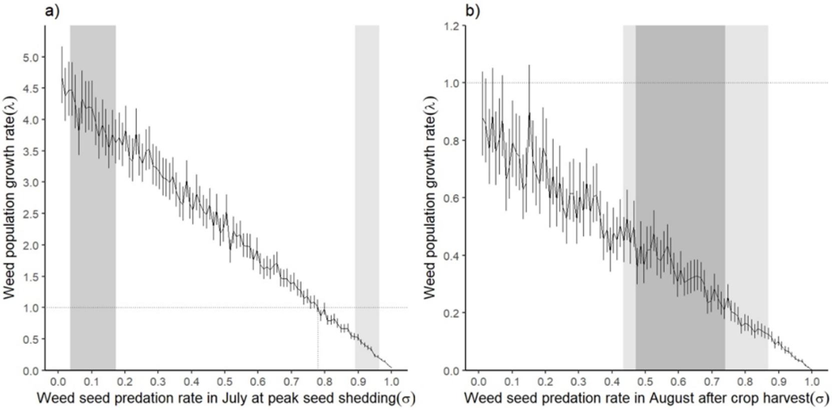


Figure 6. Population growth rate (λ) of *Alopecurus myosuroides* (blackgrass) as a function of weed seed predation (a) in July before harvest and (b) in August after harvest. In the model used, predation rate ranged from 0 to 1 at 0.01 increments. The vertical line in the diagrams indicates the seed predation value and corresponding growth rate. Dark-grey shaded areas are the 1st and 3rd quartile of field-estimated predation rates by invertebrates, while light-grey areas represent field-estimated predation rates by vertebrates. The horizontal dotted line corresponds to λ = 1. For details refer to Paper I, from where both graphs are taken.

4.2. Impact of agricultural intensity on seedbank regulation

Paper III demonstrated that weed regulation by carabid seed predators was reduced by high agricultural intensity across all four European countries studied. Three different aspects of agricultural intensity had a direct or indirect negative effect on seed predation strength and ultimately on weed seedbank regulation. Simplified crop rotations at field level and reduced landscape heterogeneity directly reduced seed predation strength, and thereby indirectly reduced weed seedbank regulation. Increasing management intensity indirectly reduced seed predation strength and weed seedbank regulation, by reducing weed seed availability (Figure 7a). There was a strong positive effect of increased seed availability on seed predation strength, suggesting a density-dependent response of carabid seed predators to seed availability. The negative effect of a simplified crop rotation on seed predation strength (Figure 7b) contributes to the growing body of work showing reduced weed seed predation estimates in intensively managed fields (Diekötter *et al*., 2010; Meiss *et al*., 2010) with simplified crop rotations (Westerman *et al*., 2005; O'Rourke *et al*., 2006). In Paper III, it was found that landscape heterogeneity enhanced seed predation strength, and indirectly weed regulation, via increased length of interface between the crop and semi-natural habitat (iSNH) (Figure 7c). This supports the positive effect of landscape heterogeneity on weed seed predation shown by some previous work (Trichard *et al*., 2013) but contradicts other observations of increased weed seed predation in simplified landscapes (Jonason *et al*., 2013). Increased proportion of natural habitat surrounding agricultural fields ensures continuity of food resources and overwintering habitats for many natural enemies and enhances their services (Tscharntke *et al*., 2012; Schellhorn *et al*., 2015; Landis, 2017). However, it is challenging to unravel the exact mechanisms by which landscape heterogeneity increases seed predation strength.

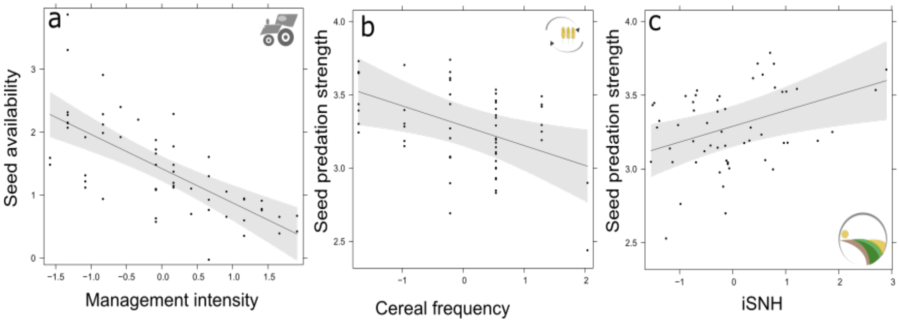


Figure 7. Direct effects of the three aspects of agricultural intensity on seed availability and seed predation strength. (a) Field management intensity had a strong negative effect on weed seed availability. (b) Cereal frequency, as a metric of crop rotation simplification, reduced seed predation strength. (c) Increased length of the interface between the crop and semi-natural habitat (iSNH), as a metric of landscape heterogeneity, had a positive effect on seed predation strength. Black lines represent prediction lines, black dots are partial residuals and shaded areas are confidence intervals. For details refer to Paper III, from where all graphs are taken.

4.3. Role of alternative prey and seed availability on weed seed predation and seedbank regulation

Availability of alternative prey decreased seed consumption per carabid (Paper II) and weed seed availability increased estimated seed predation strength (Papers III & IV). Seeds and alternative prey can both increase fecundity and abundance of certain carabid species (Fawki & Toft, 2005; Saska, 2008), which allows them to persist in agricultural fields. Paper II showed that the effectiveness of carabid seed predators to consume seeds was reduced when the availability of alternative prey increased. Specifically, with increasing biomass of Aphididae, Collembola and total biomass of alternative prey (sum of Aphididae, Collembola and Arachnida), seed consumption per carabid decreased. Carabid predators potentially switch to consumption of animal prey when it becomes highly abundant. However, this effect did not result in weed seedbank regulation. One potential reason is that weed regulation occurs during the whole year (Williams *et al*., 2009), while measurements of alternative prey availability in Paper II were based on two sampling sessions (during crop growth) and were not able to capture the annual fluctuations in alternative prey. Paper I demonstrated that predator seed demand must overlap with high seed availability, since seed losses due to predation need to reach 78% at the peak of seed shedding to reduce *A myosuroides* population growth. In periods of high seed availability, such as the peak of seed shedding, high availability of alternative prey, which was found to reduce predator seed consumption, can potentially disrupt predator potential for weed regulation. However, whether those effects can lead to an impact on population or community regulation of weeds remains to be determined.

In Papers III and IV, weed seed availability increased seed predation strength, which indirectly had a positive effect on weed seedbank regulation (Paper III). This positive correlation between seed availability and seed predation strength indicates a positive density-dependence effect of seeds on seed predation strength. Since seeds are an essential nutrient source for the carabid community (Saska 2008; Gaba *et al*., 2019), by reducing weed seed availability may actually compromise the ability of predators to control weeds. Adeux *et al*. (2019) recently demonstrated that weed diversity can mitigate yield losses. New research avenues, such introduction of non-destructive weed species for increasing weed diversity (*e.g*. Lang *et al*., 2021; Twerski *et al*., 2021) and maintaining ecosystem services, can potentially secure seed availability and thus biological weed control without yield loss.

4.4. Role of disturbances at field scale and habitat refugia at landscape scale

In Paper IV, it was found that field management intensity directly affected weed seed predation and indirectly affected community strength of seed predation via reduced seed availability. Those results are in line with similar findings indicating that weed seed predation levels are reduced in intensively managed agricultural environments (Menalled *et al*. 2007, Trichard *et al*. 2013). Additionally highlights that the frequently found negative effects of field management intensity on carabid communities (Navntoft *et al*. 2006, Shearin *et al*. 2007) can be mediated by reduced seed availability. However, the study provided no evidence that, during disturbances in the crop, either crop or non-crop refugia can support higher weed seed predation or estimated community strength of seed predation. This indicates that the natural habitat failed to enhance weed seed predation, possibly because increased management intensity compromised the ability of carabid predators to establish in the field by reducing seed availability (Tscharntke *et al*., 2016; Ricci *et al*., 2019). Additionally, the dominance of *Pterostichus melanarius* among the captured carabid species could potentially explain the absence of effect of habitat refugia on community strength of seed predation and indirectly seed card predation rates. *Pterostichus melanarious* is well adapted to intensified agroecosystems (Holland 2002) and it has a low dispersal ability (Firle *et al.* 1998) and it is potentially indifferent to the presence of SNH refugia. In addition, we found no evidence of an indirect effect of management intensity via seed predation strength on weed seed predation. This caused due to absences of a strong link between seed card predation rates and community strength of seed predation. A potential explanation for this is that other invertebrates, such as ants and carabid larvae that prey upon the weed seeds (Saska & Jarosik, 2001; Baraibar *et al*., 2011), and were not included in the calculations of predation strength, were negatively impacted by field management intensity.

4.5. Role of agricultural intensity on functional redundancy and stability of weed seed predation

By combining predator abundance estimates with molecular gut content analysis, functional redundancy in seed predation was estimated for 65 weed genera. To assess how agricultural intensity impacts upon functional redundancy (as a proxy for stability), three aspects of agricultural intensity, previously linked with a reduction in weed regulation (Paper III), were examined for possible impacts in levels of functional redundancy among different weed genera. To empirically test whether the metric of functional redundancy actually enhanced stability of weed seed predation, it was compared against independent field estimates of predation on *Poa annua* seeds.

As expected, redundancy of predation decreased with increasing field management intensity, reduced number of crops used in rotation and less landscape heterogeneity. The proportion of explained variation (R^2) from the HMSC model, fitted on the redundancy of predation across different weed genera, was 27.7%. Field management intensity accounted for the largest portion of explained variation in the redundancy of predation, accounting for 41.2% of the total variance, followed by crop rotation simplification and landscape heterogeneity, which explained 19.5% and 18% of the total variance, respectively. Since functional redundancy is important for the stability of ecosystem functions (Hooper *et al*., 2005; Thibaut & Connolly, 2013), intensively managed landscapes at both local and landscape scale are likely to show more variable weed seed predation under future disturbances. However, by reducing field disturbances, increasing the number of crops sown in rotation and increasing landscape heterogeneity surrounding the field farmers can support carabid communities that provide more reliable weed seed predation and are potentially more resilient to future disturbances.

Functional redundancy in predation of *Poa* genera led to lower coefficient of variation in *Poa annua* predation rates between agricultural fields (Figure 8). According to the insurance hypothesis or portfolio effect, redundancy in species resource use, in combination with diversity in species response to environmental fluctuations, ensures that some species will continue to supply an ecosystem service when others are lost or cannot contribute (Yachi & Loreau, 1999; Thibaut & Connolly, 2013). The positive relationship found in Paper V between functional redundancy in predation and stability of weed seed predation demonstrates the importance of biodiversity to ensure stability of ecosystem functioning. In a recent study, it was found that the variability in predation estimates for specific weed species decreased with higher diversity of small carabid seed predators (Lami *et al*., 2020), indicating that predator diversity can increase predation stability. For host-parasitoid networks, Peralta *et al*. (2014) reported stabilising effects of functional redundancy among parasitoids to community-level parasitism rates.

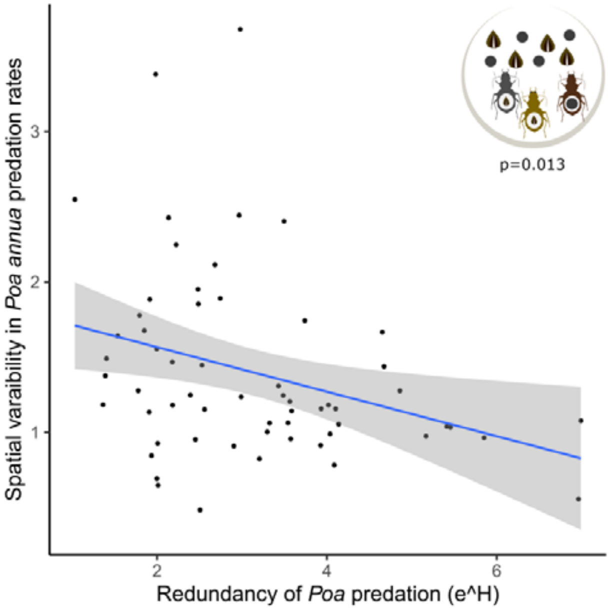


Figure 8. Relationship between spatial variability in predation estimates for *Poa annua* and redundancy of predation on *Poa*. Higher functional redundancy decreased the coefficient of variation in *P. annua* predation estimates, increasing their spatial stability. Black dots represent partial residuals, the blue line is the prediction line and the shaded areas are the confidence intervals. Figure taken from Paper V.

5. Conclusions and future directions

Weeds in agriculture have two opposing impacts on crop production, a detrimental effect that reduces crop yield (Oerke 2006) and a beneficial effect that supports several ecosystem services, such as pollination and soil quality essential for sustainable crop production (Petit *et al.* 2011). Conventional methods of weed control rely on herbicides and intensive soil cultivation to reduce the detrimental effects of weeds. However, herbicides have negative impacts on human health, beneficial organisms and the environment (Thorbek & Bilde 2004; Van Bruggen *et al*. 2018; Zhang et al. 2019; Straw *et al.* 2021), creating a need for more sustainable alternatives for weed control. One such alternative is weed control by weed seed predators - weed seed predation. The work presented in this thesis improves understanding of weed seed predation, by providing evidence that increased levels of weed seed predation can provide weed regulation. Results obtained through a combination of empirical work and modelling showed that weeds can be regulated by weed seed predation at both population and community level (papers I-III). Higher and more stable weed seed predation depends on reduced field disturbances, more diverse crop rotations and diversified landscapes surrounding the field (papers III-V).

From the farmer's perspective however, it is important to know how weed seed predation can reduce weed-related crop losses and protect crop yield. For other ecosystem services, such as pest control and pollination, benefits to crop yield are relatively well investigated (Tamburini et al. 2020; Gagic et al. 2021). For weed seed predation, there is still a lack of research describing the relationship with crop yield. Therefore, future research should specifically assess the impact of weed regulation by weed seed predation on crop yield. Clear information on this would help in the design of cropping systems that enhance weed seed predation for weed control while maintaining crop yield.

To regulate weeds at the population and community level, predation by both vertebrates and invertebrate predators is essential. This thesis showed that vertebrate predators contribute more to weed seed predation at the peak of *Alopecurus myosuroides* seed shedding, while carabid seed predators are essential for reducing the weed seedbank (Papers II & III). Therefore, management practices that maintain both vertebrate and invertebrate seed predators can support higher weed control. This thesis, focused on post-dispersal seed predators, such as carabid beetles and rodents but agricultural fields contain a very broad spectrum of weed seed predators (*e.g.*, birds, earthworms and ants) and seed predation can occur before the seed shedding (pre-dispersal predation) and in the soil seedbank. For instance, recent research has shown that in the seedbank specific species of earthworms can be important weed seed predators by reducing the survival of several weed species (Li *et al.* 2020). For biological control of weeds, most research to date has focused on post-dispersal seed predation, while the literature on pre-dispersal seed predation is limited. In addition, pre-dispersal seed losses tend to be studied in isolation from post-dispersal seed predation (DeSousa *et al.* 2003; Nurse *et al.* 2003). Hence, future research should aim to examine the combined effects of pre- and post-dispersal seed predation and belowground predation. This would improve the accuracy of predictions on the impact of weed seed predation on weed species population or community dynamics and the relative importance of different groups of predators.

Increasing agricultural intensity, in the form of increased number of field disturbances, reduced crop rotation diversity at field level and reduced landscape heterogeneity, was shown in this thesis to reduce seed predation strength and the potential for higher weed regulation (paper III). Therefore, management practices that diversify cropping systems at both field and landscape scale, and reduce field management intensity can support higher weed seed predation and better weed regulation. However, the key to higher seed predation strength is to maintain weed seed availability, (papers III and IV). Weed seeds are essential food sources for invertebrate seed predators and weed seed density can thus affect predator response to weed seeds (Carbonne *et al.* 2019). Therefore, cropping systems should not aim to eradicate weeds, but rather to maintain seed availability for higher weed control. From the farmer’s perspective, however, maintaining weed seed availability might seem a “risky” management approach. A future challenge is to ensure weed seed availability without affecting crop yield. Recent research indicates that higher weed diversity can mitigate yield losses caused by weeds (Adeux *et al.* 2019) and leading to the suggestion that introduction of rare non-destructive weed species in arable fields can increase weed diversity (Lang *et al.* 2021; Twerski *et al.* 2021). Future research should explore whether increasing weed diversity can maintain seed availability, and thereby enhance weed seed predation and improve the regulation of more destructive weeds.

High functional redundancy of predation leads to higher spatial stability in estimated weed seed predation estimates (paper V). However, higher agricultural intensity, expressed here as increased number of field disturbances, reduced crop rotation diversity at field level and reduced landscape heterogeneity, was shown to decrease the functional redundancy of predation. Consequently, the same management practices that support weed regulation in the short term (paper III) can be used to increase functional redundancy of predation across different weed genera. Functional redundancy ensures that weed seed predation is stable and resilient to future disturbances. Future work should focus on measuring weed seed predation over multiple years, to determine how temporal stability (rather than spatial stability) in weed seed predation is linked with functional redundancy. However, functional redundancy is not the only predictor of resilience of an ecosystem service to disturbances. Another key component is the level of response diversity within a functional group to changes in *e.g.* climatic or habitat conditions (Rosenfeld 2002) and, in particular how individual species respond to climatic variability (Feit et al. 2021) or land-use change (Cariveau et al. 2013). Therefore, future research should combine studies on response diversity to agricultural intensity within carabid species with determination of functional redundancy of predation, to measure the true resilience of weed seed predation against disturbances.

To conclude, to design cropping systems that rely on ecological intensification of beneficial organisms and their regulating and yield supporting services, (Bommarco et al. 2013) more knowledge is needed about ecosystem services such as weed seed predation. This thesis demonstrated that weed seed predation can be included in the ecological intensification toolbox, thus reducing the current dependence on herbicides for weed control.

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Popular science summary

Agricultural land comprises half of the Earth's habitable land. This makes agricultural landscape management and production both the cause and the solution of the world's current environmental challenges (e.g., climate change, biodiversity loss) and social challenges (e.g., unmet food demand). Agricultural intensification, a process that accelerated during the Green Revolution, via intensive use of anthropogenic inputs, reduction of crops used in rotation and loss of semi-natural habitats and landscape heterogeneity, has increased crop yields over decades but has overlooked global sustainability goals. Nowadays, it is widely recognised that "business-as-usual", meaning continued dependence on pesticides and fertilisers in crop production, is not a sustainable option to secure crop yield. Biodiversity loss and climate change questions our ability to secure food supply while allowing upcoming generations meet their own needs.

Weeds in agricultural fields have the constant attention of farmers because weed plants compete with the crop for nutrients and light, which can severely reduce crop yield. However, weeds can provide essential ecosystem services, such as pollination and improved soil quality. Additionally, for several species such as carabid beetles and rodents, weed seeds are a valuable and nutritious food source. Predation of weed seeds can reduce the number of seeds entering the soil seedbank and germinating as weed plants in the future. Herbicides are an effective tool to combat weeds, but excessive usage has led to the emergence of herbicide-resistant weed species. There are also concerns about negative effects on human health and the environment. Considering those effects, many countries have decided to apply stricter rules on herbicide use. However, this leaves farmers struggling to find ways to protect crop yield against weeds. Surprisingly, the potential of weed seed predation for weed control has been rather unexplored. Therefore, this thesis examined i) whether weed seed predation can lead to regulation of weeds at population and community level, ii) how seed predation is affected by presence of other prey types, like aphids, spiders and springtails, and by the availability of weed seeds iii) whether seed predator diversity is important to ensure stable weed seed predation and iv) how agricultural intensity affects predators' potential for high and stable weed seed predation. To answer those questions, field data obtained in experiments from four European countries were analysed.

The results showed that seed predators can reduce population growth of the herbicide-resistant weed species blackgrass. Furthermore, an increased number of carabid beetles feeding on weed seeds reduced the number of seeds of the weed species present in the seedbank at the end of the crop year. This indicated that seed predators can reduce weed communities. However, the number of carabid beetles feeding on weed seeds, increased with the availability of seeds but declined with availability of animal prey such as aphids, spiders and springtails. The stability of weed seed predation increased with the number of species feeding on the same seed species. However, agricultural intensity, reduced weed regulation and the diversity of predators feeding on the same seed via increased levels of disturbances, simplified crop rotations at the field level and reduced landscape heterogeneity.

The outcomes of this thesis suggest that we can use weed seed predators to sustainably control weeds in crop fields. However, to increase the potential of seed predators for weed control, it is essential to support their work. Specifically, to support weed seed predators and enhance weed seed predation, we need to reduce field management intensity and design cropping systems with higher diversity of crops sown in rotation and to increase heterogeneity surrounding each field. Agricultural landscapes provide humanity with the means to survive and at the same time provide habitat and resources for beneficial organisms. Without these beneficial organisms and their regulating and supporting services such as weed seed predation, it will be difficult to cope with future global environmental and social challenges.

Populärvetenskaplig sammanfattning

Jordbruksmarken täcker hälften av jordens beboeliga mark. Detta gör att förvaltning och produktion i jordbrukslandskapet både utgör en viktig orsak och lösning till världens miljömässiga (t.ex. klimatförändringar, förlust av biologisk mångfald) och sociala (t.ex. otillfredsställd efterfrågan på livsmedel) utmaningar. Intensifieringen av jordbruket, en process som accelererade under den gröna revolutionen, genom intensiv användning av antropogena insatsmedel, minskning av antalet grödor som används i växelbruk och förlust av naturmiljöer och landskapets heterogenitet, har ökat skördarna under årtionden men har förbisett de globala hållbarhetsmålen. Numera är det allmänt erkänt att "business-as-usual", dvs. fortsatt beroende av kemiska bekämpningsmedel och mineralgödsel i växtproduktionen, inte är ett hållbart alternativ för att säkra skördarna. Förlust av biologisk mångfald och klimatförändringar ifrågasätter vår förmåga att säkra livsmedelsförsörjningen samtidigt som kommande generationer kan tillgodose sina egna behov.

Ogräs på jordbruksfälten är en fråga som jordbrukarna ständigt måste uppmärksamma eftersom ogräsväxter konkurrerar med grödan om näring och ljus, vilket kan minska skörden kraftigt. Ogräs kan dock även tillhandahålla viktiga ekosystemtjänster, t.ex. pollinering och förbättrad markkvalitet. För flera arter, t.ex. jordlöpare och gnagare, är ogräsfrön dessutom en värdefull och näringsrik födokälla. Predation av ogräsfrön kan minska antalet frön som kommer ner i markens fröbank och gror som ogräsplantor i framtiden. Herbicider är ett effektivt verktyg för att bekämpa ogräs, men överdriven användning har lett till uppkomsten av herbicidresistenta ogräsarter. Det finns också farhågor om negativa effekter på människors hälsa och miljön. Med tanke på dessa effekter har många länder beslutat att tillämpa strängare regler för användning av herbicider. Detta gör dock att jordbrukarna kämpar för att hitta sätt att skydda sina skördar mot ogräs. Överraskande nog är potentialen hos predation av ogräsfrön för ogräsbekämpning ganska dåligt utforskad. I denna avhandling undersöktes därför i) om predation av ogräsfrön kan leda till reglering av ogräs på populations- och samhällsnivå, ii) hur ogräspredationen påverkas av närvaron av andra bytesdjur, som bladlöss, spindlar och springstjärtar, och av tillgången på ogräsfrön, iii) om en mångfald av fröpredatorer är viktigt för att säkerställa en stabil predation av ogräsfrön och iv) hur jordbruksintensitet påverkar predatorernas potential för hög och stabil predation av ogräsfrön. För att besvara dessa frågor analyserades fältdata från försök i fyra europeiska länder.

Resultaten visade att fröpredatorer minskade populationstillväxten hos den herbicidresistenta ogräsarten renkavle. Dessutom minskade ett ökat antal jordlöpare som äter ogräsfrön, antalet frön av olika ogräsarter i fröbanken i slutet av skördeåret. Detta tyder på att fröpredatorer kan minska hela ogrässamhällen. Rovdjurens potential för predation av ogräsfrön ökade med tillgången på frön, men minskade med tillgången på bytesdjur som bladlöss, spindlar och fjädermyggor. Stabiliteten i predationen av ogräsfrön ökade med antalet arter som livnär sig på samma fröart. Jordbruksintensiteten minskade regleringen av ogräs och mångfalden av rovdjur som livnär sig på samma fröart, via ökad störningsnivå, förenklade växtföljder på fältnivå och minskad landskapsheterogenitet.

Resultaten av denna avhandling tyder på att vi kan använda fröpredatorer för att på ett hållbart sätt kontrollera ogräs i jordbruksfält. För att öka potentialen hos fröpredatorer för ogräsbekämpning är det dock viktigt att stödja deras arbete. För att stödja fröpredatorer och öka predationen av ogräsfrön behöver vi minska intensiteten i jordbruksmetoderna och utforma odlingssystem med större mångfald av grödor som sås i växelbruk och öka heterogeniteten runt varje fält. Jordbrukslandskapet ger mänskligheten möjlighet att överleva och tillhandahåller samtidigt livsmiljöer och resurser för nyttoorganismer. Utan dessa nyttoorganismer och deras reglerande och understödjande tjänster, t.ex. predation av ogräsfrön, kommer det att bli omöjligt att klara av framtida globala miljömässiga och sociala utmaningar.

Acknowledgements

To my supervisors! Firstly to my main supervisor **Mattias**, for your guidance, trust, support and patience over the past four years. For the intellectual leadership and all the inspiring discussions that guided my often unstructured thoughts but generated great ideas. For creating a safe and inclusive working environment for me and our group where we shared our accomplishments and struggles, celebrated science and learned from each other. Even though I faced a few unlucky moments during my PhD, one thing that made me feel extremely lucky was to have you as my supervisor. **Riccardo**, for helping me broaden my ecological thinking by sharing and talking about science. For making me feel stronger when you were part of the team. **Giulia**, for the support, our catch-up discussions, sharp comments that always brought an interesting perspective to my work. For understanding what it means to miss the sun. **Ben** for your help, our intellectual and personal discussions and your stories from the desert. For trying to persuade me not to worry too much in moments of insecurity.

To my collaborators! The BioAWARE team! **Benjamin, Veronika, Hana, Britta, Pavel, Jiri, Wopke, Sandrine, Corinna, Michael** and **David** thank you for all the hours you spend working in the field, in the lab and making this fantastic dataset possible. For all the interesting discussions during our long BioAWARE meetings and sharing a beer after a long day. I hope we will have the opportunity to see each other again soon. **Alexander** for the great collaboration, vivid discussions and the opportunity to work with *Alopecurus*.

To the Biodiversity and Biocontrol group! **Sasha, Miriam, JB, Grace, Neus, Elodie** and all the Master and Bachelor students for making our lab fantastic! From sharing and discussing cool science, learning from each other and feeling that no problem is too small to share**. Sasha** special thanks to you for being always there even though you were miles away.

To Ged for your selfless and generous dedication to my project. Helping me find fields, go through samples, celebrate two long field sampling sessions and the long working days in Skåne. **Caroline** for being so supportive, helpful and understanding during all the crazy moments in Stensoffa. Without your help, it would have been impossible to survive the stressful days of fieldwork. **Carol** for always being available, for contacting all the farmers and knowing that you were always there to help. To the many people who helped to collect and convert hundreds of samples into data points! **Ruben, Anna, Lise, Gloria, Catline, Giorgos, Alec, Alexander, Hannah, Ana** and **Juliette**. **Sirirat** for all your help in all of those years. From ordering and delivering a freezer in the middle of nowhere to connecting in a webinar. **Per** for all the technical support. **Lena** for helping me with so many big and small administrative issues. I do not know how the ecology department will survive without you.

To the **ecosystem services group** for all the inspiring discussions and presentations that introduced me to some many cool research topics. To everyone at **the Department of Ecology** for creating an amazing working environment! From the Tammsalen seminars and the ecology symposium to the landscape ecology discussions and Wednesday pubs.

To all the PhD students and postdocs for the support, laughs, barbeques and so many more. **Juliana** and **Ineta** for being there for me along the way. I will always cherish and be more than grateful to have shared our PhD struggles and achievements. Thank you for the crazy moments, laughs, wine nights and so many more. My PhD years would not have been the same without you! You are both amazing! **Guille** for your never-ending willingness to help. From helping me move to a new house to deal with errors in R and administrative issues. **Chloë** for all the laughs and support and the crazy moments we shared during our fieldwork in Skåne. **Laura** for helping me with my first analysis questions, your writing advice and the opportunity you gave me to learn more about bumblebees in Lund. **Hannes** for sharing your fishing spots and tips. **Kaisa** for the laughs in the lunchroom and nice moments. **Yuval** for all the fikas, halva, cheese nights, singing and dinners. **Janina** for your enthusiasm and for making an amazing fieldwork partner in Skara. **Sara** for nice discussions and amazing dinners. **Mat** for the support and reminding me that I will be fine at the end. **Yayuan** and **Xiangyu** for the chats and dumplings evening you organised. **Merlin** for introducing us to the D&D universe. **Kate, Michelle, Julian, Adam, Kristina, Dragos, Fredrika, Tord, Tarquin, Carl, Pablo, Deanne, Svenja** for the PhD breakfasts and fun memories in Grimso. The **VPE PhD students, Elsa, James, Hui, Harimurti**, **Sokha, Rafaelle** for the chats, laughs and fikas that made our PhD journey more enjoyable. **Matthieu, Lisa** and **Elliot** for their amazing company that made me feel part of a family. **Kirsten, Giovanni** and **Yoan** for organising courses and workshops that made my first PhD struggles a bit easier to huddle.

To all members of the Poveda lab! Katja, Tim, Heather, Diana, Hayley, Anna, Laura, Kunle, Casey and **Annika** for the weekly catch-up meetings, vivid discussions, inclusiveness and so much more. I felt like a member of your group even though I was thousands of miles away. Special thanks **Katja** for being an amazing academic role model and allowing me to know so many inspiring researchers. **Heather** for all the great discussions and for spending your time giving me feedback on my manuscript. I will never forget the "bad wolf and cute baby" technique! I truly hope soon to have the opportunity to meet you all in person!

To **Dimitris** and **Jessie** for always being there for me from our first steps in Ioannina up to now. Σας αγαπώ! To **Dan** who has been there for me during the ups and downs and for making me truly happy.

To my family. Είναι δύσκολο να βρώ λόγια για να περιγράψω την ευγνωμοσύνη μου. Σας ευχαριστώ για την αγάπη, την στήριξη και την υπομονή όλα αυτά τα χρόνια που είμαι μακριά σας! Σας αγαπώ πολύ!

Acta Universitatis Agriculturae Sueciae

Doctoral Thesis No. 2021:61

Promoting ecosystem services in agriculture can help us reduce our dependency on agronomic inputs while securing crop yield. This thesis examines how the ecosystem service of weed seed predation contributes to weed regulation and how it is affected by agricultural intensification. It demonstrates that weed seed predation has the potential to provide sustainable weed control, that agricultural intensification reduces weed seed predation and that high seed predator diversity is needed to ensure reliable service delivery.

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ISSN 1652-6880
ISBN (print version) 978-91-7760-799-1
ISBN (electronic version) 978-91-7760-800-4